The semi-enclosed tidal bay Eastern Scheldt in the Netherlands: porpoise heaven or porpoise prison?

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Abstract: Harbour porpoises (*Phocoena phocoena*), the smallest of cetaceans, need to consume quantities of prey that amount to ca. 10% of their own body mass per day. They mostly feed on small fish, with the main prey species differing geographically. The $\delta^{13}C$ muscle signature of harbour porpoises sampled in the Eastern Scheldt, SW Netherlands, has indicated that animals tend to stay here for some time after they entered this semi-enclosed basin, and that they thus must feed on local prey. A relatively low primary production and low local fish biomass raises the question what there is for harbour porpoises to feed on in the Eastern Scheldt. This study reveals that there are no big differences between biological or stranding parameters of harbour porpoises found dead in the Eastern Scheldt compared with the adjacent North Sea (the "Voordelta"), but some differences in diet were found. Still, despite the low fish biomass in the Eastern Scheldt, no evidence of excessive harbour porpoise starvation was found. The main prey species for juvenile porpoises, both in the North Sea and in the Eastern Scheldt, were gobies. Gadoids were important prey for adults in both regions. Gadoid prey was supplemented by gobies and sandeels in the North Sea, and by squid and estuarine roundfish in the Eastern Scheldt. Our results demonstrate that harbour porpoises that stay in the Eastern Scheldt for a longer period of time may develop specialised feeding skills, to cope with the relatively poor prey base. Juveniles on the other hand, must settle for small and lean prey (gobies and small sepiolids) and may face competition from adults.

Keywords: Phocoena phocoena, stomach content analysis, prey composition, geographical differences, ecological trap.

Introduction

The harbour porpoise (*Phocoena phocoena)* is the most abundant, and also the smallest cetacean living in NW Europe. Cetaceans have a much higher energy metabolism than similarly sized land mammals, with the smallest species having the highest demands (Kanwisher & Sundnes 1965). Therefore, harbour porpoises need to feed at excessively high rates (Wisniewska et al. 2016) and must consume about 10% of their body mass of food per day to sustain themselves (Kastelein 1998).

Small and abundant fish species are the main prey of harbour porpoises (Santos & Pierce 2003). The prey spectrum, and hence the prey quality, varies geographically. For instance, harbour porpoises in the Kattegat and Skagerrak rely heavily on clupeids which have a high

