

Insights into the Trophic Ecology of Bottlenose Dolphins (*Tursiops truncatus*) in Irish Waters

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Abstract

The stomach contents of 12 bottlenose dolphins were examined. Ten of the 11 samples originated from dolphins that stranded on the west coast of Ireland between 1999 and 2011, while the remaining dolphin was bycaught. Ten of the stomachs contained food remains, mainly fish bones and otoliths; two stomachs were empty. A total of 37 prey taxa were identified, suggesting that they have a broad diet. The main prey items identified were five gadoid fish. Also, four species were only identified from non-otolith skeletal material, highlighting the importance of including all skeletal material in dietary studies. Three distinct populations of bottlenose dolphins have been identified in Irish waters using genetic markers. Differences in diet were found among these populations, where their stomach contents suggest that these animals might be foraging in different habitats. Significant differences were found between dolphins stranded alive and those that were found dead where the former appeared to have been feeding more on pelagic species. Significant differences were also found between male and female dolphin diet: males had eaten a wider variety of prey items than females. Annual consumption rates for the coastal bottlenose dolphin population in Irish Atlantic coastal waters are estimated to be around 1,193.8 tonnes.

Key Words: bones, bottlenose dolphins, *Tursiops truncatus*, coastal, offshore, annual consumption, feeding ecology, gadoids

Introduction

Bottlenose dolphins (*Tursiops truncatus*) are widely distributed throughout the Northeast Atlantic.

Two multinational dedicated sighting surveys carried out in the Northeast Atlantic, SCANS-II (Hammond et al., 2013) and CODA (Cetacean Offshore Distribution and Abundance [CODA], 2009), have provided abundance estimates and distribution data of bottlenose dolphins for the shelf waters and oceanic regions, respectively. Results from these surveys, and additional inshore surveys (Ingram & Rogan, 2003; Berrow et al., 2012) show that the species can occur over a wide range of habitats—from coastal waters to deeper oceanic waters. Coastal groups have been better studied in general thanks to their accessibility and year-round sightings, and photo-identification studies seem to indicate that in some areas these groups are resident. In Europe, one such group has been described in the Moray Firth, Scotland (Wilson et al., 1997), and further resident groups have been described in Ireland in the Shannon Estuary (Ingram, 2000), Cardigan Bay in Wales (Bristow & Rees, 2001), the southern Galician Rías (northwest Spain) (Fernández et al., 2011), and the Sado Estuary in Portugal (Harzen, 1998).

Bottlenose dolphins are regularly seen off the west coast of Ireland (e.g., Englund et al., 2007; O'Brien et al., 2009) where genetic information suggests that there are at least three distinct populations (Mirimin et al., 2011). One population comprises animals inhabiting the outer Shannon Estuary and Cork harbour (estimated at around 120 to 130 individuals; Ingram, 2000), while a second population is formed by dolphins that seem to range more widely, using a large but as yet undetermined stretch of the coast, including areas off Connemara (Galway) and Mayo but also showing some site fidelity (Ingram et al., 2009). A third population of unknown origin has been identified from stranded individuals only (Mirimin et al., 2011) and is characterised by high genetic

variability suggesting that they may be part of a wider ranging pelagic population, possibly with an offshore distribution. On a larger geographical scale, Louis et al. (2014) have recently suggested that there are two genetically distinct bottlenose dolphin ecotypes in the Northeast Atlantic, largely driven by habitat use: (1) a *coastal* ecotype and a (2) *pelagic* ecotype. Although genetic analysis is a useful first step in elucidating the presence of ecotypes, further work is required to more accurately define the geographical boundaries of these ecotypes, including diet analysis and skull morphometrics.

Information on the diet of bottlenose dolphins in European waters has been obtained by the examination of stomach contents of stranded and bycaught individuals with data available from Scotland (Santos et al., 2001), northwest Spain (Santos et al., 2007), France (De Pierrepont et al., 2005; Spitz et al., 2006), and east of Spain (Blanco et al., 2001). Results from these studies indicate a broad diet with many demersal and pelagic prey species along the Atlantic coasts of Scotland, France, and Spain, and the Mediterranean coast of Spain.

In this article, we use the information provided by the analysis of the stomach contents of bottlenose dolphins, in conjunction with published information on population structure (Mirimin et al., 2011) and stable isotope analysis (Rogan et al., 2011) to increase the knowledge of their

trophic ecology in the Northeast Atlantic and particularly in Irish waters, to assess the food requirements of the coastal population of bottlenose dolphins in Ireland, and to improve our understanding of the habitat use of the third population of bottlenose dolphins described in Irish waters (likely the pelagic ecotype described by Louis et al., 2014) since five of the samples examined have been assigned genetically to this population for which very little information is available.

Methods

Study Area and Sample Composition

Strandings of bottlenose dolphins in Ireland are recorded, validated, and published annually in the *Irish Naturalist' Journal* by Irish Wild Dolphin Group (www.iwdg.ie). The digestive tracts of five male and six female bottlenose dolphins that stranded along the west coast of Ireland (Figure 1) from 1999 to 2011 were analysed. Two dolphins (BND 1/01 and BND 2/01) did not contain any food remains within their digestive tracts. Animals were measured, sex determined, and, whenever possible, additional samples were collected for further studies. In addition, the stomach of a bottlenose dolphin bycaught (Table 1) in a drift net targeting albacore tuna (*Thunnus alulunga*) was examined. Five of these individuals were characterised genetically (see Mirimin et al., 2011) as belonging to the "3rd population"

