

The diet of harbour porpoises bycaught or washed ashore in Belgium, and relationship with relevant data from the strandings database



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September 2012, V2



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Cover picture:

Washed ashore harbour porpoise (image: J.Haelters/RBINS)

Funding:

This report was funded by the Federal Public Service for Health, Food Chain Safety and Environment (DG5 – Marine Environment), in the framework of the ASCOBANS North Sea Harbour Porpoise Conservation Plan.



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Summary

The harbour porpoise *Phocoena phocoena* is currently the most abundant marine mammal in Belgian waters. Large-scale changes in the distribution of this top predator in the North Sea have occurred during the last decades, possibly caused by changes in food availability. An analysis of the strandings database 1970-2011, containing data on 737 harbour porpoises, revealed that throughout the year two peaks in strandings occurred: one in spring, for an important part caused by the strandings of animals incidentally bycaught in fishing gear, and a second one during summer. Most of the stranded animals were juveniles, with a higher percentage of males than females. As could be expected, bycaught animals were on average heavier than equally sized naturally died animals, and they had a thicker blubber layer. In naturally died animals the blubber layer was thicker in winter than in summer, illustrating the insulating function of the blubber layer besides its function as an energy storage.

We investigated the stomach content of 64 harbour porpoises washed ashore or bycaught in Belgium between 1997 and 2011. Ten of the stomachs were empty. Fish contributed to most of the prey remains. In total we found the remains of 19 fish species belonging to 10 families. The numerically most important prey items in juveniles were gobies (Gobiidae). Reconstructing the original weight of the prey items revealed that gobies constituted the most important prey by weight, but that larger sandeels (Ammodytidae) and to a lesser extent gadoids (Gadidae) were also important. In adults the majority of prey items were gobies and sandeels, but the reconstructed weight of the stomach content revealed that sandeels and gadoids constituted by far the most important prey. Surprisingly, clupeids (Clupeidae) did not contribute much to the diet, although the return of the harbour porpoise is often linked to an increase in herring *Clupea harengus* stocks in the southern North Sea. Also no twaite shad *Alosa fallax* were found, although this diadromic fish is common again in the



area. A small number of smelt *Osmerus eperlanus* was found in some of the recently stranded harbour porpoises. Smelt is a diadromic fish of which densities are increasing from very low levels. The fact that juvenile harbour porpoises had apparently fed on large quantities of small bottom fish may help to explain why they were more prone to bycatch than adults. The analysis revealed that a gradual shift occurs in the feeding habits of harbour porpoises while becoming adults: from small benthic fish towards larger fish taken from the water column.

Samenvatting

De bruinvis *Phocoena phocoena* is tegenwoordig het meest algemeen voorkomende zeezoogdier in het Belgisch deel van de Noordzee. Tijdens de laatste decennia hebben zich grootschalige veranderingen voorgedaan in de verspreiding van deze toppredator binnen de Noordzee, mogelijk veroorzaakt door veranderingen in voedselbeschikbaarheid. Een analyse van de strandingen-database 1970-2011, met gegevens over 737 bruinvissen, bracht aan het licht dat jaarlijks twee pieken in strandingen voorkwamen: één in het voorjaar, voor een belangrijk deel veroorzaakt door strandingen van dieren die incidenteel in visnetten verdrongen waren, en een tweede tijdens de zomer. De meeste gestrande bruinvissen waren juvenielen, met een hoger percentage aan mannetjes dan aan vrouwtjes. Zoals verwacht werd, waren bijgevangen dieren gemiddeld zwaarder dan dieren die een natuurlijke dood gestorven waren, en ze hadden een dikkere speklaag. Bij dieren die een natuurlijke dood gestorven waren, bleek de speklaag tijdens de winter dikker dan tijdens de zomer, een illustratie van de isolerende functie van de speklaag naast de functie als energiereserve.

We onderzochten de maaginhoud van 64 bruinvissen, gestrand of bijgevangen in België tussen 1997 en 2011. Tien van de magen waren leeg. De meeste voedselresten behoorden toe aan vissen. In totaal troffen we in de magen de resten aan van 19 soorten vis, behorend tot 10 families. In de magen van juveniele bruinvissen bleken de resten van grondels (Gobiidae) veruit het hoogst in aantal. Bij een reconstructie van het originele gewicht van de prooiresten bleek dat grondels de belangrijkste prooi waren, maar dat ook de grotere zandspieringen (Ammodytidae) en in mindere mate kabeljauwachtigen (Gadidae) significant tot het dieet hadden bijgedragen. Bij adulte bruinvissen werden vooral resten van grondels en zandspiering aangetroffen, maar bij de reconstructie van het originele gewicht van de prooiresten bleken zandspiering en kabeljauwachtigen de belangrijkste prooien. Het was verassend dat haringachtigen (Clupeidae), hoewel aanwezig, niet belangrijk bleken als prooi, hoewel de



terugkeer van de bruinvis in de zuidelijke Noordzee vaak gelinkt wordt met een herstel van de stocks van haring *Clupea harengus*. Er werden geen resten van fint *Alosa fallax* aangetroffen in de magen van de onderzochte bruinvissen, hoewel deze diadrome vissoort opnieuw algemeen voorkomt in dit gebied. In recent aangespoelde bruinvissen werden de resten van een klein aantal spieringen *Osmerus eperlanus* aangetroffen. Spiering is een diadrome vissoort waarvan de dichtheid opnieuw toeneemt nadat de soort in Belgische wateren vrijwel verdwenen was. Het feit dat juveniele bruinvissen zich blijkbaar gevoed hadden met kleine bodemvisjes kan mogelijk mee verklaren waarom ze in belangrijkere mate dan adulten omkomen door incidentele vangst in visnetten. De analyse van de maaginhouden toonde aan dat een graduele verandering voorkomt in het voedingspatroon van bruinvissen bij het volwassen worden: van kleine bodemvisjes tot grotere vissen die in de waterkolom gevangen worden.





1. Introduction

In 1994 and 2005 large-scale monitoring surveys were undertaken to estimate the number of small cetaceans present in the North Sea and adjacent Atlantic Ocean (SCANS I and SCANS II surveys; Hammond et al., 2002, SCANS II, 2008). Although looking into the summer distribution was of secondary importance, it became clear from the comparison of the results of the two surveys that an important shift had occurred in the distribution of the harbour porpoise *Phocoena phocoena* during that season. While during the summer of 1994 high densities had been observed in the northern North Sea, and very low densities in the southern North Sea and eastern Channel, the situation was totally different during the summer of 2005, when harbour porpoises occurred on average much more to the south. This shift in distribution had not only been documented through the SCANS surveys. Also stranding records in The Netherlands, Belgium (Haelters & Camphuysen, 2009) and the north of France (OCEAMM; Sylvain Pézéril, personal communication) had increased markedly in the same period. In Belgium the number of stranded harbour porpoises increased from a few per year in the 1970s to the early 1990s to on average more than 65 per year during the last decade.

It has been suggested that the shift of a large part of the North Sea harbour porpoise population was a consequence of changed environmental conditions, with as an indirect consequence worsening feeding conditions for harbour porpoises in the northern North Sea. For investigating trophic changes in the North Sea ecosystem it is important to investigate, among other questions, the feeding ecology of the harbour porpoise, which is with around a quarter of a million animals one of the most commonly occurring top predators in that area. Similarly, the breeding success of seabirds in function of the availability of their prey items has been made. It was demonstrated that the survival of chicks of sandwich terns *Sterna sandvicensis* depended on the availability of suitable prey (Vincx et al., 2007). While it is usually difficult for seabirds to switch to suitable alternative breeding locations, the harbour porpoise can adjust its area of distribution on the basis of the availability of prey.

The investigation of the health, nutritional status and diet of harbour porpoises is one of the actions in the framework of the *Conservation plan of the harbour porpoise in the North Sea* (Reijnders et al., 2009), as adopted on 18 September 2009 by the Parties of the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS), a regional agreement concluded under the auspices of the Convention on Migratory Species (CMS or Bonn Convention). The implementation timeline



for parties is ‘ongoing’, with a regular (every 3 to 5 years) review of results. Such investigations can help us understand the changes in distribution of harbour porpoises that occurred in the past, describe effects of shifts in prey species, possibly caused by climate change or an improving water quality, and further predict possible climate change effects or effects of overfishing.

This report starts with the presentation of a first analysis of the strandings database, with data that might be relevant for prey availability and stomach content (e.g. location of the stranding, cause of death, nutritional condition, age, etc.). Subsequently, it gives a summary of the stomach content analysis of 64 harbour porpoises stranded or bycaught in Belgium between 1997 and 2011, as an extension of the exploratory study made in 2011 (Haelters et al., 2011a).



2. Material and methods

2.1. The collection of washed ashore and/or bycaught harbour porpoises

The investigation of bycaught or washed ashore marine mammals has been coordinated since 1995 by the Management Unit of the North Sea Mathematical Models (MUMM), currently a department of the Royal Belgian Institute of Natural Sciences (RBINS). Remains of harbour porpoises collected from the coast or from harbours were mostly transferred to Oostende to be temporarily stored in a freezer at -23°C . Afterwards, they were transported to the University of Liège, where they were subjected to an extensive necropsy using a standardised methodology (Kuiken & Hartmann, 1991; Jauniaux et al., 2002). Due to the increasing amount of carcasses washing ashore, with in 2011 a record number of 116 animals, the percentage of remains collected decreased, an increasing number of very decomposed carcasses being disposed of at a destruction facility without further investigation. We transported some selected very fresh animals immediately upon the stranding, especially for microbiological sampling in cases of the suspicion of viral/bacterial infection and for inner ear investigation (Morell et al., 2009). We established a cooperation with fishermen, resulting in a mixed success. Only one in the three to four static gear fishermen occasionally provided bycaught harbour porpoises for further investigation (Depestele et al., 2008; 2011).

2.2. The analysis of the strandings database

We analysed the data (available at MUMM) of harbour porpoises stranded and bycaught between 1990 and 2011. In some cases we only present data from 1996 or 1997 due to the availability of data or for practical purposes. The data include:

- Animals collected as well as animals not recovered from the beach or sent away for destruction;
- A small number of animals found inland (river Scheldt and tributaries);
- Live stranded animals, under the condition that they were not returned to sea immediately, but were taken to a rehabilitation facility in The Netherlands (Harderwijk) or died at the beach or during transport;
- Animals bycaught close to shore, and brought to port by a fisherman instead of discarding them at sea;



- Animals found dead at sea, close to shore, and brought to port for further investigation.

Dead animals observed at sea were not included. The strandings dataset 1990–2011 comprises data for 737 harbour porpoises. All data collected at the strandings scene and from the external examination of the collected animal (location, circumstances, external characteristics of the animal such as bycatch marks, sex, length, external parasites, etc.) were taken up in the database. Next to this, also basic necropsy data were included, such as blubber thickness and weight. The database as such contains elements relevant in the framework of diet investigations. Independently of the stomach content analyses, we made a number of analyses of relevant data in the strandings database:

- 1) We analysed trends in numbers of washed ashore harbour porpoises as there may be a link between density of harbour porpoises at sea and certain prey density.
- 2) We analysed the date/season of the strandings as certain prey may have a seasonal distribution in the southern North Sea, which may be reflected in the stomach content.
- 3) As prey in Belgian waters and as such also harbour porpoises are not evenly distributed, we looked into the geographical distribution of strandings. As some communities have a longer shoreline than others (e.g. Blankenberge 3.2 km vs. Wenduine-De Haan 10.4 km), we presented data as animals per km coastline per coastal community. We included animals found in harbours (cases at Zeebrugge, Oostende and Nieuwpoort), and in the length of the community of Zeebrugge we included the harbour (total: 5.4 km). We excluded the animals washed ashore in the river Scheldt (n=6), found at sea or bycaught at sea (n=14), and as such considered a total of 688 animals for this analysis.
- 4) As carcasses may have drifted in from elsewhere, we analysed the Condition Code (CC) of the washed ashore harbour porpoises. We used the following codes: CC 1: live animal (becoming code 2 after death on beach or in rehabilitation facility); CC 2: fresh dead, no decomposition; CC 3: moderate decomposition; CC 4: advanced decomposition; CC 5: mummified remains, or skeleton with virtually no (or liquefied) intestines left. The decomposition code is a subjective measure given to the animals (1) upon stranding or collection of the carcass, and (2) before the necropsy. Therefore it is possible that an animal in CC 2 washing ashore can evolve



to CC 3 upon collection or necropsy. Most animals washing ashore in CC 1 died on the beach (and as such became CC 2 during the necropsy). Therefore we combined animals in CC 1 and CC 2 for the analysis, as well as the very decomposed animals in CC 4 and CC 5. The total sample size was 202, 216 and 288 animals in CC 1/2, CC 3 and CC 4/5 respectively.

