Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food?

Jérôme Spitz[a, b, *], Yann Rousseau[a] and Vincent Ridoux[a, c]

[a]Centre de Recherche sur les Mammifères Marins, Institut du Littoral et de l'Environnement, Université de La Rochelle, Avenue du Lazaret, 17000 La Rochelle, France
[b]Ecole Pratique des Hautes Etudes, Laboratoire de Biogéographie et Ecologie des Vertébrés, Place Eugène Bataillon, 34060 Montpellier, France
[c]Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés, UMR 6217,CNRS-Ifremer-Université de La Rochelle, Avenue Michel Crépeau, 17042 La Rochelle, France

*: Corresponding author : Email : jspitz@univ-lr.fr

Abstract

In aquatic ecosystems, competitive interactions are occasionally described. Violent attacks on harbour porpoises by bottlenose dolphins were reported and it was proposed that this behavior could result from competitive interactions for food. This hypothesis implies that the two predators should share all or part of they prey range. In this work, we describe the diets of each predator in the Bay of Biscay and adjacent areas from stomach content analysis of stranded animals. The diet of the harbour porpoise was mostly composed of small schooling fish living close to the seafloor (98 percent by mass). The diet of the bottlenose dolphin was characterised by the presence of large specimens of demersal fish (91 percent by mass) and cephalopods. Several prey species are common in the two diets and even the length distributions of some of them, such as sardine or scads, are very similar. However, global indices such as the Mantel test or the Pianka's index indicate no or weak overlap. The dietary results suggest that the two predators show partial dietary overlap over several major dimensions of the foraging niche: prey profile, foraging habitats, prey species and size range. We suggest interference competition is plausible at the scale of a prey school that would be exploited jointly by groups of the two predators.

Keywords: interference competition; top predator; diet; *Phocoena phocoena*; *Tursiops truncatus*; North-Eastern Atlantic

1. Introduction

An accepted definition of the concept of competition is given by Keddy (1989) as "*the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability*". Then, most ecologists distinguish two forms of competition : exploitative competition when the competitive species are not in direct interaction but the consumption of food by one of them reduces resource availability to the others, and, the interference competition when direct conflicts break out between competitors (*e.g.* Keddy, 1989; Sih, 1993).

The observed diet of a marine predator is the combination of resource availability and foraging strategies. The former is determined by a combination of spatially-defined characteristics of the environment such as depth and slope, and more mobile or temporary features such as a wide variety of meso- to small-scale hydrological processes. The latter is determined by costs and benefits associated to foraging, linked to limitations in physiological, physical or social functioning. Thus, if several predators develop the same foraging technique and so, exploit the same resource, they are in a context where competition could occur. In top predators, exemplified by terrestrial carnivores (Caro and Stoner, 2003), competition can take different forms: avoidance, exploitative competition, food stealing or competitor killing. Aggressive interactions were largely documented for terrestrial predators; Palamores and Caro (1999) reviewed 97 pairs of African terrestrial carnivores shown to exhibit lethal aggressive competition.

In aquatic ecosystems, aggressive interactions are occasionally described. For marine mammals, predation by killer whales, *Orcinus orca*, on other marine mammals is largely documented (Jefferson et al., 1991), some social interactions are observed, specially, with delphinids (*e.g.* Herzing et al., 2003; Psarakos et al., 2003) and few anecdotic observations like infanticide were reported (Baird, 1998, Orr and Harwood, 1998, Patterson et al., 1998). Finally, violent interactions between bottlenose dolphins, *Tursiops truncatus*, and harbour porpoises, *Phocoena phocoena,* were reported, notably in British waters where they are estimated to be the first source of porpoise mortality in areas were both species occur (Ross and Wilson, 1996; Jepson and Baker, 1998; Santos et al., 2004). It was proposed that these attacks could notably result from competitive interactions for food (Ross and Wilson, 1996). The Bay of Biscay and the adjacent Northeast Atlantic Ocean are home to an abundant and diversified cetacean fauna, including the harbour porpoise and the bottlenose dolphin (Hammond *et al.*, 2002; CRMM/ULR, unpublished data from sighting surveys in the Bay of Biscay). The two species' ranges partly overlap in coastal and shelf waters, although the bottlenose dolphin also extensively dwells further offshore. Direct and stranding evidences (C. Vincent, unpublished field observation; O. Van Canneyt, unpublished stranding data) suggest that, similarly to what is frequently observed in Scotland, attacks of harbour porpoises by bottlenose dolphins also occur.

In this work, we describe the diets of each predators from stomach content analysis of stranded animals and examine if these species do share similar prey preference in the aim of highlighting the potential for interference competition between the two species.

2. Materials and methods

2.1. Collection of samples

In this study, 29 stomachs of harbour porpoise and 25 of bottlenose dolphin stranded along the Northeast Atlantic French coast, Bay of Biscay and western Channel, were collected (Fig. 1). These animals were recovered and examined by members of the French stranding scheme from June 1988 to April 2003. The sample set includes individuals of both sexes, with immatures and adults. After necropsy, the stomachs were ligatured and stored deep-frozen (-20°C) in polythene bags until further analyses.

2.2. Sample analysis

Sample analysis was aimed at describing the diet in terms of prey occurrence, relative abundance, calculated mass and size distribution and followed a general procedure which is now standard for marine top predators (Pierce and Boyle, 1991; Croxall, 1993; Ridoux, 1994). Each stomach was weighed, emptied in a tray and its wall weighed again to obtain the mass of the stomach content by difference. The stomach content was washed through a 0.2 mm mesh sieve. The diagnostic parts were recovered and stored dry for fish bones and otoliths or in 70% ethanol for cephalopod beaks, crustacean remains as well as any remain with flesh attached. The items found were identified to the lowest taxonomic level by using published guides (Lagardère, 1971; Clarke, 1986; Härkönen, 1986) and our reference collection of specimens caught by commercial or scientific trawlers in the Bay of Biscay and adjacent Atlantic areas. The total number of food items was estimated as the highest number given either by paired structures (otoliths, operculum, hyomandibular, dentary and premaxillary for fishes, upper and lower beaks for cephalopods and eyes for crustaceans) or impaired structures (parasphenoid for fishes, gladii for cephalopods and carapace and telson for crustaceans). Diagnostic hard parts such as beaks, otoliths and carapaces were measured by using a

digital vernier calliper (± 0.02 mm) following standards (Clarke, 1986; Härkönen, 1986). A random sub-sample of up to 30 diagnostic hard parts per prey species per stomach sample was measured.

