

# Season, sex and age variation in the diet of harbour porpoises (*Phocoena phocoena*) in the Dutch North Sea area



© Essexbiodiversity.org.uk

Ellen Nieuwenhuijsen

Season, sex and age variation in the diet  
of harbour porpoises (*Phocoena phocoena*)  
in the Dutch North Sea area

A study on prey remains in stomachs  
of 155 harbour porpoises stranded and by-caught  
in Dutch coastal waters in 2006 – 2008

A Bachelors thesis by

Ellen Nieuwenhuijsen

## **Colofon**

### **Time periods**

January–May 2009 Lab research

May–July 2010 Finalisation report

### **Realisation**

Wageningen IMARES

Location Texel

P.O. Box 167

1790 AD Den Burg

### **Contact**

Ellen Nieuwenhuijsen, Van Hall Larenstein

### **Supervisors**

Drs. Mardik Leopold (IMARES)

Drs. Peter Hofman (Van Hall Larenstein)

Drs. Arjen Strijkstra (Van Hall Larenstein)

### **Extern**

Van Hall Larenstein

P.O. Box 1528

8934 CJ Leeuwarden

## Acknowledgements

My special thanks go out to Mardik Leopold who was my supervisor during this study and who gave me valuable insight on several important aspects of this type of research: the data collection, diet analysis and the database, as well as other things to think about when studying harbour porpoises (*Phocoena phocoena*).

The other people of IMARES I would also like to thank for their support. As well as Peter Hofman and Arjen Strijkstra, my supervisors from Van Hall Larenstein. The subject matter I dealt with is potentially vast, and they were very helpful in helping me decide which information is relevant to my questions.

This work, my bachelors thesis for the HBO study Nature and Wildlife Management at Van Hall Larenstein, was part of a larger research programme on the dietary preferences and causes of death of harbour porpoises found on the Dutch shores in the North Sea, a programme supported by the Ministry of LNV. Thanks to the many people who were part of this, especially Kees Camphuysen (NIOZ), Okka Jansen (IMARES), Amber Beerman (Wageningen University) and Thierry Jauniaux (Luik University).

Ellen Nieuwenhuijsen, 30<sup>th</sup> of August 2010.

## Summary

It has been suggested that adult female harbour porpoises (*Phocoena phocoena*) in the southern North Sea could occupy a slightly higher trophic position than adult males (Das et al. 2003, from carbon and nitrogen stable isotopes ratios in 46 harbour porpoises stranded on the French, Belgian and Dutch coasts). Higher nitrogen ratios for females suggest a different diet, perhaps associated with reproductive behaviour.

In this study, diet composition of 155 beached and by-caught harbour porpoises from 2006–2008 was reconstructed. The objectives were to (i) determine whether the diet of mature females differed from that of mature males (ii) explore if and how they differentiated between the seasons, and (iii) explore if conclusions can be made on what these patterns might indicate in terms of foraging strategies, habitat use and general body condition.

Harbour porpoises have a high metabolic rate (Santos & Pierce 2003), which, combined with their limited energy storage capacity, requires them to feed frequently without long periods of fasting. Many harbour porpoise prey are also commercially exploited, and dramatic changes in North Sea fish stock have occurred in recent years. Both physiological research as abundance estimations (Santos & Pierce 2003, Camphuysen 1994) suggest that clupeids could be a more important fish order to porpoises than generally is accounted for.

To investigate whether the suggestions of Das et al. (2003) could be confirmed or not, relative contributions of individual prey taxa were assessed, as well as for prey orders (clupeids, gadoids, scombrids, gobies, squid and sandeel). Potential correlations were examined between either an offshore or inshore diet and demographics, seasonal features, and the general body condition (measured in classes 1 to 4).

The Das et al. findings on significant differences between diets of the sexes were confirmed, but not in such a substantial way that a structural higher trophic position could be assumed. Female adults took significantly more scombrids and fewer squid and gobies than the other demographic groups, and had in general a more offshore type of diet. Juvenile diet had a high proportion of gobies and in general a more inshore diet. Body condition per individual was compared on their consumption per prey order. Individuals with a better condition consumed more clupeids than the more emaciated animals.

These findings indicate complex use of energy resources and general conclusions were difficult to make. However, since the adult female group was more associated with a diet of more scombrids and in general a more offshore diet as the other demographic groups, this could indicate a different habitat use, perhaps because of (previous) higher energy requirements, caused by energy demands during the reproductive season. Further studies are needed to investigate the relationship between adult female reproductive needs, habitat use and their reactions on possible future changing availability of several prey groups, especially clupeids and scombrids.

# Index

Acknowledgements .....	5
Summary .....	6
Index .....	7
1. Introduction .....	7
1.1 Literature review .....	7
1.2 Study objectives .....	9
2. Material & methods .....	10
2.1 Data collection .....	10
2.2 Data analysis .....	11
3. Results .....	13
3.1 General results .....	13
3.2 Diets per sex and age group .....	13
3.2.1 Diet composition .....	13
3.2.2 “Offshore” or “inshore” diet .....	15
3.3 Nutritional value of diet and season .....	15
3.4 Seasonal variation in diet with regard to behaviour .....	17
3.6 Body condition index .....	17
4. Discussion .....	19
4.1 Summary of results .....	19
4.2 Discussion of the results .....	20
5. Conclusions and recommendations .....	23
5.1 Conclusions .....	23
5.2 Recommendations .....	23
6. References .....	25
Appendices .....	28

# 1. Introduction

## 1.1 Literature review

### European distribution and ecology

Harbour porpoises are one of the most common cetaceans in European waters (Santos & Pierce 2003, Leopold & Camphuysen 2006). However, through the last century, declines in their populations have occurred in some areas, particularly in the Baltic Sea, the southern North Sea and the English Channel. Several potential threats such as fishery by-catch, depletion of food resources, marine traffic and exposure to contaminants may have been responsible for such local declines of these stocks (IWC 2009, ICES 2007).

Harbour porpoises are small and have a relatively high metabolic rate (Santos & Pierce 2003), which, in combination with its limited energy storage capacity, contributes to a need to feed frequently without long periods of fasting. Their distribution and movements are perhaps closely related to the movements of their diet species (Johnston et al. 2005 in Fontaine et al., 2007). Haelters & Camphuysen (2009) noted a clear shift in distribution from northern waters towards the south between 1994 and 2005 (based on SCANS II 2008), which they assume is probably food related.

*Phocoena phocoena* forage mainly within the first 200m of the water column (Bjorge 2003 in Fontaine et al. 2007). They may feed at the sea floor in shallow waters, or pelagically on midwater prey, either in shallow or in deeper waters. In the southern and central North Sea area, depth varies from less than 40m in the south until a maximum depth of circa 100m in the central parts, except for the Doggerbank. A peak in numbers in coastal waters of the southern North Sea is reached between February and April (Haelters & Camphuysen 2009). During summer, sightings were less in number, more widespread and occurred mainly in northwestern regions, at or around the Doggerbank, and outside the Dutch sector of the North Sea (Camphuysen & Leopold 1993 in Booij, 2004).

Harbour porpoises are considered to be opportunistic feeders. Their diet consists of many different species of fish, cephalopods, crustaceans and even polychaetes. Several European studies indicate different primary prey species per location (Santos et. al 2004, Leopold & Camphuysen 2006, Haelters & Camphuysen 2009, Fontaine et al. 2007). Total food intake is between 4 and 9.5% of the total body weight, representing between 8000 and 25000 kJ/day (Kastelein et al. 1997 in Bouquegneau et al. 2007).

Young are mostly born between May and August, after a gestation period of 10 to 11 months. A peak in births occurs in June and July (Addink et al. 1995, in Haelters & Camphuysen 2009). Their nursing period is usually less than one year. Interestingly, there is a very short resting period between pregnancies, and females are often pregnant and lactating at the same time (Read et al. 1997, in Santos & Pierce 2003). Porpoises are sexually mature at an age of three to four (males) and four to five years (females), and longevity is around twenty years (Haelters & Camphuysen, 2009).

### Food type and trophic status: differences between adult females and adult males?

According to Das et al. (2003) adult females in the southern North Sea occupy a slightly higher trophic position than adult males. They measured nitrogen stable isotope ratios in the muscle tissue of 46 harbour porpoises and other marine mammals and several prey species. Of their investigated individuals, 17 were adult, 9 female and 8 male. Naturally occurring stable isotope ratios have a slight selective retention of the heavier isotope and excretion of the lighter one in biological tissues.

They are derived from assimilated food of the consumer and reflect dietary input over a longer period of time. Therefore, they are a good addition to studies on the last meal of individuals before stranding or by-catch. The isotopic ratio of nitrogen is generally used to indicate the trophic level of a predator. It shows the enrichment in its tissue, as compared to its prey. Mature female harbour porpoises had a significantly higher nitrogen ratio in their muscles than mature males: a mean of 16.5‰ versus 15‰. Stable isotope values did not differ between porpoises that had died with poor, moderate and good body conditions.

However, interpretation of isotopic ratio studies remains complex and inconclusive. Several of the results were in contradiction with other diet studies (Lick 1991 in Das et al. 2003, Santos & Pierce 2003, Leopold & Camphuysen 2006, Yang 1982 in Jennings et al. 2002). Furthermore, within a species many feed on higher trophic levels as they grow, but not all. Herring appeared to feed at lower trophic levels as they increased in size, and some flatfishes shift from feeding on predatory polychaetes to deposit- or filterfeeding bivalves as they grow (Braber & De Groot 1973 in Jennings et al. 2002). Future studies on stable isotope ratios possibly need to be based on increased replication over larger sea areas (Jennings et al. 2002).

