



Are starving harbour porpoises (*Phocoena phocoena*) sentenced to eat junk food?

Mardik F. Leopold, Eileen Heße, Lonneke L. IJsseldijk, Lineke Begeman, Lara Mielke, Tara Schelling, Lizzy van der Steeg, Erik Meesters, Guido O. Keijl, Thierry Jauniaux, Sjoukje Hiemstra, Andrea Gröne & Jaap van der Meer



3



Abstract

The distribution of harbour porpoises *Phocoena phocoena* in the North Sea has shifted southwards in recent years. Apparently, many animals left areas previously rich in sandeels and moved to a region where much leaner gobies and gadoids are important prey. This shift in range, and presumably in diet, does not seem to have affected the body condition of all porpoises in the South. Body condition varies in stranded specimen found in The Netherlands, from very good to very poor. Emaciation is a common cause of death in this species, indicating that periods of decreased quantity or quality of prey can be detrimental to the species. The question thus arises whether emaciated harbour porpoises could not find sufficient food or whether their food was of insufficient quality. Stomachs of emaciated animals are not necessarily empty but, in fact, often contained food remains. In this study we examine these remains and compare the prey composition of well-nourished porpoises to that of progressively leaner specimens, collected between 2006 and 2014. We hypothesize that porpoises might starve by eating relatively too much prey with a low fat content that has a low energy density. Such food may be referred to as junk food: prey that is too lean for maintaining a good body condition. Results show that there is a significant difference in prey composition between animals in a good body condition and animals in a poor body condition, that starving animals have fewer prey remains in their stomachs, and that these prey, on average, are of lower quality. Healthy harbour porpoises take a mixture of fatty fish and leaner prey: the “big four” in dietary terms are clupeids and sandeels with a relatively high fat content, and gadoids and gobies, which are leaner prey. Our findings show that there is a negative correlation between the loss of body mass and the ingestion of fatty fish. This indicates that the emaciation is likely due to a lack of energy-rich prey, and that harbour porpoises need these prey in their diet to prevent starvation.

Keywords: diet, prey composition, prey quality, stomach content analysis, nutritional condition, body mass

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Introduction

With more than 200,000 individuals, harbour porpoises *Phocoena phocoena* are the most numerous cetaceans in the North Sea (Hammond *et al.* 2013), but local abundances have varied considerably over time. In the second half of the 20th century, porpoise densities were relatively low in the southern parts of the North Sea, but have recently shown a steep increase here (Camphuysen 2004; 2011; Witte *et al.* 1998; Thomsen *et al.* 2006; MacLeod *et al.* 2009; Haelters *et al.* 2011; Wenger & Koschinski 2012; Peschko *et al.* 2016), possibly at the expense of more western and north-western parts (Hammond *et al.*, 2013; Peltier *et al.* 2013). Apparently, many animals shifted from areas where they could feed on sandeels (MacLeod *et al.* 2007a,b) or herring (Evans & Scanlan 1989) to a region where much leaner gobies, gadoids and even flatfishes are important prey (Lick 1991;1993; Benke *et al.* 1998; Siebert *et al.* 2001; Santos *et al.* 2005; Leopold & Camphuysen 2006; Haelters *et al.* 2012).

Harbour porpoises have a relatively small body mass to body surface ratio, and as a result, a high rate of heat loss (Kanwisher & Sundnes 1965; Spitz *et al.* 2012). Therefore, porpoises need large amounts of food per day relative to their body mass to sustain themselves, which leaves them quite intolerable to starvation (Kanwisher & Sundnes 1965; Yasui & Gaskin 1986; Kastelein *et al.* 1997a; Koopman *et al.* 2002; Bjørge 2003; Lockyer 2003). Harbour porpoises should thus eat prey with a high energy density (Spitz *et al.* 2012; 2014). Indeed, diet studies have shown that harbour porpoises worldwide tend to have fatty schooling roundfish species as an important component of their diets. However, mixtures of several dozens of different prey species are generally found in single studies, suggesting that porpoises are generalist predators, taking a broad prey spectrum. Still, in each part of their range, one to four prey species tend to dominate the prey composition of the diet (expressed as percentage of total reconstructed prey mass) and at least one major prey species has a high energy content. Such key prey species include: herring *Clupea* spp., sprat *Sprattus sprattus*, pilchard *Sardina pilchardus*, Pacific sardine *Sardinops sagax*, anchovies *Engraulis* spp., capelin *Mallotus villosus*, pearlides *Maurolicus*

spp., scad *Trachurus trachurus*, mackerel *Scomber scombrus*, and sandeels Ammodytidae (Fink 1959; Sergeant & Fisher 1957; Neave & Wright 1968; Smith & Gaskin 1974; Recchia & Read 1989; Smith & Read 1992; Gaskin *et al.* 1993; Fontaine *et al.* 1994; Aarefjord *et al.* 1995; Raum-Suryan 1995; Sekiguchi 1995; Kenney *et al.* 1996; Read *et al.* 1996; Malinga *et al.* 1997; Gannon *et al.* 1998; Walker *et al.* 1998; Birkun 2002; Börjesson *et al.* 2003; Lockyer & Kinze 2003; Lockyer *et al.* 2003a; Vikingsson *et al.* 2003; Santos & Pierce 2003; Santos *et al.* 2004; Spitz *et al.* 2006; Haelters *et al.* 2012; Koponen 2013; Leopold *et al.* 2015a). Diet studies have shown that harbour porpoises do not restrict themselves to such energy-rich prey. Considerable proportions of their intake may consist of prey types that have rather low energy contents, such as gadoids, gobies, or squid.

Presumably, however, a diet with a high proportion of lean prey could be detrimental to porpoise health (MacLeod *et al.* 2007a,b; Spitz *et al.* 2012, 2014). Of porpoises that washed up dead in the southern North Sea, a considerable proportion of non-neonates were emaciated. The body condition in stranded animals was found to vary, from very good to very poor, indicating that at least some animals had thrived on the prey locally available (Jauniaux *et al.* 2002; 2008; Siebert *et al.* 2006; Deaville *et al.* 2010; Gröne *et al.* 2012; Haelters *et al.* 2012). The question thus arises whether emaciated animals had a different prey composition than animals in good condition, and if so, if the diet of emaciated animals specifically lacked fatty fish species. Stomachs of emaciated animals were not always empty. In this study we examine the stomach contents and compare the prey composition of emaciated porpoises to that of individuals in good condition. We hypothesise that porpoises might starve by eating relatively too much lean prey and too little energy-rich prey.

Lean prey has been described as junk food. The junk food hypothesis was formulated in the early 1990's for marine predators (Piatt & Anderson 1996), stating that when preferred prey is replaced by less nutritious prey, the consumer faces reduced fitness (Whitfield 2008), even when animals can feed *ad libitum* on such prey (Rosen & Trites 2000, Donnelly *et al.* 2003, Wanless *et al.* 2005, van Gils *et al.* 2006). Such a change in diet might result from an ecosystem shift that reduces the availability of preferred prey (Rosen & Trites 2000; Litzow *et al.* 2002; Jodice *et al.* 2006; MacLeod *et al.* 2007ab; Österblom *et al.* 2008), or the energy content of preferred prey (Wanless *et al.* 2005) or from easy access to low quality food, such as fishery waste (Pichegru *et al.* 2007). Slightly confusing, junk food for wild animals is exactly the opposite of human junk food. While human junk food is fatty fare, the opposite applies to animals in the wild - food without enough fat and energy to sustain them (Whitfield 2008).