2.3. Dietary data analysis

The occurrence of a given prey taxon is the number of stomachs in which this taxon was observed. The relative abundance is given by the number of individuals of the same taxon found throughout the sample set. The calculated biomass is given by the product of the average calculated body mass and the number of individuals of the same taxon in each sample, summed throughout the sample set. These three indices can be expressed by their percentage frequency with, respectively, percentage of occurrence (%O), percentage by number (%N) and percentage by biomass (%M) :

$$\%O_i = n_i / N * 100$$

where n_i is the number of stomachs where the prey i was found and N the total number of stomachs ;

$$\%N_i = x_i / X * 100$$

where x_i is the number of prey i found and X the total number prey ;

$$\%M_i = (\sum_j x_{i,j} * \overline{Y}_{i,j} / \sum_i \sum_j x_{i,j} * \overline{Y}_{i,j}) * 100$$

where $x_{i,j}$ is the number of prey i found in the sample j and $\overline{Y}_{i,j}$ the average individual body mass of prey i in sample j.

Individual prey body length and body mass were back-calculated by using relationships that either came from the literature (Clarke, 1986; Härkönen, 1986) or were fitted from measurements performed on specimens of our reference collection. Body size distribution was established on the basis of the whole series of individuals of each prey i. Therefore, size distributions were established at sample j level from the 30 measured individuals or prey i, level-headed to total number of prey i individuals in sample j and summed throughout the sample series. These prey size distributions were constructed both as the percentage by number and the percentage by mass contributed by each size class, since these two variables convey quite different information about the importance to the diet of prey of varying body lengths.

Thus, the diets of these cetaceans were described by the following indices: occurrence, number and reconstructed mass as well as body size distributions for each prey species. 75% percentile for the compositions by number and by mass were generated by non-parametric bootstrap simulations allowing sampling error to be estimated (Reynolds and Aebischer, 1991). The bootstrapping routine was written by using the *R* software (Ihaka and Gentleman, 1996). Random samples were drawn with replacement and the procedure was repeated 300 times. Possible biases related to subsampling for length measurements and to erosion of diagnostic parts were not estimated.

2.4. Comparison of diets

Firstly, some descriptive index were calculated to estimate and compare the characteristics of dietary niches. The specific richness (R) is the number of species found in the diet of a given predator. The common specific richness (Rc) is the number of species found in the diets of both predators. The biodiversity of prey was calculated by the Shannon-Wiener index (H') which considers both the specific richness and the number of specimens for each species.

$$H' = - \sum p_i \log_2 p_i$$

where p_i is the percentage by number of the prey i founded in the diet.

The equitability gives the balance between the percentage by number of each prey. It varies from 0 to 1; 1 indicating that each prey has the same percentage by number.

$$E = H' / \log_2 R$$

The dietary overlap in number or in mass is obtained by the Pianka index (respectively O_n et O_m). It varies from 0 (no overlap) to 1 (complete overlap).

$$O = \frac{\sum p_{iA} p_{iB}}{\sqrt{\sum p_{iA}^2 \sum p_{iB}^2}}$$

where p_{iA} is the percentage by number (or mass) of the prey i founded in the diet of predator A and p_{iB} is the percentage by number (or mass) of the prey i founded in the diet of predator B.

The dispersion of our samples was examined by performing Correspondence Analyses (CAs). CA routines were done by using the software XLSTAT© v5.1 (Addinsoft). CAs allowed the homogeneity of the samples and the existence of sub-groups to be highlighted. The matrix was constituted by 0 (absence of prey species) or 1 (presence of prey species). According to Patterson (1986), the difference in prey taxa utilisation was estimated by using a Mantel test, a nonparametric statistical test for comparing two distance matrices. The first matrix consists of 0 and 1 depending on whether the species are the same or not ; the second one contains overlap values (Pianka's index) based on prey taxa. This correlation test was generated by the software XLSTAT© v5.1 (10000 randomisations).

To compare differences in prey length distributions, the univariate Mann-Whitney test was used because of non-normal data.

3. Results
3.1. Diet of harbour porpoise
3.1.1. General
The total mass of examined food material was 5300g, *i.e.* an average stomach content mass of 182 ± 227 g (N=29; range 6 – 839). Identifiable material was retrieved from 26 out of 29 stomachs.
A total of 1728 prey individuals were found. They accounted for a total reconstructed biomass of 24072 g. Fish, cephalopods and crustaceans were identified and represented a species richness of 19 (respectively 13, 5 and 1 species). The average prey diversity was 3.4 ± 2.2 species per sample (N = 26 non empty stomachs). Fish dominated the diet (Table 1) both by number (85 %) and mass (98 %). Crustaceans, represented by only one species, northern krill, *Meganyctiphanes norvegica*, reached 13 % in relative abundance but were negligible in reconstructed mass. Cephalopods accounted for a low fraction of the diet either by number or by mass.

3.1.2. Specific composition
The diet of harbour porpoise along the Northeast Atlantic French coast was composed of a combination of groundfish (*e.g.* Gadidae, Atherinidae, Merluccidae) and some pelagic fish (*e.g.* Clupeidae, Carangidae, Scombridae). In terms of species importance, 6 fish species held more than 80 % by number and 95 % by mass (Table 1). Blue whiting, *Micromesistius poutassou*, was the most frequent prey with 39 % of occurrence and it amounted to 19 and 21 % in relative abundance and mass, respectively. Despite their lower relative abundance, sardine, *Sardina pilchardus*, scads, *Trachurus trachurus* (or/and *T. mediterraneus*) and whiting, *Merlangius merlangus*, represented the remainder of reconstructed biomass with 21, 28 and 20 % respectively, as a result of their comparatively larger body size (Fig. 2). By contrast, gobies represented 22 % by number but, owing to their very small body size (44 ± 11 mm body length), only 1 % by mass. Similarly, northern krill (29 ± 0 mm) accounted for 13 % by number and only 0.2 % by mass.

3.1.3. Prey sizes
The overall prey size distribution ranged from 8 to 307 mm with the mean at 130 mm (Fig. 3). Overall, 77 % of all prey individuals (mainly *Trisopterus* spp, *gobidae*, *Meganyctyphanes norvegica*) were smaller than 100 mm and only 9 % (mainly *Sardina pilchardus*, *Merlangius merlangus*, *Trachurus* spp) were larger than 190 mm body length. Contrastingly, prey individuals smaller than 100 mm represented only 7 % of the reconstructed biomass, whereas those over 190 mm accounted for 70 % by mass.

3.2. Diet of bottlenose dolphin
3.2.1. General
The total mass of food remains was 27200 g, *i.e.* an average of 1300 ± 1229 g per sample (N=25; range 60 – 4398) and identifiable material was found in 21 out of 25 samples. A total of 1060 prey individuals were found, which accounted for a total reconstructed biomass of 174875 g, with a species richness of 33 (25

fish species, 3 cephalopods and 1 crustaceans). The diet was mostly composed of fish, with limited amounts of cephalopods and crustaceans as well. The average prey diversity was 4.7 ± 2.1 species per sample (N=21 non empty stomachs). Fish largely dominated (Table 2) by both number (94 %) and mass (91 %). Cephalopods represented 9 % reconstructed mass and crustaceans accounted for a very low fraction of the diet either by number or mass.