In the Bay of Fundy, on the eastern shore of Canada, Smith & Gaskin (1983) reported that six lactating females consumed larger prey with a mean length of 46.4 cm ( $\pm 10.2$  cm) than seven non lactating nor pregnant females (mean 14.0 cm,  $\pm 3.1$  cm) and three mature males (mean 12.2 cm,  $\pm 5$  cm). The lactating females had a more diversified diet as well. In addition to their normal prey (herring, mackerel, gadoids, smelts) they took species that were not found in other stomachs examined (redfish, ocean pout, hagfish). The authors concluded that a different size range of fish and the more frequent occurrence of anomalous species “is further evidence that these females were searching for food in areas not generally utilized by other porpoises, in order to meet their energy requirements.” This is in agreement with Iverson & Lockyer (2004, in Santos et al. 2005), who found that females took in a greater variety of taxa than males in a sample of 72 by-caught harbour porpoises from Danish waters.

### **Other dietary aspects**

Clupeids could be of importance to harbour porpoises. Dudok van Heel (1962, in Santos & Pierce 2003) observed that captive porpoises fed on young cod lost weight, but this weight loss was halted when the diet was changed to the same amount of herring. Switching from high calorific prey like herring to one with lower calorific density could have long-term effects on survivorship and productivity of harbour porpoise populations, and since dramatic changes in North Sea fish stock do occur, prey quality could be an important aspect of porpoise ecology to look into. In addition to clupeids, MacLeod et al. (2007) suggest that sandeel are also important for porpoises. Changes in their availability have had major effects on the breeding success of other marine predators, such as seabirds (Wanless et al. 2005, Woo et al. 2008).



## ***1.2 Study objectives***

The dietary differences between adult males and females found in both the Das et al. (2003) and Smith & Gaskin (1983) studies are intriguing. The authors mentioned a possible link with reproductive behaviour, in the latter study this is more obvious than in the first study, however, it could be the case for both. In addition, females are in general significantly larger and weigh more than males (76 kg versus 61 kg, Santos et al. 2004). Both the larger size as the (past) periods of pregnancy and lactating could demand higher energy requirements.

Prey species like herring could perhaps meet these higher energy requirements. And especially during autumn, herring and several other fish are calory richer than in spring. Do adult females consume more of these fish than adult males? And more so in autumn? What about malnourishment: is there a link between the higher or lower nutrional state in which a harbour porpoise was found and its consumed prey? Answers to these questions could generate more insight in energy requirements in different stages of harbour porpoise lifes.

In this study, diets of 155 beached and by-caught harbour porpoises were reconstructed from the contents of their stomachs. The objective was to investigate whether different energy requirements of adult males and females during their lives translate into lasting differences in diets.

Main question: *Are diets of adult males and females significantly different?*

*-In prey species?*

*-In prey size?*

Sub questions:

- *Do these diets differ between the seasons?*
- *Are there differences in how they differ between the seasons?*
- *Is there a relationship between diets and nutritional state/body condition?*

## 2. Material & methods

### 2.1 Data collection

Between 2006 and 2008, 172 stranded and by-caught harbour porpoises were collected along the coasts and fisheries of the Netherlands. 155 Of these could be later analysed on diet. The sample included individuals of both sexes, immatures and adults. The post-mortem condition of the carcasses varied from very fresh to decomposed. The carcasses were stored at -18°C until dissection. Animals found in 2006 were stored at the NIOZ at Texel, those found in 2007/2008 at the University of Utrecht. During each dissection, individual characteristics of each animal were recorded and some tissues were sampled for further analyses (histopathology, virology, bacteriology, parasitology, toxicology, fatty acids and DNA), following the protocols from Kuiken and Hartmann (1991), and Jauniaux et al. (2002 in Leopold & Camphuysen 2006).

Date and location of stranding was recorded, as well as state of health, gender, length, weight and blubber thickness. Teeth were sampled in order to determine the age by counting the dentinal growth layers of the teeth, assuming that one layer equals one year (Gaskin & Blair 1977; Myrick et al. 1983; Lockyer 1995 in Leopold & Camphuysen 2006). Not all teeth have been processed at the time of writing this thesis. State of health was assigned into one of four categories: 4 (not emaciated), 3 (slightly emaciated), 2 (moderately emaciated), or 1 (severely emaciated, characterized by weight loss, reduced blubber layer thickness and dorsal muscle atrophy). Where possible, necropsy included assessment of disease status and cause of death.

The four stomach compartments were taken out and cut open. The stomach content was recovered and washed. All parts; food items, other swallowed elements, including macro-parasites of prey fish, were stored at -20°C in polythene bags for further analysis. After sorting, fish bones and otoliths were stored dry, and cephalopod beaks, crustacean remains as well as any remains with attached tissue were stored in 70% ethanol.

All prey hard parts were further analysed and measured under a microscope at IMARES on Texel. All derived data was recorded in a database. Maarten Debruyne and Angela Folmer started data acquisition on 2006 samples in 2007, Martijn Moorlag continued with 2007 samples in 2008. In 2009, I and my colleague Amber Beerman entered the 2008 sample data. Food items such as otoliths, fish bones, vertebrae, jaws and scales were determined to species, by using literature (Clarke 1986, Härkönen 1986, Watt et al. 1997, Leopold et al. 2001) and a reference collection of specimens caught by commercial or scientific trawlers in the Texel Wadden sea area. Otoliths and jaws were aligned by size, and paired if possible. Matching pairs or single items were considered being of one prey. Of each otolith or jaw, length and width was measured and recorded. If an otolith was broken, only the width was measured. Non food items were measured, weighed and recorded.

The size of the otolith was corrected by 5 to 20%, depending on the degree of wear and the species (Leopold & Winter 1997; Leopold et al. 1998). After this procedure the original size of the otoliths was assessed. Original prey sizes were estimated, by means of regression analyses of Clarke (1986, squid); Leopold et al. (2001, fish); Zwarts & Esselink (1989) and Leopold & van Damme (2003, worms) and Doornbos (1984, shrimp). Fish bones were measured and the original fish size was assessed via regression comparisons in Watt et al. (1997) and Couperus (unpubl., for mackerel). After that, the fish length was estimated. No correction was applied on items such as claws of shrimp, or jaws of worms (Doornbos 1984; Leopold & van Damme 2003). Finally, the prey weight was calculated via regression comparisons, from earlier mentioned publications and reference material.

## 2.2 Data analysis

Neonates, animals of unknown sex, animals with decomposed bodies, empty or missing stomachs, or stomachs containing only fish eyes that could not be identified to species, were excluded from further analyses. Of the original 172 harbour porpoises, the sample comprised of 155 porpoises after this deduction. The relative importance of individual prey taxa was assessed in terms of percentage by number, weight and kJ, expressed in %N, %W and %kJ, respectively. Temporal variation in diet preferences and nutritional state was investigated at seasonal scales, defined as “spring” (February until the end of June) and “autumn” (August to end of December).

Age classes used were “adults” and “immatures” (both calves and juveniles, in this study immatures and juveniles are used synonymously). At the time of writing this report, data on exact age and reproductive status per animal were not available. Therefore body length was used as an approximation for age and maturity. When over 130 cm long, the animals were considered adult (Haelters & Camphuysen 2009). Adult females formed one demographic group, and were compared to the other demographic groups, especially to adult males.

Each individual porpoise diet sample was examined and each was categorized as resembling either “offshore” or “inshore” types of diet. A diet was considered “offshore” if it contained >55% of offshore prey species in weight intake, and “inshore” if it had >45%W of inshore prey. Only one “inshore” prey eater had a mixed diet of 48% inshore fish and 52% offshore. The lowest value of the other “inshore” eaters was 80%W inshore prey, and most were close to 100%W inshore prey. Only two “offshore” types had mixed diets, both of circa 55%W offshore and 45%W inshore fish. Most of the other “offshore” type eaters consumed 80–90%W offshore prey.

Taxa considered “offshore” (migrating) were: whiting (*Merlangius merlangus*), Atlantic cod (*Gadus morhua*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), bib (*Trisopterus luscus*), poor cod (*T. minutus*), horse mackerel (*Trachurus trachurus*), mackerel (*Scomber scombrus*) and twait shad (*Alosa fallax*, anadromous). “Inshore” taxa were: gobies (*Gobiidae*), all North Sea squid species (*Loligo*, *Sepiolo* and *Rossia* spp.), sandeel (*Ammodytidae* spp.), all flatfish species (*Pleuronectiformes*), smelt (*Osmerus eperlanus*), European seabass (*Dicentrarchus labrax*, immatures), European perch (*Perca fluviatilis*), golden grey mullet (*Liza aurata*), eelpout (*Zoarcidae*), common dragonet (*Callionymus lyra*), silverside (*Menidia menidia*), hooknose (*Agonus cataphractus*), shrimp (*Crangon crangon*), mussels (*Mytilus edulis*), crabs (*Ebalia*, *Carcinus*, *Liocarcinus* spp.), pipefish (*Syngnathus rostellatus*) and worms (*Nereis virens*) (Arnold 1979, ICES fishmaps).

Literature was used to estimate prey energy density per species, and if possible per month, based on kilojoules (kJ) per gram dry weight, as assessed by bomb calorimetry. Table 1 shows the references per species. The kJ per gram was then multiplied by the estimated weight of the prey. However, calorific variation over the year is generally poorly known. Much of the differences in caloric intake is mainly attributable to differences in estimated prey mass, and to a lesser extent in seasonal fluctuations in energy density. Important exceptions to this are herring, whiting and Atlantic cod; of these species more is known.

Demographic features of the “offshore” and “inshore” diet groups were analysed for significant differences. To test whether the data on distributions of the diets were homogeneous among the groups, contingency table analyses on the simple frequencies of numbers was performed, via the chi-square test with Yates' continuity correction and Wilks' G<sup>2</sup> test of independence between the rows and the columns. Z-tests and two sample t-tests were used to compare the mean consumption of a specific prey species and prey group, (measured in %W and %N), per harbour porpoise group, and to note any variances, Fisher's F-tests were rendered. The Bonferroni correction for multiple testing was considered, but was decided against due to its conservative effect which could generate

too many false negatives. If p-values were less than 0.05, differences were considered to be statistically significant.