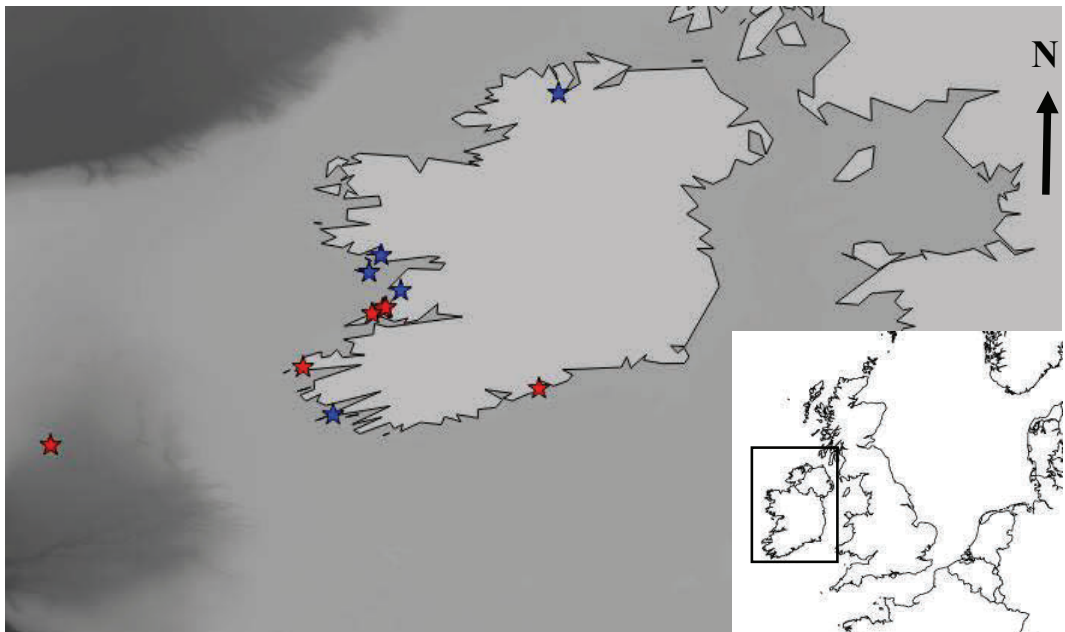


Figure 1. Map showing the locations of stranded and bycaught bottlenose dolphins (*Tursiops truncatus*) used in this study. Two females stranded on the same beach. Red stars are females, and blue stars are males.

Table 1. Data on stranded and bycaught bottlenose dolphins (*Tursiops truncatus*) in Ireland for which stomach contents were analysed (N = 11); # indicates live strandings. ST = 3rd population of unknown origin, SH = Shannon (from Mirimin et al., 2011), * indicates stable isotope samples, ND = not determined, and BY = bycaught. Season: W = Winter, Sp = Spring, S = Summer, and A = Autumn. Estimated dolphin weight was calculated using the Kastelein et al. (2002) formula based on dolphin body length.

Code	Pop.	Year	Season	Sex	Length (cm)	Estimated weight (kg)	Location of stranding
BND 1/99#	ST	1999	W	Male	309	396.8	Ballydonegan Co. Cork
BND 2/99	ND*	1999	S	Male	330	543.7	Lahinch Co. Clare
BND 1/01#	ST	2001	S	Male	340	631.7	L. Swilly Co. Donegal
BND 2/01	SH*	2001	S	Female	320	467.9	Doonbeg Co. Clare
BND 3/01	ST	2001	A	Female	288	289.6	Ventry Co. Kerry
BND 1/02	ND	2002	S	Female	280	256.8	Doonbeg Co. Clare
BND 1/05	ST*	2005	S	Female	287	285.3	Doonbeg Co. Clare
BND 2664#	ND	2005	Sp	Male	295	321.7	Aran Islands Co. Galway
BND 3241#	ND	2008	A	Male	310	402.8	Rossaveel Co. Galway
BND 3617		2011	Sp	Female	300	346.7	Kilkee, Co. Clare
BND 1/12#	ST	2012	Sp	Female	280	256.8	Pilmore Co. Cork
JB T3H6 (BND 1/96)	BY*	1996	S	Female	--	--	51° 18' 99" N 13° 01' 38" W

(p. 349) of unknown origin and one was assigned to the Shannon/Cork population (Table 1).

Prey Identification and Quantification of Diet

Stomachs and intestines were thawed, and their contents were washed into sieves of decreasing mesh-size (0.35, 0.25, and 0.1 mm). Recovered fish bones and otoliths were stored dried, while cephalopod beaks and crustacean remains were stored in 70% ethanol. Identification of all fish prey remains was carried out to the lowest possible taxon using a reference collection held at University College Cork (Ireland), digital image library of the fish material held at University of Aberdeen (Scotland), and published guides (e.g., Härkönen, 1986; Watt et al., 1997; Tuset et al., 2008). Cephalopod remains (lower and upper mandibles or beaks) were identified using published guides (Clarke, 1986) and reference material held at the University of Aberdeen. Usually, cephalopods can only be identified to the genus

level, and Hastie et al. (2009) was used to confirm cephalopod species occurrence in the study area.

Cephalopod beaks, fish bones, and otoliths were measured using a microscope fitted with an eyepiece graticule (< 1 cm) or a digital callipers (0.01 mm) otherwise. Length and weight of the fish prey and cephalopods were extrapolated from standard otolith/bone and beak measurements, respectively, using published regressions (Clarke, 1986; Härkönen, 1986; Watt et al., 1991; Hernandez-Milian et al., 2005). For some species—European eel (*Anguilla anguilla*), European conger (*Conger conger*), horse mackerel (*Trachurus trachurus*), and *Scyliorhynchus* spp.—regressions were not available in the literature, and new ones were derived using the fish reference collections of the University College Cork and the University of Aberdeen.

During the digestion process, prey remains suffer different degrees of erosion depending on the type of structure and robustness; therefore,

prey sizes can be underestimated. Grellier & Hammond (2006) developed digestive coefficient factors for some fish prey species occurring in captive grey seal diets to improve the biomass estimation after they had passed through the entire digestive tract and were collected in scats. The application of these digestion coefficient factors depends on the degree of erosion of the otoliths. Only otoliths from samples BND 2664 and BND 3241 (29 and 57 otoliths, respectively) were found eroded enough to apply coefficient factors. There were not digestion coefficient factors for all species, and factors given by Grellier & Hammond (2006) for similar otoliths in shape and robustness were applied; the digestion coefficient factor for whiting (*Merlangius merlangus*) was applied to blue whiting (*Micromesistius poutasou*), while otoliths' digestion coefficient factors for cod (*Gadus morhua*) was used for pollack (*Pollachius pollachius*) and saithe (*P. virens*). To investigate if these coefficient factors were significantly increasing the total biomass consumed, differences in prey length and weight estimations before and after applying coefficient factors were calculated using Wilcoxon Signed Rank statistics, using *R Statistical Software* (www.r-project.org) as data were not normally distributed.