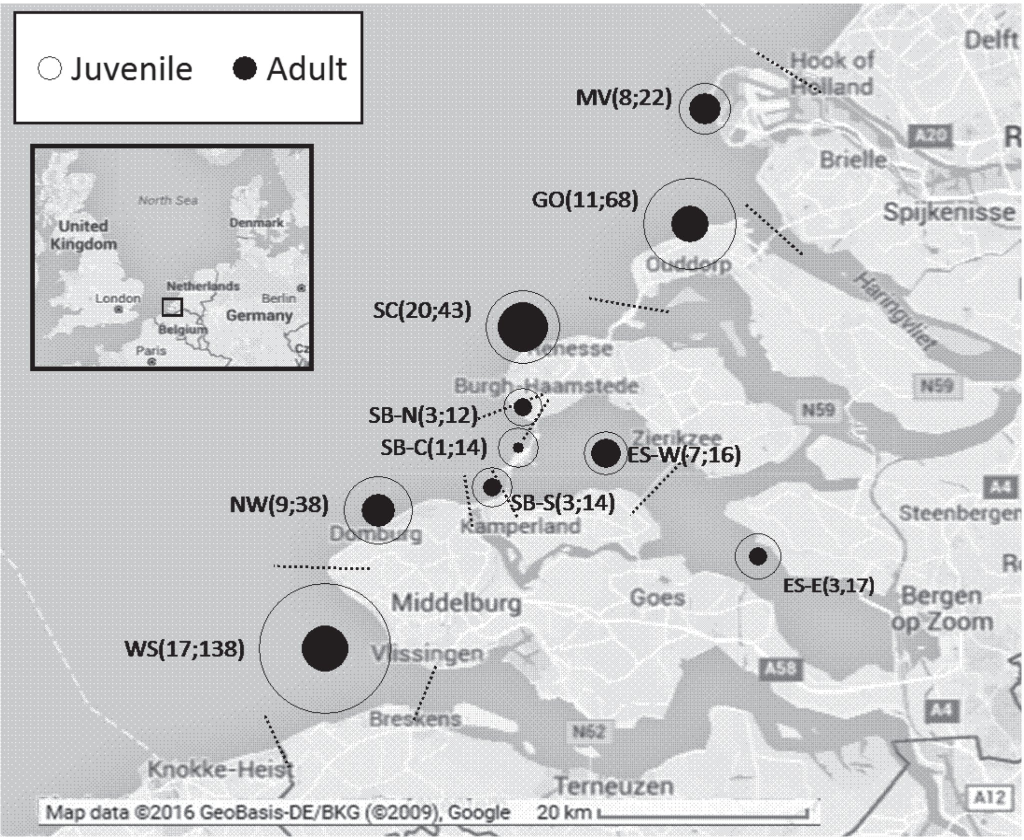

Figure 1. Study area. Stranded harbour porpoises (n-adults; n-juveniles 2006-2015) in geographically divided groups: MV = Maasvlakte, GO = Goeree, SC = Schouwen, SB-N = Storm surge Barrier-North, SB-C = Storm surge barrier-Central, SB-S = Storm surge barrier-South, NW = North-west Walcheren, WS = Western Scheldt estuary, ES-W = Eastern Scheldt-West, ES-E = Eastern Scheldt-East.

energy density, while porpoises in the eastern North Sea feed mainly on gobies and gadoids which are much leaner prey (Börjesson et al. 2003, Leopold & Meesters 2015).

Although harbour porpoises may move around a great deal in the open seas and oceans, and may thus encounter different prey in different seasons, porpoises living in a semi-enclosed tidal bay, the Eastern Scheldt (SW Netherlands), have been shown to have a distinct, local $\delta^{13}C$ muscle signature, indicating prolonged feeding on local prey (Jansen et al. 2013). Prolonged feeding in one place could be indicative either of good feeding conditions, or the impossibility to leave. Unless porpoises were born in the Eastern Scheldt, they must have entered the tidal bay from the outside, through openings in the storm surge barrier (Jansen et al. 2013). A relatively low fish biomass in the Eastern Scheldt, as compared to adjacent North Sea waters (Tulp 2015) in combination with long residence times of porpoises would suggest that the Eastern Scheldt is an ecological trap (Jansen et al. 2013).

Primary production within the Eastern Scheldt has been steadily decreasing since the onset of measurements and has halved between 1995 and 2010 (Smaal et al. 2013). This trend is reflected in higher trophic levels. With low nutrient concentrations and large stocks of grazing bivalves (Smaal et al. 2013), relatively low quantities of the local primary production may be available to secondary producers and top predators, such as fish and harbour porpoises. Total fish biomass in the Eastern Scheldt is comparatively low and shows a decreasing trend, in contrast to the situation in the North Sea (Tulp 2015). In this study, we aim to find out if the diet of harbour porpoises in the Eastern Scheldt is different from that of their counterparts in the adjoining part of the North Sea, by comparing the stomach contents of stranded harbour porpoises, as well as prey fish densities in these two areas.

Methods

Study area

The Eastern Scheldt (SW Netherlands, figure 1) is a former open estuary. It was turned into a semi-enclosed tidal bay by the construction of a storm surge barrier, that was built from 1979-1986. This barrier has 62 openings, each 42 m wide, that allow water to flow through, albeit at a reduced rate. Two auxillary compartment dams, built further upstream from 1977-1987, have closed off the fresh water input through the rivers Scheldt and Rhine. The Eastern Scheldt now covers a surface of 350 km^2, including 118 km^2 of tidal flats, and it has a smaller tidal range, higher salinity and water transparancy, a longer water residence time and lower nutrient concentrations than the former open estuary (Nienhuis & Smaal 1994, Jansen et al. 2013, Smaal et al. 2013). The area is sub-divided in an Eastern and Western compartment, separated by a 5 km long bridge ('Zeelandbrug'), built on pillars that are 72.5-95 m apart. The openings in both the outer storm surge barrier and the inner bridge are large enough for harbour porpoises to pass through and porpoises can be found in the Eastern Scheldt on either side of the bridge.