Material and Methods

Assessing the nutritional status of the harbour porpoises

The nutritional state of stranded porpoises was assessed for each carcass during standard necropsies (Jauniaux *et al.* 2008, Begeman *et al.* 2013), using the Nutritional Condition Codes (NCC) as defined by Kuiken & García Hartmann (1991, see ES-1). Animals were assessed as NCC=1 (very good); 2 (good); 3 (slightly emaciated); 4 (bad), 5 (very bad) and 6 (extremely bad). NCC was only assessed in porpoises that were reasonably fresh, i.e. that had Decomposition Codes (DCC) 1-3 (ES-1). A total of 510 intact carcasses of DCC1-3 were measured and weighed and their NCC was scored. These carcasses ranged from a length of 77 cm, the smallest porpoise which had hard prey remains in its stomach, to 168.5 cm long, and from 6.0-62.0 kg (Table 1). Note that sample sizes presented in the following tables may differ slightly due to unknown variables (1 with gender unknown, 5 without stranding date, 4 without stranding location).

Table 1. Number, length (L, in cm, measured from the tip of the snout to the notch in the tail fluke) and body mass (kg) of examined harbour porpoises, per NCC-class.

NCC	n	avg L	min(L)	max(L)	SD(L)	avg Mass	min(Mass)	max(Mass)	SD(Mass)
1	65	112.8	78.0	161.5	19.4	26.2	6.8	57.5	11.6
2	82	120.7	78.0	162.0	22.0	29.6	6.0	62.0	13.3
3	97	116.5	77.0	161.0	22.1	24.8	6.3	57.5	12.2
4	109	119.0	78.0	166.0	22.2	23.3	7.9	57.5	11.8
5	110	121.4	77.0	168.5	22.7	23.4	6.9	51.0	12.0
6	47	112.9	79.5	157.5	18.9	18.5	7.3	43.0	8.3

Next to NCC, which is an assessment rather than a true measurement, blubber thickness (mm) was measured at three standard locations along the left side of the body: dorsally, laterally and ventrally, just anterior of the dorsal fin. The average of these three values was compared to NCC, to evaluate the merits of the latter. We have shown earlier (Leopold *et al.* 2015b) that NCC can be used as a continuous variable. We assumed a non-linear relationship (general model: $M=a(L)^b$) to the data for each NCC class, where L is porpoise length in cm, and M is porpoise body mass in kg. This was transformed to: $Y=\ln(a) + bX$, where $X=\ln(L)$ and $Y=\ln(M)$.

We fitted four models to the data for the different NCC classes $i=0,\dots,6$:

Model 1: $Y = \ln(a_i) + b_iX$

Model 2: $Y = \ln(a_i) + bX$

Model 3: $Y = \ln(a_i) + 3X$

Model 4: $Y = \ln(a) + bX$

These models are nested and may be represented as a nest plot (Figure 1):

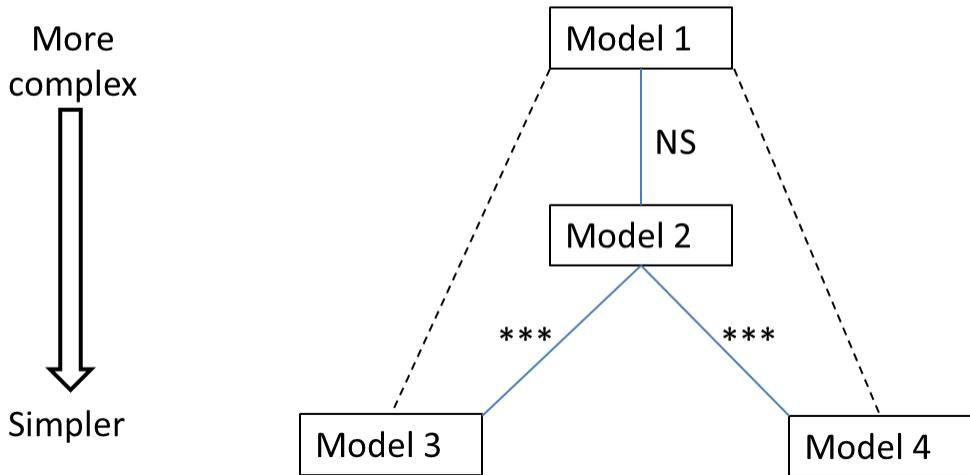


Figure 1. Nest plot of the four models tested to the Length-Mass per NCC data.

Model 1 did not perform significantly better than Model 2 (F-test, $P > 0.05$). Neither Model 3 nor model 4 differed significantly from Model 2 (F-test, $P < 0.001$ for both comparisons). Model 2 was therefore chosen as the best model to fit the data.

Stomach content analysis and assigning energy density of prey guilds

Prey remains, first and foremost fish sagittal otoliths, were used to identify fish species and to estimate fish length and weight. In addition to the otoliths, fish bones, eye lenses, scales, cephalopod and annelid jaws, crustacean exoskeleton parts, and copepoditic parasites of gadoids and clupeids were used to identify as many different prey as possible (cf. Tollit *et al.* 2003). Prey were identified and prey sizes back-calculated, using our reference collection, and Härkönen (1986), Clarke (1986) and Leopold *et al.* (2001), following the methods outlined in Leopold *et al.* (2015a). A total of some 70 different prey species were found, that were subsequently grouped into ten prey guilds: small schooling clupeids, sandeels, estuarine roundfish, pelagic roundfish, schooling gadoids, gobies, flatfish, (other) demersal roundfish, squid and other invertebrates (ES-2). We consider clupeids, sandeels, estuarine roundfish and pelagic roundfish to be energy-rich prey ($>5 \text{ kJ} \cdot \text{g}^{-1}$ wet weight) and prey in the other guilds to be low in energy ($<5 \text{ kJ} \cdot \text{g}^{-1}$ wet weight; MacLeod *et al.* 2007a, Spitz *et al.* 2014) acknowledging that species-specific energy densities might vary, between seasons, years, and prey size (Pedersen & Hislop 2001, Wanless *et al.* 2005).

Statistical analysis

Stomach contents were studied in 381 harbour porpoises for which at least NCC and body length were also known. For each porpoise the number of prey (minimum number of individuals per species) was estimated, and for each prey the length and mass. The importance of energy-rich, versus lean prey across the various NCC groups was assessed using four standard indices. Within each group the percentage of animals with empty stomachs was determined, and among the animals with non-empty stomachs ($n=301$) we determined the frequency of occurrence of energy-rich and lean prey (%FO); the percentage of energy-rich prey by number (%N); and the percentage of energy-rich prey by reconstructed mass (%M). The latter three indices were also combined in the 'Index of Relative Importance (IRI)' (Pinkas *et al.* 1971; Hyslop 1980) as: $(\%N + \%M) \times \%FO$, where %N is the (number of energy-rich prey $\cdot 100$) divided by the total number of prey items found; %M is the combined (mass of all energy-rich prey $\cdot 100$) divided by total prey mass; and %FO is the percentage frequency of occurrence of each prey group. Note that we used reconstructed prey mass rather than prey volume, as used by Hyslop (1980).