The importance of individual prey species/ taxa in each stomach was evaluated in terms of presence/absence, number, and summed reconstructed prey weight. Overall diet was described using three standard indices—(1) frequency of occurrence, %F; (2) percentage by number, %N; and (3) percentage by reconstructed weight, %W. Following Hyslop (1980), we also used the Index of Relative Importance (IRI) to measure the importance of each prey:

$$\text{IRI} = (\%N + \%W) \times \%F \text{ (eq. 1)}$$

where %F is the percentage frequency of occurrence of each prey, %N is the percentage of importance by number of each prey, and %W is the percentage of importance by weight.

Annual Food Consumption and Statistical Analysis

Annual food consumption rate (C, tonnes/y) was calculated using the equation from Col et al. (2012):

$$C = \Sigma N * E * \text{Res} * T \text{ (eq. 2)}$$

Where N is the estimated number of bottlenose dolphins in the area (obtained from the SCANS II survey estimate for Block R – south and west coast of Ireland of 313 (78 to 1,259, CV = 0.81) dolphins (Hammond et al., 2013; P. S. Hammond, pers. comm.), E the daily individual consumption,

Res the residential ratio, and T the time, which is 365. Col et al. (2012) reported a residential ratio of 0.66 for bottlenose dolphin in the northeast U.S. continental shelf; in Ireland, there is no residential value of the population, but, based on occupancy rates in the Shannon Estuary, it is likely to be similar, and we used a residential ratio of 0.66 in this study as well.

The individual's daily consumption (kg/d) E was calculated using the model suggested by Innes et al. (1987) for adult Odontoceti:

$$E = 0.313 * W^{0.66} \text{ (eq. 3)}$$

Where W is the weight (in kg) of an average dolphin. Weight is not routinely measured during *postmortem* examination, and, therefore, bottlenose dolphin weight was calculated from dolphin length for each of the animals examined using the equation from Kastelein et al. (2002):

$$W = 17.261 e^{0.0156(L-100)} \text{ (eq. 4)}$$

Where L is the length of the dolphin (tip of rostrum to tail fluke in cm).

Col et al. (2012) calculated a general annual food consumption of different marine mammal species without reference to prey types. In this study, we also calculated the annual food consumption (tonnes/y) for the main prey items by using the equation in Pierce et al. (2007):

$$I = N \times P_i \times F \times T \text{ (eq. 5)}$$

Where N is the abundance estimate used in equation 2, P_i is the proportion of prey species i by weight in the diet, F is the average weight of food taken daily by the dolphin, and T is the time, which is 365.

Pierce et al. (2007) used three different approaches to estimate the annual food consumption: (1) by using the data from the individuals with food in their stomachs (No Weighting), (2) by using the average body weight of all bottlenose dolphins stranded on the Irish coastline (E Weighting), and (3) by using the average bottlenose dolphin weight published in the literature (D Weighting).

Differences in food consumption in comparison to average landings during the study period of the main commercial prey groups were investigated. Within the flatfish family, only landings of plaice (*Pleuronectes platessa*), megrim (*Lepidorhombus wiffiagonis*), and sole (*Solea* spp.) were available, and the average of these three species was used as landings of all flatfish.

Comparison of diet between dolphins stranded alive and dolphins stranded dead, and between

sexes were investigated using Chi-square tests. Other comparisons such as differences in diet between season and areas were not carried out due to small sample size. All analyses were carried out using *R Statistical Software*.

Results

Study Area and Sample Composition

From 1999 to 2011, 90 bottlenose dolphins were reported to strand on the Irish coast at a rate of 6.15 per annum. Only 13% ($n = 12$) of the animals were recovered for *postmortem* examination.

In total, five animals stranded alive, six stranded dead, and one was bycaught. Five of the 12 dolphins studied were males, while seven were females. Digestive tracts of 10 out of 12 bottlenose dolphins analysed contained prey items (Figure 1). Half of the dolphins with food remains in their stomachs stranded alive, and four of these were male. The estimated body length ranged from 295 to 340 cm in males and from 280 to 320 cm in females (Table 1).

Prey Identification and Quantification of Diet

Of the digestive tracts examined, 333 prey items were identified, with 96.4% of all items being identified to at least genus level (Table 2). The number of fish identified using both bones and otoliths was 8.2%, higher than using otoliths alone, and four species were identified using skeletal structures other than otoliths—*Scyliorhinus* spp., Atlantic salmon (*Salmo salar*), *Phycis* spp., and ling (*Molva molva*). Fish occurred in 88.9% of the stomachs and constituted 82.4% of the diet by number and 98.9% by weight. At least 26 fish taxa were identified belonging to 22 families; Gadiformes species comprised 54.1% by number (76.8% by weight; $n = 187$), with five species occurring in over 60% of the stomachs (whiting, blue whiting, pollack, saithe, and haddock); flatfish made up 4.3% by number (0.9% by weight; $n = 15$), followed by dogfish, conger eel, and horse mackerel (Table 2). On the other hand, IRI values showed that pollack/saithe/haddock were the main prey ingested by the dolphins followed by whiting/blue whiting and pelagic fish (Atlantic mackerel and horse mackerel) (IRI = 845) (Table 2).

Table 2. Prey species identified from stranded and bycaught bottlenose dolphins in Irish coasts and waters ($N = 10$); N is number of prey, and W is reconstructed weight of prey in grams. Each prey is shown as percentage frequency of occurrence (%F), percentage importance by number (%N), percentage importance by weight (%W), and index of relative importance (IRI).

Prey species	%F	N	%N	W	%W	IRI
Chondrichthyes						
<i>Scyliorhinus</i> spp.	10	12	3.5	4,297.1	1.1	45.3
Egg capsule of <i>Scyliorhinus</i> spp.	10	1	0.3	NA	NA	NA
Osteichthyes						
Anguilliformes						
Unidentified eel	10	1	0.3	290.5	3.6	5.3
<i>Conger conger</i>	20	15	4.3	64,798.0	16.0	406.0
Salmoniformes						
<i>Salmon salar</i>	10	2	0.6	3,668.6	0.9	14.8
Gadiformes						
<i>Micromesistius poutassou</i>	30	8	2.3	8,681.3	2.1	133.5
<i>Merlangius merlangus</i>	30	11	3.2	6,071.9	1.5	140.3
<i>M. merlangus/M. poutassou</i>	30	34	9.8	3,542.2	0.9	321.0
<i>Melanogrammus aeglefinus</i>	30	17	4.9	21,547.1	5.3	306.6
<i>Pollachius virens</i>	10	11	3.2	50,185.1	12.4	155.4
<i>P. pollachius</i>	20	11	3.2	52,196.9	12.9	320.8
<i>Pollachius</i> spp.	20	6	1.7	11,829.5	2.9	93.0
<i>Pollachius</i> spp./ <i>M. aeglefinus</i>	10	14	4.1	6,936.9	1.7	57.6
<i>Trisopterus esmarki</i>	10	3	0.9	6.3	0.0*	8.7
<i>T. luscus</i>	2	6	1.7	1,261.9	0.3	40.9
<i>Trisopterus</i> spp.	30	21	6.1	4,287.5	1.1	213.8
<i>Gadiculus argenteus thori</i>	10	3	0.9	30.4	0.0*	8.8
<i>Phycis</i> spp.	10	2	0.6	498.6	0.1	7.0
<i>Molva molva</i>	40	10	2.9	63,074.1	15.5	737.1
Unidentified Gadidae	30	3	0.9	352.7	0.1	28.6
<i>Merluccius merluccius</i>	30	27	7.8	81,332.0	20.0	1,391.9