Yearly total population counts (2009-2015, conducted between May and September) of harbour porpoises in the Eastern Scheldt suggest a population size of about 30-60 animals (rugvin.nl). Numbers in the North Sea are considerably larger; two aerial line transect surveys in August 2009 off the Dutch mainland coast (including the Voordelta) and in the Belgian sector of the North Sea have yielded estimated population sizes of 5795 (Scheidat et al. 2012) and 186 (Haelters et al. 2011), respectively, while subsequent surveys in July 2010, 2014 and 2015 off the Netherlands produced estimates 10,098, 18,778 and 11,674 animals, respectively (Geelhoed et al. 2015).

The stomach contents of stranded, dead harbour porpoises found in the Eastern Scheldt from 2006 to 2015 were compared with those of porpoises found along the shores of the North Sea, between Hook of Holland and the Belgian border, further referred to as North Sea, in the same period.

Available fish biomass and sizes of fish

Fish biomass data (kg.ha^{-1} per fish species and length class) were obtained from standard annual demersal fish surveys of the Eastern Scheldt and the adjacent North Sea waters (Voordelta), 2006-2015 (data taken from Tulp (2015) and Dr Ingrid Tulp, Wageningen Marine Research, personal communication). In these years the surveys in the Voordelta were mostly done in the third week of October, while surveys in the Eastern Scheldt were done circa five weeks earlier, around mid-September. Fish growth between the two sampling periods was assessed for herring (*Clupea harengus*) and whiting (*Merlangius merlangus*), using daily fyke catches at Texel over the years 2006-2015 (waddenzeevismonitor.nl/monitoring.html; data courtesy Dr Henk van der Veer, NIOZ). We restricted the analysis of relative fish abundance to roundfish, as these comprise 97% of the prey mass taken by harbour porpoises in the Netherlands (Leopold & Meesters 2015). Biomass data for squid and other invertebrates were not available. Total lengths of fish, both found in the fish survey data and in the stomachs of the porpoises, were assigned to 1 cm (below) length classes, with a length between e.g. 10.0 and 10.99 cm assigned to length class 10, etc.

Stranded harbour porpoises

A total of 505 dead stranded harbour porpoises were collected in our study area between 2006 and 2015 by members of the Dutch strandings network. The carcasses were transported to the Department of Pathobiology, Faculty of Veterinary Medicine, Utrecht University, for necropsy following the protocol of Kuiken & Garcia Hartmann (1991). Porpoise age was assessed as neonate (*n*=41; these were omitted from the analyses as these were still fully dependent on their lactating mothers), juvenile or adult. Non-neonates <130 cm were classed as juveniles and animals ≥130 cm as adults, unless gonad development showed otherwise. Over the years, 43 non-neonate porpoises were collected in the Eastern Scheldt and 421 along the coastline of the North Sea waters.

Age class, stranding date and location were recorded for each animal. Carcass freshness was scored using the Decomposition Condition Code (DCC; 1 (stranded (probably) alive) to 5 (very old, mummified carcass)) for each carcass. The Nutritional status (in terms of the Nutritional Condition Code, NCC; from 1 (very fat and muscular) to 6 (extremely emaciated); Kuiken & Garcia Hartmann 1991) of the collected porpoises and cause of death was established only for reasonably fresh specimen (DCC 1-3). Figure 1 depicts the geographical distribution of harbour porpoises strandings in the Eastern Scheldt and in the adjacent North Sea waters.

Stomach content analysis

Stomach contents of juvenile (North Sea: *n*=349; Eastern Scheldt: *n*=33) and adult (North Sea: *n*=72; Eastern Scheldt: *n*=10) animals were analysed separately, because diet is known to vary with porpoise age (or length; Leopold & Meesters 2015). Stomach contents were analysed using the methods as outlined in Leopold et al. (2015). In brief, stomach contents were washed and prey hard parts were collected under a dissecting microscope, identified to the lowest possible taxon, measured, their size corrected for wear and paired if possible. From these measurements, prey sizes and masses were estimated (Leopold et al. 2001). All prey species were assigned to one of the following prey groups; clupeids, sandeels, gobies, gadoids, other demersal roundfish, pelagic roundfish, estuarine roundfish, flatfish, squid, and other invertebrates (cf. Leopold & Meesters 2015). %FO (frequency of occurrence; stomachs containing a certain prey group, as a percentage of all stomachs), %N (number of prey; the number of individuals of one prey group, as a percentage of all prey found in all stomachs) and %M (mass of prey; the total reconstructed mass of one prey group, as a percentage of the total prey mass in all stomachs) were calculated for all prey groups. This was done separately for the North Sea and the Eastern Scheldt and separately for juveniles and adults, across all porpoises within each sample. As these three indices each provide a different representation of the diet, they were also combined in an index of relative importance IRI (cf. Pinkas et al. 1971) in which %M replaces % prey volume in the original IRI (cf. Carrassón et al. 1997):