3.2.2. Specific composition

The diet of bottlenose dolphin along the Atlantic French coast was composed of a combination of large groundfish and squid (*e.g.* Merluccidae, Mugilidae, Sparidae, Gadidae, Loliginidae) and some pelagic fish (*e.g.* Carangidae, Moronidae, Clupeidae) (Table 2). Hake, *Merluccius merluccius*, was the most important prey in this diet with 20 % by number and 41 % by mass. Scads and mullets, family Mugilidae, represented 13 % and 12 % by reconstructed biomass and 15 % and 5 % by number respectively. All these three species were represented by large specimens (Fig. 2). Secondary fish species included pouts (7 % by mass), sea bass, *Dicentrarchus labrax* (6 % by mass), sea bream, *Spondyliosoma cantharus* (4 % by mass) and sardine (3 % by mass). Finally, blue whiting and sprat, *Sprattus sprattus*, represented respectively 13 % and 11 % by number but, owing to their very small body size (9 and 12 cm), less than 1 % by mass. Among cephalopods, only *Loligo spp.* (*L. vulgaris* and/or *L. forbesi*) was found, and reached more than 9 % by reconstructed biomass.

3.2.3. Prey sizes

Overall prey size distribution ranged from 18 to 667 mm with the mean at 228 mm (Fig. 3) and displayed three modes. Prey <160 mm and prey from 160-320 mm accounted for 41 % and 44 % by number respectively, whereas prey > 320 670 mm represented 16 % by number. Prey larger than 160 mm provided about 96 % by mass of the diet.

3.3. Comparison of the diet of harbour porpoise and bottlenose dolphin

Bottlenose dolphin appeared to feed on a more diversified diet (33 species) than the harbour porpoise (18 species). But, more than 70% of the harbour porpoise prey (13 species) were found in the diet of the bottlenose dolphin. Similarly, dietary diversity was higher in bottlenose dolphin than in harbour porpoise (H'$_{Tursiops}$ = 3.58, 95%CI: 3.31-3.58, compared to H'$_{Phocaena}$ = 2.83, 95%CI: 2.76-2.98). Again, equitability was also higher in the bottlenose dolphin than in the harbour porpoise (E$_{Tursiops}$ = 0.72, 95%CI: 0.70-0.75, compared to E$_{Phocaena}$ = 0.63, 95%CI: 0.64-0.69). The niche overlap calculated with the Pianka index was of 0.45 by relative abundance and only 0.25 by mass.

Statistical testing of dietary differences gave equivocal conclusions. On a general point of view, the Mantel test indicated that the diets of harbour porpoise and bottlenose dolphin differed significantly in prey composition (P<0.05) and prey length distributions as well (P<0.001) (Fig. 3). However, on a more specific points of view, the projection of stomach contents in the CAs (Fig. 4) showed some samples were very close in their prey species composition between the two predators. Similarly, there was important overlaps in length distributions for many shared prey species (Table 3) such as scads, mackerel, anchovy or sand-smelt; moreover, length distributions for sardine were statistically identical (P<0.001) in both predators.

4. Discussion

4.1. General

The present work is the first quantitative study of the diet of the harbour porpoise and the bottlenose dolphin in the Bay of Biscay, two of the main top-predators of coastal and shelf habitats in the area.

Several limitations are inherent to a small sample of stomach contents from stranding schemes. Thus, for a comparison of the diet of two predators, the results could be affect by the pooling of the data across time and space. However, in this study, the two samples were comparable because distributed across all sex and age classes (sex identified at necropsy, age identified from teeth sections; ULR/CRMM unpublished data), the repartition of stranding were similar for the two cetaceans across years and seasons and mostly came from the same large area, the Bay of Biscay and the western channel. Secondly, a characteristics of stranded materials, compared to material obtained from freshly by-caught animals is that the stomach content is often reported to be merely made up of digested material (Pierce and Boyle, 1991). However, in this work, the mass of food material collected represented 22% and 16% of the reconstructed mass for harbour porpoise and bottlenose dolphin respectively, a ratio not very different from figures obtained in by-caught dolphins (24% in common dolphin, 21% in striped dolphin, Ringelstein et al*.,* in press; Pusineri et al., in press). Nonetheless, this is likely to cause some biases in the quantification of the importance by number and by mass of the different species as the various diagnostic parts used in the analyses do not have the same retention times in the stomachs (*e.g.* Murie, 1987; Pierce and Boyle, 1991; Santos et al., 2001b).

This effect is evidenced, principally for bottlenose dolphins, since remains of large species found were mostly accumulated material. Consequently, the contribution of this kind of prey, here hake, mullets or squids, may be overestimated. Given these limitations shared by both species in this study, the present work nonetheless provides new quantitative figures on the dietary composition of these two top predators on the continental shelf of Bay of Biscay and adjacent areas and allows assessment of dietary overlap.

The diet of the harbour porpoise was mostly composed of fish (98%M). The assemblage of species revealed the prevalence of small schooling fish living close to the seafloor. The ingested biomass was essentially made up of four species accounting for an approximately equal share of the diet: scads, sardine, blue whiting and whiting. A striking aspect of this study was the presence of some offshore prey species such as northern krill, pearlsides (*Maurolicus muelleri*) and, to a lesser extent, blue whiting, suggesting that the harbour porpoise is not strictly limited to coastal waters. The diet of the bottlenose dolphin was characterised by the presence of large specimens of demersal fish and cephalopods. Fish made up a total of 91 %M. Hake was the central prey with 41 %M, complemented by mullets, scads, pouts, sea bass and *Loligo* squids.

The comparison of the two diets suggests that these predators essentially share the same prey profile, with demersal prey being the most important complemented by some pelagic species. Several prey species are common in the two diets and even the length distributions of some of them, such as sardine or scads, are very similar. However, global indices such as the Mantel test or the Pianka's index indicate no or weak overlap. A fair amount of segregation is also obtained in terms of prey size ranges, as bottlenose dolphin preys on larger specimens (*c.* 200-600 mm) than harbour porpoise does (*c.*100-300 mm).Seemingly, the former tends to forage further offshore, in deeper waters as shown by the abundance of hake and particularly of large specimens on the outer shelf (Poulard, 2001) and the stomach contents as well (this work). On this latter point however, overlap between the two species also exists as shown by the presence in the food of the harbour porpoise of blue whiting, pearlsides and northern krill, three species that are more likely to be found close to the slope than along the coast (Mauchline, 1960; Quéro et al., 2003).

4.2. Comparisons with previous studies
The diets of these small cetaceans have been studied in many regions. The diet of the harbour porpoise is generally composed of gadids and clupeids, complemented by sandeels and gobies, but at prey species level its composition varies between areas (*e.g.* Börjesson et al., 2003; Rae, 1965; Santos et al., 2004; Smith and Gaskin, 1974, present work). Thus, the harbour porpoise can be considered as a predator of small demersal prey (although clupeids are pelagic fish, they often dwell near the seafloor). The diet of the bottlenose dolphin varies a lot between study areas, possibly as a result of local prey availability combined with highly flexible foraging tactics. Pelagic and demersal fish, cephalopods and even crustaceans can be locally predominant in the diet (*e.g.* Cockcroft and Ross, 1990; Barros et al., 2000; Santos et al, 2001a); however, the bottlenose dolphin is also often described as a strictly demersal feeder (Gunter, 1942; Tomilin, 1957; Evans, 1980; Barros and Odell, 1990; Blanco et al., 2001; present work). In terms of foraging tactics, the bottlenose dolphin is extremely flexible among delphinids as it was shown to develop original feeding techniques such as crater-feeding (Rossbach and Herzing, 1997) or inducing fish schools to strand on mud banks (Lewis and Schroeder, 2003).