Prey species	%F	N	%N	W	%W	IRI
Perciformes						
<i>Trachurus trachurus</i>	40	43	12.4	7,908.2	2.0	575.0
<i>Scomber scombrus</i>	10	1	0.3	4,586.1	1.1	14.2
Gobiidae	10	1	0.3	3.3	0.0*	2.9
Atheriniformes						
<i>Atherina presbyter</i>	10	1	0.3	13.1	0.0*	2.9
Myctophiformes						
Myctophidae	10	1	0.3	27.0	0.0*	3.0
Pleuronectiformes						
<i>Platichthys flesus</i>	20	3	0.9	1,250.5	0.3	23.5
<i>Pleuronectes platessa</i>	10	1	0.3	995.0	0.3	5.3
<i>Limanda limanda</i>	10	1	0.3	144.3	0.0*	3.3
<i>Hippoglossoides platessoides</i>	20	7	2.0	780.9	0.2	44.3
<i>Scophthalmus rhombus</i>	10	1	0.3	233.8	0.1	3.5
<i>Solea solea</i>	10	2	0.6	441.0	0.1	6.9
Unidentified fish	20	4	1.2	NA	NA	NA
Cephalopods						
Theuthida						
<i>Loligo</i> spp.	30	3	0.9	933.3	0.23	32.9
<i>Alloteuthis</i> spp.	10	1	0.3	6.5	0.0	2.9
<i>Todarodes sagittatus</i>	10	1	0.3	NA	NA	NA
<i>Illex</i> spp./ <i>Todaropsis</i> spp.	10	1	0.3	363.2	0.1	3.8
Unidentified Ommastrephid	10	1	0.3	10.3	0.0*	2.9
<i>Brahioteuthis rissei</i>	30	17	4.9	119.3	0.0*	148.3
<i>Gonatus</i> spp.	10	8	2.3	1,055.6	0.3	25.7
<i>Teuthowenia megalops</i>	10	20	5.8	409.1	0.1	58.8
Octopoda						
<i>Octopus vulgaris</i>	20	5	1.5	1,097.2	0.3	34.3
<i>Eledone cirrhosa</i>	10	2	0.6	681.1	0.2	7.5
Unidentified cephalopod	20	2	0.6	NA	NA	NA
Crustacean	10	1	0.3	NA	NA	NA
Total	10	346		40,5946.8		

Two of the stomachs contained eroded gadoid otoliths that could not be identified to species level. These otoliths were grouped (Table 2) into two categories: (1) whiting/blue whiting and (2) pollack/saithe/haddock. The degree of erosion of these otoliths was not severe and, therefore, low digestion grade coefficient factors were used in all these cases; most of the otoliths could be grouped as low digestion grade. The overall estimated reconstructed prey weight increased by 67.2 kg if these digestion coefficient factors are applied—a significant increase (Wilcoxon Rank, $p < 0.005$).

The estimated length of all the gadoid species varied and ranged from 59 to 1,143 mm (Figure 2a & 2b). Almost 50% of the Gadiformes were found to be below 300 mm (Figure 2), which is considered to be below the minimum landing size (MLS) for some marketable Gadidae spp. (e.g., whiting and blue whiting) for the area (www.ices.dk). In contrast, most of the saithe and pollack were found to be larger than the MLS as was European

hake (*Merluccius merluccius*). *Trisopterus* spp. ranged in length between 59 and 495 mm, but 50% of these fish were larger than 210 mm (the maximum length at sexual maturity for one species, *T. luscus*, is 216 mm; www.fishbase.org). In general, most of the fish species recorded were less than 300 mm (Figure 3), and 58% of fish prey was below MLS. Although 12% of the horse mackerel estimated size was found below MLS (150 mm; www.ices.dk), 33% of the horse mackerel were below the sexual maturity length (239 mm; www.fishbase.org), ranging from 101.0 to 366.2 mm (average = 257.3 mm).

Cephalopods were the second main prey found in the diet occurring in 61%F of the stomachs, but its contribution by number and weight was relatively small (Table 2). Ten species within six families were identified, and oceanic cephalopods made up 15.6% by number ($n = 47$). It was the third most important prey group (including fish) when using IRI values (1,034). Within the cephalopod