- 5) As there might be an evolution in prey with age of the harbour porpoises, we tried to analyse the age distribution of stranded animals. As a proxy for age we used the length of the animals, with animals of 0.90 m or shorter catalogued as newborns (or stillborns), those longer than 130 cm as adults, and the ones in between as juveniles. This is only a proxy within a population in which large individual differences exist, and with 'grey zones' in between the classification as newborn, juvenile and adult: very short animals washed ashore outside the calving season are as such classified as newborns (but should probably be considered as juveniles), and fully functional reproductive organs have been observed during the necropsy of some animals classified here as juveniles, while some animals longer than 130 cm apparently were not sexually active yet. The two stranded animals described in Haelters & Everaarts (2011) for instance were very short considering the period in which they washed ashore (December and April, and a length of respectively 92 and 89 cm).
- 6) The sex ratio of the harbour porpoises might reveal that males and females have a different preference for certain prey species.
- 7) The cause of death is important in diet analysis, as the stomach content of animals having died due to bycatch might be more representative for the population and unbiased due to disease or starvation. As the link between the strandings database managed by MUMM and the database on necropsy results managed by the University of Liège is not fully operational yet, the data on the cause of death and the analysis based on these data are preliminary, certainly for 2010 and 2011.
- 8) The nutritional condition of the animals may have had an influence on the latest prey composition and its volume.

There are different ways to describe the nutritional condition of washed ashore harbour porpoises. A subjective description can be given on the basis of the dorsal fat/muscle and the dorsal region behind the head: emaciated animals mostly have a longitudinal concave appearance in the dorsal and lateral area around and distally from the dorsal fin, with in



extreme cases the underlying spine and rib cage being defined externally. In animals in a good nutritional condition this appearance is mostly convex (Figure 1). Also, in emaciated animals the dorsal region behind the head shows a concavity, with a neck-like appearance.

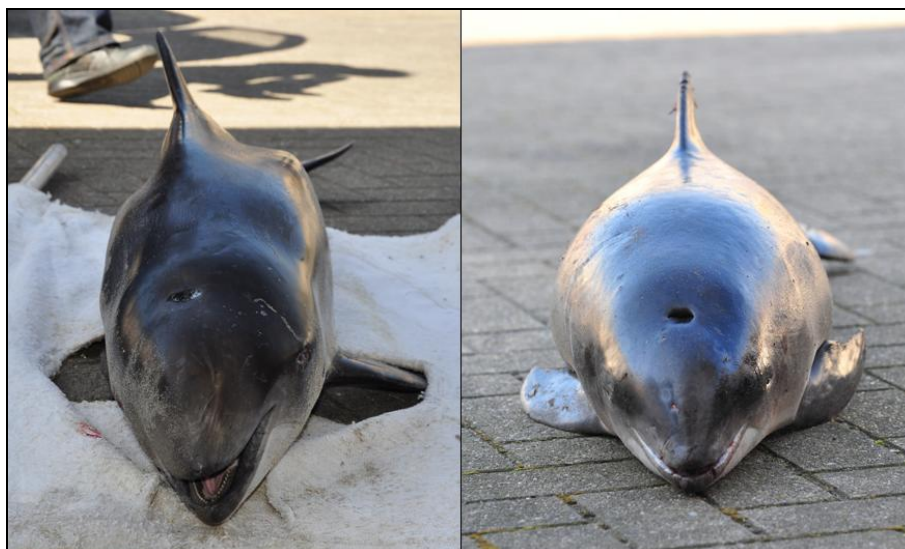


Figure 1. External appearance of harbour porpoises as a proxy for their nutritional condition: on the left a harbour porpoise in a very poor nutritional condition, with a clear concave dorsal side due to the disappearance of fat and dorsal muscle atrophy, and a concavity behind the head; on the right a harbour porpoise in a good nutritional condition, with a convex dorsal region and no clear concavity behind the head (images: RBINS/MUMM).

However, more quantified proxies to describe the nutritional condition exist. Firstly, the length – weight relationship can be used, as animals failing to get enough food become lighter while remaining approximately at the same length. To establish a length-weight distribution in stranded animals, only those animals were considered of which it was estimated that only a limited weight loss occurred after their death. As such we excluded animals with a CC 4 or CC 5 from the assessment, and eliminated also those animals that had lost body parts or were heavily scavenged upon. We did not include a very large but extremely emaciated adult (1.7 m, 41 kg) that was bycaught, as we considered it an outlier. The data were thus comprised of 349 animals, of which 115 animals that died of trauma, 183 animals that died through natural causes, and 51 animals for which the cause of death remains unknown.

Also the thickness of the blubber layer can serve to describe the nutritional condition (Lockyer, 1995; Lockyer et al., 2003a). As the blubber serves as an energy storage, it becomes thinner in animals failing to get enough food (Figure 2). However, there is also a seasonal aspect, with a blubber layer becoming thicker in the colder seasons, as was demonstrated by Lockyer et al. (2003b) in two captive harbour porpoises. We used the thickness of the dorsal blubber layer, measured a few cm distally from the dorsal fin. The



blubber layer can be influenced by the state of decomposition, becoming thinner with the advance of the decay. Therefore we only used it when obtained from animals with a CC 2 or CC 3.



Figure 2. The dorsal blubber thickness was measured to obtain a quantified proxy for nutritional condition (image: RBINS/MUMM).

2.3. Collecting and preparing stomach contents

For the collection of the stomach contents we used the methodology described in Haelters et al. (2011a). This method can be summarised as the rinsing of the content of the first stomach, second stomach and oesophagus (Figure 3) over a 315 μm square meshed sieve. After a visual inspection, with a subjective description of the freshness of the remains and a retrieval of invertebrate remains, the content was transferred to a beaker with enzymatic washing powder Biotex GreenTM and left to macerate for 1 to 3 days at 40°C. After rinsing and drying, a sample remains which may contain fish remains (bones, eyeballs) and/or cephalopod beaks.

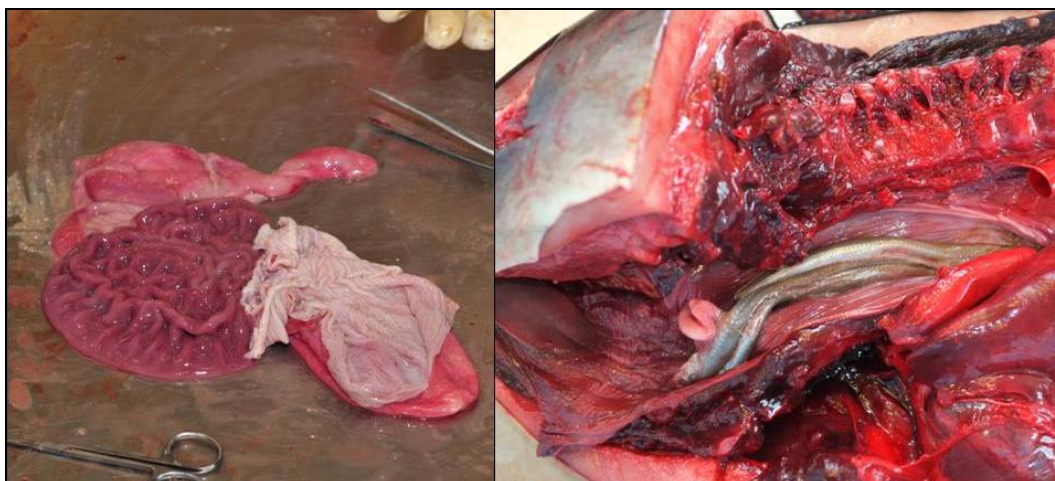


Figure 3. Left: the stomach of a harbour porpoise is a sequence of chambers: first chamber (where most fish remains are found) visible on the right, second chamber on the left, and third and fourth chamber in the background; right: sometimes fresh fish (in this case sandeels) are found in the oesophagus, constituting one of the indications of bycatch (images: RBINS/MUMM).

For this study, we investigated the stomach content of 64 harbour porpoises washed ashore or bycaught and brought to port by fishermen between 1997 and 2011. Of the stomachs investigated, 10 were empty and were not further considered here. Most of these stomachs originated from animals washed ashore in 2010 ($n=8$) and all of them washed ashore between May and August. Most of the animals with a non-empty stomach had washed ashore between 2003 and 2011 ($n=52/54$), with only one animal having washed ashore in 1997 and one in 2000.

The animals of which the stomachs were investigated for this study, together with details about the location and date of stranding, their size, sex, etc., are presented in Annex 1. The sex ratio in the animals with a non-empty stomach ($n=54$) was almost equal, with 28 males, 24 females and 2 animals with an unknown sex, and 41 animals were classified as juveniles against 13 adults. In this sample 30, 12 and 12 stomachs originated from animals that had died due to drowning in fishing gear, due to a natural cause and due to unknown reasons respectively. Of the animals with an empty stomach ($n=10$), 1, 7 and 2 had died due to drowning in fishing gear, due to a natural cause and due to unknown reasons respectively.

Given the low sample size, especially in adults, and the seasonal distribution of the stranded animals (37 out of the 54 animals with a non-empty stomach had washed ashore between February and April), no analysis of the seasonal aspect of prey choice was performed, nor of the differentiation of prey according to the sex in the different age classes.



2.4. Analysis of the stomach contents

We investigated the dry remains of the stomach content under a binocular microscope. As the main prey of harbour porpoises consists of different fish species, the stomach contains fish bones, of which the most important ones for this study are the sagittal otoliths or sagittae. These are mineralised, solid compact structures forming part of the inner ear of fish. They are fairly resistant to stomach acids, and can be used to identify the species of fish they belonged to. From their size, the original fish size and weight can be extrapolated (see for more details Haelters et al., 2011a).

To the extent possible we identified sagittae to species level and coupled them into pairs. If many otoliths of one species were present, their number was divided by two and rounded to the higher number to estimate the minimum number of fish of that prey species in the stomach. For most goby (Gobiidae) and sandeel (Ammodytidae) otoliths, we made no attempt to identify them to the species they belonged to, although this would be possible to a certain extent (but would be very time-costly). We classified them as respectively *Pomatoschistus* sp. and *Ammodytes* sp. Also some small pout (*Trisopterus* sp.) otoliths were not identified to species level. *Scophthalmus* sp. was not identified to the species level as the otoliths originated from juveniles (it either concerned *S. rhombus* or *S. maximus*).

We measured sagittae to extrapolate the original length and weight of the fish (Leopold et al., 2001; Härkönen, 1986): for coupled otoliths we used the average size, unless one otolith of the couple was damaged. In case of many otoliths of the same species, we measured a subsample without trials to couple them. In case of broken otoliths, we measured the width and used a corresponding otolith width/fish length regression model. We applied no correction to the length or width due to the erosion of the otoliths, and as such the lengths and weight of the prey should be considered as a minimum. For the otoliths that were not identified to species level, we used the regression curves of what we considered the most common species in the respective groups: *Pomatoschistus minutus*, *Ammodytes tobianus* and *Trisopterus luscus*. While it is very likely that other species are included in the samples of those otoliths, their regression curves would be similar, as the different species in the groups have a similar shape, and are in some cases even as a fresh fish difficult to distinguish from one another.

In the absence of otoliths, other fish bones were used to identify prey remains. The otoliths and fish bones were identified using a reference collection available at MUMM and a



number of publications (Härkönen, 1986; Nolf & Stringer, 1992; Watt et al., 1997; Leopold et al., 2001; Conroy et al., 2003; Svetocheva et al., 2007; Tuset et al., 2008; Nolf et al., 2009). In most cases we made no efforts to identify invertebrate remains such as from shrimps, cephalopods and polychaetes to species level. The analysis was non-destructive, and all stomach contents remain available for further investigation.