The compositions of the food of both the harbour porpoises and bottlenose dolphins in the Bay of Biscay largely differ from the diet of the common dolphin, *Delphinus delphis*, the other abundant small cetacean in the area. This latter, known to be a cooperative pelagic feeder, locally displays a diet almost exclusively composed of small schooling pelagic fish, such as anchovy, sardine, scads and mackerel (CRMM/ULR, unpublished data).

4.3. Ecological significance
The dietary results suggest that the two predators show partial dietary overlap over several major dimensions of the foraging niche: prey profile, foraging habitats, prey species and size range. Is this amount of overlap sufficient to generate interference competition?
In marine ecosystems, resource is patchily distributed; this is often reported for schooling forage species like scads or clupeids but it is also the case for most demersal species. The optimal foraging theory MacArthur and Pianka, 1966) suggests that top marine predators would have to go from patch to patch in order to maximize the ratio between foraging benefits and costs. If interference competition is hardly conceivable when one considers bottlenose dolphins and harbour porpoise living sympatrically at the scale of the whole Bay of Biscay and western Channel, such behaviour is more plausible when one considers the scale of a prey school that would be exploited jointly by groups of the two predators. Consequently, even if only one prey is shared by two predators, interspecific interaction can occur. The risk of such competition

would be a function of the size of the prey aggregation, the number of predators present in the same patch and the duration of the mixed-predators association. For example, no interference competition was observed in the Azores in mixed-species feeding aggregation of dolphins, large tunas and seabirds (Clua and Grosvalet, 2001). In this case, prey constitute large patches and predation results in and relies on the formation of a compact and transient "ball" of several thousands of fish close to the surface; in that case the mixed-predators aggregations were of short duration (5 to 20 minutes). However, other conditions seem to be more propitious to aggressive interactions. For instance, between spotted dolphins, *Stenella frontalis*, and bottlenose dolphins in the Bahamas, aggressions on spotted dolphins by bottlenose dolphins were recorded in situations of mixed-species foraging that lasted up to more than a day and targeted bottom resources (Herzing and Johnson, 1997; Herzing et al., 2003). Moreover, interference competition would be more likely to induce aggressive interactions in case of marked asymmetries between the two predators involved (differences in body size, strength or group size) (Maynard Smith, 1982). In the present study case, the bottlenose dolphin is clearly larger and stronger than the harbour porpoise and it generally forages in larger groups than the harbour porpoise does.

These elements suggest that all circumstances are gathered to facilitate aggressive behaviors on harbour porpoises by bottlenose dolphins when they forage together on the same prey patch. This hypothesis is strengthened by dietary results from Scotland, an area well known for the frequency of aggressive interactions between harbour porpoises and bottlenose dolphins. A recent study showed that sandeels are more abundant in the stomach contents of porpoises killed by *Tursiops* compared to other causes of death (Santos et al., 2004) and in this area, sandeels are also the second more abundant prey in the diet of bottlenose dolphins (Santos et al., 2001b).

If this interference competition is frequent enough, it could cause some shift in habitat or resource use in the weaker species. An illustration of such an effect could be the higher proportion of small prey items in the diet of the harbour porpoise, according to the principle stated by Milinski (1982) for the less successful competitor. In some cases, high rates of competition killing are sufficient to limit population size of the killed species (Laurenson, 1995). In the North Sea, harbour porpoises largely outnumber bottlenose dolphins (Hammond et al., 2002), consequently, attacks by bottlenose dolphin should only have a limited impact on harbour porpoise population. By contrast in the Bay of Biscay, where the ratio between the two species is well in favour of the larger more successful species, these interactions may be an additional pressure that contribute to limit harbour porpoise populations in the area.

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Table 1: Prey found in stomach contents of *Phocoena phocoena* stranded on the Northeast Atlantic French coast

Table 2: Prey found in stomach contents of *Tursiops truncatus* stranded on the Northeast Atlantic French coast

Table 3: Common species in the diets of harbour porpoise and of bottlenose dolphin

Table 1: Prey found in stomach contents of *Phocoena phocoena* stranded on the Northeast Atlantic French coast

	Occurrence	Number			Body length (mm)		Body mass (g)		Biomass	
	%O	%	P75%	n	x ± σ	Range	x ± σ	Range	%	P75%
FISHES	**88.5**	**84.5**							**98.2**	
Engraulidae										
Engraulis encrasicolus	15.4	0.5	0-1	12	116.3 ± 24.2	81.1 - 157.7	9.9 ± 6.4	2.6 - 23.2	0.3	0-1
Clupeidae										
Sardina pilchardus	30.8	2.3	1-7	67	199.8 ± 29.9	116 - 245.9	128 ± 21.9	69.8 - 163.8	21.3	11-38
Sternoptychidae										
Maurolicus muelleri	3.8	0.2	0-1	4	29.4 ± 3.1	25 - 33.7	0.1 ± 0.2	0 - 0.4	0.0	0
Merluccidae										
Merluccius merluccius	11.5	0.3	0-1	12	182 ± 70.7	79.7 - 258.7	56.1 ± 39.2	5.2 - 110.7	1.4	0-3
Gadidae										
Gadiculus argenteus	7.7	0.2	0-1	6	67.1 ± 9.4	58 - 80	2.1 ± 1.3	0.9 - 4	0.0	0
Trisopterus spp	34.6	28.7	3-36	57	54.3 ± 14	15.7 - 156.7	1.9 ± 2.9	0 - 36.3	3.9	1-9
Merlangius merlangus	15.4	2.5	0-8	38	233.4 ± 40.8	117.4 - 291.1	111.2 ± 51.2	12.3 - 209.1	20.3	11-41
Micromesistius poutassou	38.5	18.5	14-27	154	121.3 ± 38.3	109.8 - 290.1	16.1 ± 13.6	9.1 - 119.7	21.3	5-22
Carangidae										
Trachurus trachurus	26.9	5.2	2-16	152	187 ± 56	70.3 - 276.9	73.8 ± 52.2	4.2 - 190.5	27.6	18-45
Scombridae										
Scomber scombrus	3.8	0.1	0-1	2	305.4 ± 1.3	304.1 - 306.7	214.8 ± 2.7	212.1 - 217.5	0.9	0-2
Gobiidae										
Undeterminated gobiidae	23.1	21.5	12-33	117	44 ± 10.8	22.4 - 86.7	0.7 ± 0.7	0.1 - 6.6	1.1	0-2
Atherinidae										
Atherina presbyter	7.7	0.3	0-1	6	86.3 ± 15.9	68.7 - 114.1	4.66 ± 2.9	2.1 - 9.9	0.1	0-1
Others Fish										
Undeterminated fishes	23.1	4.1	0-12	-	-	-	-	-	-	-