All four indices are presented in ES-2. We used the prey biomass data for further analysis. These showed a large range in values, both between prey guilds and between individual porpoises, and were therefore fourth root transformed before calculating Bray-Curtis dissimilarities between individuals (Bray & Curtis 1957). The resulting distance matrices were analysed using the PERMANOVA routine included in the Primer 6+ software package (Anderson 2001, McArdle & Anderson 2001, Anderson *et al.* 2008), to test for differences between the six NCC groups.

Several co-variables which might have an effect on prey composition were tested, also with PERMANOVA. We considered porpoise gender, age and the season and location of strandings. Gender might influence prey composition if males and females have different energetic requirements or a different distribution at sea. This seems unlikely for young animals, even though there is a slight size difference between the sexes (Lockyer 2003b; Olafsdóttir *et al.* 2003). However, adult females may have higher energy requirements than adult males, during pregnancy and lactation (Smith & Gaskin 1983; Aarefjord *et al.* 1995; Santos & Pierce 2003; Das *et al.* 2004) and must accompany neonates in summer and autumn, while adult males do not face these constraints. Gender was therefore examined in concert with age. Age itself is also likely to influence prey composition, as older animals are larger and also more experienced predators. They may thus have both the need and the skills to catch larger prey or prey with a higher energy density. On the other hand, juveniles need extra energy for growth. Within our samples, we considered three age classes. Animals <100 cm long, that had stranded between 1 May and 31 December were considered calves; animals <100 cm that stranded after 31 December and animals between 100 cm and 130 cm long were considered juveniles. Animals >130 cm were considered adult (cf. Lockyer 2003b, for North Sea harbour porpoises), unless gonad

inspection revealed otherwise. Animals that were clearly neonates were excluded. The distinction between neonates and calves was not always clear however and we set the division at a body length of 77 cm, the smallest animals in our samples that had solid food remains in its stomach.

Diet is likely to vary with season as many fish species are migratory to some extent and show different behaviours during the year that will affect their availability as prey. We considered four seasons: winter (December-February), spring (March-May), summer (June-August) and autumn (September-November).

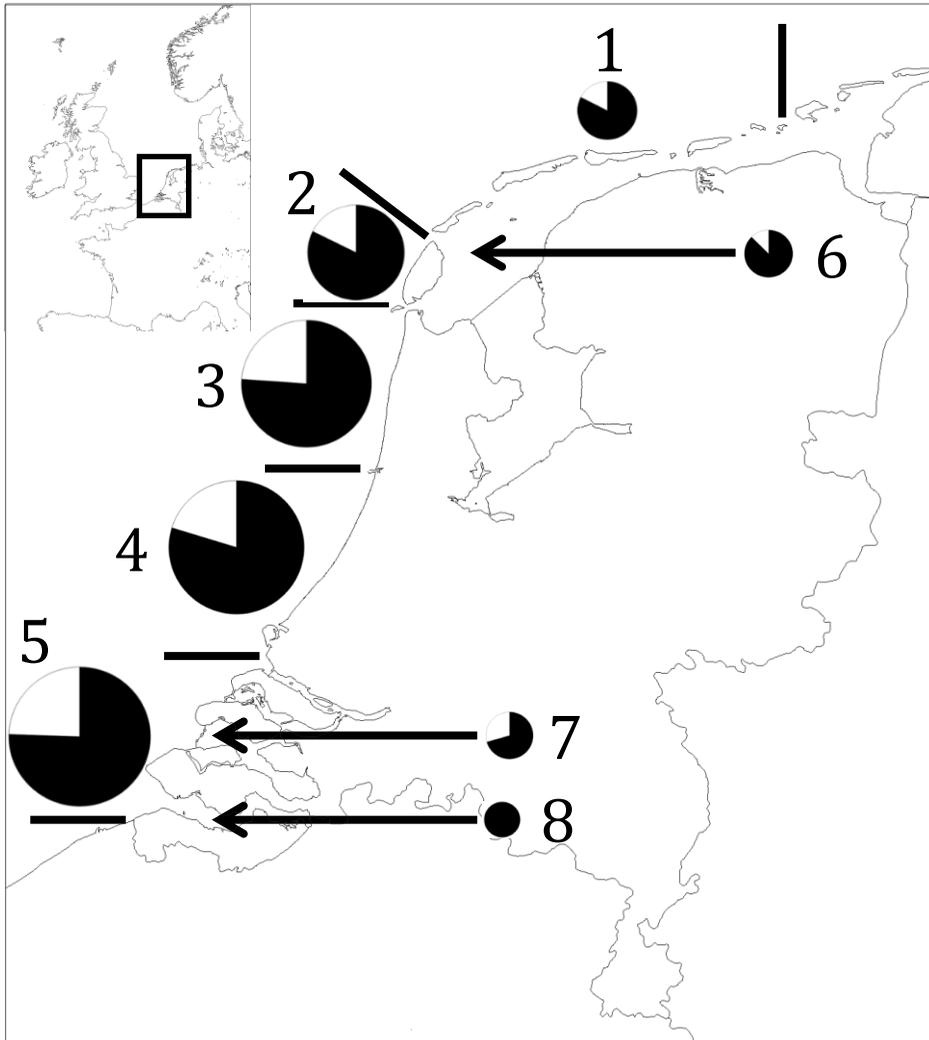


Figure 2. Regions (#1-8: see Table 6) used as geographical subdivisions. Circles are scaled to the relative numbers of porpoises for which the stomach content was studied; black: with prey; white: empty. Estuarine waters indicated by arrows.

We also considered possible regional differences in diet, even though the Dutch part of the North Sea constitutes only a small part of the distribution range of the harbour porpoise in NW Europe. We consider five regions along the Dutch North Sea coast: the Eastern Wadden Islands (Rottum-Vlieland), Texel, North-Holland (mainland coast from Den Helder to IJmuiden), South-Holland (mainland coast between IJmuiden and Hook of Holland), and the Voordelta in the SW of the county; as well as three estuarine waters: the Wadden Sea, the Eastern Scheldt, and the Western Scheldt (Figure 2). The latter three regions are all connected with the North Sea: the Wadden Sea via tidal inlets between the various barrier islands, the Eastern Scheldt by openings in the storm surge barrier separating this former estuary from the North Sea, while the Western Scheldt is an open river. Prey composition of porpoises found in the Eastern and Western Scheldt has been found to be slightly different from animals found along the North Sea coastline (Jansen *et al.* 2013, Chapter 5); no specific study has yet been done on porpoises found in the Wadden Sea.

Prey composition may also vary with year, as fish stocks show large year to year variations (cf. MacLeod *et al.* 2007a). However, porpoises were only available for a few different years, with considerable differences in numbers per month and per year, precluding a meaningful analysis of year to year variation of diets. A full multi-variate analysis of the effects of the various covariates on porpoise diet is presented elsewhere (Chapter 2). Here, we evaluate the effects of each co-variate in turn and consider if any of these co-variates would seriously hamper the analysis of the effects of NCC.

Results

Co-variables

Gender and age

Juveniles, of both sexes, were the most numerous age class within our samples. Adult females were more numerous than adult males, while males were more numerous among the younger ages. Age and gender categories were distributed slightly differently between porpoises in good and poor body condition (Table 2). Most cells are filled, but very lean adults (NCC 6) were very rare.

Average NCC was very similar across age classes and between males and females (T-test: $P > 0.1$ for all comparisons; Table 3) and we conclude that any interaction between gender or age with NCC will not seriously hamper an analysis of the effect of NCC on prey composition.