$$IRI = (\%N + \%M)^* \%FO$$

The value of IRI is a rather meaningless figure, with the unit $\%^2$, and is only fit for comparing the relative contributions of different prey groups within a sample of predators. Therefore, we used the percentage IRI, which is a dimensionless number between 0 and 100:

$$\%IRI = (IRI_x/\Sigma(IRI_{a-z}))^*100,$$

being the IRI of prey group x divided by the sum of the IRIs of all (a…z) prey groups * 100 (cf. Carrassón et al. 1997).

Statistical analysis

Differences in porpoise lengths between the North Sea and the Eastern Scheldt, for juveniles and adults separately, were assessed using the two-sample *t*-test allowing unequal variances. Harbour porpoises with known Decomposition Condition Codes (DCC) and Nutritional Condition Codes (NCC) were divided in the same regional/age groups and these data were also tested with a two-sample *t*-test allowing unequal variances. Before testing for differences in diet between the North Sea and the Eastern Scheldt, the possibility of latitudinal differences in diet was explored by regressing %M for each prey group per individual porpoise against the latitude of the stranding location (North Sea strandings only).

The total reconstructed biomass per prey group was calculated for each harbour porpoise. Initially, we considered eight groups of porpoises, based on age class (juveniles vs adult), season (summer (May-October) vs winter (November-April) and region (North Sea vs Eastern Scheldt) of stranding. Months with no porpoise strandings in one of the two regions were excluded from the analysis. For this reason, adults stranded in winter could not be analysed. Primer (Clarke & Gorley 2015) version 7.0.7 was used to perform a multivariate analysis. First the data was 4th root transformed and the Bray-Curtis dissimilarity was calculated of each matrix. Differences in diet between groups were assessed using Permanova (Anderson 2001, McArdle & Anderson 2001), with variable region (North Sea vs Eastern Scheldt).

Table 1. Numbers and sizes (average with standard deviation, in cm) of herring (<16 cm) and whiting (<26 cm) in daily catches at Texel, 2006-2015 for September and October.

Month	Species	*n*	AVG	STD
September	Herring	158,834	6.66	0.95
October	Herring	46,630	8.72	1.67
September	Whiting	137	17.07	2.92
October	Whiting	407	19.14	2.92

Average fish length was calculated per prey group for fishes caught between 2006 and 2015 during the annual surveys both in the North Sea and the Eastern Scheldt. Differences in fish lengths between the two regions were assessed using two-sample *t*-tests allowing unequal variances. Significance level $\alpha=0.05$ was used as a criterion for effect.

Results

Available prey

Prey fish biomass per surface area in the Eastern Scheldt was much lower than in the North Sea, across a wide variety of taxa (figure 2). Moreover, herring and whiting were found to be smaller in the Eastern Scheldt as compared to the North Sea, but this was probably due to fish growth between September, when the Eastern Scheldt was sampled, and October, when the North Sea was sampled. Average sizes of herring and whiting in the daily fyke catches at Texel showed similar differences between September and October (table 1).

Several within-group differences were found between the Eastern Scheldt and the North Sea. For instance, within the gobies, the comparatively large black goby (*Gobius niger*) comprised 12% of the biomass in the Eastern Scheldt (vs virtually zero in the North Sea). Within the gadoids, bib (*Trisopterus luscus*) made up 52% of the biomass in the Eastern Scheldt (vs 5% in the North Sea, while the reverse was true for whiting: 40% vs 89%). Within the clupeids, sprat (*Sprattus sprattus*) was virtually absent from the East-

Table 2. Causes of death for the animals sampled in the North Sea and Eastern Scheldt. Acute deaths include seal victims and fisheries bycatches; non-acute deaths include various diseases and emaciation.