2.5. Expressing stomach content: diet indices

We used the following quantified measures to describe the remains in the stomachs investigated (only based on otolith remains):

- 1) Overview of prey species in the stomach.
- 2) Number of fish prey remains.
- 3) Number of fish prey species by harbour porpoise.
- 4) Frequency of occurrence of each fish prey species in the stomach, or the presence/absence of fish or other prey species (i) in the stomach, as a percentage of the total number of stomachs analysed (n), excluding those that were empty:

$$\% O_i = \frac{n_i}{n} \times 100 \text{ with } n_i \text{ the number of stomachs in which prey item } i \text{ was found.}$$

- 5) The numerical importance N_i of each prey species i (or the numerical importance of each fish prey species):

$$\% N_i = \frac{N_i}{N} \times 100 \text{ with } N \text{ the total number of prey items.}$$

- 6) Proportion of each species by fresh weight:

$$\% W_i = \frac{W_i}{W} \times 100, \text{ with } W \text{ the total estimated fresh weight of the prey.}$$

- 7) The average length of the prey taken by each harbour porpoise.

Aspects of the prey investigated were differences in prey according to age (size). Due to the limited time available for this project, no statistical analysis was performed.

Investigating stomach contents is one of the best methods (and in many cases the only one available) to obtain detailed information about the feeding ecology of marine mammals.



However, there are some sources of bias inherently connected to this method (Pierce & Boyle, 1991; Wijnsma et al., 1999; Santos & Pierce, 2003; Granedeiro & Silva, 2000). The sample itself is based on stranded and bycaught animals, and may as such be biased. The remains in the stomach only represent the most recent prey items, and there is a different digestion rate of prey per species or per size, and a differential degradation of otoliths. Also, prey may only be ingested partly, or part of the stomach content may represent secondary prey. Errors occur in the measurements of the otoliths and the assessment of correction factors applied to correct for erosion, and there is an individual, regional and seasonal variability in the relationship between fish length and weight.





3. Results

3.1. Results of the analysis of the strandings database and relevance to the diet study

3.1.1. Trends in the number of stranded animals

In Figure 4 we present the number of records of stranded animals between 1990 and 2011. It comprises in total 737 animals. Strandings were not evenly distributed throughout this period, with on average only 5.7 animals per year between 1990 and 2000, and 61.3 animals per year between 2001 and 2011.

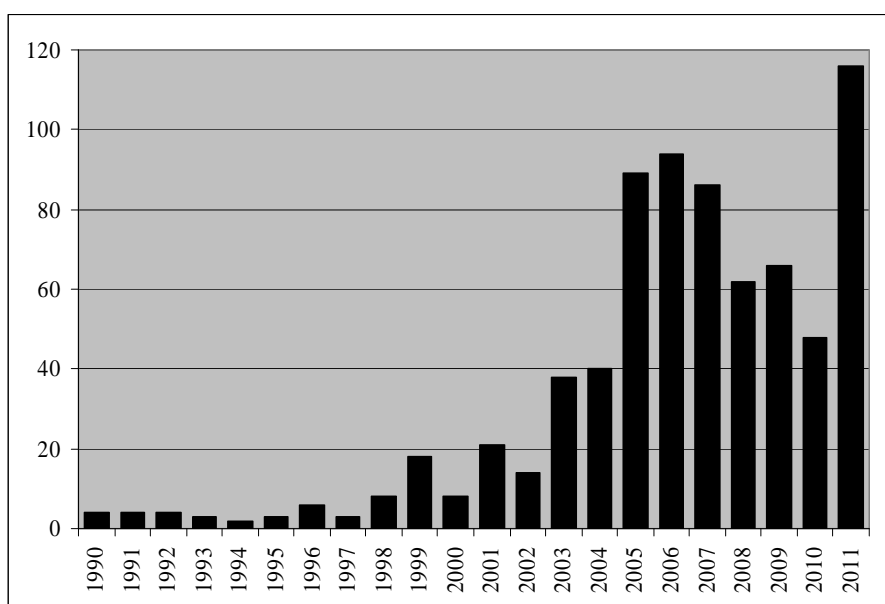


Figure 4. Number of harbour porpoises washed ashore annually between 1990 and 2011.

There is a clear increase in the number of stranded animals since the beginning of the 21st century. A similar increase, occurring somewhat earlier however, was observed in The Netherlands (Haelters & Camphuysen, 2009). After a slight decrease between 2008 and 2010, the number peaked again in 2011 with an unprecedented 116 stranded animals.



3.1.2. Seasonality of strandings

In Figure 5 we present the number of stranded animals per month and per triennium between 1997 and 2011.

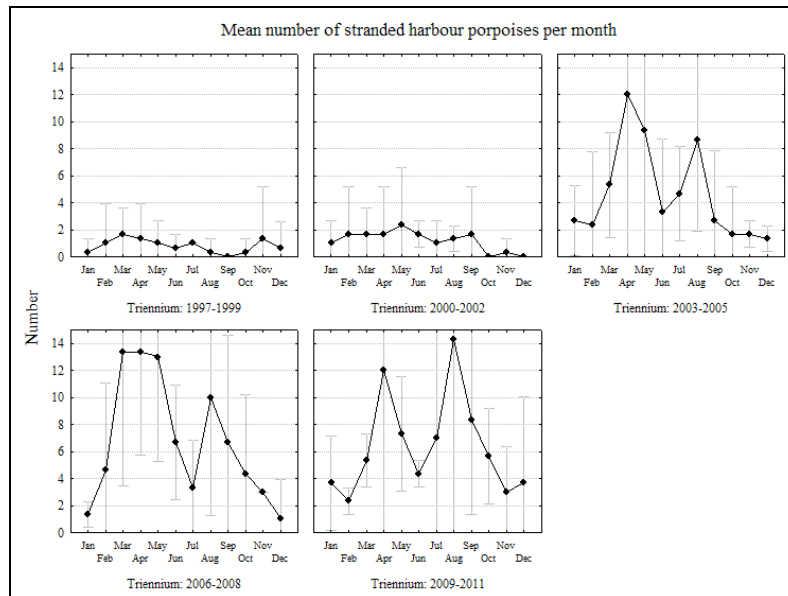


Figure 5. Numbers of harbour porpoises washed ashore per month and per triennium between 1997 and 2011 (including Confidence Interval CI).

There is a clear seasonality in strandings, with since the start of the increase in the number of strandings (around 1999, but more pronounced from 2003 onwards) a peak in late winter-spring and a second one during summer. During the last triennium the summer peak is more pronounced than the spring peak, in contrast to the two previous trienniums with a more pronounced peak centred around April. A consistent observation is the low number of stranded animals during June and between October and January.



3.1.3. Geographical distribution of strandings

Figure 6 presents the total number of stranded harbour porpoises according to the location along the coast (division per coastal community) between 1995 and 2011. It also gives the total number of animals washed ashore per km coastline per coastal community.

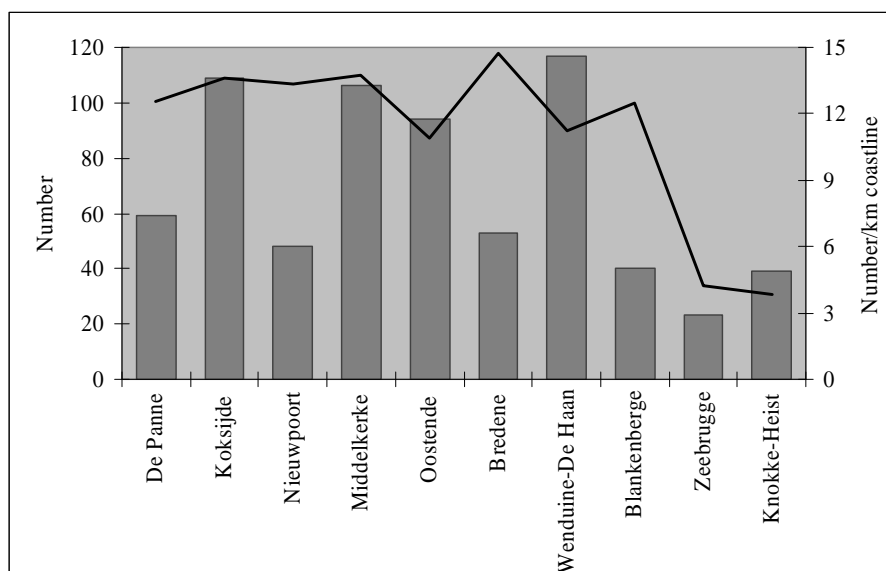


Figure 6. Number of washed ashore harbour porpoises per coastal community (bars) and per km per coastal community (line) between 1995 and 2011.

The number of stranded animals/km coastline/coastal community is fairly constant between De Panne and Blankenberge (approximately 13 animals/km coastline between 1995 and 2011). There are fewer strandings per km coastline at Zeebrugge and Knokke-Heist.

3.1.4. Decomposition of stranded animals

Figure 7 and 8 present the condition code (CC) of stranded animals between 1995 and 2011 (n=706). The highest percentage of fresh animals is found between December and March. In absolute values, the highest number of fresh animals is found in March (Figure 7). The highest number of very decomposed animals is found in April, May and August (Figure 7), with the highest percentages from April to November (on average almost half of the animals; Figure 8). The lowest percentage of fresh animals is found from May to November.

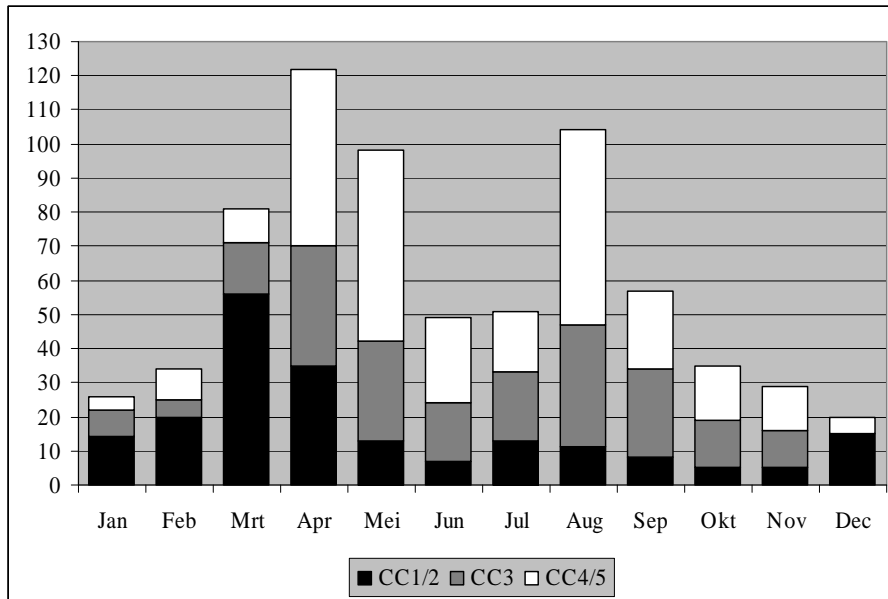


Figure 7. Monthly numbers of animals in CC 1-2, CC 3 and CC 4-5 between 1995 and 2011.