Table 2. Distribution of harbour porpoises for which the stomach contents were analysed over the different age and gender categories, per NCC class. Shading indicates sample size: empty cells (white), relatively low sample size (1-5; light grey), medium sample size (6-10, medium grey) and large sample size (>10, dark grey).

Age,Gender/NCC	1	2	3	4	5	6	Totals
Calf-Male	8	3	7	9	4	7	38
Calf-Female	1	1	5	3	6	2	18
Juvenile-Male	18	15	23	42	28	10	136
Juvenile-Female	8	20	19	18	20	14	99
Adult-Male	7	6	11	4	10	0	38
Adult-Female	4	9	7	17	12	2	51
Juvenile-(gender ?)	1						1
Totals	47	54	72	93	80	35	381

Table 3. Average NCC (with Standard Deviation and sample size) for each age group and gender. Differences between groups are tested by Student's T-test.

Age/NCC	Avg-NCC	SD-NCC	n	Comparison	t	df	p
Calf	3.66	1.64	56	Calf/Juvenile	0.292	290	>0.1
Juvenile	3.59	1.50	236	Calf/Adult	0.982	143	>0.1
Adult	3.38	1.40	89	Juvenile/Adult	1.070	323	>0.1
Gender							
Male	3.47	1.52	212	Male/Female	-1.297	378	>0.1
Female	3.67	1.47	168				

Season

Relatively many animals were available for spring and summer (Table 4). In summer, NCC values were significantly higher than in winter and spring, but not statistically different from the values found in autumn. Autumn values were intermediate between those in summer and in winter and spring (Table 5). The sampled harbour porpoises tended to be leaner in summer than in spring and winter. There is thus an interaction between season and NCC, and possibly prey composition.

Table 4. Distribution of harbour porpoises for which the stomach contents were analysed over the different seasons, per NCC class. Shading as in Table 2.

Season/NCC	1	2	3	4	5	6	Totals
winter	15	10	15	12	16	4	72
spring	14	26	21	34	22	7	124
summer	6	10	23	26	25	17	107
autumn	10	7	12	21	16	7	73
Totals	45	53	71	93	79	35	376

Table 5. Average (with Standard Deviation and sample size) NCC for each season. Differences between groups were tested by Student's T-test.

Season/NCC	Avg-NCC	SD-NCC	n	Comparison	t	df	p
Winter	3.22	1.59	72	Winter/Spring	-0.616	194	>0.1
Spring	3.36	1.43	124	Winter/Summer	-3.280	177	<0.01
Summer	3.98	1.41	107	Winter/Autumn	-1.631	143	>0.1
Autumn	3.64	1.51	73	Spring/Summer	-3.311	229	<0.001
				Spring/Autumn	-1.282	195	>0.1
				Summer/Autumn	-1.523	178	>0.1

Location

Most animals were collected along the various stretches of North Sea coastline (regions 1-5), with increasing sample size from NE to SW. Lower sample sizes were available from the estuarine waters (Table 6, Figure 2). Overall, numbers of animals were rather equal across NCC-classes. Animals found on the North Sea coasts of the eastern Wadden Sea Islands were somewhat leaner ($p < 0.1$) than those found along other stretches of North Sea coastline, while those found South-Holland were marginally fatter (Table 7). There was no clear NE-SW trend in NCC along the North Sea coastline, as animals in the SW had NCC values not different from the other stretches of North Sea coastline combined and were, in fact, slightly leaner than those in South-Holland (with borderline significance: $t = 1.811$, $df = 171$, $p = 0.075$). Animals from the Wadden Sea (region 6) had similar NCC values compared to those found on the seaward sides of the Wadden Sea Islands (regions 1 & 2 combined; $p > 0.1$). Animals found in the Eastern Scheldt (region 7) were marginally fatter ($p < 0.1$) than those in the adjoining Voordelta (region 5), while those found in the Western Scheldt (region 8) were leaner ($p < 0.05$), but note relatively small sample sizes for the estuarine waters. We conclude that regional differences in NCC were slight, or related to small sample sizes and that region is unlikely to affect an analysis of the effect of NCC on prey composition.

Table 6. Distribution of harbour porpoises for which the stomach contents were analysed over the different regions, per NCC class. Shading as in Table 2.

Stranding location/NCC	1	2	3	4	5	6	Totals
1. Eastern Wadden Sea Islands North Sea coast	1	3	4	3	9	3	23
2. Texel North Sea coast	6	5	10	15	12	3	51
3. North Holland North Sea coast (DH-IJM)	9	15	20	19	13	12	88
4. South Holland coast (HoH-IJM)	14	14	14	17	16	4	79
5. NL-SW (Voordelta)	12	9	18	24	22	9	94
6. Wadden Sea	2	2	1	6	4	1	16
7. Eastern Scheldt	1	4	4	8	0	0	17
8. Western Scheldt		1		1	3	3	8
9. Unknown	2	1	1	0	1	0	5
Totals	47	54	72	93	80	35	381

NCC and body mass

Model 2 has a fixed slope parameter $b = 2.56778$, that is equal for all NCC classes, but a different intercept, a . We also added porpoise gender as a factor to Model 2, but this did not improve the model, so even though male and female porpoises reach different asymptotic lengths and also reach maturity at different lengths (Lockyer 2003b, Learmonth *et al.* 2014), this difference in growth apparently did not significantly impact their length-mass relationships. The values for the intercept a_i are given for each NCC class in Table 8. Predicted body masses for NCC 1,...,6 become progressively smaller. Relative body mass compared to animals with NCC_i equals $\exp(a_i - a_1)$ and is, for example, for NCC 6 animals 30.6% lighter.

The available data are plotted in Figure 3a (ln-transformed) and the predicted L-M curves for each NCC class are plotted in Figure 3b.

Table 7. Average (with Standard Deviation and sample size) NCC for each region. Differences between groups are tested by Student's T-test.

Stranding location/NCC	Avg-NCC	SD-NCC	n	Comparison	t	df	p
1. E-Wadden Islands North Sea coast	4.09	1.44	23	1 vs (2,3,4,5)	1.859	333	<0.1
2. Texel North Sea coast	3.61	1.42	51	2 vs (1,3,4,5)	-0.321	333	>0.1
3. North Holland (DH-IJM)	3.55	1.53	88	3 vs (1,2,4,5)	0.049	333	>0.1
4. South Holland (HoH-IJM)	3.24	1.53	79	4 vs (1,2,3,5)	-2.095	333	<0.05
5. Voordelta	3.66	1.5	94	5 vs (1,2,3,4)	-0.817	333	>0.1
6. Wadden Sea	3.69	1.49	16	6 vs (1,2)	-0.172	88	>0.1
7. Eastern Scheldt	3.12	0.99	17	7 vs 5	-1.891	109	<0.1
8. Western Scheldt	4.88	1.36	8	8 vs 5	2.415	100	<0.05
9. Unknown	2.40	1.67	5				

Table 8. Model 2 parameters for each NCC class.