Region	Unknown	Acute	Non-acute
North Sea	252 (60%)	87 (21%)	82 (19%)
Eastern Scheldt	25 (58%)	8 (19%)	10 (23%)

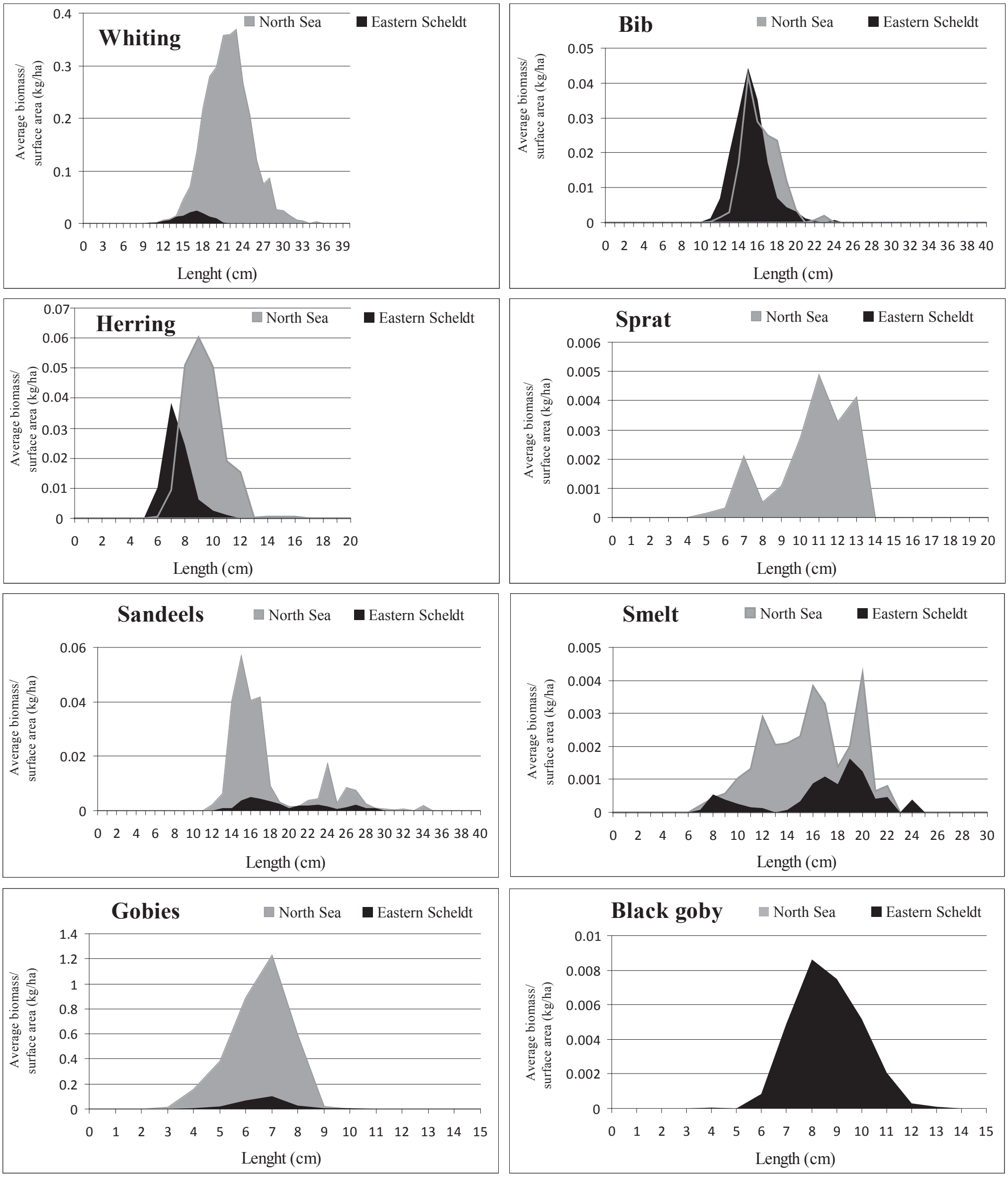

Figure 2. Average (2006-2015) fish biomass (kg·ha^{-1}), for the most important prey species and prey groups, per cm (below) length class for the North Sea (grey) and the Eastern Scheldt (black). Note different scalings.

ern Scheldt samples while it made up 8.4% of clupeid biomass in the North Sea catches. In the group of estuarine roundfish, smelt (*Osmerus eperlanus*) contributed relatively less to the biomass in the Eastern Scheldt than in the North Sea, due to the dominance of sand smelts (*Atherina presbyter*) and pipefishes (Syngnathidae) in the Eastern Scheldt samples. However, as energy densities of different members within fish families are generally rather similar, this probably does not have large consequences for the porpoises.