The nutritional quality of both prey groups, offshore and inshore (measured in average kJ and weight) was compared by z-tests and two sample t-tests, in general and per season. The same comparison was made per species per season; sandeels, goby spp., squid spp., herring, sprat, whiting, cod, horse mackerel, mackerel, poor cod and bib (these last two taxa were combined). Average prey weight intake and kJ intake (per porpoise as well as per prey per porpoise) differences between gender and age classes were analysed by z-tests and two sample t-tests. This was repeated on seasonal fluctuations.

Table 1. References on nutritional value per prey species. \*Paiva conversion means that a conversion of energy density of dry weight to energy density of wet weight was made according to energy density values of Paiva et al., 2006.

Species	Reference
Whiting, herring	Pedersen & Hislop 2001
Bib, poor cod	Pedersen & Hislop 2001 value for Norway pout
Cod	Average of Härkönen & Heide-Jørgensen 1991 and Steimle & Terranova, 1985
Sprat, months 2, 3, 12	Hilton et al 2000
Sprat, months 4, 7, 8, 9	Wanless et al 2005 based on Hislop et al 1991
Sand eel	Wanless et al 2005
Greater sand eel	Average sand eel, after Pedersen & Hislop 2001
Horse mackerel	Hammond & Fedak 1994, based on Murray & Burt 1977
Squid spp.	Hammond & Fedak 1994
Mackerel, <i>Loligo spp</i>	Worthy, 2001
Goby spp.	Average of Andersen 1999 and Temming & Herrmann 2000
Smelt	Temming & Herrmann 2003
Twait shad	Rand et al. 1994, value taken for <i>A. pseudoharengus</i>
Plaice	Prime & Hammond 1988
Other flatfish	Prime & Hammond 1987
Seabass, silverside	Paiva et al 2006
Dragonet, hookfish,	Murray & Burt 1977; value for Gurnard
Eelpout	Härkönen & Heide-Jørgensen 1991
Perch	Schrenckenbach et al. 2001
Shrimp spp.	Average of Massias & Becker 1990 and Andersen 1999
Crab spp.	Bomb calorimetry N. Daan, unpubl with Paiva conversion*
Mussel spp.	Bert Brinkman in litt.
Pipefish	M.P. Harris, in litt.
Sandworm	Cummins & Wuycheck 1971

Seasonal variation in feeding ecology, measured in number of porpoises using “offshore” or “inshore” diets, was analysed via the chi-square test with Yates' continuity correction and Wilks' G<sup>2</sup> test.

In addition, the general body condition (in classes 1–4) per specimen was taken into account. The nonparametric Mann-Whitney U-test was performed to compare differences among groups when variances were not homogenous, and to investigate if there is a relationship between the average body condition and (i) the seasons, (ii) the demographic groups and (iii) the diets. For the four groups per season, chi-square tests and Wilks' G<sup>2</sup> test were performed. Evidence is building that fishorders differ widely in lipid content, calorific value per gram and perhaps in their influence on porpoise physiology and health (see Introduction). %W, %kJ, and %N of animals with body condition 4 (highest) were compared in t-tests and z-tests to those of animals with body condition 1 (lowest). This was repeated in comparisons between body conditions 3 and 4 to those of 1 and 2.

The statistical analyses were carried out using the computer program XLSTAT 2010 (Addinsoft).

### 3. Results

#### 3.1 General results

The sample contained 155 porpoises; 19 male adults, 24 female adults, 61 male immatures (juveniles and calves) and 51 female immatures. The demographical distribution is presented in figure 1. The body conditions of the dissected porpoises ranged from score 4: no emaciation, to 1: severely emaciated. The majority of the animals were in poor body condition when they died, with scores 1 and 2 (figure 2). 8 Porpoises had an unknown condition.

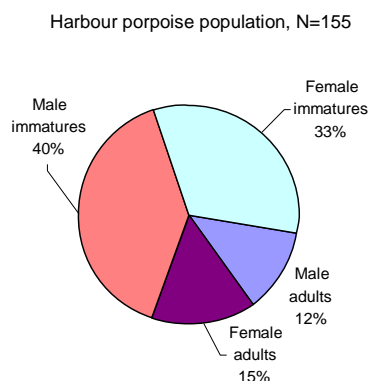


Figure 1. The demographic groups.

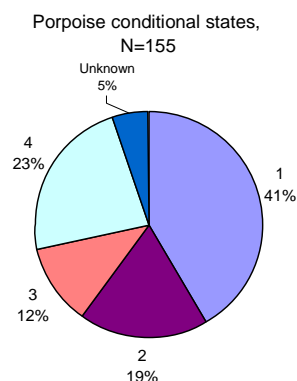


Figure 2. General body conditions.

70 Animals were found in “autumn” (August-December), and 73 were found in “spring” (February-June). 12 Were found in the periods in between; January and July.

A total of 19,330 prey individuals were found. 63 Porpoises consumed mainly “offshore” fish and 92 consumed mainly “inshore” fish. Adults tended to have offshore diets, immatures had more inshore diets. In spring, many seemed to forage “inshore” type prey, in autumn, the distribution is almost equal.

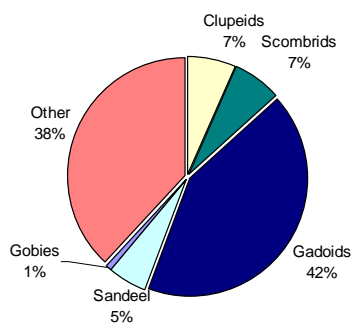


Figure 3. Total biomass per fish group.

Figure 3 shows the ingested biomass measured in fish order groups. Clupeids account for 5.2 kg in total biomass, with a mean of 20.7 g per item. Scombrids are the largest prey, with also 5.2 kg in total biomass, but a mean of 159 g per item. There were only 33 scombrids taken by mostly adult females. Gadoids were 32.8 kg in total, 77.5 g per item. Sandeel 4 kg in total, 4.7 g per item. Gobies 686 g in

total, 0.6 g

#### 3.2 Diets per sex and age group

##### 3.2.1 Diet composition

Adult females ate significantly more scombrids compared to adult males (in %W,  $p=0.028$ ; in %kJ  $p=0.029$  mean of two tailed z-test and t-test, but %N  $p>0.05$ ). When adult females were compared

to the other porpoises it revealed a diet of relatively more scombrids (both %W and %kJ:  $p=0.030$ , but %N is nonsignificant with  $p>0.05$ ) and few gobies (%W  $p=0.009$ , %kJ  $p=0.004$ , %N  $p=0.009$ ) and squid (%W  $p=0.005$ , %kJ  $p=0.002$ , %N  $p=0.045$ ) for the mature females. Figure 4 shows the differences per fish order between adult male and adult female diets.

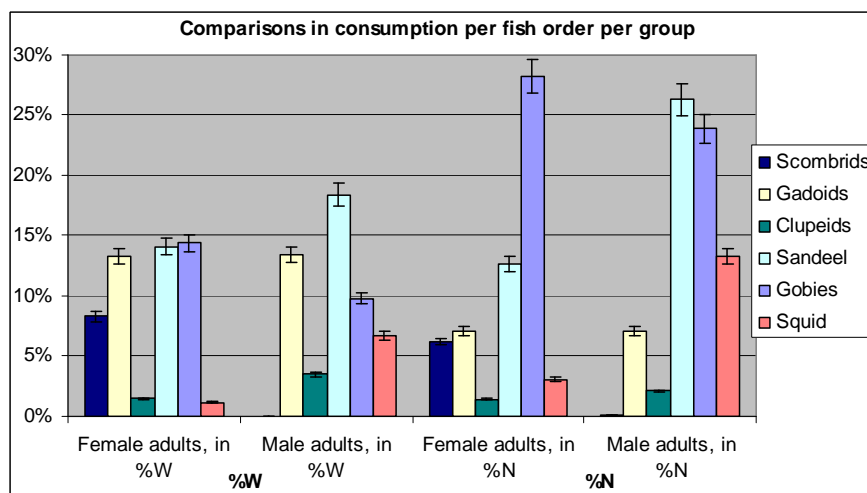


Figure 4. Consumption per fish order of adult females and adult males, measured in %W and %N. Intake of scombrids, %W  $p=0.028$ . %N plus the intake of the other orders:  $p>0.05$

There were also significant differences between the age groups. Adults took in more scombrids than immatures (%W  $p=0.035$ ; %kJ  $p=0.037$  both the mean of t-test and z-test, but %N  $p>0.05$ ). Also they took more gadoids (%W and %kJ both  $p=0.036$ , %N  $p>0.05$ ), and sandeel (in %N  $p=0.017$ ; z-test  $p=0.020$ ; t-test), but not significantly more in %W and %kJ. Matures took less gobies than juveniles ( $p<0.0001$ , z-test and t-test, on %W, %kJ and %N).

Adult females took relatively large and therefore energy rich prey. Their prey was significantly larger compared to the three other demographic groups measured together as one group (weight  $p=0.037$ , kJ  $p=0.036$ , mean of both t-test and z-test) and compared to the juvenile female group (weight  $p=0.028$ , kJ  $p=0.027$  mean of both tests). Adult males tended to take smaller prey compared to adult females, but these differences were not significant. Adults took heavier ( $p=0.007$  mean of z-test and t-test), and therefore energy richer prey (kJ  $p=0.004$  z-test;  $p=0.007$  t-test) prey than juveniles. There were no significant fluctuations between the demographic groups in mean kJ consumption per harbour porpoise, nor by mean prey weight intake per porpoise, in other words immatures make up for the lesser weight and energy intake per item by eating relatively more but smaller prey. The differences are shown in figures 15 and 16.