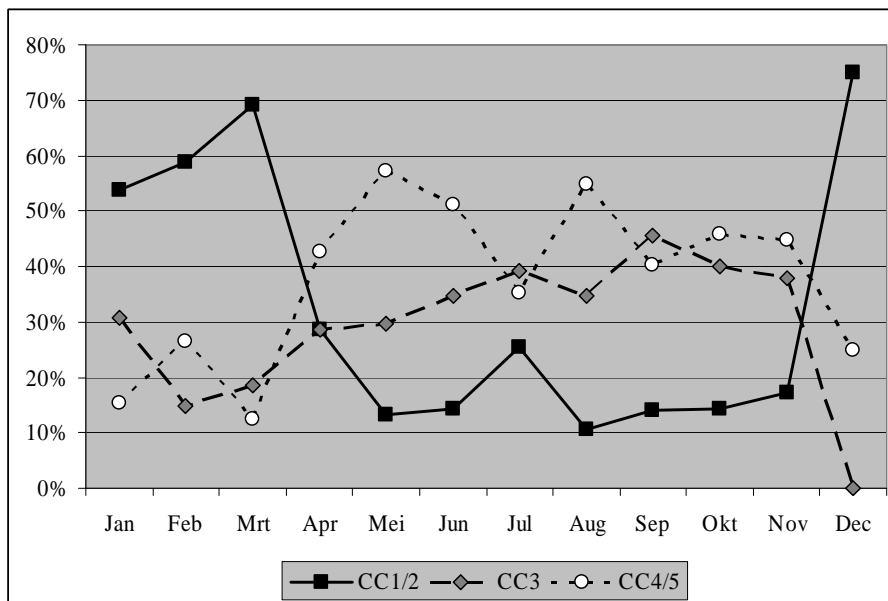


Figure 8. Monthly percentage of animals in CC 1-2, CC 3 and CC 4-5 between 1995 and 2011.

3.1.5. Age distribution in stranded animals

Figure 9 presents the age distribution of stranded animals between 1995 and 2011.

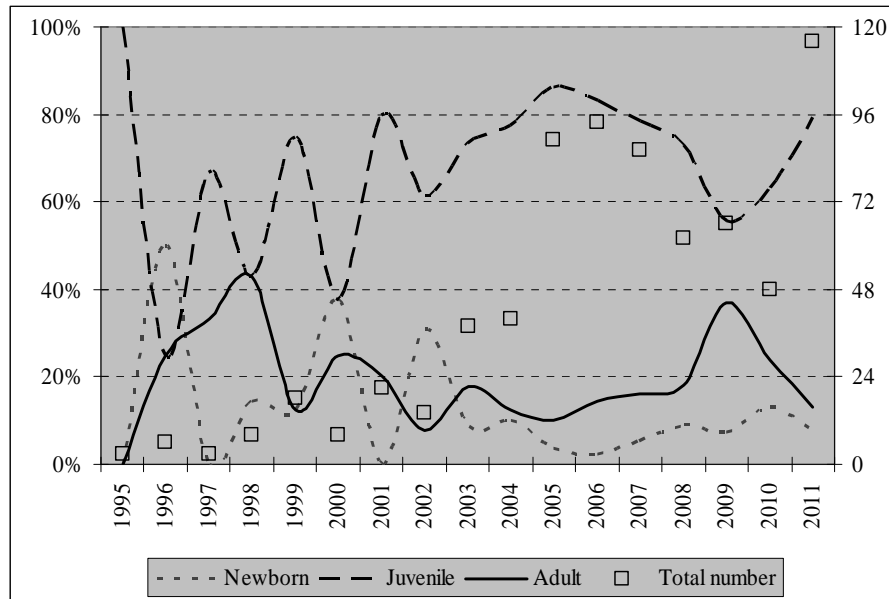


Figure 9. Yearly age distribution of stranded animals between 1995 and 2011.

The age distribution between 2003 and 2008 is fairly constant, with in total 6%, 80% and 14% of newborns, juveniles and adults respectively. There is an anomaly in 2009 and 2010, years with relatively few strandings, with 10%, 59% and 31% of newborns, juveniles and adults respectively. In 2011 similar figures as between 2003 and 2008 are found. Figure 10 presents the seasonality in the length distribution of stranded animals, by plotting day and month of the stranding of the animals vs. their length.

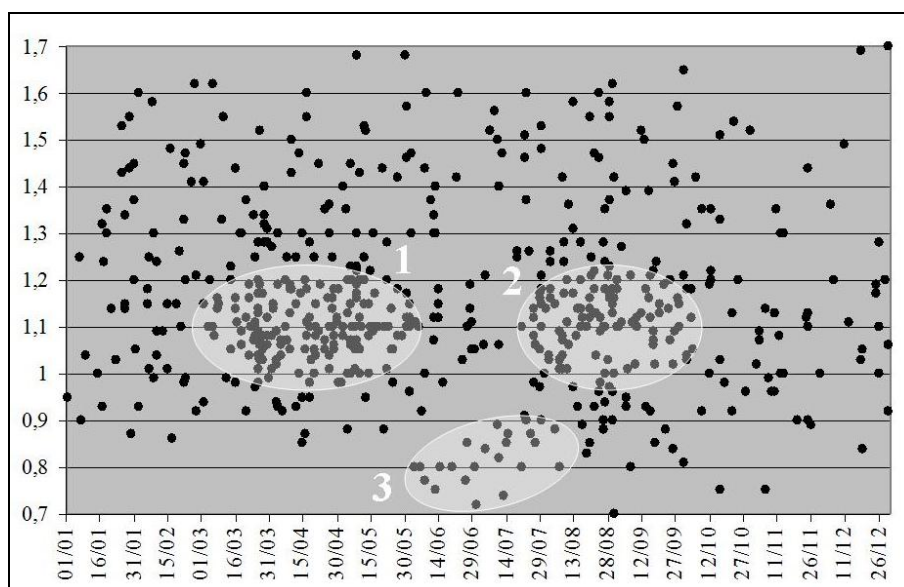


Figure 10. Length vs. day and month of stranding, indicating a high number of juveniles in spring (1) and summer (2), and the main occurrence of animals supposed to be newly born or stillborn (3).



The relatively high number of animals of 1.0 to 1.2 m in length washed ashore in spring are indicated, and a less pronounced peak of relatively short juveniles in summer. Also, the season in which newly born harbour porpoises washed ashore can be discriminated; the start of this season lies around the beginning of June, to last into August; however, there are many animals that were catalogued as newly born outside this period.

3.1.6. Sex ratio in stranded animals

Figure 10 presents the percentage of females in stranded animals divided in age groups (newborn/stillborn animals, juveniles, adults). For the age distribution, the length was used as a proxy. For in total 566 animals the length (~ age) and sex was known.

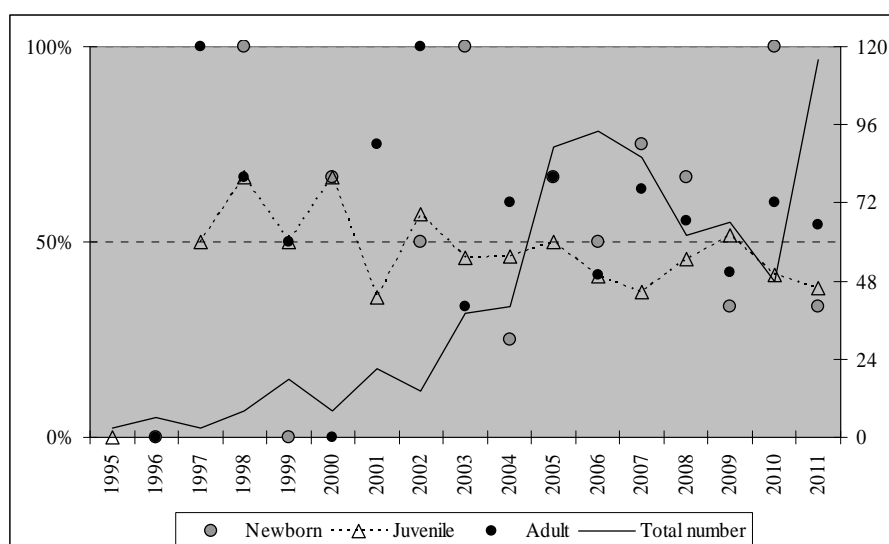


Figure 11. Yearly percentage of females in newborn, juvenile and adult animals washed ashore (left Y-axis), together with the absolute number of stranded animals (full line; right axis). The percentage females in juveniles is indicated by a dotted line.

Important fluctuations can be observed in the sex ratio of newborn/stillborn animals and adults, especially during the period in which few animals washed ashore. In the 21st century, with more animals available, the sex ratio stabilised. For newborn/stillborn animals and for adults the sex ratio in the total number of animals stranded between 1995 and 2011 for which a length and sex is known is fairly even, with as many females as males (respectively 50% and 52% females). However, in juveniles there seems to be a downward trend in the percentage of females, and in total there are clearly more males than females (44 % females between 1995 and 2011).



3.1.7. Causes of death in stranded animals

For 398 animals we could identify the most probable cause of death: we diagnosed 140 animals as having certainly or probably drowned in fishing gear, 1 animal was probably hit by a ship, and 257 animals probably died a natural death (including disease, starvation, death at birth or while giving birth, or killed by a seal; Haelters et al., 2012a). As such, bycatch can be considered as the major human-induced cause of mortality. For 309 animals it was not possible to establish the cause of death. The total number of bycaught animals (Figure 12) shows a peak in 2005 and 2006. Data for 2010 and 2011 are preliminary.

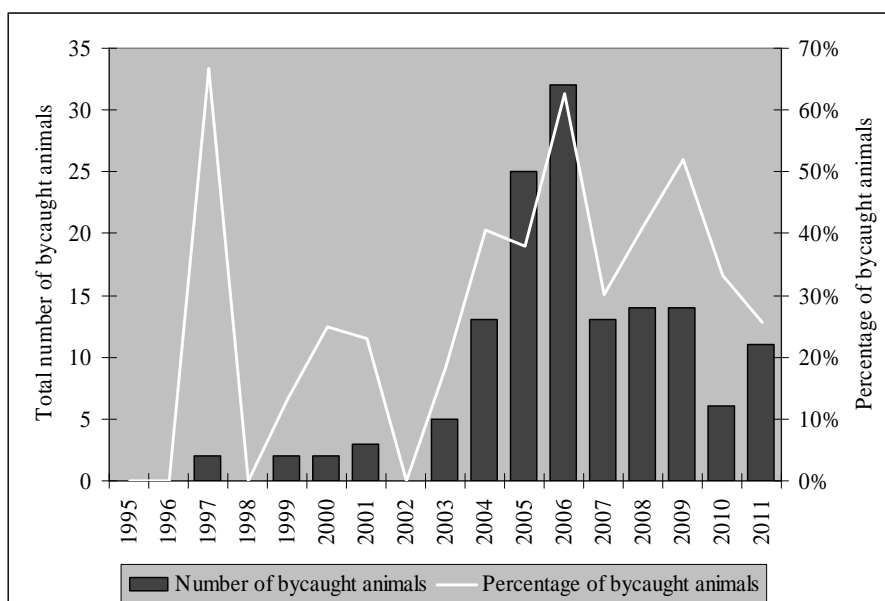


Figure 12. Total number of bycaught animals registered annually between 1995 and 2011, and percentage of bycaught animals (based on the total number of animals for which the most probable cause of death could be identified).

Bycatch records show a distinct seasonal pattern (Figure 13), with most of the bycaught animals found in March and April, and many of the animals found in May having probably died (drowned) already during April (Haelters et al., 2006). During those months more than 50% of the recovered animals was diagnosed as having been bycaught.

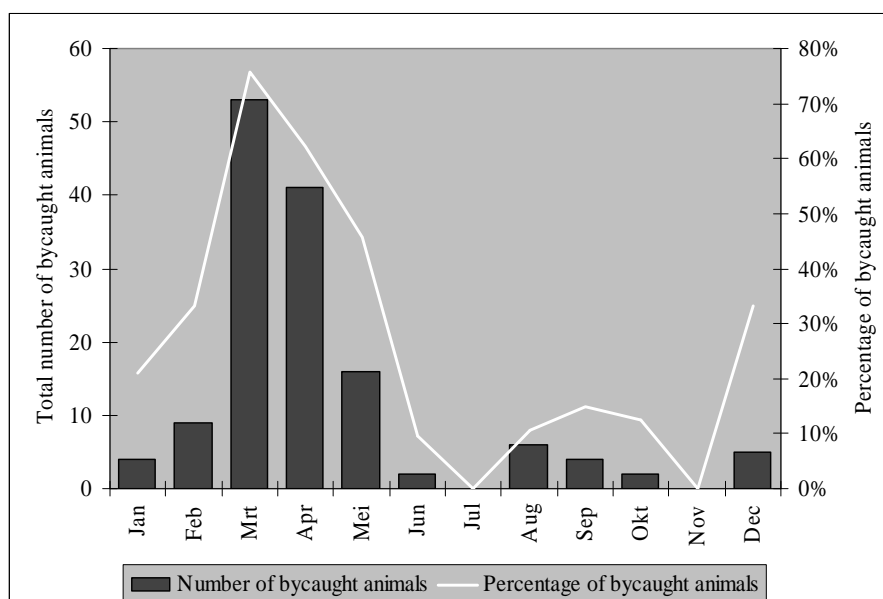


Figure 13. Total number of bycaught animals registered per month between 1995 and 2011, and percentage of bycaught animals (based on the total number of animals for which the most probable cause of death could be identified).