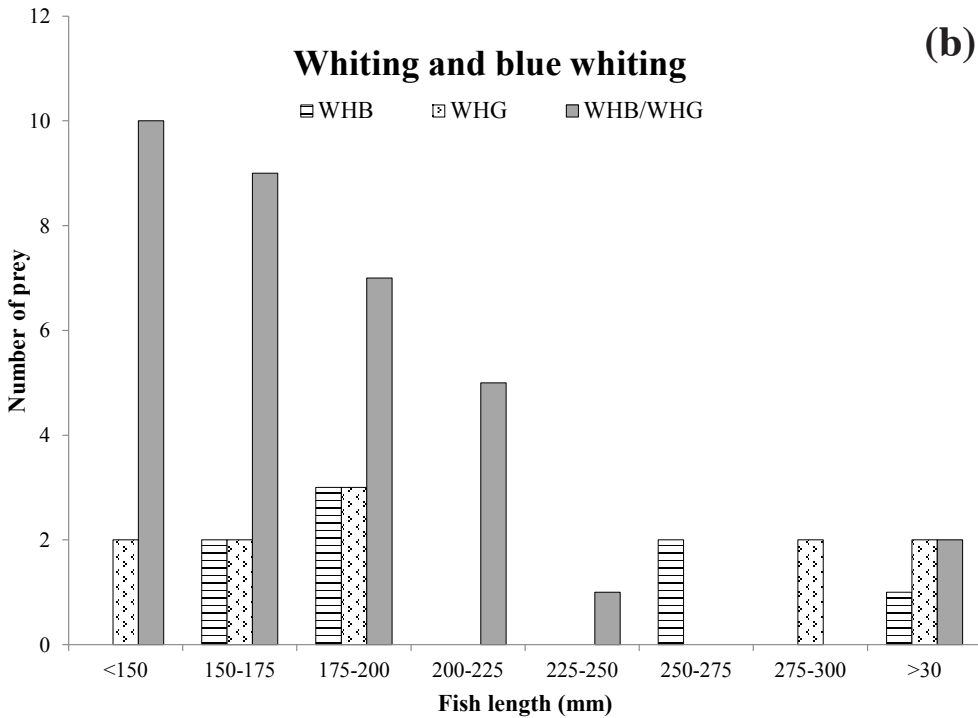
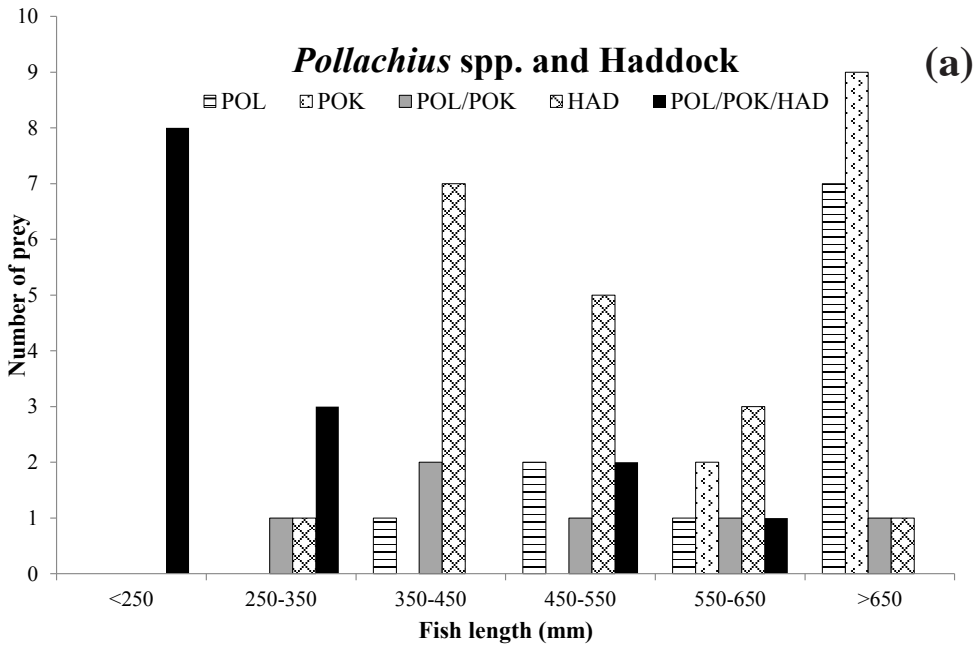


Figure 2. Estimated size for (a) pollack (POL), saithe (POK), and haddock (HAD), and (b) blue whiting (WHB) and whiting (WHG) prey items; minimum landing size (MLS) for whiting, pollack, saithe, and haddock are 27, 30, 35, and 30 cm, respectively. There is no blue whiting MLS in this region; however, 14 cm is the MLS for northwest of Spain.

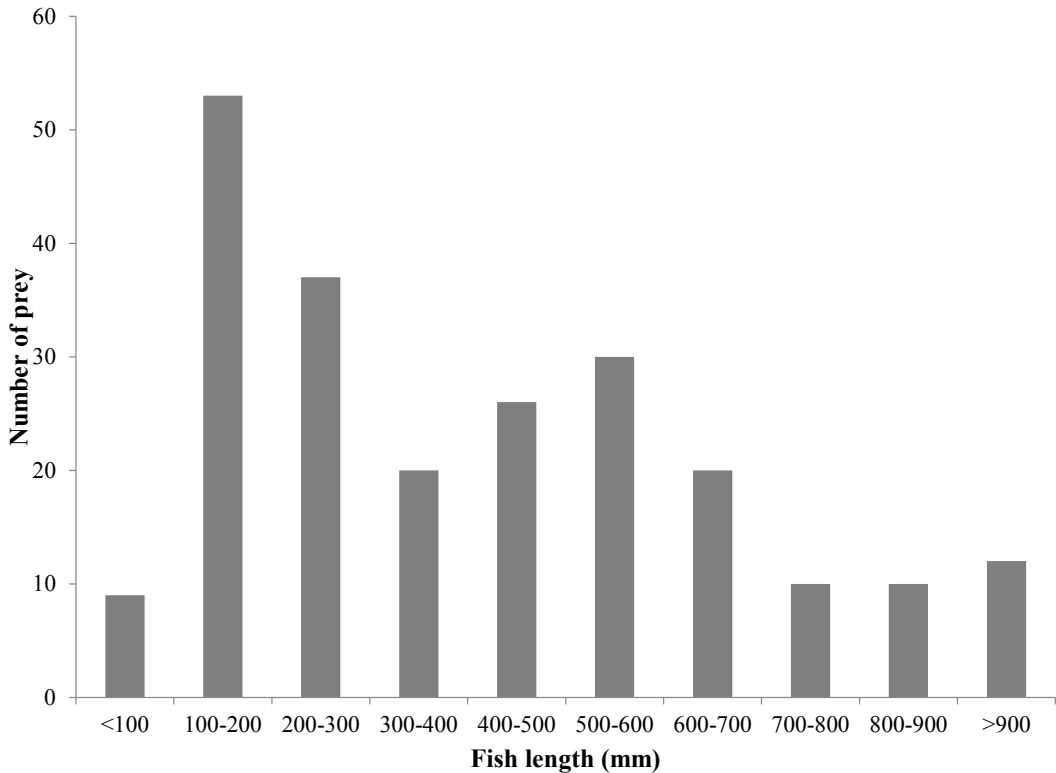


Figure 3. Estimated size for the main fish prey combined

prey category, the most abundant were the oceanic cephalopods, *Teuthowenia megalops*, followed by *Gonatus* spp. and *Brachioteuthis* spp. But these oceanic species mainly occurred in one of the stranded dolphins and in the bycaught one. The coastal cephalopods were mainly octopuses and squid, and they occurred in similar frequencies (Table 2). Two species of octopus were identified: *Octopus* spp. and *Eledone cirrhosa* (Table 2). Most of the cephalopod prey sizes ranged from 58 to 180 mm (80.9%) mantle length (ML) and weighed less than 130 g (79.3%).