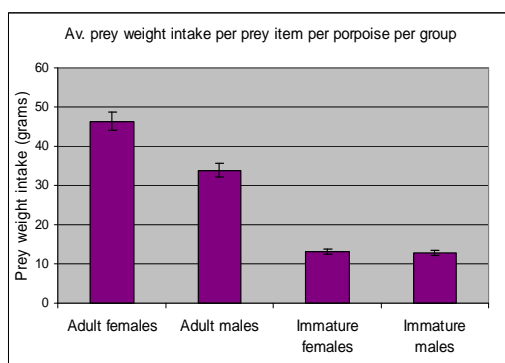


Figure 15. Mean prey weight intake per group.

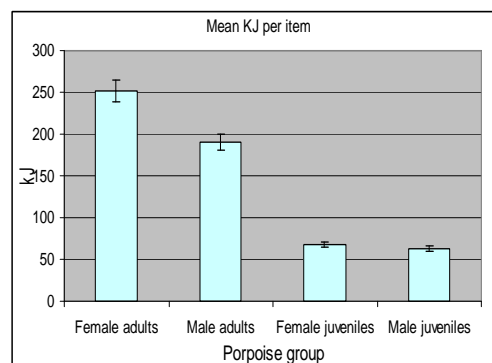


Figure 16. Mean kJ intake per item per group.

### 3.2.2 “Offshore” or “inshore” diet

“Offshore” fish eating porpoises take up a significantly larger proportion of the total adult sample population of porpoises, and a lower proportion of the total juvenile sample population. For “inshore” fish eaters the opposite was found: they take up a significantly lower proportion of the total adult sample population, and higher proportion of the juveniles (Fishers exact test;  $p=0.002$ , Chi-square with Yates' continuity correction,  $p=0.003$ ). Between the genders there were no significant differences.

To assess the four demographic groups in one take, both the chi-square test for homogeneity was used, as well as the Wilks'  $G^2$  test of independence between the rows and the columns. Both tests revealed a significant difference: adult females are significantly overrepresented in the “offshore” fish eating group and underrepresented in the “inshore” fish eating group ( $p=0.029$ ). The adult male group had no significant differences compared to the three other demographic groups. The results are shown in the figures 5 and 6.

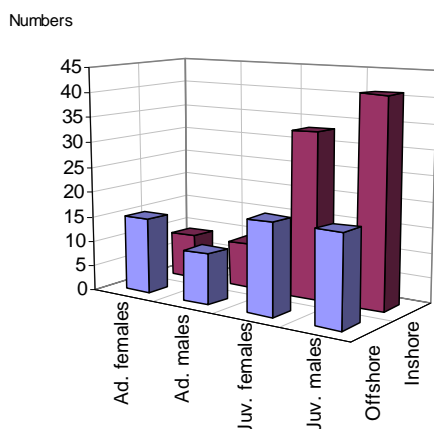


Figure 5. 3 D view of the contingency table in diets per group ( $p=0.029$ ).

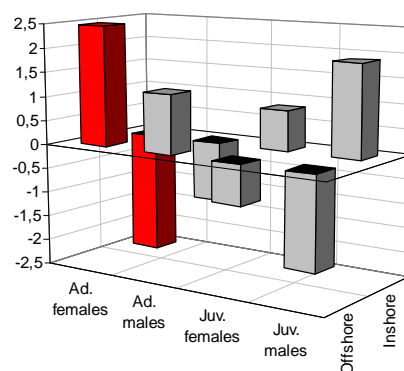


Figure 6. The adjusted residuals.

### 3.3 Nutritional value of diet and season

As was expected, “offshore” fish were significantly richer in average kJ and weight per prey than “inshore” fish (both  $p<0.0001$ , two sample t-test and z-test). This was confirmed by the significantly higher average weight and energy content values for “offshore” prey in “autumn,” compared to “spring” (both  $p<0.0001$ ). In contrast, “inshore” prey had no significantly higher mean kJ value and weight in “autumn” compared to “spring” ( $p>0.05$ ). “Offshore” fish eaters again had significantly higher scores on average biomass and kJ taken per prey item per porpoise compared to “inshore” fish eaters (both  $p<0.0001$ , both the t-test as z-test). Total kJ per individual stomach content was also significantly higher for “offshore” foragers (z-test;  $p=0.020$ , t-test;  $p=0.023$ ). No significant differences were found in total biomass taken in per porpoise.

In “autumn,” all differences in energy intake were significant, both expressed in biomass and in kJ per prey ( $p<0.0001$ , both tests), total biomass intake per porpoise ( $p=0.014$ , mean of both tests) and total kJ intake per porpoise ( $p=0.0025$ , mean of both tests). In the “spring” data, none of these differences were significant. KJ and weight values per prey item per diet per season are shown in figures 7 and 8.

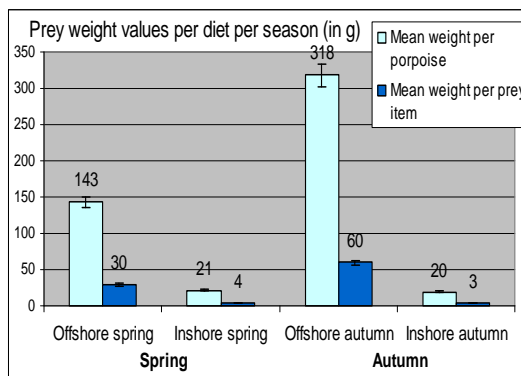


Figure 7. Average weight value per prey item per diet per season. Autumn:  $p < 0.0001$ , Spring:  $p > 0.05$ .

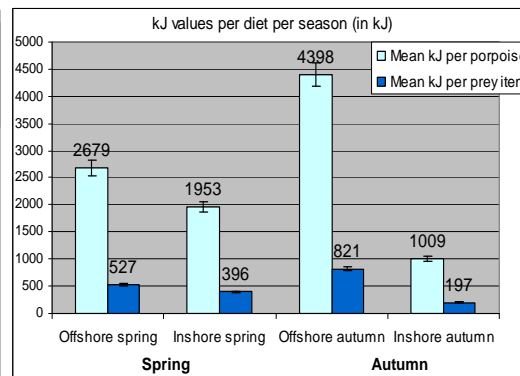


Figure 8. Average kJ value per prey item per diet per season. Autumn:  $p < 0.0001$ , Spring:  $p > 0.05$ .

The specifics for the individual prey taxa were also considered. All “offshore” species that were taken into account – whiting (%kJ and %W  $p=0.001$ ), cod (%kJ and %W  $p=0.004$ ), bib/poor cod (%kJ and %W  $p=0.0001$ ), herring (%kJ  $p=0.004$ ; %W  $p=0.018$ ), sprat (both measurements  $p=0.002$ ) and horse mackerel (both measurements  $p<0.0001$ ) – were significantly heavier and containing more calories in autumn than in spring, see figures 9 and 10. Like “offshore” fish, sandeel was significantly richer in both weight as kJ in autumn than in spring ( $p<0.0001$ , both measurements). Squid had no significant shifts in kJ and weight between the seasons. Interestingly, gobies were in *spring* significantly heavier and richer in calories than in autumn ( $p<0.0001$ , both measurements). Figures 11 and 12 show the average weight and kJ values for the inshore prey taxa.

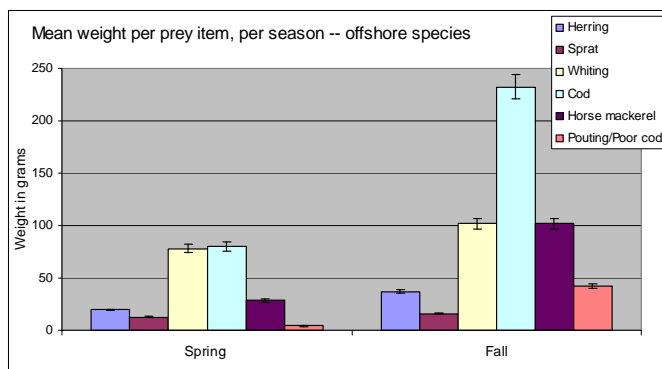


Figure 9. Average weight value per prey item specified per diet per season. Herring  $p = 0.004$ , sprat  $p = 0.002$  whiting  $p = 0.001$ , cod  $p = 0.004$ , horse mackerel  $p < 0.0001$ , bib/poor cod  $p = 0.0001$ .

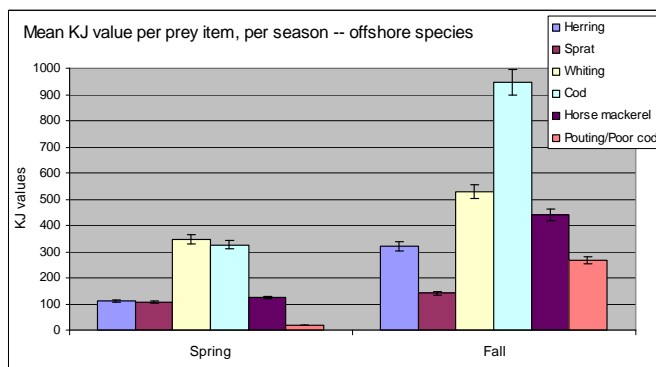


Figure 10. Average kJ value per prey item specified per diet per season. Herring  $p = 0.018$ , sprat  $p = 0.002$  whiting  $p = 0.001$ , cod  $p = 0.004$ , horse mackerel  $p < 0.0001$ , bib/poor cod  $p = 0.0001$



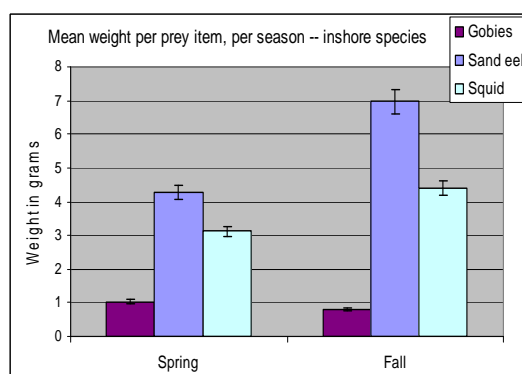


Figure 11. Average weight value per prey item specified per diet per season. Gobies  $p < 0.0001$ , sandeel  $p < 0.0001$ , squid  $p > 0.05$ .