Of the juvenile females 43% was diagnosed as having been bycaught, while this was only the case for 38% of juvenile males (animals for which a cause of death was established, sample size: 285; 116 females, 169 males). In adults, with a much smaller sample size (females: n=40, males: n=36), 23% of females was bycaught against 39% of males.

3.1.8. Nutritional condition of stranded harbour porpoises

Length-weight distribution

The body weight (W, in kg) at length (L, in m) relationship (Figure 14) obtained was:

$$W = 1.4587 \cdot \exp(2.244 \cdot L)$$

As it can be expected that bycaught animals would be healthier than stranded animals that died due to disease or starvation, they were supposed to be heavier, and were discriminated from the other animals in figure 15 (together with the single animal that probably died due to a collision). The different weight – length relationships obtained are the following:

$$W = 1,205 \cdot \exp(2,3414 \cdot L) \text{ (naturally died animals)}$$

$$W = 2,4826 \cdot \exp(1,9221 \cdot L) \text{ (animals died due to trauma)}$$

$$W = 1,2776 \cdot \exp(2,28 \cdot L) \text{ (animals with an unknown cause of death)}$$

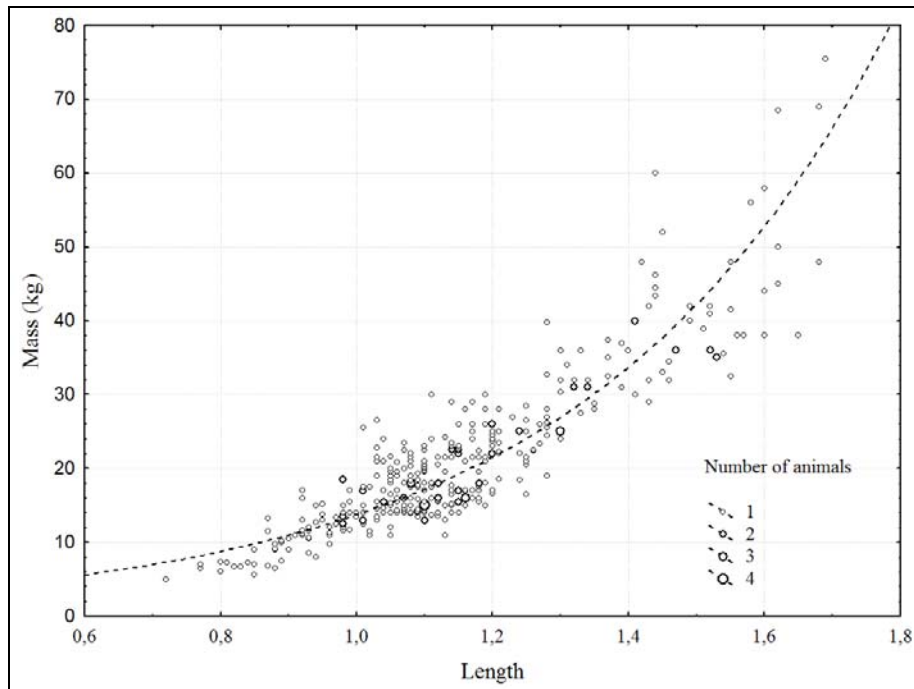


Figure 14. Weight at length of all harbour porpoises for which this could be obtained, and which were not considered as having lost a significant amount of weight after death.

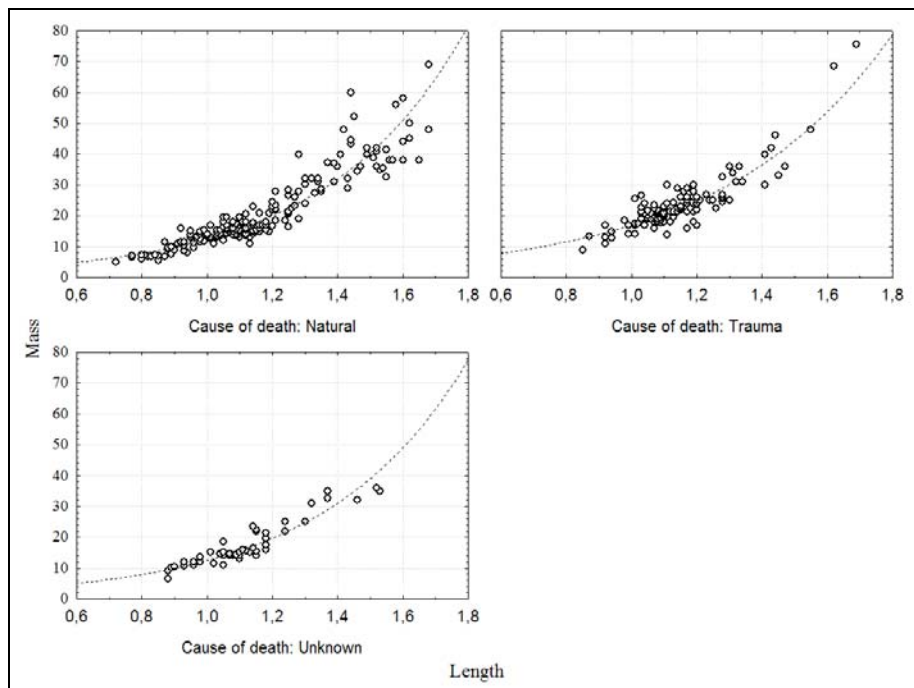


Figure 15. Length–weight relationship in harbour porpoises that died due to natural causes (top left), due to (human-induced) trauma (top right) and due to unknown reasons (bottom).

Figure 15 demonstrates that bycaught animals were in most cases juveniles. Relatively few adults and animals categorised as newborns were bycaught. Figure 16 demonstrates that bycaught juvenile animals (n=104) were heavier than naturally died juveniles of a similar



length (n=142). The average difference ranges from around 3 kg in the smallest animals to around 5 kg in the larger ones.

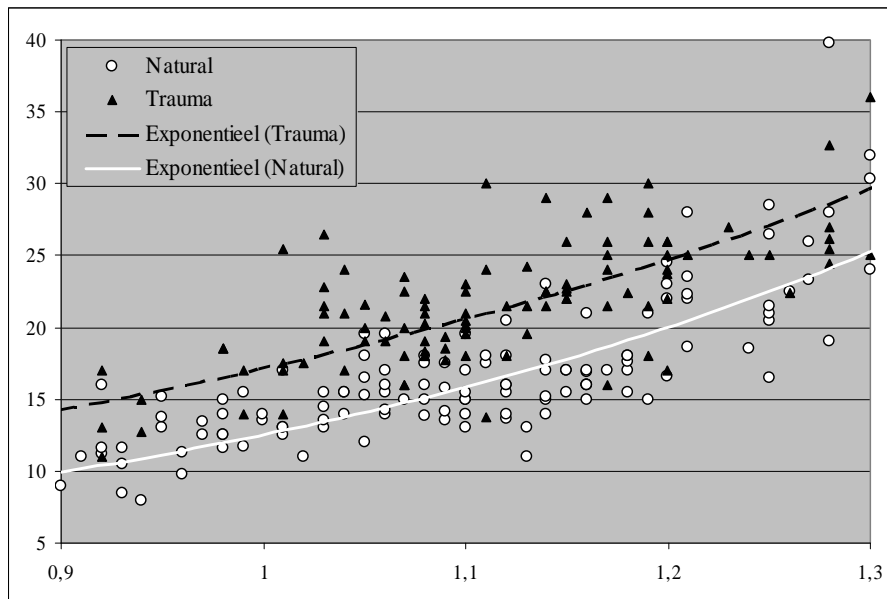


Figure 16. Comparison of the length (X-axis, m) - weight (Y-axis, kg) relationship in naturally died juvenile harbour porpoises vs. animals that died of trauma (mostly bycatch).

Blubber thickness

Figure 17 shows that the average blubber layer is around 0.8 cm thicker in animals bycaught than in naturally died animals of the same length.

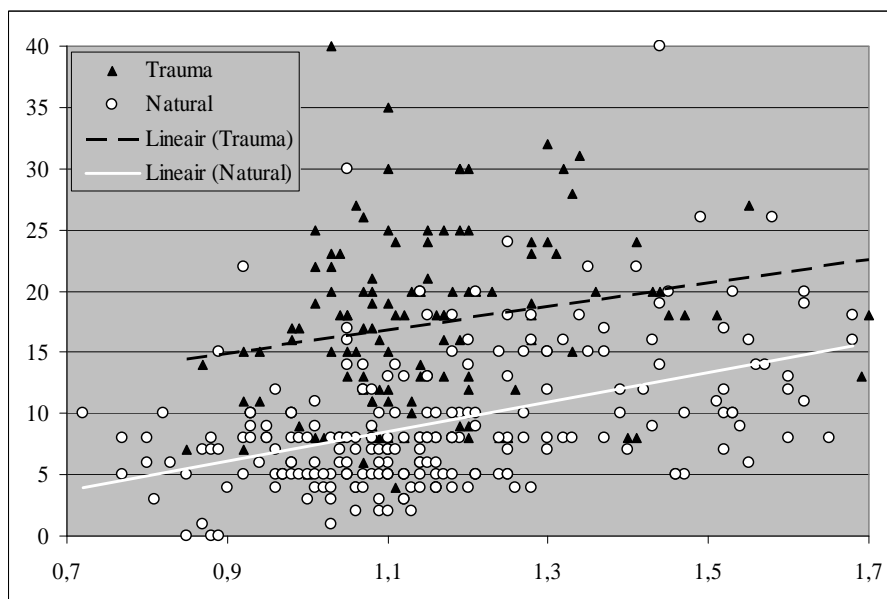


Figure 17. Comparison of the length (X-axis, m) – blubber thickness (Y-axis, mm) relationship in naturally died harbour porpoises vs. animals that died of trauma (mostly bycatch).



A seasonality (and relationship with water temperature) in blubber thickness is demonstrated in Figure 18, with the blubber thickness of 1.00 to 1.20 m long animals (CC1 to 3) that died a natural cause of death (n=93) and were bycaught (n=83). While in winter and early spring a number of naturally died animals had a blubber thickness of more than 1 cm (still very thin!), the blubber thickness of naturally died animals that washed ashore during summer months was systematically thinner than 1 cm, indicating that they had used up most of their energy reserve. Figure 18 also indicates that amongst the bycaught animals we find also relatively emaciated and therefore unhealthy animals.

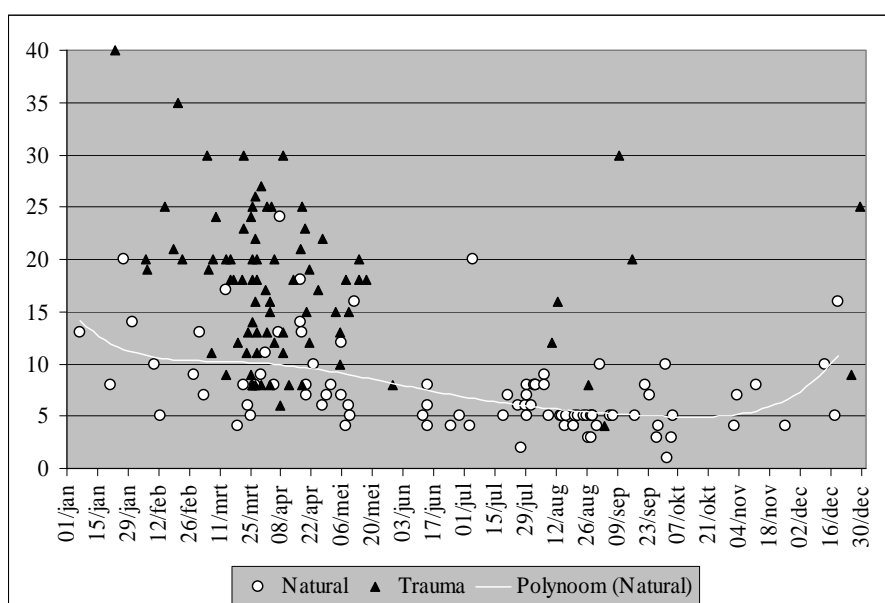


Figure 18. Seasonality (day/month; X-axis) in blubber thickness (Y-axis, in mm) of animals between 1.00 and 1.20 m in length (only CC 1 to 3 considered) washed ashore between 1995 and 2011. For illustrative purposes, a polynomial function (6th order function) is indicated for the blubber thickness in naturally died animals.