Only one crustacean was found, and it was not possible to identify it to a lower taxonomic level (Table 2).

Five bottlenose dolphins were genetically assigned the 3rd/unknown origin population (Mirimin et al., 2011), and their stomach contents presented a variety of species from coastal (e.g., octopuses and conger eel in BND 3241) to oceanic pelagic prey (e.g., *T. megalops* and *M. poutassou*, BND 1/99 and BND 3/01, respectively), suggesting a wide ranging habitat use for this population.

Annual Food Consumption and Statistical Analysis

The estimated weights of the dolphins studied ranged between 257 and 632 kg (Table 1). The annual food consumption was estimated using the average estimated weight (394.3 kg), and the bottlenose dolphin population estimate, derived from SCANS II for Block R (297.5 to 4,081.9), was 1,193.8 t.

The annual food consumption for the main groups of prey was estimated using the Pierce et al. (2007) equation. Differences between the three approaches are shown in Table 3.

When comparing food consumption and landings in Ireland of the main prey groups, all prey groups were consumed on a very small scale (Figure 4). The only species consumed in a notable manner were *Pollachius* spp., whiting, and haddock that represent approximately 24, 10, and 12%, respectively, of the landings reported.

Significant differences were found in prey occurrence between the two stranding categories (dead and alive) ($\chi^2 = 27.9, p < 0.005$) and between sexes ($\chi^2 = 97.8, p < 0.005$). While 47.9% of the prey items found in live-stranded dolphins were identified as belonging to gadoid fish, followed by cephalopods (35.2%N, $n = 48$) and Atlantic hake

Table 3. Annual food consumption ($t \times 10^3$) of the main prey of bottlenose dolphins without rescaling (No Weighting), after applying equal weighting (E Weighting), and after applying the weighting related to the body weight of the animal (D Weighting). Percentage of diet related to average landings during the study period is in brackets.

	No weighting	E weighting	D weighting
Whiting/blue whiting	28.32 (< 0.0)	81.49 (< 0.0)	29.77 (< 0.0)
Pollack/saithe/haddock	220.87 (1.5)	116.69 (0.8)	272.65 (1.8)
<i>Trisopterus</i> spp.	8.60 (0.2)	19.24 (0.4)	10.11 (0.2)
European hake	125.89 (0.8)	141.13 (0.9)	159.59 (1.0)
Horse mackerel	12.24 (< 0.0)	9.62 (< 0.0)	15.47 (< 0.0)
Flatfish	5.95 (< 0.0)	4.25 (< 0.0)	4.33 (< 0.0)
Pelagic squid	4.49 (0.1)	80.24 (1.3)	4.0 (0.1)
Octopuses	2.75 (0.2)	2.31 (0.1)	2.20 (0.1)
Total	409.11	454.97	498.13

(12.8%N, $n = 10$), only 5.4%N ($n = 13$) of the prey were cephalopods in the dead stranded dolphins, with a further 36.8% comprising the three main Gadidae groups, 11.8% eels and dogfish, and 6.9% flatfish species. Significant differences were found between males and females ($\chi^2 = 97.8$, $p < 0.005$): females fed on 43.5% of the three main groups of gadoids, followed by horse mackerel (27.9%) and Atlantic hake (17.7%); males also fed on the three main groups of gadoids (39.7%), while cephalopods and eels/dogfish were also found to be important prey items (28.6% and 13.6%, respectively).

Discussion

Bottlenose dolphins have been described as generalist predators feeding mainly on pelagic fish and squid prey (e.g., Barros & Wells, 1998; Walker et al., 1999; Lopez, 2009). In Europe, studies on bottlenose dolphin diet have reported a wide variety of prey, including demersal species and some pelagic prey (Santos et al., 2001, 2007; Spitz et al., 2006). In Scotland, bottlenose dolphins ($N = 10$) were reported to feed mainly on whiting, followed by saithe and cod (Santos et al., 2001). In France ($N = 25$), the main Gadiformes species preyed on was European hake, followed by blue whiting and *Trisopterus* spp. (Spitz et al., 2006). Off northwest Spain ($N = 82$), bottlenose dolphins preyed mainly on blue whiting and hake (Santos et al., 2007); and in the western Mediterranean ($N = 15$), they preyed predominantly on European hake (Blanco et al., 2001).

The low rate of recovery of bottlenose dolphin carcasses in Ireland is caused mainly because this species is usually found in an advanced state of decomposition or they disappear with the next tide before examination. Although our sample size is small, results are consistent with previous studies (Blanco et al., 2001; Santos et al., 2001, 2007; Spitz et al., 2006). Bottlenose dolphins stranded

along the southwest and west of Ireland are eating a mixture of pelagic and demersal fishes, predominantly Gadiformes species such as the pollack-saithe-haddock group followed by whiting/blue whiting group and *Trisopterus* spp. In general, the main prey items could be considered benthic or benthopelagic species, suggesting feeding activity in coastal or relatively shallow waters. However, the presence in our sample of mesopelagic fish and squid species in the stomachs of dolphins from the 3rd population and a bycaught dolphin might suggest that individuals are also able to forage either in more oceanic waters and/or at deeper depths (bottlenose dolphins are capable of diving deeper than 450 m; Klatsky et al., 2007).

Horse mackerel was also reported in the diet of bottlenose dolphins in French (Spitz et al., 2006) and Spanish (Santos et al., 2007) Atlantic waters, but the size range consumed was larger in dolphins stranded in Ireland than those studied in France (Spitz et al., 2006). However, most of the horse mackerel (95.2%) occurred in dolphins that were classified within the 3rd population. West and southwest Irish waters are included within Area VII of the ICES areas, and this area has been reported to be important for the migration and spawning of pelagic fish species such as mackerel and horse mackerel (Uriarte & Lucio, 2001; Marine Institute [MI], 2010).