	N	M	P75%	n	x ± σ	range	x ± σ	range	M	P75%
CEPHALOPODS	**46.2**	**2.8**							**1.6**	
Loliginidae										
Loligo spp	11.5	0.2	0-1	3	39.2 ± 22.1	8.3 - 58.9	9 ± 5.2	1.9 - 14.2	0.1	0-1
Alloteuthis spp	19.2	0.6	0-1	5	96.7 ± 25.9	62.5 - 128.6	11.1 ± 5.8	5.5 - 28	0.5	0-1
Sepiolidae										
Underteminated Sepiolidae	23.1	1.7	1-5	6	15.8 ± 0.2	15.6 - 16.1	1.5 ± 0.1	5.6 - 6	0.2	0-1
Ommastrephidae										
Underteminated ommastrephidae	3.8	0.1	0-1	2	77 ± 5.3	66.8 - 77.3	27.5 ± 5.5	22 - 33	0.2	0-1
Octopotidae										
Underteminated Octopotidae	3.8	0.1	0-1	2	56.5 ± 21.3	35.3 - 77.8	55 ± 46	9 - 100.9	0.7	0-3
Others Cephalopods										
Undetermined Cephalopods	7.6	0.2	0-1	-	-	-	-	-	-	-
CRUSTACEANS	**11.5**	**12.7**							**0.2**	
Euphausiacea										
Meganyctiphanes norvegica	11.5	12.7	0-16	45	28.6 ± 0.2	27.6 - 29	0.2 ± 0.1	0.01 - 0.6	0.2	0-1

N, number of each prey ; P75%, 75% percentile ; n, number of measurement ; M, total mass of each prey in gram ; x, mean value ; σ, standard deviation

Table 2: Prey found in stomach contents of *Tursiops truncatus* stranded on the Northeast Atlantic French coast

	Occurrence %O	Number %	Number P75%	n	Body length (mm) x ± σ	Body length (mm) Range	Body mass (g) x ± σ	Body mass (g) Range	Biomass %	Biomass P75%
FISH	**100**	**94.2**							**90.6**	
Clupeidae										
Sardina pilchardus	23.8	4.8	2-8	86	199.8 ± 28.9	126.1 - 269.2	107.6 ± 36.5	36 - 186.9	3.1	1-6
Sprattus sprattus	4.8	10.6	0-21	30	119.2 ± 15.3	74.2 - 147.1	14.8 ± 6.4	2.3 - 30.1	0.9	0-2
Engraulidae										
Engraulis encrasicolus	14.3	2.4	1-4	42	123.1 ± 27.9	62.2 - 173.4	12.7 ± 7.4	2.7 - 31.7	0.2	0-1
Argentinidae										
Argentina sp	4.8	0.2	0-1	4	127.6 ± 25.4	94.5 - 153.3	13.8 ± 8	4.3 - 22.2	0	-
Merluccidae										
Merluccius merluccius	52.4	20.2	12-28	244	337.9 ± 109.2	78.4 - 666.8	333.1 ± 354.9	5 - 2040.3	40.8	34-48
Gadidae										
Gadiculus argenteus	4.8	0.1	0-1	1	43.6	-	0.3	-	0	-
Merlangius merlangus	9.5	0.3	0-1	5	168.2 ± 20.8	140 - 192.2	39.6 ± 14.1	21.3 - 57	0.1	0-1
Micromesistius poutassou	33.3	13	2-24	64	87.9 ± 34.3	15.1 - 239.1	7.2 ± 8.4	0.5 - 68.5	0.6	0-1
Trisopterus spp	66.7	10.8	8-15	218	153.5 ± 74.1	17.7 - 286.6	101.9 ± 81.1	0.1 - 295.6	6.6	4-10
Moronidae										
Dicentrarchus labrax	9.5	4.2	0-9	77	296.3 ± 45.3	187 - 431.8	218.8 ± 33.5	138.4 - 319.6	5.5	0-10
Cepolidae										
Cepola macrophthalma	4.8	0.2	0-1		240	-	650	-	0.1	0-1
Carangidae										
Trachurus spp	57.1	15.6	8-23	150	239.3 ± 51.2	75.6 - 355.6	139.8 ± 70.2	5.1 - 393.1	13.2	7-19
Sciaenidae										
Sciaena aquila	4.8	0.1	0-1		250	-	156.1	-	0.1	0-1
Sparidae										
Spondyliosoma cantharus	23.8	2.4	1-4	25	252.2 ± 36.7	195.4 - 313.9	268.5 ± 119.8	111.4 - 501.1	3.8	2-6
Diplodus sp	4.8	0.1	0-1	1	270	-	402.6	-	0.2	0-1
Pagrus sp	4.8	0.1	0-1	2	335.5 ± 9.3	326.3 - 344.8	621 ± 54.2	566.8 - 675.2	0.4	0-1
Sparidae B	4.8	0.2	0-1	4	204.2 ± 16.4	178.4 - 219.1	130.9 ± 30.9	83.4 - 160.2	0.2	0-1
Ammodytidae										
Undetermined sandeels	9.5	2.6	0-6	32	129 ± 14	102.3 - 168.7	6.2 ± 2.1	3.1 - 13	0.1	0-1

	N		P75%	n	M					P75%
Scombridae										
Scomber scombrus	9.5	0.9	0-2	8	374.8 ± 26.8	333.1 - 417.5	396.5 ± 83.3	276.1 - 538.9	2.3	1-4
Gobidae										
Undetermined gobids	9.5	0.3	0-1	6	86.9 ± 16.4	67.9 - 109.7	8.1 ± 5.8	2.6 - 16.6	0	-
Mugilidae										
Undetermined mullets	19	4.5	1-8	32	314.5 ± 99.3	221.7 - 543.3	411.8 ± 515.5	92.4 - 1942.8	12.1	6-18
Atherinidae										
Atherina presbyter	4.8	0.1	0-1	1	73.1	-	2.5	-	0	-
Soleidae										
Undetermined soleids	4.8	0.2	0-1	2	294 ± 6.5	287.6 - 300.5	249.9 ± 18.2	231.7 - 268	0.3	0-1
Others fish										
Others flatfish	14.3	0.3	0-1	5	239.2 ± 48	184.6 - 307.2	107.4 ± 76.4	34 - 225.4	0.2	0-1
Unknow A	4.8	0.2	0-1		-	-	-	-	-	
Undetermined fish	4.8	0.2	0-1							
CEPHALOPODS	**42.9**	**2.8**							**9.4**	
Loliginidae										
Alloteuthis spp	9.5	1.1	0-2	11	63.6 ± 10.6	46.6 - 83	4.6 ± 1.5	2.6 - 7.4	0	
Loligo spp	38.1	2.5	2-4	23	235.5 ± 119.8	42 - 466	603.3 ± 562.4	2.2 - 1614.7	9.3	3-15
Sepiidae										
Sepia sp	4.8	0.1	0-1	1	36.2	-	1.2	-	0	-
CRUSTACEANS	**19**	**2**							**0**	
Crangonidae										
Crangon crangon	4.8	1.5	0-4		40		24	-	0	-
Pasiphaeidae										
Pasiphaea multidentata	4.8	0.2	0-1		100		8	-	0	-
Undetermined shrimp	14.3	0.4	0-1		-					