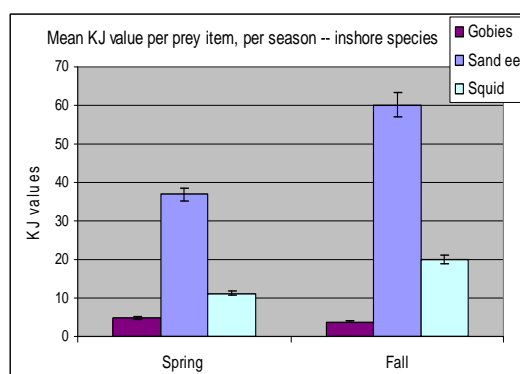


Figure 12. Average kJ value per prey item specified per diet per season. Gobies  $p < 0.0001$ , sandeel  $p < 0.0001$ , squid  $p > 0.05$ .

### 3.4 Seasonal variation in diet with regard to behaviour

To analyse if the animals use the higher caloric value and biomass of “offshore” fish in “autumn,” a Fisher’s exact test was applied. Indeed did harbour porpoises use significantly more “offshore” fish and less “inshore” fish in “autumn” ( $p = 0.037$ ). Conversely, the porpoises took more “inshore” and less “offshore” fish in “spring” (figures 13 and 14).

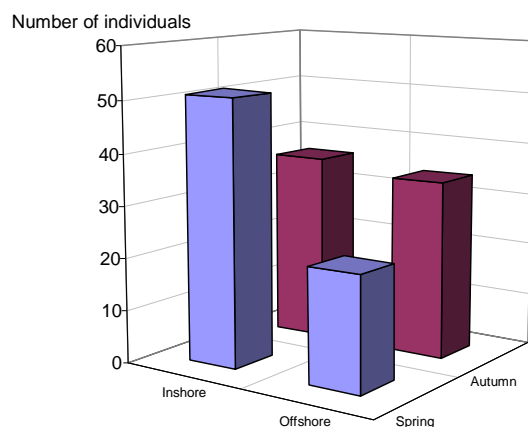


Figure 13. 3D view of the contingency table on seasonal variation in diet ( $p = 0.037$ ).

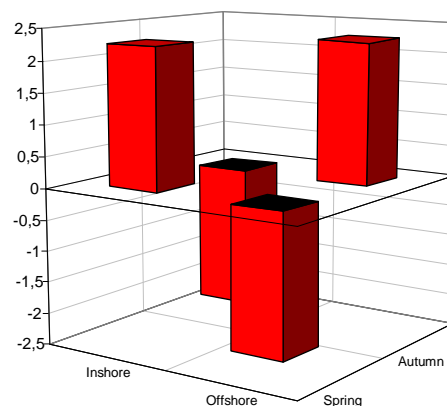


Figure 14. The adjusted residuals.

Tests per specific prey revealed that in “autumn,” porpoises consumed significantly more scombrids than in “spring” (%W  $p = 0.033$ , %N  $p = 0.047$  mean z-test and t-test), however measured in %kJ, the difference was not significant.

### 3.6 Body condition index

The Mann-Whitney U test was used to assess possible relationships between demographic group and their diet and general body condition (set in classes 1–4). “Offshore” fish eaters had a significantly higher body condition than “inshore” fish eaters ( $p = 0.004$ ). Adults had a significantly higher condition than juveniles ( $p = 0.015$ ). For males and females there were no significant differences in general condition.

When all demographic groups were assessed for differences in body condition at once, the chi-square test for homogeneity was used, as well as the Wilks’  $G^2$  test, and both gave significant conclusions ( $p = 0.016$  chi-square;  $p = 0.017$  Wilks’  $G^2$  test). Highest condition 4 stands out, as it is

clearly positively associated with an offshore diet and negatively with a inshore diet. The outcomes can be seen in the figures 15 and 16.

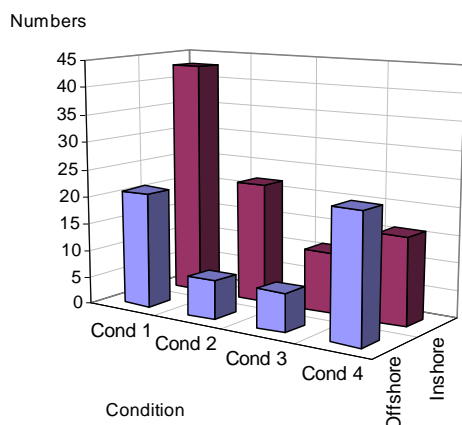


Figure 15. 3 View of the contingency table per condition per season.  $P=0.016$ .

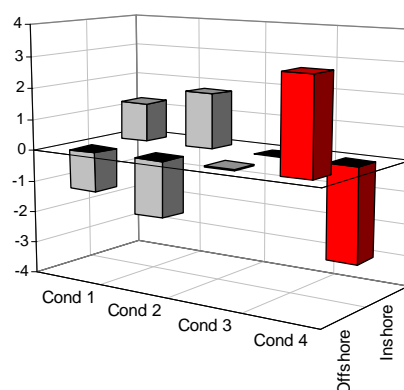


Figure 16. The adjusted residuals show that condition 4 is overrepresented in the offshore diet and underrepresented in the inshore diet.

A further breakdown of the data was performed to analyze the seasonal variances. Again, “offshore” diets are positively associated with higher conditions, particularly in “spring,” and negatively with lower conditions, especially in “autumn” ( $p=0.001$ ). For “inshore” diets, the inverse pattern could be observed. The graphics are shown in Appendix I.

Also in general, without looking at diets, the animals found in “spring” were in better condition ( $p=0.003$ , Mann-Whitney). This was supported by a contingency table, per body condition per season ( $p=0.018$ ). The graphics are shown in Appendix I.

Evidence was found for a positive association between clupeid consumption and good body condition. Animals with a higher condition index ate significantly more clupeids (sprat, herring and twait shad combined). First, the extremes were assessed (conditional state 1 and 4) on their diet, and later the higher and lower classes combined (conditional classes 1 and 2 with those of classes 3 and 4). In both comparisons, individuals with a better overall condition took significantly more clupeids. In the tests of the extremes; class 1 versus 4, the results were:  $p=0.005$  %W;  $p=0.003$  %kJ; and  $p=0.007$  %N, all mean of the z-test and t-test. In the tests of classes 1 and 2 versus classes 3 and 4, the results were:  $p=0.007$  %W;  $p=0.005$  %kJ; and  $p=0.004$  %N. Note however, that the mean percentages of clupeid consumption remain low, also at the highest value which was for condition 4 (no emaciation); 6.9%W.

Animals in good condition had more scombrids and less squid, gobies and sandeel (in both ways of testing, in all measurements) in their diet, but this was not significant.

## 4. Discussion

### 4.1 Summary of results

Adult females took significantly more scombrids and fewer squid and gobies than the other groups, and were in general more associated with an offshore diet. However, on body condition no significant differences between adults females and the other groups were found.

In table 2 the most important significant group comparisons are shown. All intake is measured in percentage of the total weight consumed (%W). “>” Means significantly more than the other group compared; “<” means significantly less than the other group.

Table 2. Summary of the most important significant differences found.

Feature/group	Feature/condition	P-value
<b>Adult females (vs. Adult males)</b>	>Scombrid intake	0.028
<b>Adult females (vs. Rest)</b>	>“Offshore” diet	0.029
	>Scombrid intake	0.030
	>Mean prey weight	0.037
	<Goby intake	0.009
	<Squid intake	0.005
<b>Adults (vs. Juveniles)</b>	>“Offshore” diet	0.003
	>Scombrid intake	0.035
	>Gadoid intake	0.036
	>Mean prey weight	0.007
	<Goby intake	<0.0001
<b>“Offshore” diet (vs. “Inshore”)</b>	>Body condition 4	0.016
<b>Conditional state 4 (vs. 1)</b>	>Clupeid intake	0.005
<b>Conditional state 3 &amp; 4 (vs. 1 &amp; 2)</b>	>Clupeid intake	0.007

As one can see, individuals in good condition consumed more clupeids than the more emaciated animals. However, the percentage remains relatively low (6.9%W for condition 4; not emaciated, versus 1.5% for condition 1, severely emaciated).

Species such as whiting, cod, bib/poor cod, herring, sprat and horse mackerel contained significantly more kJ and biomass in autumn than in spring. Clupeids ranged from 4.6 (spring) to 11.9 kJ g<sup>-1</sup> (autumn), and gadoids ranged from 3.8 to 5.4 kJ g<sup>-1</sup> (see subchapter 2.2). Correspondingly, in autumn, the mean kJ and prey weight consumption per porpoise was higher than in spring. There is no information on energy density of squids or gobies over the year, but given that gobies were larger in spring than in autumn, they may also have yielded more kJ per fish in spring.

This difference is used; in spring, harbour porpoises took more prey items, indicating a lifestyle of feeding on small prey, like gobies and sandeel. In autumn, it is more equally distributed, due to the large proportion of juveniles in the sample. Most of them continue to consume coastal prey, while adults have a more offshore lifestyle, feeding on larger prey that become more energy dense in that period.

## ***4.2 Discussion of the results***

Adult females eating more scombrids and generally more offshore prey is an interesting result, and this could indicate changes associated with reproductive behaviour.

In a study on stomach content, Smith & Gaskin (1983) found a larger average prey seize for six lactating females compared to seven other mature females and three mature males in Canada.