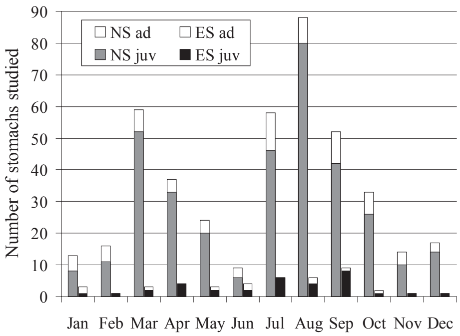

Figure 3. Seasonal distribution of harbour porpoise strandings for the North Sea (grey) and Eastern Scheldt (black), separately for adults (open) and juveniles (closed), total *n*=464 (2006-2015).

Seasonality in strandings

Overall, 464 porpoises were available for stomach content analyses, of which 421 came from the North Sea coastline. These show a bi-modal pattern in stranding time (figure 3), with peak numbers in spring (March/April) and summer (July through September). The temporal distribution of strandings in the Eastern Scheldt more or less follows that of the pattern found in the North Sea, but with only 43 porpoise carcasses collected from the Eastern Scheldt, a peak in spring strandings is not apparent.

Age, gender, condition, cause of death

Not all porpoises that stranded in the Eastern Scheldt or in the Voordelta could be collected and studied, therefore the characteristics of collected carcasses were compared to avoid bias due to incomplete sampling. Females comprised a minority among the stranded porpoises in both areas with 40.9% and 39.5% of the collected harbour porpoises, in the North Sea and the Eastern Scheldt, respectively. Most animals were juveniles: 83% among the North Sea strandings and 77% in the Eastern Scheldt. Animals classified as adults measured 145.5 ± 9.5 cm (*n*=63; range: 128-164 cm) in the North Sea and 146.7 ± 10.6 cm (*n*=10; range: 130-161 cm) in the Eastern Scheldt; for juveniles these figures were respectively 109.2 ± 10.6 cm (*n*=313; range: 81-138 cm) and 105.3 ± 10.8 cm (*n*=29; range: 85-127 cm) (*t*-tests: $P>0.05$ for both age classes). DCC and NCC did not differ significantly between the two regions (*t*-tests; $P>0.05$) and with an overall average DCC of 3.33, most carcasses were quite decomposed. This hampered establishing cause of death, which remained unknown in 277 (59.7%) cases. Among the porpoises for which a cause of death could be established, 56% of the animals had died from disease or starvation in the Eastern Scheldt (table 2). In the North Sea this percentage was 49%. From these comparisons we conclude that porpoises sampled in the two areas were similar, with only a slight difference in age composition (slightly more juveniles among the animals sampled in the North Sea).

Diet

Of the 464 examined stomachs, 369 contained prey remains and 95 were empty (20%). Among the animals found in the North Sea, 89 had empty stomachs (21%). In the Eastern Scheldt six out of 43 (14%) porpoises had empty stomachs. The probability of finding empty stomachs peaked in summer (July/August; figure 4).

Among the porpoises that were found with prey remains in their stomachs, both juveniles and adults showed a bi-modal pattern in strandings in the North Sea (figure 5). Peak numbers were found in early spring and in late summer/early autumn. Juveniles in the Eastern Scheldt showed a similar pattern. Numbers of adults with prey remains in their stomachs found in the Eastern Scheldt were too small to evaluate a temporal pattern.

No significant latitudinal trends in diet (%M per prey group) were found along the North Sea coastline, so this region will be treated as one, and compared to the Eastern Scheldt in

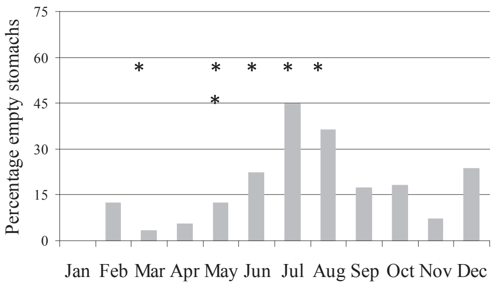

Figure 4. Percentage of empty stomachs among porpoises collected along the North Sea coastline (grey bars, *n*=89), and individual cases in the Eastern Scheldt (*, *n*=6).