3.2. Results of the stomach content analyses

3.2.1. Prey species present in the stomachs

Most of the prey remains in the stomachs had belonged to fish. We found the remains of other organisms (cephalopods, crustaceans and polychaetes) in small quantities and in less than 10% of the stomachs. We suspect that in many cases these concerned remains of secondary prey. Amongst the fish species we identified 19 species belonging to 10 families. The remains of *Loligo vulgaris* concerned a gladius, the remains of *Sepiolo* sp. concerned beaks, and the remains of the polychaetes concerned chitinous jaws.



Table 1. List of species found in the stomach of the investigated harbour porpoises.

Species	Family
Fish	
<i>Clupea harengus</i>	Clupeidae
<i>Sprattus sprattus</i>	Clupeidae
<i>Osmerus eperlanus</i>	Osmeridae
<i>Gadus morhua</i>	Gadidae
<i>Merlangius merlangus</i>	Gadidae
<i>Trisopterus luscus</i>	Gadidae
<i>Trisopterus minutus</i>	Gadidae
<i>Dicentrarchus labrax</i>	Serranidae
<i>Trachurus trachurus</i>	Carandigidae
<i>Mullus surmuletus</i>	Mullidae
<i>Ammodytes marinus</i>	Ammodytidae
<i>Ammodytes tobianus</i>	Ammodytidae
<i>Hyperoplus lanceolatus</i>	Ammodytidae
<i>Pomatoschistus lozanoi</i>	Gobiidae
<i>Pomatoschistus microps</i>	Gobiidae
<i>Pomatoschistus minutus</i>	Gobiidae
<i>Gobius niger</i>	Gobiidae
<i>Platichthys flesus</i>	Pleuronectidae
<i>Scophthalmus sp.</i>	Scophthalmidae
Invertebrates	
<i>Crangon crangon</i>	Crustacea, Crangonidae
<i>Pagurus bernhardus</i>	Crustacea, Paguridae
<i>Sepiola sp.</i>	Mollusca, Sepiolidae
<i>Loligo vulgaris</i>	Mollusca, Loligidae
Polychaete sp.	Polychaeta, Nereidae

3.2.2. Number of fish prey remains

We identified the remains of 16.932 prey items (excluding polychaete jaws), of which 16.924 were fish prey. The average number of prey items was 319 per harbour porpoise: 367 (SD 511) per stomach in juveniles and 146 (SD 296) per stomach in adults. The number of prey items was not equally distributed among prey species; table 2 indicates that the high number of fish prey items per stomach could be attributed to the presence of a sometimes very high number of goby remains.



Table 2. Average number of remains of fish belonging to different families (including minimum and maximum number, SD) in the stomachs (in which prey remains of that species group were present).

Family	Average	Minimum	Maximum	SD
Gobiidae	371,8	1	2800	520,7
Ammodytidae	45,0	1	302	91,3
Gadidae	6,8	1	80	17,1
Clupeidae	2,6	1	7	2,2
Serranidae	9,7	1	42	15,4
Osmeridae	3,0	1	6	1,9
Carangidae	5	5	5	-
Mullidae	1	1	1	-
Pleuronectidae	1	1	1	-
Scophthalmidae	2	2	2	-

3.2.3. Number of fish prey species per harbour porpoise

On average the remains of 2.5 fish prey species were present in the stomachs, both in juveniles (1 to 8 fish species/stomach; SD 1.6) and in adults (1 to 4 species/stomach; SD 1.3).

3.2.4. Frequency in occurrence of prey

The overall frequency of occurrence of fish prey is indicated in figure 19. Gobies occurred in almost 80 % of all stomachs investigated, while also sandeels, gadoids and clupeids were found in a large percentage of the stomachs.

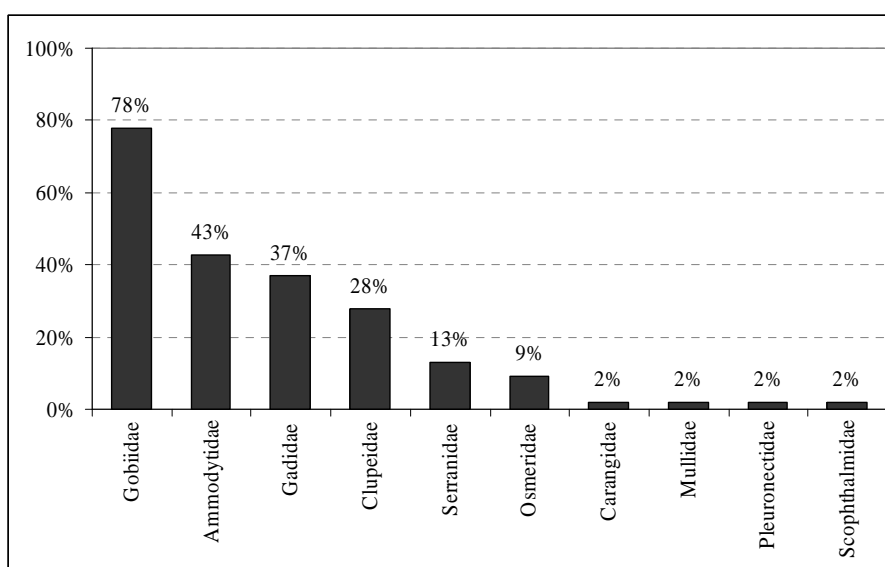


Figure 19. Frequency of occurrence of prey in the stomach of all investigated harbour porpoises.



However, as indicated in figure 20, the occurrence of prey in juveniles (n=41) is different than from that in adults (n=13), where sandeels are the group of species most commonly encountered. Sea bass *Dicentrarchus labrax* (only remains of juvenile fish) and smelt *Osmerus eperlanus*, relatively small fish, were only encountered in juvenile harbour porpoises, as were the few bottom dwelling red mullet *Mullus surmuletus* and flatfish encountered.

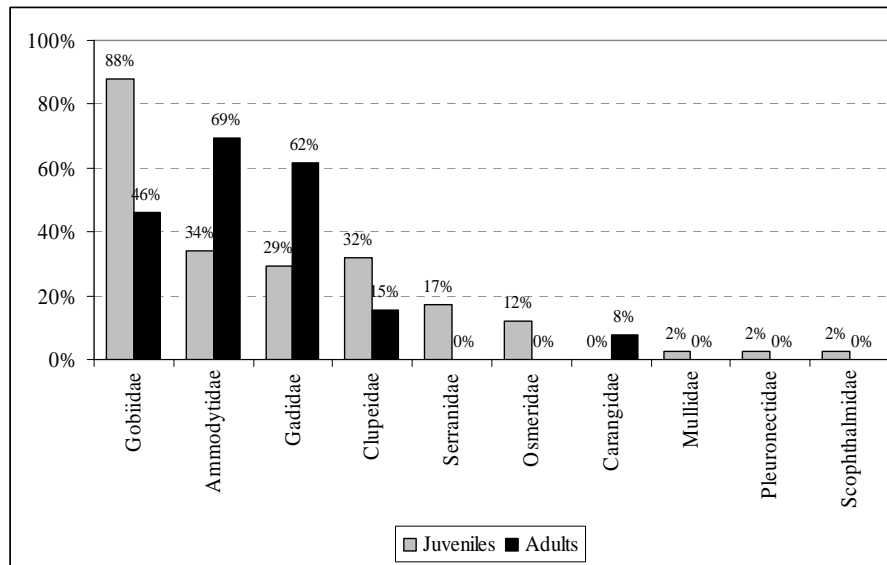


Figure 20. Frequency of the occurrence of prey in the stomach of juveniles (n=41) and adults (n=13).

3.2.5. The numerical importance of each fish prey species

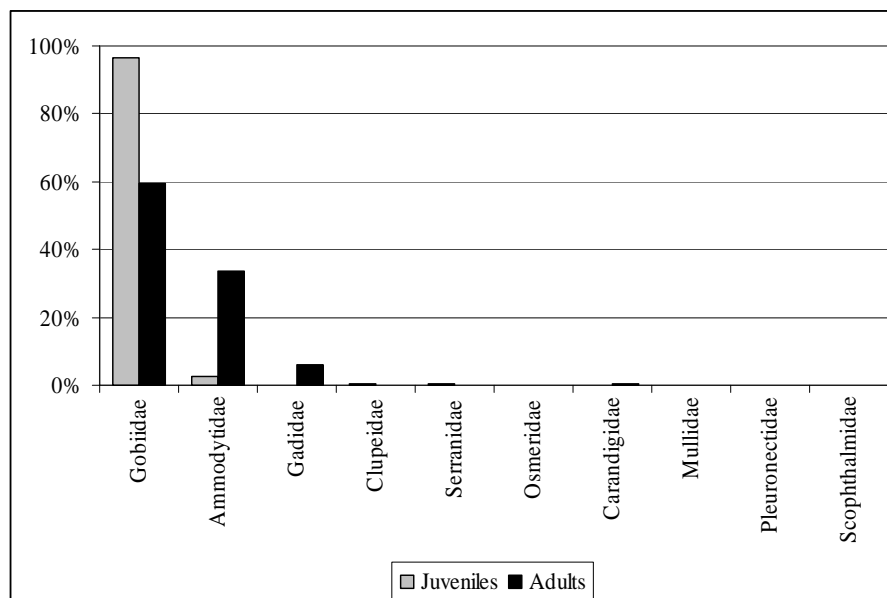


Figure 21. Numerical importance (in %) of the different fish prey item remains (by family) in the stomach of juveniles and adults



The prey remains most frequently encountered in juveniles originated from gobies, while in adults these were gobies and sandeels (Figure 21). Besides those, the only other prey that was numerically important was gadoids in adults.

3.2.6. Proportion of each species by fresh weight

We estimated the average original weight of the fish prey remains in the stomachs at 0.66 kg: 0.444 kg in juveniles and 1.281 kg in adults. The most important prey by weight in juveniles were gobies and sandeels, while in adults this was sandeels and gadoids (figure 22). The relatively large Atlantic horse mackerel *Trachurus trachurus* were only found in one adult harbour porpoise.

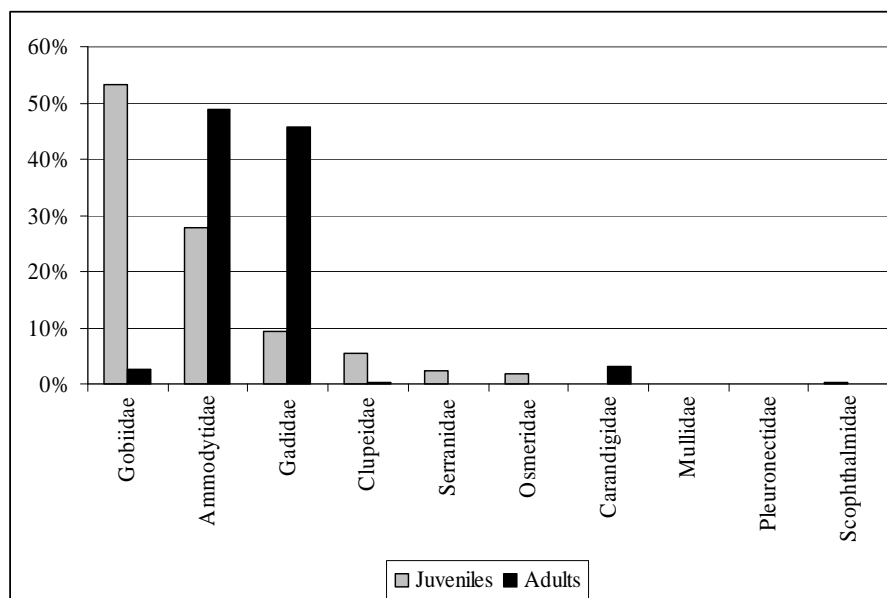


Figure 22. Importance by weight (in %) of the different fish prey item remains (by family) in the stomach of juveniles and adults.