NCC	a_i	% of M_{NCC1} -predicted
1	-8.91101	100
2	-8.99337	92.1
3	-9.08421	84.1
4	-9.19976	74.9
5	-9.25373	71.0
6	-9.27690	69.4

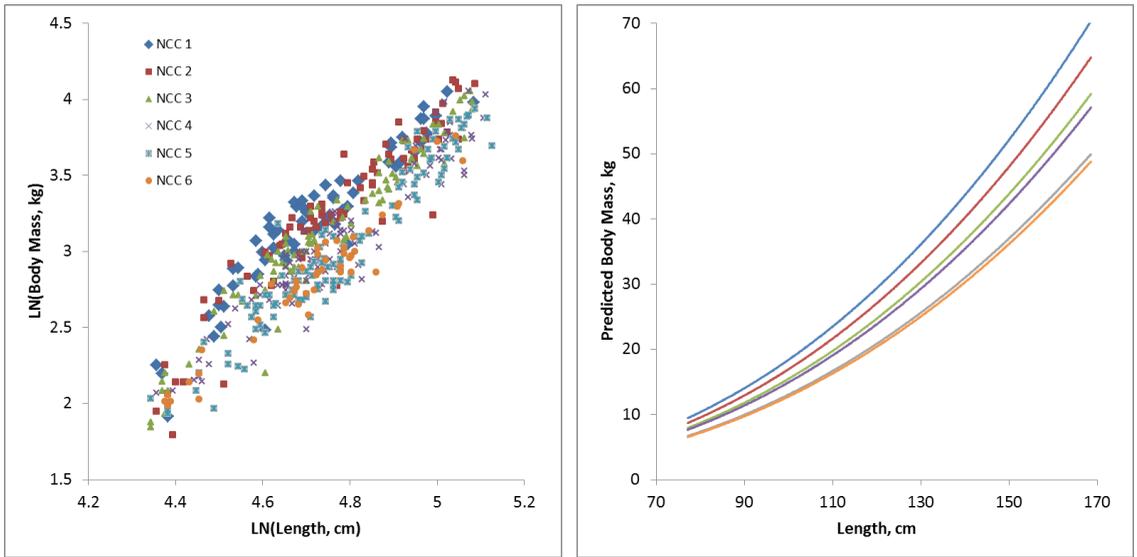


Figure 3a (left). Body mass as a function of body length, for NCC1...6 (ln-transformed).

Figure 3b (right). Predicted porpoise length-mass curves for NCC1...6 (top to bottom; parameters: Table NCC).

NCC and blubber thickness

NCC closely mirrors the blubber thickness of harbour porpoises and both measures vary with month (Figure 4). The porpoises were fattest from January through March, and leanest in August, with animals gradually losing blubber from April through August and regaining a thicker blubber layer from September through December. NCC thus appears to be a good proxy for the body condition of harbour porpoises.

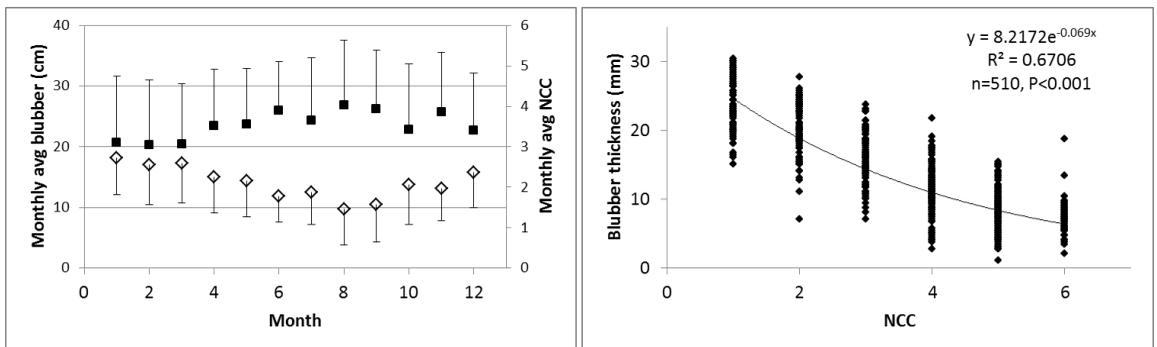
Prey composition

Empty stomachs

Around 17% of all porpoises of NCC1,...,4 did not have any hard prey remains in their stomachs, without a clear trend in this percentage across NCC classes. The leanest porpoises, however, had higher percentages of empty stomachs (Table 9).

Table 9. Numbers of harbour porpoises with non-empty and with empty stomachs, per NCC class.

NCC	non-empty	empty	% empty
1	38	9	19.1
2	46	8	14.8
3	60	12	16.7
4	76	17	18.3
5	58	22	27.5
6	23	12	34.3

**Figure 4a (left).** Monthly average (with SD) blubber thickness (open symbols; left Y-axis) and NCC (closed symbols; right Y-axis).**Figure 4b (right).** Relationship between NCC and blubber thickness.

Gender and age

The overall difference in prey composition of males (n=169 non-empty stomachs) and females (n=131; Table 10) was significant, but very small (only 1.2% of the variance explained; Table 11). Considering adults only, however, this percentage increased to 5.6% (p=0.015). For neither juveniles (p=0.245), nor calves (p=0.344) were the diets significantly different between the sexes. Adult males had taken relatively more clupeids and sandeels and less pelagic roundfish and gadoids than adult females. Similar differences were found among the juveniles, but their prey compositions were not significantly different.

Adults had generally taken more gadoids and fewer gobies than juveniles. Prey compositions of adults, juveniles and calves all differed significantly from each other (Table 11). The diet of calves was dominated by gobies, but the contribution of gobies

declined as porpoises got older. Adult diet was dominated by gadoids, irrespective of gender (Table 10).

Table 10. Percentages of total prey mass in male and female porpoises per age class. N-values represent numbers of porpoises with non-empty stomachs. The figures at the bottom rows give the average reconstructed prey mass per individual porpoise (for respectively all animals and with empty stomachs excluded).

Prey guild/Porpoise group	Adult ♂ (n=32)	Adult ♀ (n=42)	Juvenile ♂ (n=121)	Juvenile ♀ (n=84)	Calf ♂ (16)	Calf ♀ (5)
Clupeids	13.93	3.51	14.10	11.01	0.07	1.58
Sandeels	18.83	8.32	18.02	8.47	3.99	0.00
Est. roundfish	1.03	0.67	3.07	7.02	0.00	2.11
Pel. roundfish	0.26	12.25	0.15	3.76	0.00	0.00
Gobies	2.19	2.91	36.73	20.37	94.21	95.92
Gadoids	59.96	70.50	25.30	48.61	1.51	0.00
Dem. roundfish	0.04	0.64	0.68	0.23	0.15	0.00
Flatfish	1.49	0.09	0.44	0.05	0.00	0.00
Squid	1.92	0.93	1.36	0.19	0.03	0.39
Other invert.	0.35	0.18	0.16	0.28	0.04	0.00
per individual (all stomachs)	1006	1293	598	547	172	83
per individual (non-empty)	1194	1570	672	645	407	298

Table 11. Pair-wise comparison of the prey composition of calves, juveniles and adults.

Age, Gender	%-expl.	P(perm)	Unique perms
Calves - Juveniles	12.2	0.001	999
Calves - Adults	38.5	0.001	999
Juveniles - Adults	8.3	0.001	999
Males - Females	1.2	0.022	998
Ad-male - Ad-female	5.6	0.015	998
Juv-male - Juv-female	-	0.245	997
Calf-male - Calf-female	-	0.344	979

Season

Diets were dominated by gadoids, in all seasons. In summer, overall stomach filling was considerably lower than in the other seasons and porpoises relied more on sandeels and estuarine roundfish than in other seasons. High-energy prey (clupeids, sandeels, estuarine and pelagic roundfish) were relatively scarce in autumn. Conversely, leaner prey, mostly gadoids and gobies, had the highest contribution in autumn and the lowest in spring.