N, number of each prey ; P75%, 75% percentile ; n, number of measurement ; M, total mass of each prey in gram ; x, mean value ; σ, standard deviation

Table 3: Common species in the diets of harbour porpoise and of bottlenose dolphin

SPECIES	%N$_{Pp}$	%N$_{Tt}$	%M$_{Pp}$	%M$_{Tt}$	L75%$_{Pp}$	L75%$_{Tt}$
Trachurus trachurus	5.2	15.6	27.6	13.2	110-270	180-290
Sardina pilchardus	2.3	4.8	21.3	3.1	160-240	160-240
Trisopterus spp	28.7	10.8	3.9	6.6	40-70	50-250
Micromesistius poutassou	18.5	13.0	21.3	0.6	130-170	50-120
Merlangius merlangus	2.5	0.3	20.3	0.1	180-280	150-190
Merluccius merluccius	0.3	20.2	1.4	40.8	80-250	190-430
Gobiidae	21.5	0.3	1.1	0.0	30-60	70-110
Scomber scombrus	0.1	0.9	0.9	2.3	300-310	340-400
Engraulis encrasicolus	0.5	2.4	0.3	0.2	90-150	90-160
Atherina presbyter	0.3	0.1	0.1	0.0	70-90	70-80
Gadiculus argenteus	0.2	0.1	0.0	0.0	60-80	40-50
Loligo spp	0.2	2.5	0.1	9.3	50-60	110-270
Alloteuthis spp	0.6	1.1	0.5	0.0	70-100	50-80

%N, percentage of number ; %M, percentage of mass ; L75%, length range including 75% of prey

species ; Pp, *Phocoena phocoena* ; Tt, *Tursiops truncatus*

Fig. 1: Locations of harbour porpoises (dark triangles) and bottlenose dolphins (grey circles) strandings

**Fig. 2:** Size distributions of main preys in the diets of the harbour porpoise and/or of the bottlenose dolphin in percent number

Fig. 3: Overall prey-size distribution in the diets of the harbour porpoise and of the bottlenose dolphin in percent number and percent mass