3.2.7. Length of prey taken by harbour porpoises

Figure 23 shows the average original length of the prey remains in the stomach of each harbour porpoise (vs. length of the harbour porpoise). This figure is probably biased due to secondary prey: the average length of harbour porpoises with gadoid and goby remains in their stomach may be in many cases too low, as the small gobies may have been the prey of the much larger gadoids. From the figure it is clear that larger harbour porpoises take larger prey.

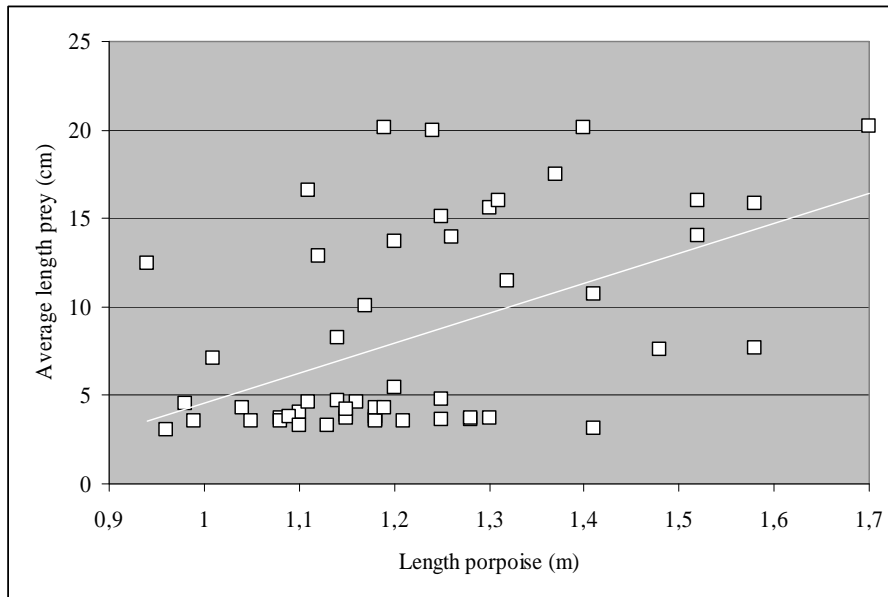


Figure 23. Average original size of the fish of which remains were found in the stomach of each harbour porpoise, expressed as a function of the length of the harbour porpoise.



4. Discussion

4.1. Analysis of the strandings database

A stranding rate of on average almost 2 animals/km coastline/year, as in 2011, can be considered as very high. As the number of stranded animals can be used as a proxy for the density at sea in the wide vicinity of the stranding location, it can be assumed that the harbour porpoise, once a rare animal, has returned in numbers to the coastal waters of the Southern North Sea. As a reason for shifts in the distribution of marine predators, habitat changes have been suggested which potentially affect food availability – although this remains difficult to prove (Alfonsi et al., 2012; McLeod et al., 2005; 2007; Simmonds & Isaac, 2007). Also in this case the change in distribution might well be prey related, with a decrease in the prey availability in more northerly waters, an increase in the prey availability in the Southern North Sea, or a combination thereof (Haelters & Camphuysen, 2009). While the number of stranded animals could be used as a proxy for the density of animals at sea, one should consider the many sources of bias:

- A higher bycatch rate during spring, with a higher static gear fishing effort;
- A bias due to weather conditions, the movement of carcasses being influenced by wind speed and direction, next to water currents;
- The decomposition rate of animals influenced by water temperatures, with during summer more animals greatly decomposed falling apart and not washing ashore, and possibly a floating/sinking sequence during different stages of decomposition;
- A differential mortality in the population, with for instance a high mortality rate in neonates (with animals being born in late spring – summer) and juveniles.

However, given the consistent nature of the seasonal strandings pattern, one can safely assume that during the 21st century there has been a higher density in harbour porpoises in Belgian and surrounding coastal waters between February and May, and between July and September, and that densities were lower in May-June and between October and January. At least the spring peak has been clearly demonstrated through aerial surveys, with consistent estimates for instance of an average of more than 2 animals/km² in Belgian waters during March 2011 (Haelters et al., 2012b). The increasing trend in strandings during summer, especially in the last triennium, might be explained by a return of the harbour porpoise to the coastal waters of the Southern North Sea during summer months. Indeed, while an analysis of



anecdotal sightings data (1970-2007) in The Netherlands and Belgium did not reveal that a high density of harbour porpoises might occur in these waters during summer months (Haelters & Camphuysen, 2009), the number of sightings reported during summer has clearly increased since 2010 (data MUMM, unpublished). Also an aerial survey performed in July 2010 indicated that harbour porpoises were not rare in Belgian waters, with on average 0.42 animals/km², in contrast to the results of an aerial survey during August 2009 yielding an average density of only 0.06 animals/km² (Haelters et al., 2011b). Seasonal migrations may be due to different stages in the life cycle of the harbour porpoise, such as birth and mating, and to the availability of food which may differ in the central – southern North Sea depending on the season.

There were fewer strandings per km coastline at Zeebrugge, possibly due to reporting issues, the long outer harbour walls, and the difficulties for dead animals to enter and be recovered in the port. The lower stranding rate at Knokke-Heist might be due to the shadow-effect of the harbour of Zeebrugge, limiting the number of strandings in the prevailing west to east currents. Although prey availability is probably uneven throughout Belgian waters, leading to an uneven distribution of harbour porpoises, the detailed location of the stranding was not further considered as a factor determining the stomach content, given the high mobility of harbour porpoises and many uncertainties, for instance in the origin of the carcass.

As could be expected given the low water temperatures, and as such a relatively slow decomposition rate, the highest percentage of fresh animals was found between December and March. The highest number of fresh animals was found in March, but this number was biased due to a high bycatch rate in this month (see further). The highest stranding rate of decomposed animals, and the lowest of fresh animals, coincided with the months with the highest water temperatures. The more decomposed an animal is, the more uncertainty exists about its origin. Therefore, the prey items in very decomposed animals may not originate from animals that had their last meal in Belgian waters. It has been demonstrated that carcasses can float in from considerable distances (Haelters et al., 2006; Peltier et al., in prep.). Therefore, if choice is possible or a selection is needed, prey analysis should by preference be performed on fresh animals.

It is difficult to indicate whether animals considered as newborns but washed ashore outside the calving season in fact concern newly born animals, naturally very small individuals (eg. grown very slowly after birth), or animals measured wrongly. It is very



unlikely to find any prey item in truly newborn animals, and evidently in stillborn animals the stomach is always empty. However, prey items may be found in animals shorter than 91 cm washed ashore outside the calving period, indicating that these animals should have been classified as juveniles.

It is difficult to interpret the sex ratio in stranded animals, with more juvenile males than females. This was likely not the consequence of a higher bycatch rate in males. In at least one other odontocete (the sperm whale) males disperse more than females, and on the basis of a study of stranded harbour porpoises in the UK and adjacent waters Walton (1997) suggested that this was also the case in harbour porpoises.

Bycatch was an important cause of death of the washed ashore harbour porpoises. Especially in 2006 a relatively high number of harbour porpoises were bycaught in recreational beach fisheries, probably due to a high effort in this fishery combined with a distribution of harbour porpoises unusually close to shore – perhaps due to the high density of a favoured prey item. However, it is likely that in the early years of the research some bycaught animals were not recognised as such, as some experience is needed to recognise the sometimes subtle signs of bycatch. A seasonality in the bycatch rate was due to the high static gear fishing effort during March and April, mostly close to shore. This activity targets predominantly the highly valuable migrating sole *Solea solea* and it coincides with the highest density of harbour porpoises in the coastal waters of the Southern North Sea.

Juvenile bycaught animals were, as expected, heavier than juveniles of a similar length that died naturally, given that natural death in many cases is preceded by weight loss. When animals are not feeding anymore, they use their blubber, and especially the blubber of the thorax, as the site of lipid deposition and mobilization (Koopman et al., 2002). A comparison of the thoracic blubber layer (measured at a standardised location) in naturally died vs. bycaught animals confirmed that animals that died due to starvation or disease had a thinner blubber layer than animals that drowned in fishing gear, and that they were lighter at a similar length. The fact that the blubber layer in juvenile naturally died animals was thicker in winter stranded animals than in summer stranded animals can be explained through the second function of the blubber layer: it also serves as an insulation against the outside temperatures. While harbour porpoise with a thin blubber layer and as such an impaired insulation could survive in warm summer water (up to around 20°C) for a short period of time, this is not the case anymore in winter, with temperatures dropping to a few °C.



4.2. Stomach content analysis

The most important prey species remains encountered in juvenile harbour porpoises originated from gobies, of which hundreds to thousands must have been consumed per day in some harbour porpoises. The foraging by these animals must have taken up a considerable amount of their time. It might help to explain why juvenile harbour porpoises drown in fishing nets in higher frequencies than newborns or adults. Whereas a harbour porpoise might be able to detect static gear in the immediate vicinity while echolocating, this is only the case when this static gear is located in front of it. Most gobies occur on the bottom, and a harbour porpoise feeding on them must be hanging vertically above the seafloor, slowly moving with the tidal current, and possibly oblivious of what is happening around it. As such it may be temporarily unaware of static gear in the vicinity.

Whereas juveniles predominantly fed on bottom dwelling fish, the stomachs of the small sample of adults investigated contained a higher proportion of pelagic and demersal fish, as well as sandeels. Sandeels have a pelagic and benthic life stage: they are buried in the sand during part of the day, and turn to a pelagic life stage to feed. Winslade (1974) studied the supposedly diurnal pattern in the behaviour of Raitt's sandeel *Ammodytes marinus* and found that it was active in the water column during daytime when food was available, and remained buried in the sand at night. Terns also feed on sandeels, and catch them during daytime in the water column close to the surface (Eric Stienen, personal communication). It is not known whether harbour porpoises can take sandeels in the water column or while these fish are buried (but other odontocetes can detect buried prey). As we did not find sand in many of the stomachs investigated, and as other pelagic fish were taken, we presume that the sandeels were taken in the water column, but this remains to be investigated. The apparent importance of sandeels in the diet indicates that sandeels may form a more important staple food species in the Southern North Sea than could be expected from research on fish stocks; the methods used in fish sampling, such as shrimp trawls or relatively large-meshed pelagic nets may not be the most suitable ones to reveal the density of sandeels.

Interesting in the (relatively recent) prey composition is the presence of juvenile sea bass (considered as a southern species) and smelt. Smelt is a diadromous fish which had nearly disappeared until a decade ago from the southern North Sea, and was rarely observed



in Belgian waters. Slowly the numbers of this small fish are increasing. In Germany these fish have, together with twaite shad *Alosa fallax*, returned in numbers to spawn in the rivers Jade, Elbe and Weser in March to May. In 2012 they were even presumed to be one of the reasons why so many harbour porpoises were observed swimming far upstream in these rivers in March to return to sea in May (GRD, 2012). While March to May is the period in which harbour porpoises are particularly common in shallow waters bordering the Southern North Sea, no link (except for the increase in harbour porpoises far upstream in Germany in 2012) has been laid so far between this phenomenon and the yearly migration of diadromous fish to rivers. At least in our study no twaite shad remains were found in the stomachs investigated (although our sample did not contain many adult harbour porpoises in a good nutritional condition). Poll (1947) reported that this formerly abundant fish was decreasing in the Southern North Sea, and it had disappeared from the Scheldt, Meuse and Rine by 1950. In the 1950s also the harbour porpoise disappeared from Dutch and Belgian waters (Camphuysen & Peet, 2006). Adult twaite shad were caught again in the Scheldt in 2003 (Maes et al., 2004), and the species was suspected of reproducing again in the river Scheldt by Stevens et al. (2011). The abundance of this fish in the Southern North Sea is clearly increasing, together with the amelioration of the water quality of rivers. While Poll (1947) reported smelt as abundant far upstream rivers, Rappé & Eneman (1988) considered it as rare. Our own observations indicate that this fish has become common again in the Belgian coastal waters since 2010 (Kerckhof, 2012), and Stevens et al. (2009) reported that it was reproducing again in the Scheldt.