The occurrence of conger eels in the diet of bottlenose dolphins from European waters was previously reported from animals stranded along the Spanish coasts, both from northwest of Spain and the Mediterranean coast (Blanco et al., 2001; Santos et al., 2007). Although conger eels seemed to be important in terms of weight in this study, they mainly occurred in a single dolphin. The occurrence of this prey species could be related to individual prey preferences or foraging strategy.

Small elasmobranchs have been found to occur in the diet of bottlenose dolphins from the Northwest Atlantic (e.g., Barros & Wells, 1998;

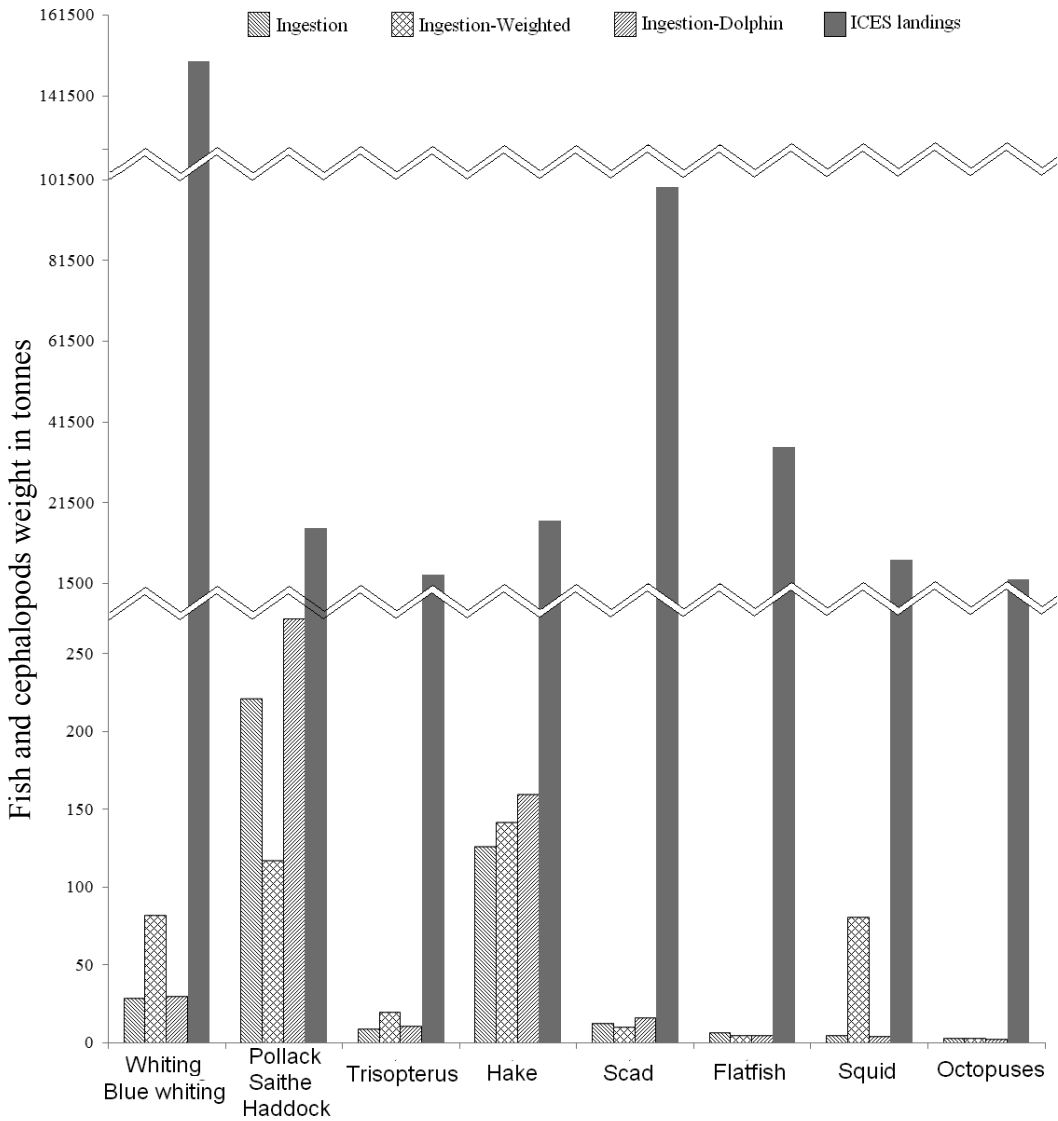


Figure 4. Landings and estimated consumption of the main prey groups for the coastal population in Ireland; estimations were calculated using percentage of weight (Ingestion), equal weighting percentage (Ingestion-Weighted), and weighting related to the body weight of the dolphin (Ingestion-Dolphin). Landings were obtained using the available data from ICES (www.ices.dk, ICES-landings) during the study period.

Gannon & Waples, 2004). However, within European waters, dogfish has only been previously reported in the diet of the Mediterranean monk seal (*Monachus monachus*) (Pierce et al., 2011). Dogfish are one of the most common small elasmobranch species around the Irish coast, and the landings in Ireland are around 2,000 tonnes/y (Central Statistics Office, 2002), mainly by recreational fisheries; they also are caught and discarded from bottom-set gillnets (Borges et al.,

2005). The occurrence of this species at different digestion stages in one bottlenose dolphin accompanied with other unusual prey species (Hernandez-Milian & Rogan, 2011) suggested that the dolphin might be feeding in an area where dogfish are abundant. However, the importance of elasmobranchs in the diet of bottlenose dolphins is difficult to quantify due to their relatively high digestibility that complicates the identification of elasmobranch fishes, which is only possible by

direct feeding observation or when the stranded animal was feeding very recently and digestion of hard remains has been limited.

The occurrence of salmon in the diet is also of note. Although only found in one stomach (BND 1/05), movement of bottlenose dolphins into the Shannon Estuary following the salmon run has been suggested as one of the reasons for an increase in bottlenose dolphins in the estuary over the late spring/summer months (Ingram, 2000). Direct observations of bottlenose dolphins feeding on salmon have also been reported in the Shannon Estuary (along with garfish [*Belone belone* L. 1761]; Ingram, 2000; E. Rogan, pers. obs.) and in Cork Harbour (Ryan et al., 2010), and, therefore, salmon might be more prevalent in the diet than was found in this study as was suggested in bottlenose dolphins stranded and bycaught in Scottish waters (Santos et al., 2001).