Fig. 4 : Plots of the correspondence analysis from the mass of prey per dolphin. The two axis explained 23% of total inertia
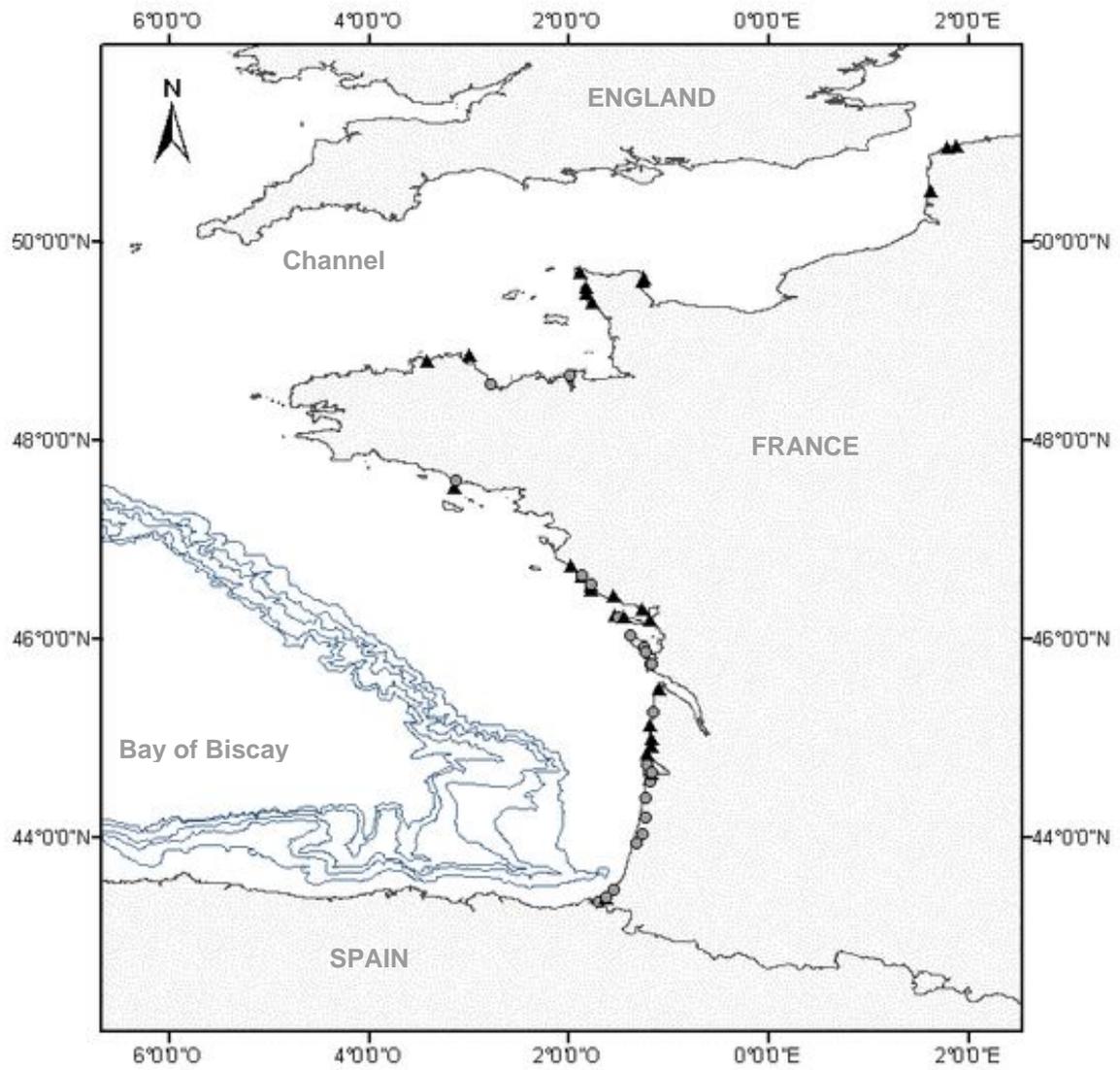
Fig. 1: Locations of harbour porpoises (dark triangle) and bottlenose dolphins (grey circles) strandings
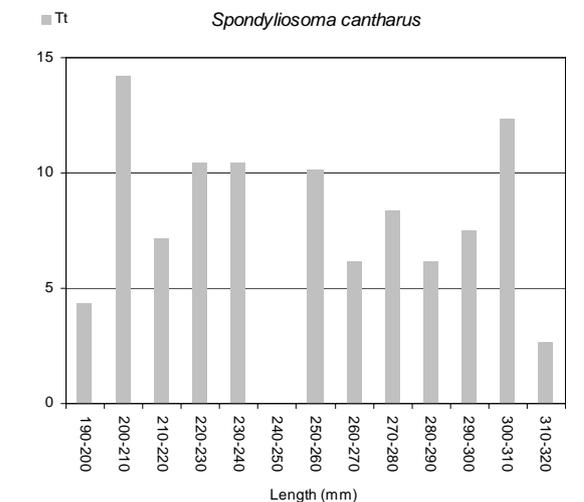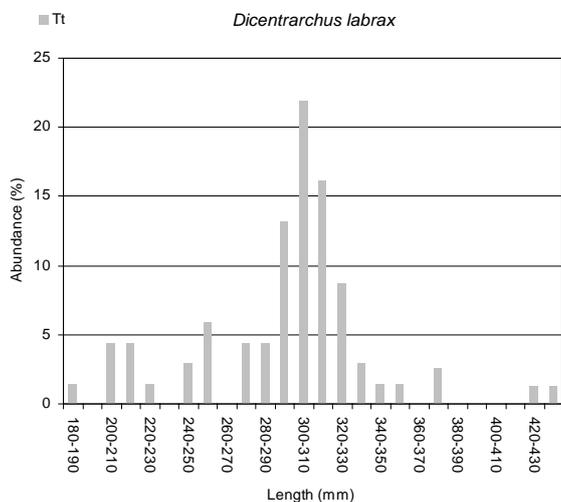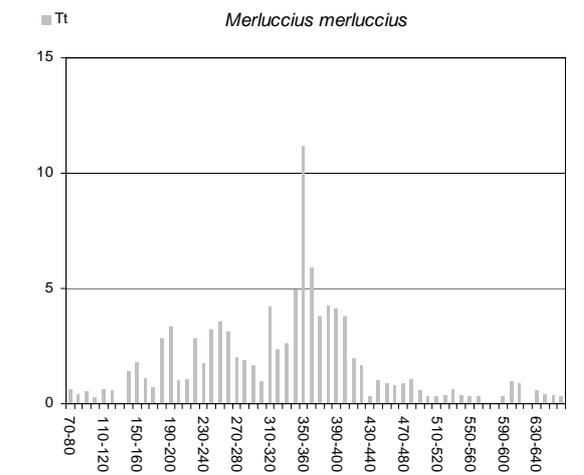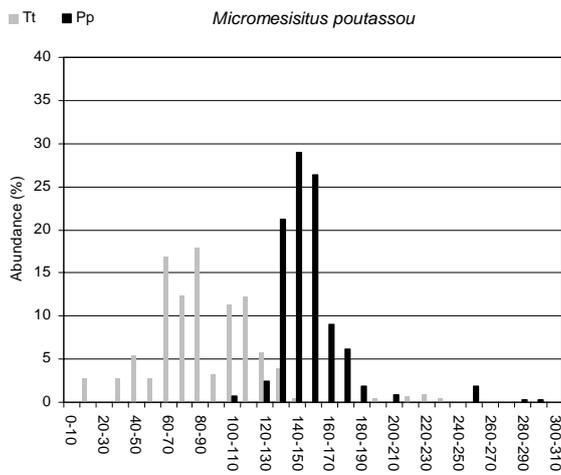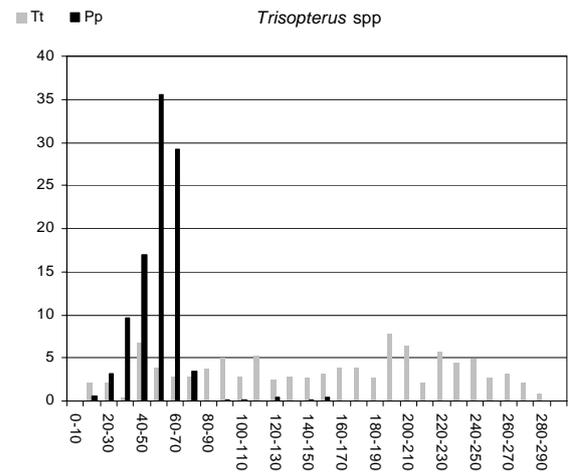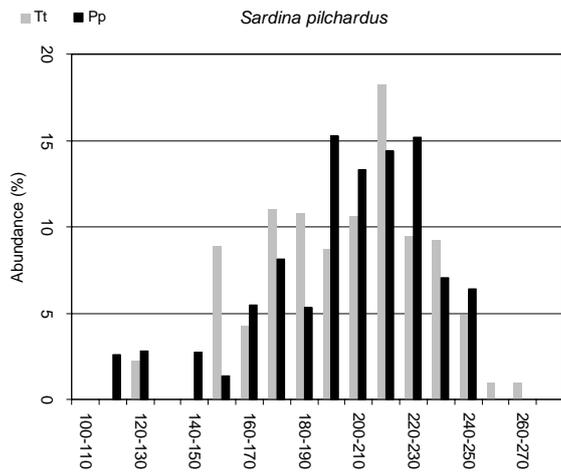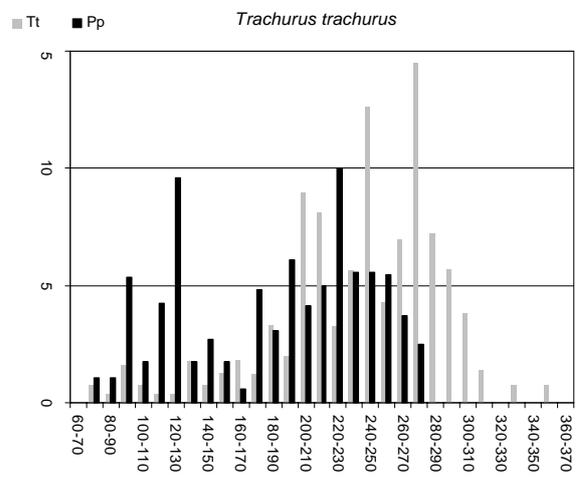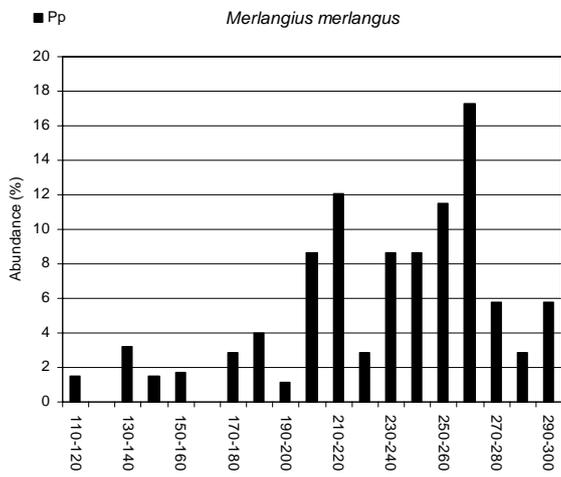
Fig. 2: Size distributions of main preys in the diets of the harbour porpoise and/or of the bottlenose dolphin
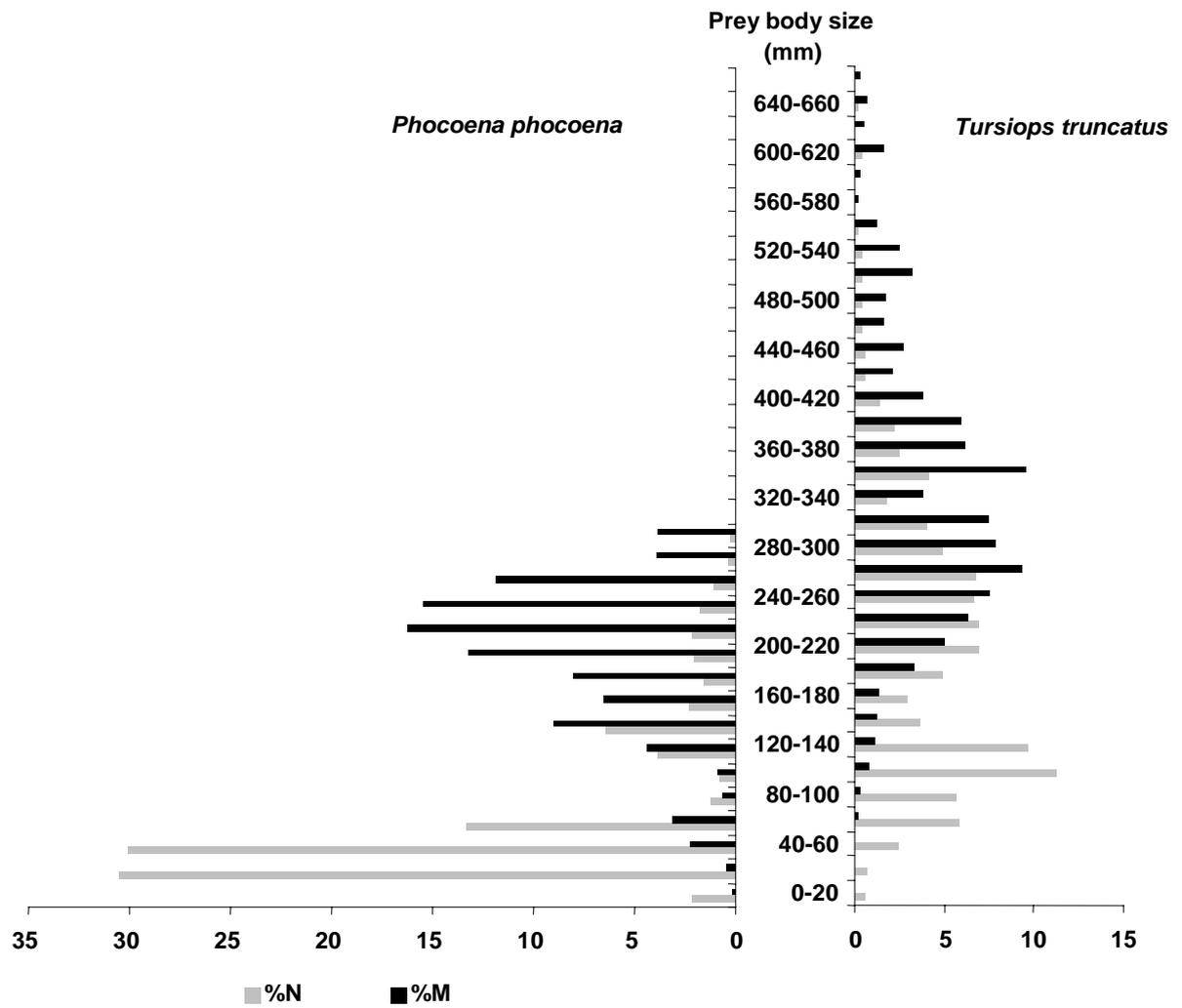
in percent number