There were no significant differences body condition index between adult males and adult females. This could be due to the small sample of these groups: porpoises stranding in the Netherlands are mostly immatures.

An age-related change from a largely inshore diet to a more offshore diet (Germany; Lick 1991, Benke & Siebert 1996, Sweden; Börjesson & Berggren 1996 in Santos et al. 2004) was confirmed by our study. The diet change mostly indicated a shift from gobies to scombrids. Whiting and clupeids were eaten more by adults, but this was not significant. Mature animals tend to take larger prey. This is reflected in a higher mean body condition. These findings, combined with the fact that immatures dominated this stranding sample as well as other studies (Fontaine et al. 2007, Santos et al. 2004, Das et al. 2003), suggest that the juvenile stage is very difficult for porpoises, with low survival chance, perhaps more so than in other marine mammals in the North Sea.

Offshore fish (sprat, herring, whiting, cod, horse mackerel, mackerel, bib, poor cod, and twait shad) have overall higher weight and kJ values per individual compared to inshore fish (gobies, sandeels, flatfish species, smelt, seabass, perch, golden grey mullet, eelpout, common dragonet, silverside, hooknose, shrimp, mussels, crabs, pipefish, worms, and the North Sea squid species) and the difference becomes larger in autumn. Clupeidae are highly calorific prey with a range from 4.6 to 11.9 kJ g<sup>-1</sup>, whereas calorific values for gadoids range from 3.8 to 5.4 kJ g<sup>-1</sup>. Scombridae are in between with 4.34 to 5.59 kJ g<sup>-1</sup> (see subchapter 2.2). Gadoids (mainly whiting) were the dominant group, contributing 42% of the porpoise diet in biomass. Clupeids compromised for only 7%, as did scombrids. The seasonal difference in calorific value is used; porpoises take more offshore fish in autumn, and in spring, they forage more on inshore species, especially sandeel and gobies. However it should be noted that the nutritional value of offshore prey may have been overestimated, since these fish generally are faster and require higher energetic investments of catching them, which might be lowering the total benefit of the catch.

The changing consumption of the respective prey species in the seasons follows partly their changing availability. Sandeel are more eaten in spring, when they become more abundant; at that time they come out of the sand, and are at their peak in numbers in the southern North Sea. Conversely, offshore prey like horse mackerel, mackerel and whiting are at their peak in quarter 3 and 4 (until October). The other offshore species important in this study; sprat, cod, gobies, bib and poor cod have a more homogenous distribution throughout the year (ICES, 2007).

Dudok van Heel (1962) found that weight loss occurred in ex situ porpoises when they were fed with young gadoids, and that the weight loss was halted when they ate the same amount of clupeids.

A small (and rough) exploration into this matter strengthened this hypothesis. Feeding regimes were compared to the degree of emaciation. Body condition was determined in classes of 1 to 4. The extremes were compared – class 4 good body condition versus class 1 severely emaciated – as well as the classes combined – class 3 and 4 versus class 1 and 2. In all comparisons, the animals in the better shape consumed more clupeids. Although this is a rough test, the results can indicate that clupeids, especially herring, indeed are physiologically important for harbour porpoises.

Observational evidence suggests that porpoises in the North Sea consume more clupeids when these fish become more abundant, the massive decline in North Sea herring stocks might have forced changes in food preference to lower-quality fish, and as the stock recovered in recent years, herring proportions in porpoise diet increased (Rae, 1965, 1973 in Santos & Pierce 2003, Bouquegneau et al. 2007, Saana 2006). Before the collapse, between 1959 and 1971, herring and sprat were the most frequent prey of harbour porpoises in Scotland (Rae 1965, 1973, in Santos & Pierce 2003). And after the recovery, herring and sprat were found to be the main food of harbour porpoises stranded and by-caught during 1988–93 in the Swedish Skagerrak and Kattegat Seas (Berggren 1996 in Santos & Pierce 2003). However, in Scottish porpoise diet, the increase in herring stock was not yet reflected. Sandeel and whiting still comprise 80% of the diet (Santos et al. 2004). Other studies as well showed various different species being dominant in porpoise diet; sandeel (UK; Martin 1996, Eastcoast UK; Santos et al. 2004), gadoids (Shetlands; Santos et al. 2004), cod, whiting, sandeel, gobies (Danish North Sea & Baltic Sea; Aarefjord et al. 1995) Gobies, herring and cod (Baltic Sea; Benke & Siebert 1996, all in Santos et al. 2005).

Scombrids as substantial part of porpoise diets are less often mentioned, most reports go back to the time before the collapse of the North Sea mackerel population in the early 1970s. The population was decimated as a consequence of extreme overexploitation in the 1960s and 1970s and has not recovered. To this day, scombrids and especially mackerel remain severely depleted in the North Sea and considered to be in need of maximum protection (Hardy 1959, Slijper 1962, Andersen 1965, Anon. 2002 in Santos & Pierce 2003, ICES 2007).

As stated above, the relatively high scombrid consumption by adult females compared to the other groups could be related to reproductive behaviour, but the nutritional benefits to porpoises of these relatively large fish are still unknown. It could indicate that pregnant or lactating females travel further in search of energy rich prey, like Smith & Gaskin (1983) found. Major dietary studies after the 1970s never found these fish being a primary resource of porpoises. However, they are still dominant in other marine mammal diets, such as bottlenose dolphins (*Tursiops truncatus*, Pauly et al. 1995, Spitz et al. 2006). Perhaps interspecies competition combined with depleted stocks is causing porpoises to feed on other resources.

Clupeids are becoming much more available. On the westside of the Atlantic, evidence of a porpoise tendency towards consuming herring seems more clear. Their consumption of herring closely followed herring abundance, declining as herring became scarcer and other prey, such as sandeels increased. After herring stocks increased almost sixfold between the 1980s and 1990s, their contribution in porpoises diet increased as well (Read 2001, Overholz & Link 2007). Herring consumption by harbour porpoises averaged slightly over 5000 tonnes during the years 1977–1981, increased to an average of 12,000 t in the early 1990s, and peaked at 22,000 t in 2002. This was mirrored in almost all marine mammals in the area, as well as predatory fish (Overholtz & Link 2007). Diets of harbour porpoises in the West Atlantic are now dominated by herring; which encompasses 80% of their calorific intake (Gannon et al. 1998 in Read 2001).

At Ramsey Sound, off Wales, increases in porpoise densities in winter coincided with concentrations of herring (Gannon et al. 1998 in Baradell 2009). Pierpoint (2008) observed harbour porpoise foraging behaviour in the area, which is a high energy spot with steep trenches, tidal currents and upwellings. At ebb tide, porpoises visited the area regularly to feed. Tidal currents and the steep walls of the trench are believed to concentrate prey which is funnelled towards the waiting porpoises. Harbour porpoise foraging in a tide race habitat is reported from more locations within their range (Bay of Fundy, Canada and the northern California Current System, Watts & Gaskin 1985, Tynan et al. 2004 in Soona 2006). Currents are known to concentrate aggregations of zooplankton and herring, and, to a lesser extend, other fish as well (Soona 2006, Baradell 2009). In addition, harbour porpoises surprisingly regularly frequented North Sea offshore gas installations, especially at night (Todd et al. 2009). Offshore installations can act as artificial reefs, accumulating plankton and therefore attracting many species of fish (Stanley & Wilson 1991, Keenan et al. 2003 in Todd et al. 2009).

However, as the herring stocks increase, so does the commercial fishery. And the significant rise of net entrapment of porpoises could indicate a link (Bouquegneau et al. 2007). In the Bay of Fundy, Canada, Tripper et al. (1999) observed lower harbour porpoise entanglement rates during years of low herring abundance.

The current state of the sprat stock is not well known with large natural fluctuations in annual stock biomass. Recruitment appears to be highly variable and can influence the abundance of the species rapidly due to the short life-span (Santos & Pierce 2003, ICES 2007). Wanless et al. (2005) found evidence for a decline in sandeel size, and possibly also sprat size, which could be due to changes in the plankton community.

Clupeids and scombrids could be more important to harbour porpoise populations than what is generally thought. Observed porpoise foraging behaviour, increase in their herring intake as stocks become more abundant (especially in the West Atlantic, but also in the North Sea, but not conclusively and not for Scotland, which could be due to local circumstances) and evidence on positive physiological effects of clupeids for porpoises indicate that these fish might be more important to harbour porpoises than what is generally concurred, and that porpoise health might be compromised in case this fish group should decline again in the future (Santos & Pierce 2003). Wanless et al. (2005) found evidence of a possible decline in sprat size, and sandeel size, which, because of the combined reduction in energy value, is something to look into. The same could be applied for scombrids of which less is known. These relatively large fish are still far from abundant in the North Sea and are hunted and eaten significantly more by adult female harbour porpoises. Pregnant or lactating females might travel further in search of energy rich prey. However, gadoids (mainly whiting) remain the dominant prey measured in biomass, as it is the case in other studies, perhaps as prey of secondary choice.

Herring numbers are increasing. But the persisting low numbers of Atlantic mackerel stock, combined with the uncertainty concerning sprat stocks due to their short life-spans, and downward trend in whiting abundance (ICES 2007) could pose a threat to harbour porpoise abundance in the North Sea. However, these statements must be made with caution, as data are not conclusive and many ecological aspects like harbour porpoise foraging behaviour and their physiological needs are still unknown.

## 5. Conclusions and recommendations

### 5.1 Conclusions

The main question was: *Are diets of adult males and females significantly different?*

They are: females consumed more scombrids.

All harbour porpoises consumed significantly more offshore prey in autumn, female adults slightly more than male adults. This difference was not significant.

There is a relationship between diets and nutritional state/body condition. Animals with a higher body condition consumed significantly more clupeids.