In general, the estimated size of 50% of Gadiformes was below the MLS established for the different species (www.ices.dk). Saithe and pollack eaten by bottlenose dolphins were estimated to be above the MLS, while the opposite was true for whiting/blue whiting group and *Trisopterus* spp. Most of the items that were not identified to species level in *Pollachius* spp./haddock group were estimated to be below 280 mm after applying the correction factors, and 300 mm is considered the MLS for the smallest species (haddock).

The identification of non-otolith bones in marine mammal diet studies to improve our understanding of feeding ecology has become more common (e.g., Santos et al., 2007; Gosch et al., 2014). In this study, for example, four fish species—European eel (*Anguilla anguilla*), *Salmo* spp., common dab (*Limanda limanda*), and dogfish—were identified from bones (e.g., dentary, premaxilla), and this information would have been lost if only otoliths had been used to characterise the diet of the sampled dolphins. Digestion coefficient factors to take otolith size loss due to gastric erosion into account have been derived from experimental trials in the lab (e.g., Wijnsma et al., 1999) or by feeding otoliths to captive seals (e.g., Grellier & Hammond, 2006). However, no comparable information is available for cetaceans. When the erosion coefficients were applied to our data, the estimated weight of prey consumed increased 300% for some groups such as gadoids (e.g., pollack, saithe, and haddock) and hake, and 200% for mackerel and plaice.

The prey diversity indicates that the diet of bottlenose dolphins might be composed mainly of locally available prey species as suggested previously by Barros & Odell (1990). Indeed, stable isotope analysis carried out on bottlenose

dolphins in Irish coastal waters showed differences in diet (Rogan et al., 2011). Walker et al. (1999) studied stable isotopes in bottlenose dolphins in the Northwest Atlantic and found that coastal dolphins were mainly fish feeders, while offshore ones were mainly squid feeders. The bycaught dolphin examined in this study had pelagic squid in its stomach, and stable isotope analysis showed a high $\delta^{34}\text{S}$ value (Rogan et al., 2011), suggesting that this animal might be related to a more pelagic population. The majority of prey items from the stomach contents of animals that are genetically classified as belonging to the 3rd population indicate that these animals were foraging on the continental shelf and close to the shelf edge, suggesting that these animals represent a community that feeds in the continental shelf/neritic zone. Reconstructing diet from stomach content analysis of dead dolphins has obvious caveats associated with it, but in this case, stable isotopes (Rogan et al., 2011) and genetic analysis are consistent with the results that the bottlenose dolphins feed on locally available species.

A few studies have estimated food consumption by marine mammal populations (e.g., Barlow et al., 2008; Col et al., 2012). Barlow et al. (2008) investigated the accuracy of different models to calculate the annual food consumption in marine mammals; however, these authors do not consider migration/residential patterns. Bottlenose dolphins in Irish waters present a complex structure with resident and highly mobile populations (Mirimin et al., 2011), and the residency ratio suggested by Col et al. (2012) of 0.66 is likely applicable in our study area. Dolphin body mass estimation obtained in published literature was calculated using different studies around the world; those studies are often of smaller animals than the ones inhabiting Irish coastal waters and, therefore, the annual consumption is likely underestimated. Kastelein et al. (2002) obtained a body mass estimation studying 16 captive bottlenose dolphins that ranged from 220 to 280 cm in length and found that the asymptotic growth occurred at 270 cm. In our study, all of the animals were over this length. Kastelein et al. suggested that dolphins between 155 to 225 kg might consume between 2 to 4% of their body mass per day. Using 4% of body mass as a metric for consumption, the mean annual food consumption estimation in Irish coastal waters is around 1,190 t. As captive dolphins are expected to have lower consumption rates (Barlow et al., 2008), it might be expected that the annual food consumption of bottlenose dolphins in Irish coastal waters might be higher. Interestingly, the annual consumption of this species in Ireland showed that competition with fisheries might not be strong—particularly

considering that all animals in this study were adults—and, therefore, annual food consumption is likely overestimated. Although consumption of pollack and saithe were found to be high, more than 80% of this prey was consumed by the animal stranded in 2001 when landings of these species was also high, suggesting that this animal was feeding on species that were highly abundant.

Significant differences were found in the diet of male and female bottlenose dolphins in this study despite the small sample size, something that has been reported in other areas (e.g., Blanco et al., 2001; Santos et al., 2007). Santos et al. (2007) investigated the diet of dolphins related to cause of death (bycaught dolphins vs unknown and other causes) and found no significant differences in the diet. In our study, only one animal was bycaught, and only offshore-pelagic squid was found in its digestive tract; a third of the animals stranded alive. In the literature, live strandings have often been associated with disorientation, non-familiar habitat, and illness, and with animals that likely have not been feeding normally. Therefore, differences in diet might be expected between these groups and the remaining samples. In our study, live-stranded dolphins were mainly feeding on gadoids and cephalopods, while dead-stranded dolphins were found to have greater prey diversity. It is also possible that live strandings could comprise individuals that usually reside in more oceanic/neritic type habitats.

Of the animals sampled and for which genetic origin is known, five individuals were identified as belonging to the 3rd population in Irish waters of unknown origin. It appears that these animals were feeding on species that can occur both in coastal waters and on the continental shelf; these results suggest that the 3rd population might be inhabiting or feeding on the continental shelf or slope. These results appear to be consistent with a recently published genetic study by Louis et al. (2014) who showed that there are genetic differences between *coastal* and *pelagic* bottlenose dolphins in the Northeast Atlantic.

Complementary analysis with stable isotope techniques has been carried out recently (Rogan et al., 2011) and has confirmed diet results. Rogan et al. (2011) reported a low $\delta^{13}\text{C}$ in animals that were feeding mainly on demersal prey, while animals with high $\delta^{13}\text{C}$ preyed on pelagic prey. Also, results on $\delta^{34}\text{S}$ confirmed the suggestion that some animals are coastal, while others are neritic, with the possibility of another group feeding within the oceanic area (BND 1/96; Table 1).

Quantifying the diet of a species through the examination of its digestive tracts provides valuable information towards understanding its ecological requirements as well as informing

conservation efforts and future management plans. In addition, it provides some of the data needed to parameterize the tools that would allow us to explore how the ecosystem can react to possible future scenarios; for example, mass-modeling simulations, such as *Ecopath* with *Ecosim* (www.ecopath.org), need dietary information in terms of biomass to obtain a trophic model ecosystem.

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