Fig. 3 : Overall prey-size distribution in the diets of the harbour porpoise (left) and the bottlenose dolphin

(right) in percent number (%N) and percent mass (%M)
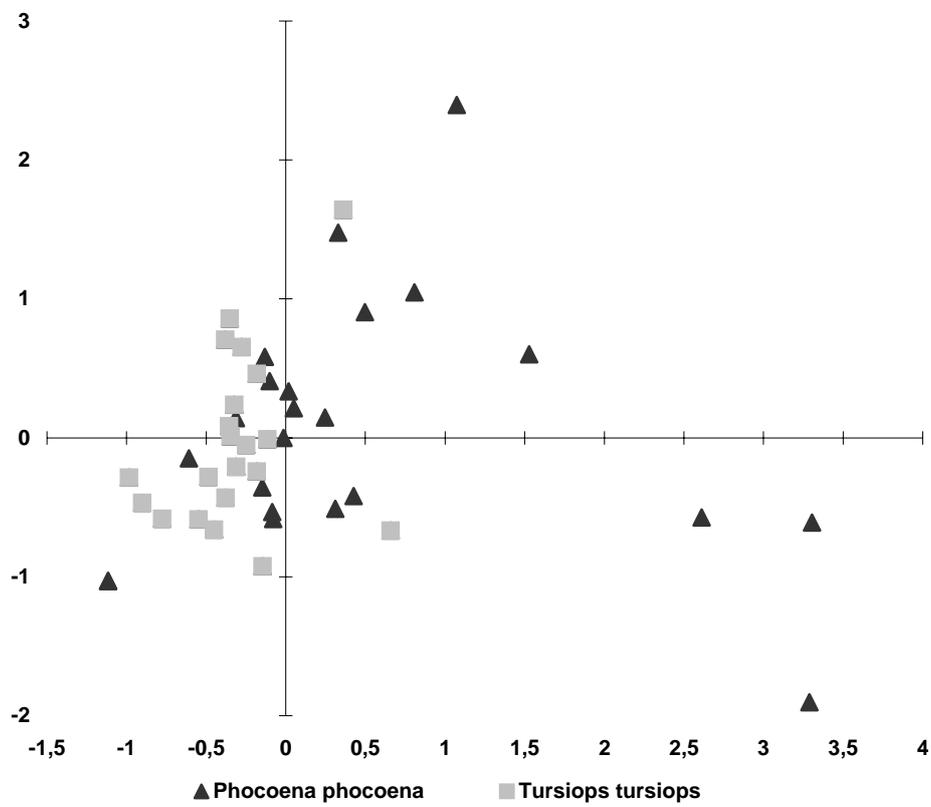
Fig. 4 : Plots of the correspondence analysis from presence or absence for each prey species per cetacean.

The two axis explained 19% of total inertia