### 5.2 Recommendations

The harbour porpoise is one of the smallest cetaceans and its habitat and life history impose very high energy demands. Understanding its distribution in relation to its environment, especially its prey, is vital for the conservation of the species.

However, the effects of the various possible factors influencing porpoise diet (year, season, area, cause of death, age, sex and size) are to this day still difficult to disentangle. For example, some authors consider harbour porpoises to be opportunistic feeders (Haelters & Camphuysen 2009, Fontaine et al. 2007).

However, the idea that the importance of each type of prey in the diet is related to its availability has rarely, if ever, been tested (Santos et al. 2004). This study, and others (see Discussion), found evidence of positive correlations between scombrid and clupeid contributions to the diet on one hand, and age, growth, possible better health and possible experience of high energetic needs during pregnancy and lactation, on the other. Further research is needed to either confirm or reject these possible links.

Stomach studies of stranded or by caught individuals are a valuable tool to examine the diets, and continuation of these are necessary, to keep monitoring the diet, cause of death, and other ecological factors, as well as possible future threats for the North Sea population. If possible, the necropsies should be coordinated internationally for the countries around the North Sea. These studies should distinguish between diets of lactating and non-lactating females, as it seems that differences between diets of males and females are most likely to be seen when females are nursing calves (Santos et al. 2005). Changing energy needs of lactating females should be studied more, as sudden changes in North Sea fish stock do occur and could pose a future threat to harbour porpoise recruitment.

Stable isotope ratios in mammalian muscle tissue can retain dietary information on a time scale of a few months (Das et al. 2003, Jennings et al. 2002, Santos et al. 2005). Cadmium in kidney tissue can retain this for even longer time periods; in the order of years (Fontaine et al. 2007). On seals, analyses of fatty acid composition of the blubber have also generated insight in diet composition of individuals of over longer periods, and this is a possibility to use for harbour porpoises as well. However, this technique is relatively new and still has practical complications in its use (Iverson 1997 in Santos & Pierce 2003). One or more of these techniques could help on long term dietary information and could be considered for harbour porpoises and their potential prey, especially on herring contribution to their diet, and on diet in relation to porpoise health status (Bouquegneau et al. 2007). Jennings et al. (2002) emphasize that future attempts to estimate the mean trophic levels

of fishes from stable isotope ratios will need to be based on increased replication over larger sea areas. Estimation of trophic levels is complicated and sometimes intraspecific differences are larger than interspecific differences, due to changes in diet and habitat use as the fish grows. Often the fish climbs in trophic level as it grows (gadoid species), but in some species it is the opposite (herring) (Braber & De Groot 1973 in Jennings et al. 2002). However, these techniques are expensive compared to stomach analyses, but should be considered as a complementary source of information on diets (Santos et al. 2005).



## 6. References

- Andersen, N.G 1999. *The effects of predator size, temperature, and prey characteristics on gastric evacuation in whiting*, Journal of Fish Biology 54: 287–301.
- Arnold G.P 1979. *Squid. A review of their biology & fisheries*, Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, United Kingdom.
- Baradell, M.G. 2009. *Fine Scale Use of Ramsey Sound, Pembrokeshire, West Wales, by Harbour Porpoise (Phocoena phocoena)*, BSc Honours Dissertation, Pembrokeshire College, Wales, UK.
- Booij, J. 2004. *Improving the Dutch part of the North Sea as a cetacean habitat*, Trainee report, University of Leiden.
- Borjesson, P., P. Berggren & B. Ganning 2003. *Diet of harbour porpoises in the Kattegat and Skagerrak seas: Accounting for individual variation and sample size*. Marine Mammal Science 19: 38–58.
- Bouquegneau, J.M, K. Das, O. Drouguet, M. Fontaine, L. Holsbeek, T. Jauniaux, J. Michaux & C. Joiris, 2007. *Viability of the Northeast Atlantic harbour porpoise and seal population, genetic and ecological study*, Scientific Support Plan for a Sustainable development Policy, Belgian Science Policy, Brussels, Belgium.
- Das K., G. Lepoint, Y. Leroy, J.M. Bouquegneau, 2003. *Marine mammals from the southern North Sea: feeding ecology data from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measurements*, Marine Ecology Progress Series 263: 287–298, 2003.
- Debruyne M. & A.. Folmer 2007. *Dieetonderzoek bruinvissen (Phocoena phocoena). Een onderzoek op harde prooi-resten van bruinvissen gestrand aan de Nederlandse kust in 2006*. Bachelor thesis, Van Hall Larenstein/IMARES.
- Fontaine, M.C, K. Tolley, U. Siebert, S. Gobert, G. Lepoint, J. Bouquegneau & K. Das 2007. *Long-term feeding ecology and habitat use in harbour porpoises (Phocoena phocoena) from Scandinavian waters inferred from trace elements and stable isotopes*, BMC Ecology, 7:1, Biomed Central.
- Jennings, S., S. Greenstreet, L. Hill, G. Piet, J. Pinnegar & K. Warr 2002. *Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics*, Marine Biology (2002) 141: 1085–1097.
- Greenstreet, S.P.R., J. McMillan & F. Armstrong 1998. *Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance?*, ICES Journal of Marine Science, 55: 121–133.
- Haelters, J. & K.C.J. Camphuysen 2009. *The harbour porpoise in the southern North Sea. Abundance, threats and research- and management proposals*, International Fund for Animal Welfare, EU Office, Brussels, Belgium, and IFAW Dutch Office, The Hague, Netherlands.
- Hislop, J.R.G., M.P. Harris & J. G. M. Smith 1991. *Variation in the calorific value and total energy content of the lesser sandeel (Ammodytes marinus) and other fish preyed on by seabirds*, Journal of Zoology London 224:501-517.

Härkönen, T. & M. P. Heide-Jørgensen 1991. *The harbour seal (Phoca vitulina) as a predator in the Skagerrak*, Ophelia 34: 191–207.

ICES Fishmap Herring, 2007, ICES, Copenhagen, Denmark

ICES Fishmap Whiting, 2007, ICES, Copenhagen, Denmark

ICES Fishmap Cod, 2007, ICES, Copenhagen, Denmark

ICES Fishmap Sprat, 2007, ICES, Copenhagen, Denmark

ICES Fishmap Horse mackerel, 2007, ICES, Copenhagen, Denmark

ICES Fishmap Mackerel, 2007, ICES, Copenhagen, Denmark

ICES Fishmap Bib, 2007, ICES, Copenhagen, Denmark

ICES Advice, Book 6, 2009, ICES, Copenhagen, Denmark

Leopold M.F. & C.J. Camphuysen 2006. *Bruinvisstrandingen in Nederland in 2006:*

*Achtergronden, leeftijdsverdeling, sexratio, voedselkeuze en mogelijke oorzaak*, IMARES Rapport C083/06, NIOZ Report 2006 5.

MacLeod C., M. Begona Santos, R. Reid, B. Scott & G. Pierce, 2007. *Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises?* Biology Letters 2007: 185–188.

O'Brien, J., S. Berrow, D. McGrath & P. Evans 2009. *Cetaceans in Irish waters: A review of recent research*, Biology and Environment: Proceedings of the Royal Irish Academy, Vol. 109B, No. 2, 63–88.

Overholtz, W.J. & Link, J.S. 2007. *Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine–Georges Bank Atlantic herring (Clupea harengus) complex during the years 1977–2002*, ICES Journal of Marine Science, 64: 83–96.

Pierpoint, C. 2008. *Harbour porpoise (Phocoena phocoena) foraging strategy at a high energy, near-shore site in south-west Wales, UK*, Journal of the Marine Biological Association of the United Kingdom, Volume 88, Special Issue 06, pp 1167–1173.

Paiva, V.H., J.A. Ramos, T. Catry, P. Petro, R. Medeiros, J. Palma 2006. *Influence of environmental factors and energetic value of food on little tern (Sterna albifrons) chick growth and food delivery*, Bird Study, 53: 1–11.

Pedersen, J. & J. Hislop 2001. *Seasonal variations in the energy density of fishes in the North Sea*, Journal of Fish Biology 59: 380–389.

Read, A.J. 2001. *Trends in the maternal investment of harbour porpoises are uncoupled from the dynamics of their primary prey*, Proceedings of the Royal Society of London. Series B. Biological Sciences 268(1467): 573–577.

Saana, I. 2006. *Coastal habitat use of harbour porpoise (Phocoena phocoena) in Cardigan Bay Special Area of Conservation (Wales)*, Bachelor's thesis, University of Jyväskylä, Finland.

Santos M.B. & G.J. Pierce, 2003. *The diet of harbour porpoise (Phocoena phocoena) in the northeast Atlantic*, Oceanography and Marine Biology: an Annual Review 41: 355–390.

Santos M.B., G.J. Pierce & J.A. Learmonth 2004. *Variability in the diet of harbour porpoises (Phocoena phocoena) in Scottish waters 1992–2003*, Marine Mammal Science, 20: 1–27.

Santos M.B., G. Pierce, E. Ieno, M. Addink, C. Smeenk, C. Kinze & M. Sacau 2005. *Harbour porpoise (Phocoena phocoena) feeding ecology in the eastern North Sea*, ICES CM 2005/Theme session R:15 (Marine Mammals: Monitoring Techniques, Abundance Estimation, and Interactions with Fisheries), ICES, Copenhagen, Denmark.

Smith G.J.D. & Gaskin D.E. 1983. *An environmental index for habitat utilization by female harbour porpoises with calves near Deer Island, Bay of Fundy*. *Ophelia* 22: 1-13.

Spitz, J., Y. Rousseau & V. Ridoux 2006. *Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food?*, *Estuarine, Coastal and Shelf Science* 70: 259–270.

Steimle, F.W., & R.J. Terranova, 1985. *Energy equivalents of marine organisms from the continental shelf of the temperate Northwest Atlantic*, *Journal of Northwest Atlantic fishery science*, 6: 117–124.