Among these lean prey, the relative contribution of gobies was highest in spring, that of gadoids in autumn (Table 12). With nearly twice as many animals studied in spring as compared to the other seasons and with animals in spring having a relatively good condition (Table 5), overall results for the lower NCC classes will be slightly biased towards gobies, relative to gadoids. However, animals found in winter were in even better condition and their gadoids-dominated diet will balance this out to some extent.

Significant differences were found between seasonal diets, except between summer and autumn (Table 13), which are both characterised by high contributions of gadoids and low contributions of gobies (Table 12).

Table 12. Percentages of total prey mass found per season. N-values represent numbers of porpoises with non-empty stomachs. The figures at the bottom rows give the average reconstructed prey mass per animal (for respectively all individuals and with empty stomachs excluded).

Prey group/Season	Winter (=66)	Spring (n=109)	Summer (n=61)	Autumn (n=60)
Clupeids	14.00	12.33	1.77	4.68
Sandeels	12.20	16.12	22.82	8.25
Estuarine roundfish	0.58	3.80	4.82	2.12
Pelagic roundfish	3.09	8.34	0.01	1.98
Gobies	18.36	33.06	14.01	11.73
Gadoids	48.40	24.44	55.51	69.92
Demersal roundfish	0.85	0.12	0.04	0.56
Flatfish	0.18	0.96	0.42	0.04
Squid	2.09	0.60	0.38	0.53
Other invertebrates	0.23	0.24	0.21	0.19
per capita (all stomachs)	1123	642	188	820
per capita (non-empty)	1225	730	330	997

Table 13. Pair-wise comparison of seasonal prey composition.

Age	%-expl.	P(perm)	Unique perms
Winter - Spring	4.2	0.001	999
Winter - Summer	8.9	0.001	998
Winter - Autumn	3.9	0.006	999
Spring - Summer	7.4	0.001	999
Spring - Autumn	4.2	0.001	998
Summer - Autumn	-	0.195	999

Region

Considering all available stomach contents (n=376 porpoises of known location (Table 6), of which 296 contained hard prey remains (Table 14), only a few near-significant differences were found between the North Sea regions 2 to 5, with the largest sample sizes. All other regional prey compositions were not significantly different (Table 15). Because the prey composition along the Eastern Wadden Islands North Sea coasts (region 1) was similar to that in the Voordelta (region 5: p=0.9194), there was no clear NE-SW gradient.

Table 14. Percentages of total prey mass found per region (1-9: see Figure 2 and Table 6). N-values represent numbers of porpoises with non-empty stomachs. Prey guilds (abbreviated) are, respectively: Clupeids, Sandeels, Pelagic roundfish, Estuarine roundfish, Demersal roundfish, Flatfish, Gadoids, Gobies, Squid and Other invertebrates.

	N	CL	SE	PRF	ERF	DRF	FF	GA	GO	SQ	O
1.	19	10.14	17.41	0.00	3.99	0.25	0.08	31.18	36.22	0.42	0.32
2.	42	3.46	7.13	5.11	0.04	0.72	0.03	62.82	17.97	2.40	0.32
3.	67	10.15	8.48	0.38	1.72	0.09	0.26	56.45	21.73	0.52	0.21
4.	63	16.43	31.31	9.04	0.46	0.20	1.09	21.82	19.12	0.34	0.20
5.	71	11.23	11.23	3.82	4.37	0.93	0.51	49.39	17.19	1.18	0.15
6.	14	15.62	7.11	0.00	13.65	0.00	0.00	3.39	59.32	0.29	0.62
7.	12	6.06	4.82	0.21	5.15	0.00	0.00	20.56	62.46	0.51	0.22
8.	8	12.59	2.82	15.01	26.62	0.00	0.00	17.09	25.65	0.18	0.04
9.	5	10.76	0.80	0.00	19.07	0.00	0.00	64.08	5.10	0.00	0.18

Table 15. Pair-wise comparison of regional prey composition.

Region	%-expl.	P(perm)	Unique perms
Region 1 - 2	-	0.252	997
Region 1 - 3	-	0.788	998
Region 1 - 4	-	0.190	999
Region 1 - 5	-	0.919	998
Region 2 - 3	-	0.210	999
Region 2 - 4	-	0.242	998
Region 2 - 5	1.7	0.075	999
Region 3 - 4	1.8	0.054	999
Region 3 - 5	-	0.36	999
Region 4 - 5	1.5	0.072	999
Regions 1&2 - 6	-	0.209	998
Region 5 - 7	-	0.203	998
Region 5-8	-	0.763	999

NCC and prey composition

The prey compositions of animals of NCC 1,...,6 are shown in Figure 5 in so-called modified Costello diagrams (Amundsen *et al.* 1996, Ringelstein *et al.* 2006). These graphs combine the information on the proportions of porpoises that had taken certain prey(group), irrespective of the amount of prey (%FO along the X-axis) with the contribution of that prey to the diet in terms of mass (%Mass along the Y-axis). Prey that are eaten by the majority of animals and that are also important in terms of mass contribution show up in the upper right corner of these graphs; prey that are found only rarely and constitute little mass are placed near the origin.

Animals in good condition had four main prey groups that constituted a mix of two energy-rich prey types (Spitz *et al.* 2012): sandeels and clupeids, and two leaner prey types: gobies and gadoids. All other prey types were marginally important, particularly in terms of mass-contribution. As porpoises got leaner (higher NCCs), the fatter prey disappeared from the diet: first the clupeids (from NCC 3) and next the sandeels (from NCC 4). In very lean porpoises (NCC 5 and 6) this trend continued as fewer animals still took clupeids or sandeels (Figure 5).

Gadoids and gobies remained important prey as NCC increased, with gadoids always dominating total prey mass, while gobies were always found most frequently. The loss of sandeels and clupeids from the diet in starving porpoises was not compensated by other energy-rich prey, so overall, starving porpoises had a much leaner diet than porpoises in a good body condition. There is no indication that alternative food sources (e.g., invertebrates) were more prominently included in the diet of starving porpoises: they rather stopped eating energy-rich prey.

Differences in prey composition were not significant between successive NCC classes, but were significant, or near-significant, between successive pairs of NCC classes (NCC 1&2; 3&4; 5&6; Table 16).

Table 16. Pair-wise comparisons of prey composition for different combinations of NCC classes.