In the past clupeids constituted an important part of the diet of harbour porpoises. This apparently changed after the collapse of the herring *Clupea harengus* stock (Santos, 1998). Although herring is becoming more common again, we could not find evidence that clupeids (relatively fat fish, and therefore from an energetic point of view interesting prey for the harbour porpoise) formed an important part of the diet of harbour porpoises. It cannot be excluded however that this is the case during summer in the central North Sea – after all, the stomach contents only reveal the most recent prey taken, and thus the prey taken close to the stranding location.

Although our sample is still small, the small number of prey species encountered so far in the stomach of the harbour porpoises was surprising. We would have expected at least the presence of other common species, such as dragonets (Callyonimidae), rocklings (Lotidae),



sea-snail (*Liparis liparis*) and more flatfish, abundantly occurring in between gobies. We also expected, especially in adults, species such as twaite shad, occurring now commonly in Belgian waters, and perhaps also other common species such as mackerel *Scomber scombrus*, sea trout *Salmo trutta trutta*, thinlip mullet *Liza ramada* and garfish *Belone belone*. Apparently harbour porpoises are not as opportunistically feeding as sometimes described.

5. Conclusions

- The harbour porpoise is the most abundant top predator (excluding birds) in Belgian marine waters, with in 2011 on average almost 2 stranded animals per km coastline. There are currently two peaks in strandings: one in March-April, with a high mortality due to bycatch, and one during summer. Trends in occurrence may be prey related.
- The seasonal strandings rate of fresh and decomposed animals is partly related with the water temperature, with a higher percentage of decomposed animals washing ashore during months with warmer water temperatures.
- Most of the washed ashore harbour porpoises are juveniles, and the sex ratio among them is uneven, with a higher percentage of males. This could be due to a higher dispersion rate of males compared to females.
- Juvenile bycaught animals were on average heavier and had a thicker blubber layer than juvenile naturally died animals; this is due to the fact that the blubber layer is used as a reserve, and is consulted in weakened animals. In naturally died animals the blubber layer was thicker in winter than in summer, illustrating the second function of the blubber layer: insulation.
- Investigating stomach remains is useful in revealing trophic relationships; it can demonstrate changes through time, and as harbour porpoises need to feed every day, help explain changes in the distribution, more local movements and seasonal migrations of harbour porpoises.
- Investigating stomach remains can be useful to detect changes in the distribution and abundance of prey (such as of clupeids and smelt).



- Stomach content analysis may reveal how harbour porpoises feed, and as such assist in explaining how bycatch technically occurs.
- Sandeels probably form a more important staple food species in the Southern North Sea than generally thought.
- Putting together and comparing the results of diet analyses from different countries bordering the North Sea would be interesting to further reveal the reasons behind seasonal movements of harbour porpoises.
- The number of untreated stomach samples available (and growing) is appropriate to allow for a more in depth study to detect individual differences, seasonal differences, trends throughout the years, and differences throughout age groups.

6. Acknowledgements

This study was supported by the Federal Public Service for Health, Food Chain Safety and Environment (DG5 – Marine Environment), in the framework of the ASCOBANS North Sea Harbour Porpoise Conservation Plan.



Literature

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Annex 1. Overview and details of the animals of which the stomach content was investigated; cause of death is the most probable cause of death, or remained unknown; animals with an empty stomach shaded.

Date	Location	Sex	Length (m)	Age	Weight (kg)	Blubber (mm)	Cause of death
4/04/1997	Koksijde	Female	1,19	Juvenile	28	25	Bycatch
18/04/2000	Oostende	Female	1,12	Juvenile	20,5	13	Natural
18/01/2003	Oostende	Female	1,24	Juvenile	25	15	Unknown
5/03/2003	Middelkerke	Male	1,2	Juvenile	23,7	30	Bycatch
23/03/2003	Wenduine-De Haan	Male	1,1	Juvenile	22,5	11	Bycatch
22/04/2003	De Panne	Female	1,09	Juvenile	15	8	Natural
13/05/2003	Middelkerke	Male	1,52	Adult	42	17	Natural
12/03/2004	Middelkerke	Male	0,99	Juvenile	17	17	Bycatch
17/03/2004	Oostende	Female	1,11	Juvenile	30	18	Bycatch
3/04/2004	Nieuwpoort	Female	0,94	Juvenile	15	11	Bycatch
12/05/2004	Blankenberge	Male	1,53	Adult		10	Unknown
17/01/2005	Koksijde	Male	1,32	Adult	32	8	Natural
12/04/2005	Koksijde	Female	1,25	Juvenile	25	8	Bycatch
22/02/2006	Koksijde	Female	1,33	Adult	27,5	8	Natural
2/03/2006	Nieuwpoort	Female	1,41	Adult	40	24	Bycatch
29/03/2006	Koksijde	Male	1,28	Juvenile	25,5	18	Bycatch
30/03/2006	Blankenberge	Female	1,28	Juvenile	32,7	24	Bycatch
27/04/2006	Wenduine-De Haan	Female	1,3	Juvenile	25	32	Bycatch
28/04/2006	Found at sea	Male	1,14	Juvenile	23,5	20	Unknown
28/04/2006	Nieuwpoort	Female	1,25	Juvenile	38	36	Bycatch
9/05/2006	Oostende	Male	1,19	Juvenile	22,1	13	Unknown
3/08/2006	Knokke-Heist	Male	1,26	Juvenile		18	Natural
8/09/2006	Oostende	Female	1,11	Juvenile	16	7	Unknown
29/12/2006	Koksijde	Male	1,2	Juvenile	26	25	Bycatch
6/02/2007	De Panne	Male	1,18	Juvenile	22,4	20	Bycatch
15/02/2007	Nieuwpoort	Male	1,15	Juvenile	14	8	Unknown
26/02/2007	Blankenberge	Male	1,41	Adult	40	22	Natural
16/03/2007	Oostende	Male	0,98	Juvenile	18,5	17	Bycatch
9/04/2007	Koksijde	Male	1,05	Juvenile	19	13	Bycatch
20/04/2007	Wenduine-De Haan	Male	1,25	Juvenile	21,5	8	Natural
21/03/2008	Middelkerke	Male	1,37	Adult		20	Bycatch
21/01/2009	Oostende	Female	1,14	Juvenile	17,7	3	Unknown
30/03/2009	Koksijde	Male	1,31	Adult	34	23	Bycatch
3/05/2009	Middelkerke	Female	1,4	Adult		8	Bycatch
13/08/2009	Koksijde	Male	1,17	Juvenile	24	16	Bycatch



Annex 1 (continued)

Date	Location	Sex	Length (m)	Age	Weight (kg)	Blubber (mm)	Cause of death
21/03/2010	Koksijde	Male	1,16	Juvenile	21,5	18	Bycatch
22/03/2010	Middelkerke	Female	1,04	Juvenile	24	23	Bycatch
26/03/2010	Koksijde	Female	1,01	Juvenile	14	8	Bycatch
1/05/2010	Middelkerke	Male	1,18	Juvenile	18	8	Natural
16/05/2010	Middelkerke	Male	1,3	Juvenile	25,5	12	Unknown
31/05/2010	Middelkerke	Female	1,57	Adult		10	Natural
12/06/2010	Oostende	Female	1,07	Juvenile	14	12	Unknown
20/06/2010	Koksijde	Female	0,8	Newborn	5	4	Natural
29/07/2010	Koksijde	Male	0,97	Juvenile		5	Natural
2/08/2010	Wenduine-De Haan	Male	1,04	Juvenile	15,5	8	Natural
5/08/2010	Bycatch at sea	Male	1,15	Juvenile	22,5		Bycatch
13/08/2010	Koksijde	Female	1,58	Adult			Unknown
16/08/2010	Middelkerke	Male	1,14	Juvenile	16,5		Natural
25/08/2010	De Panne	Female	0,98	Juvenile	4	9	Natural
29/08/2010	Bredene	Female	1,58	Adult	39	10	Unknown
12/09/2010	Found at sea	Female	1,52	Adult	36	12	Unknown
30/12/2010	Wenduine-De Haan	Female	1,7	Adult	41	18	Bycatch
28/02/2011	Oostende	Male	0,96	Juvenile	11,6	5	Natural
9/03/2011	Koksijde	Male	1,13	Juvenile	26	24	Bycatch
11/03/2011	Oostende	Female	1,48	Adult	41,5	16	Natural
24/03/2011	Blankenberge	Male	1,08	Juvenile	18	13	Bycatch
26/03/2011	Wenduine-De Haan	Female	1,21	Juvenile	26,2	23	Bycatch
1/04/2011	De Panne	Female	1,08	Juvenile	21,5	17	Bycatch
7/04/2011	Blankenberge	Male	1,1	Juvenile	19,6	13	Natural
9/04/2011	Bredene	Male	1,18	Juvenile	21,5	15	Unknown
17/04/2011	Bredene	Male	1,18	Juvenile	17,6	18	Natural
29/04/2011	Wenduine-De Haan	Unknown	1,18	Juvenile	17	4	Unknown
14/05/2011	Wenduine-De Haan	Unknown	1,15	Juvenile	22	18	Bycatch
24/05/2011	Middelkerke	Male	1,14	Juvenile	17	10	Bycatch



Annex 2. Fish species mentioned in the report

Scientific name	English	Dutch	French
<i>Ammodytes marinus</i>	Raitt's sandeel	Noorse zandspiering	Lançon nordique
<i>Ammodytes tobianus</i>	Lesser sandeel	Kleine zandspiering	Lançon équille
<i>Belone belone</i>	Garfish	Geep	Orphie
<i>Callionymus lyra</i>	Dragonet	Pitvis	Lavandière - callionyme
<i>Clupea harengus</i>	Atlantic herring	Haring	Hareng
<i>Dicentrarchus labrax</i>	Seabass	Zeebaars	Bar
<i>Gadus morhua</i>	Cod	Kabeljauw	Cabillaud
<i>Gobius niger</i>	Black goby	Zwarte grondel	Gobie noir
<i>Hyperoplus lanceolatus</i>	Greater sandeel	Smelt	Grand lançon
<i>Liparis liparis</i>	Sea-snail	Slakdolf	Limace de mer
<i>Liza ramada</i>	Thinlip mullet	Dunlipharder	Mulet porc
<i>Merlangius merlangus</i>	Whiting	Wijting	Merlan
<i>Mullus surmuletus</i>	Red mullet	Koningsvis - Mul	Rouget
<i>Osmerus eperlanus</i>	Smelt	Spiering	Eperlan
<i>Platichthys flesus</i>	Flounder	Bot	Flet
<i>Pomatoschistus lozanoi</i>	Lozano's goby	Lozano's grondel	Gobie de Lozano
<i>Pomatoschistus microps</i>	Common goby	Brakwatergrondel	Gobie commun
<i>Pomatoschistus minutus</i>	Sand goby	Dikkopje	Bourgette
<i>Salmo trutta trutta</i>	Sea trout	Zeeforel	Truite de mer
<i>Scomber scombrus</i>	Mackerel	Makreel	Macquereau
<i>Scophthalmus maximus</i>	Turbot	Tarbot	Turbot
<i>Scophthalmus rhombus</i>	Brill	Griet	Barbue
<i>Solea solea</i>	Dover sole	Tong	Sole
<i>Sprattus sprattus</i>	Sprat	Sprot	Esprot
<i>Trachurus trachurus</i>	Horse mackerel	Horsmakreel	Maquereau bâtard
<i>Trisopterus luscus</i>	Pout - bib	Steenbolck	Tacaud
<i>Trisopterus minutus</i>	Poor cod	Dwergbolck	Petit tacaud