Temming A. & Herrmann J.P 2003. *Gastric evacuation in cod. Prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models*, *Fisheries Research* 63: 21–41.

Todd, V.L.G., W. Pearse, N. Tregenza, P. Lepper, & I. Todd 2009. *Diel echolocation activity of harbour porpoises (Phocoena phocoena) around North Sea offshore gas installations*, *ICES Journal of Marine Science*, 66: 734–745.

Trippel, E.A., M.B. Strong, J.M. Terhune, & J.D. Conway 1999. *Mitigation of harbour porpoise (Phocoena phocoena) by-catch in the gillnet fishery in the lower Bay of Fundy*, *Canadian Journal of Fisheries and Aquatic Sciences* 56(1): 113-123.

Wanless, S., M. P. Harris, P. Redman & J. R. Speakman 2005. *Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea*, *Marine Ecology Progress Series*, 294: 1–8.

Woo, K.J., K. Hamish Elliott, M. Davidson, A. Gaston & G. Davoren 2008. *Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour*, *Journal of Animal Ecology*, unknown pages.

Worthy, G. A. J. 2001. *Nutrition and Energetics*. In: L. A. Dierauf & F. M. D. Gulland (Eds.). *CRC handbook of marine mammal medicine* 2nd ed. pp. 791–827. CRC Press, Boca Raton, Florida. 1063 pp.

## Appendix I – additional graphics

Graphics of associations between higher and lower body conditions and seasons.

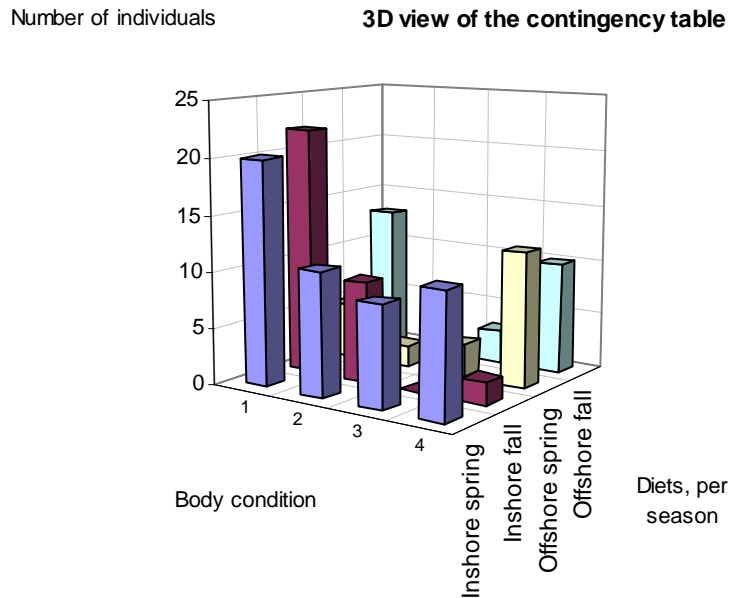


Figure 17. 3 View of the contingency table per condition per season per diet.  $P = 0.001$ .

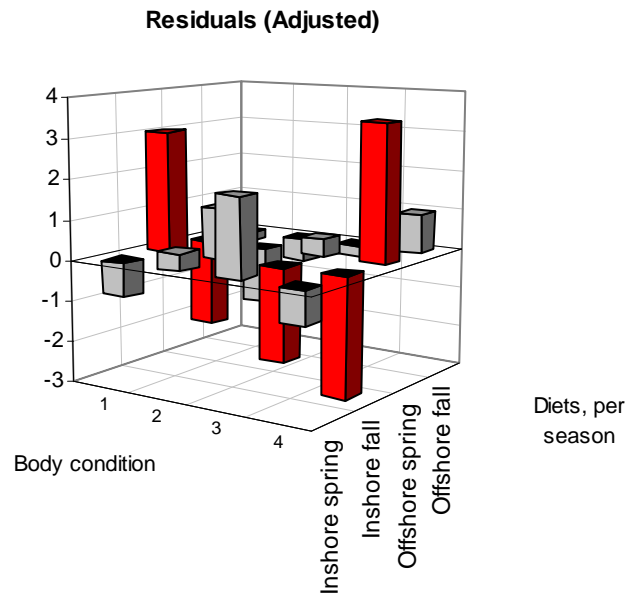


Figure 18. The adjusted residuals.

	<i>Inshore, spring</i>	<i>Inshore, autumn</i>	<i>Offshore, spring</i>	<i>Offshore, autumn</i>
Condition 1	-0,494	1,985	-1,493	-0,156
Condition 2	0,299	0,979	-1,122	-0,449
Condition 3	1,446	-1,901	0,381	-0,214
Condition 4	-0,562	-2,215	2,691	0,739

Residuals (Pearson) per cell.

	<i>Inshore, spring</i>	<i>Inshore, autumn</i>	<i>Offshore, spring</i>	<i>Offshore, autumn</i>
Condition 1	-0,832	<b>3,039</b>	<b>-2,174</b>	-0,237
Condition 2	0,422	1,254	-1,366	-0,569
Condition 3	1,934	<b>-2,312</b>	0,441	-0,258
Condition 4	-0,822	<b>-2,946</b>	<b>3,404</b>	0,974

Adjusted residuals per cell. The values displayed in bold are significant at the level  $\alpha=0.05$ .

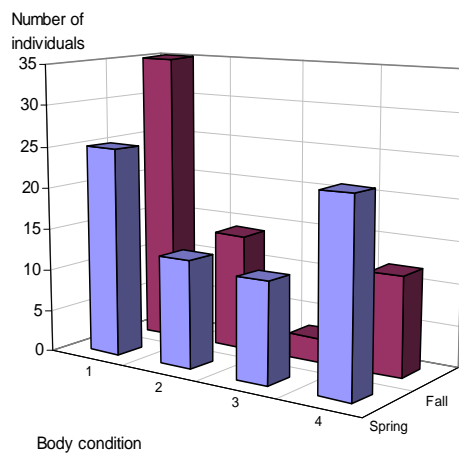


Figure 19. 3 D view of the contingency table, per condition per season.  $p = 0.018$ .

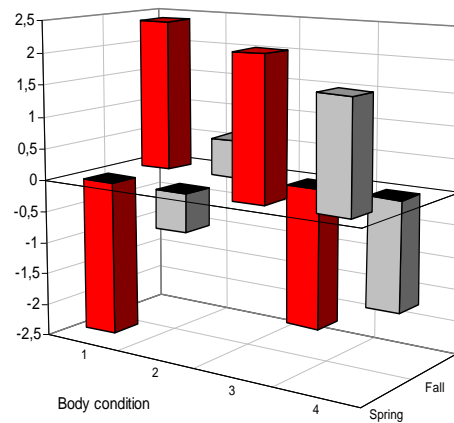


Figure 20. The adjusted residuals show that condition 1 is underrepresented in spring and overrepresented in autumn.

	<i>Spring</i>	<i>Autumn</i>		<i>Spring</i>	<i>Autumn</i>
Condition 1	-1,233	1,317	Condition 1	<b>-2,406</b>	<b>2,406</b>
Condition 2	-0,366	0,391	Condition 2	-0,597	0,597
Condition 3	1,417	-1,514	Condition 3	<b>2,198</b>	<b>-2,198</b>
Condition 4	1,007	-1,076	Condition 4	1,708	-1,708

Residuals (Pearson) per cell.

Adjusted residuals per cell. The values displayed in bold are significant at the level  $\alpha=0.05$ .

## **Appendix II – remarks on methods**

Energy density calculations could have been over- or underestimated. The lack of information on specific and/or comprehensive sampling times in the literature make it difficult to decipher which parameters most strongly affect energy density.

At the time of writing this work, data on which porpoises from the sample were stranded and which were by-caught were not yet available, and therefore this could not be taken into consideration and compared with dietary aspects.

This study did not distinguish between diets of lactating and non-lactating females. However, due to their ecology, differences between diets of males and females are most likely to be seen when females are nursing calves. Lactating or pregnant females at the time of stranding could generate more knowledge on the energy needs during this highly demanding time of their lives. There is evidence that dietary differences between lactating females and other groups are possibly vast (see 5.1). Furthermore, it was not determined whether an animal had actually reproduced or not. Body length was used as a proximate for age and maturity, animals of >130 cm were considered sexually mature (Haelters & Camphuysen 2009). If more was known, that could have yielded important information on reproduction and diet habits. Several authors (see 5.1 and Introduction) indicate that adult females that have reproduced might have different diets than juveniles or males due to their experience in which they have had high energy needs. This was not considered during this study, as all females were just accounted on their length and age.

Seasonal classification (spring; February until June and autumn; August until December) was chosen based on shifts in energy density of several prey taxa, to investigate if porpoises “use” that change in energy density, by foraging offshore during autumn, when almost all offshore species are richer than in spring. Like stated above, they appeared to do that. While this generated interesting results, an alternative classification could have been based on shifts in energy needs of the porpoises, with a cold season and warm season. Another major factor in the classification could have been the herring peak (October until March).

Stomach content analyses can generate a lot of information and are valuable research methods. However, they are but a snapshot of the last meal and perhaps a meal before that, with no possibility of repeated samples of the same animal. Furthermore, the most recent meal is not necessarily representative of the typical diet. Stomach content studies are therefore a potentially biased view of the diet, especially if the porpoise was weakened by disease or on the other hand, if the animal was by-caught, which could bring in a bias towards the target species of the fishery (Santos et al. 1994, Santos & Pierce 2003, Das et al. 2003). In this study, these diet groups were purely based on their last meals and we can therefore not be certain if the animal really had a preference towards an inshore or offshore foraging strategy or a specific fish order.

Finally, it is possible that some of the smaller food items such as gobies and small whiting have been introduced secondarily and do not reflect true prey (Borjesson et al. 2003).