NCC	%-expl.	P(perm)	Unique perms
NCC 1 - 2	-	0.746	997
NCC 1,2 - 3	-	0.134	998
NCC 3 - 4	-	0.532	999
NCC1,2 - 3,4	2.2	0.01	998
NCC 4 - 5	-	0.444	998
NCC 3,4 - 5	0.9	0.099	998
NCC 5 - 6	-	0.635	996
NCC 3,4 - 5,6	2.2	0.088	998

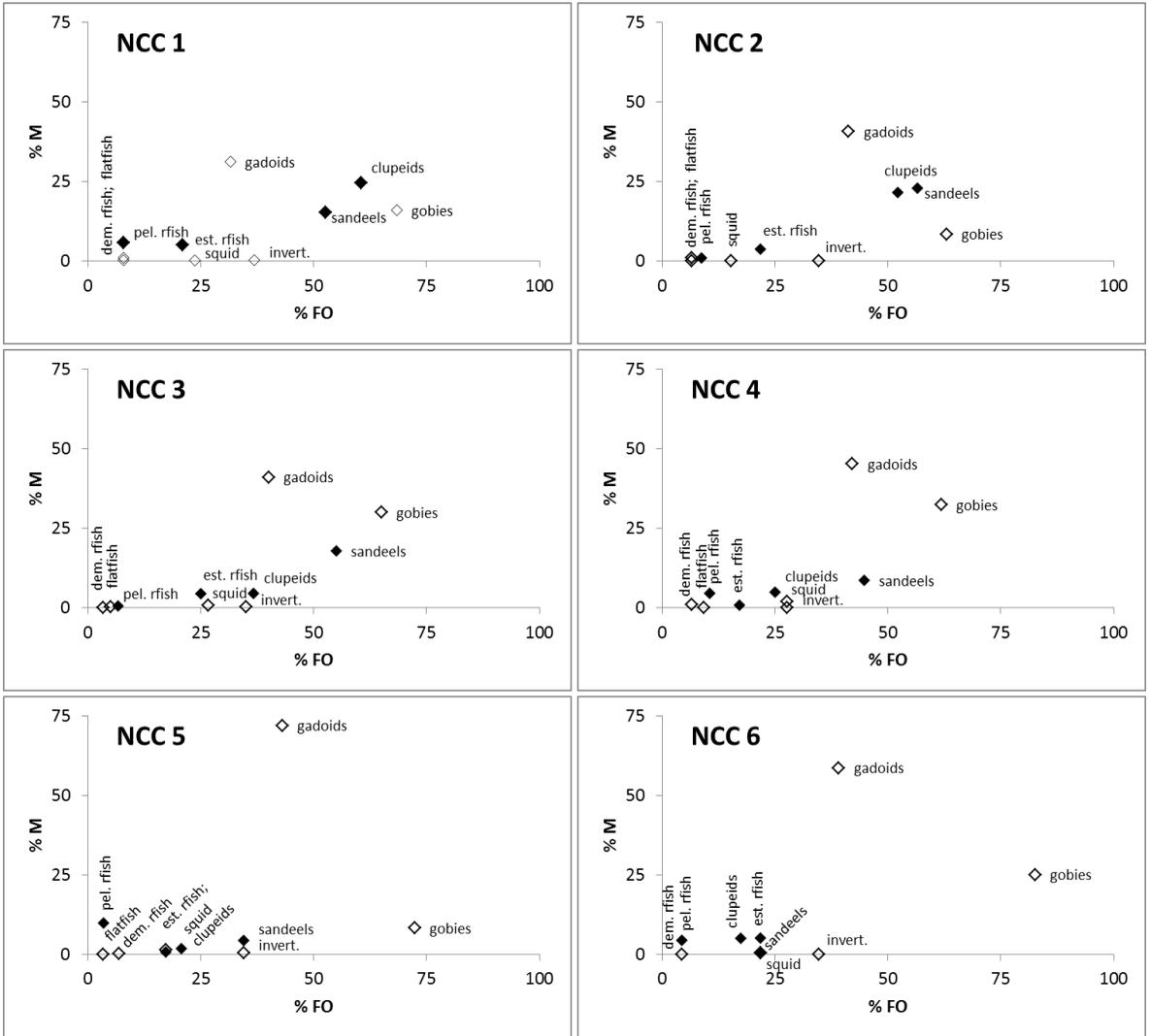


Figure 5. Costello diagrams, scatterplots of all prey groups according to their % of occurrence and their importance by mass for porpoises at body conditions going from good (NCC 1; upper left) to extremely bad (NCC 6; bottom right). Open symbols: lean prey. Closed symbols: energy-rich prey.

Discussion and Conclusion

Marine top predators with high metabolic rates are evolutionary geared towards having energy-rich diets (Österblom *et al.* 2008). Spitz *et al.* (2012) suggested that harbour porpoises are such predators, that need to eat prey with a high energy content. However, diet studies have shown that although energy-rich prey are often an important component of their diet, porpoises also eat considerable amounts of prey of a relatively low energy content. The reason for this is unknown but may be that low-quality prey are easier to catch than high-quality prey or are necessary for growth as these are relatively rich in protein or other essential components. Should, however, energy-rich prey be essential for porpoise fitness, porpoises should not be able to stay fit on a diet without such prey, no matter how easy to catch and how abundant low-quality prey may be. In this sense, lean prey could be seen as junk food, if taken in too large amounts. For porpoises in the southern North Sea, this would imply that they can only be successful here, if they manage to find and eat sufficient amounts of fatty fish, such as sandeels or clupeids, in addition to staple foods such as gadoids and gobies.

From the range of prey types available, predators should always harvest prey that have a high energy to mass ratio (Whelan & Brown 2005). Harbour porpoises should therefore always eat at least some fish with a high fat content, that is, fish with a high energy density. It is unknown how long a porpoise can stay fit on a low-energy diet, but in all likelihood, they should strive to, at least periodically, have meals of energy-rich prey. Finding no remains of energy-rich prey in a porpoise's stomach is not necessarily a sign of starvation, as these cetaceans have short gut-residence times (Gaskin 1978; Kastelein *et al.* 1997b) and may alternate meals of lean prey with meals of energy-rich prey and may not feed continuously. Indeed, 19% of the NCC 1 and 2 animals that had non-empty stomachs had no remains of energy-rich prey in their stomachs, while another 17% of these animals had empty stomachs. For the animals of NCC 3 and 4 these figures were 29% and 18%, and for the animals of NCC 5 and 6 these were 38% and 30%, respectively. Leaner animals thus had a higher probability of dying with empty stomachs and had on average eaten prey of lower energy density.

Another constraint for predators, however, is the amount of time (searching time plus handling time) needed to catch different prey, offset against the energy gain of that prey. Prey that are rare may need a long searching time and should probably only be taken when encountered incidentally, e.g., while searching for more common prey. Also, prey that are very fast swimmers, such as mackerel, may not be worth pursuing for less able porpoises, such as younger individuals. This may be the reason why porpoises, when faced with a poor availability of clupeids and sandeels, cannot switch to other high-energy fish, such as mackerel or horse mackerel. In the end, porpoises should only take foods that yield more energy than they require for catching, and they should acquire sufficient energy to sustain themselves.

Given their large surface to volume ratio, harbour porpoises need large amounts of energy to maintain their body temperature. Healthy porpoises have an insulating subcutaneous blubber layer that is at least 1.5 cm thick, the thickness depending on porpoise age and on season (Kastelein *et al.* 1997a, Lockyer *et al.* 2003b, this paper). Maintaining this also requires energy, which is probably the reason that porpoises reduce blubber thickness in summer, at relatively high ambient temperatures. Harbour porpoises are also leaner in the presence of predators/aggressors, supposedly because they need to be more mobile to evade these (MacLeod *et al.* 2007c). Blubber thickness also varies seasonally in captive animals (Kastelein *et al.* 1997a, Lockyer *et al.* 2003b) that are safe both from starvation and predation. Apparently, porpoises balance the costs for maintaining their blubber layer against the cost for thermoregulation and the risk of predation. Apart from insulation, blubber also functions as a safeguard against starvation and porpoises should not deplete their blubber too much, as this will increase heat loss and costs for thermoregulation, and decrease hydrodynamics. Consequently, blubber loss needs to be compensated later by an increased energy intake (Rosen *et al.* 2007), and will decrease the buffer against fatal emaciation.

The fact that NCC values were highest in summer, and blubber thickness was at its lowest, might simply be a response to higher water temperatures. However, stomach filling was also found to be lowest in summer, while the diet lacked (fatty) clupeids and pelagic roundfish. The probability of dying with an empty stomach was much higher in summer (43%) than in the other seasons (8-18%), while the percentage of energy-rich prey was low in both summer (28%) and autumn (25%), compared to winter (38%) and spring (39%). Rather than being a time of plenty and easy living, summer appears, for harbour porpoises, to be a time of scarcity, particularly of energy-rich prey. In addition, gobies, the prey most frequently taken by the porpoises, also seem in short supply (Table 12), both in summer and in autumn. In summer, porpoises must rely heavily on gadoids and with their already thin blubber layer, appear to run a relatively high risk of starvation, if they find these in insufficient quantities, or find too few sandeels, the main energy-rich additional prey in this season.

The gradual decrease of the contributions of clupeids and sandeels from the diet with increasing NCC values (Figure 5) may be seen as support for the junk food hypothesis. This can be interpreted in three different ways:

1. New, relatively low-quality food types are added to the diet, or
2. Prey types are kept constant, but the quality of key prey is reduced, or
3. Relatively high-quality food types are dropped from the diet.

We can rule out the possibility that new, unsuitable prey types had been taken by the starving porpoises, unless such prey would have no identifiable hard parts (e.g. jellyfish). None of the alternative prey groups found in this study was of increased importance in the

emaciated groups. It seems unlikely that the porpoises had been consuming large masses of prey without hard parts, such as jellyfish. We have no records of jellyfish or similar soft-bodied prey (freshly ingested) in porpoise stomachs, in animals that died suddenly, with full stomachs, e.g., in fishing nets (Chapter 4) or from predation by grey seals (Leopold *et al.* 2015a).

In this study, it is important to note that the second possibility cannot be directly assessed from stomach contents analysis. Prey masses, and their quality are assessed from remaining prey hard parts and not measured directly. Should the energy density of certain prey fish be particularly low in the SE North Sea as compared to other parts of the distribution range of porpoises, or should energy density of prey be comparatively low in certain years or seasons (cf. Wanless *et al.* 2005), this cannot be inferred from e.g. otoliths. Estimated relative prey masses therefore take no account of possible regional, year-to-year or seasonal variation within fish species. Prey fish may show dramatic changes in energy density (Wanless *et al.* 2005), and in case e.g. clupeids or sandeels would be exceptionally lean, they prey would probably not be worth pursuing. Such a situation would probably be linked to a certain year (cf. Wanless *et al.* 2005) and although a weak correlation is present in our data between the yearly average NCC and the overall percentage of energy-rich prey, this is not significant ($R^2 = 0.3064$, $n=9$, $p>0.1$).

Harbour porpoises should feed on high quality food which corresponds with high metabolic costs of living (Spitz *et al.* 2012), or at least on a sufficient mix of lean and fatty prey (this study). Therefore, the SE North Sea might only be a suitable habitat for harbour porpoises if they can find sufficient amounts of such high-quality prey, next to more lean prey types (gobies, whiting, flatfish) that seem to be abundantly available here. Sandeels (summer), alternating with clupeids (winter and spring), and to a lesser extent pelagic and estuarine roundfish are probably critical dietary components. With increased porpoise densities in the southern North Sea and no evidence of overall decreasing availability of prey fish here (Tulp *et al.* 2008; Tulp 2015) the most likely cause of starvation is temporary shortage of energy-rich prey, particularly clupeids and sandeels. Such shortages may be short-term (days or weeks), given the low tolerance to starvation in harbour porpoises, or seasonal, as indicated by the yearly peak in summer strandings in The Netherlands.

Interestingly, many starving porpoises had still been able to find, catch and eat gobies and gadoids, but failed to consume sufficient amounts of fatty fish. It is impossible to determine which came first: failure to find suitable prey, resulting in starvation, or a reduced body condition leading to a loss of ability to catch high-energy prey. In any case, porpoises that fail to eat sufficient amounts of high-quality fish appear to be at a serious risk of starvation. Starving animals apparently could not compensate for the lack of high-energy prey by consuming more lean prey. In summer, when efficient foraging seems to be most difficult, both a lower mass of both energy-rich and energy-poor prey was found in the stomachs.

A similar pattern was found by MacLeod *et al.* (2007a,b) for starving porpoises in Scotland. Apparently, compensating for loss of energy-rich prey by ingesting more low-energy bulk, is not an option for starving porpoises (cf. Whelan & Brown 2005): quantity of food cannot always replace its quality (Spitz *et al.* 2012).

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Chapter 3

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Electronic supplement

ES-1. NCC and DCC codes used, following Kuiken & Garcia Hartmann (1991):

NCC (Nutritive condition code):

The nutritive state of the animal should be evaluated immediately before and during the necropsy, as a general impression based on several details, both externally (the general body shape) and internally (fat and muscular condition).

NCC1: Very good nutritive condition, very well nourished, abundant blubber, significant other subcutaneous fat present in the dorsal neck and -sometimes- on the lateral thorax, pleural fat present, *Longissimus dorsi* and neck are convex, the whole animal shows a "round, barrel-like" body shape.

NCC2: Good nutritive condition, well nourished, abundant blubber, some subcutaneous fat, *Longissimus dorsi* and neck are straight or slightly convex.

NCC3: Normal nutritive condition, blubber is normal thickness, no subcutaneous fat present, neck and *Longissimus dorsi* are straight, on movement of the animal sometimes slightly convex.

NCC4: Bad nutritive condition, blubber is on the thin side, sometimes skin thickness increased, neck and *Longissimus dorsi* visibly concave.

NCC5: Very bad nutritive condition, blubber is thin, skin thickness most often increased, *Longissimus dorsi* and neck clearly concave.

NCC6: Extremely bad nutritive condition, severely emaciated, blubber is very thin, neck and *Longissimus dorsi* are severely concave, the contour of the scapula (especially the *Spina scapulae*) may be visible externally.

DCC (Decomposition condition code):

The decomposition condition code (DCC) is based on the external and internal decomposition signs of the carcass.

DCC 1: Very fresh, less than 48 hours dead, may show signs of rigor mortis (<24h), blood still separates serum (24-48h), rigidity of eyes is diminished but not very flaccid, cornea is not cloudy.

DCC 2: Fresh, first signs of decomposition visible, eyes and surface quality of the skin reveal decomposition, otherwise good state, organs look intact, blood does not separate from serum, no smell of decomposition.

DCC3: Putrefied, skin peeling, moderate but clear signs of decomposition (changes in colour and consistency) of skin and organs, not suitable for bacteriology because of overgrowth, moderate smell of decomposition.

DCC4: Very putrefied, advanced decomposition, skin and organs clearly altered, the loss of consistency changes the organ's shape, clear smell of decomposition, not suitable for any tissue analysis, even gross pathology is very unclear and can hardly be interpreted at all.

DCC5: Remains, organs are beyond clear recognition or absent, may be mummified or reduced to mere bones.

ES-2: Base data:

A second ES will be supplied with this paper, once published. In an Excel table, the total numbers, mass, and frequencies of occurrence, as well as %N, %M, %FO and IRI will be supplied for each prey guild and each prey species. This (lengthy and wide) table is not reproduced here.