the analyses. The %FO, %N and %M for all prey groups, for juveniles and adults in the North Sea and the Eastern Scheldt are given in tables 3, 4 and 5. Gobies dominated juvenile diets, in both summer and winter and in both the North Sea and the Eastern Scheldt, but particularly in the latter. In the North Sea, juvenile porpoises had eaten (in terms of prey mass) much more gadoids, clupeids and sandeels, while squid was far more important prey in the Eastern Scheldt. In terms of energy density of prey, North Sea juvenile porpoise diet (%M) included 24% (summer) to 33% (winter)

Table 3. Energy density, %FO, %N and %M for every prey group found in juveniles stranded during the summer (Jun-Oct) in the North Sea and the Eastern Scheldt. Relative energy densities of prey after Pedersen & Hislop (2001), MacLeod et al. (2007), Spitz et al. (2014), Leopold & Meesters (2015).

Juvenile summer		North Sea			Eastern Scheldt		
Prey group	Energy density	%FO (137)	%N (8913)	%M (33550)	%FO (18)	%N (5280)	%M (12599)
Gobies	low	65.69	87.78	22.75	77.78	96.27	58.37
Gadoids	low	34.31	3.25	49.14	38.89	0.30	4.77
Clupeids	high	5.11	0.11	0.19	11.11	0.15	0.54
Sandeels	high	22.63	4.23	12.81	22.22	0.09	0.45
Estuarine roundfish	high	8.76	1.44	11.13	33.33	1.04	4.09
Pelagic roundfish	high	0.00	0.00	0.00	0.00	0.00	0.00
Other demersal roundfish	low	1.46	0.02	0.04	5.56	0.02	0.04
Flatfish	low	0.73	0.01	0.17	5.56	0.06	0.08
Squid	low	33.58	2.55	2.38	50.00	2.05	31.66
Other invertebrates	low	18.98	0.61	1.40	5.56	0.02	0.00

Table 4. Energy density, %FO, %N and %M for every prey group found in juveniles stranded during the winter (Nov-Apr) in the North Sea and the Eastern Scheldt.

Juvenile winter		North Sea			Eastern Scheldt		
Prey group	Energy density	%FO (120)	%N (46,553)	%M (103,702)	%FO (10)	%N (2311)	%M (7622)
Gobies	low	85.00	93.13	34.58	90.00	94.81	72.98
Gadoids	low	35.83	0.86	23.63	30.00	0.65	17.69
Clupeids	high	49.17	1.62	13.00	30.00	0.26	3.07
Sandeels	high	40.00	2.12	10.14	60.00	1.47	3.89
Estuarine roundfish	high	35.00	0.95	8.28	20.00	0.22	0.61
Pelagic roundfish	high	15.83	0.22	1.99	20.00	1.04	1.09
Other demersal roundfish	low	3.33	0.06	0.49	0.00	0.00	0.00
Flatfish	low	5.00	0.10	0.33	0.00	0.00	0.00
Squid	low	21.67	0.55	7.41	20.00	1.17	0.51
Other invertebrates	low	30.83	0.39	0.13	40.00	0.39	0.16

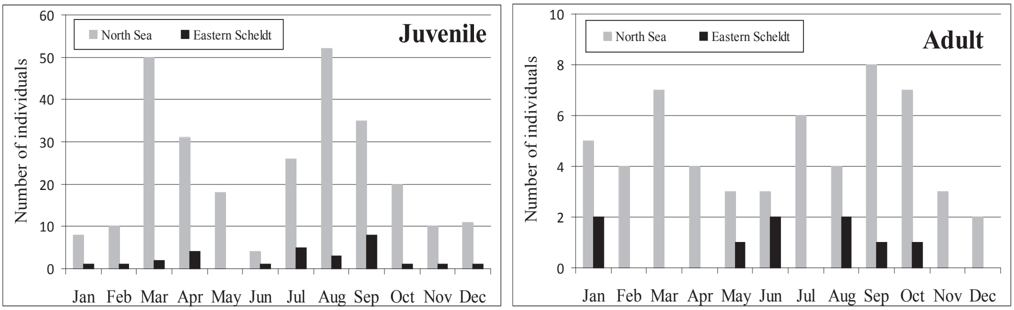

Figure 5. Stranded juvenile (left panel) and adult (right panel) harbour porpoises with prey remains in their stomach, from the North Sea (grey) and Eastern Scheldt (black).

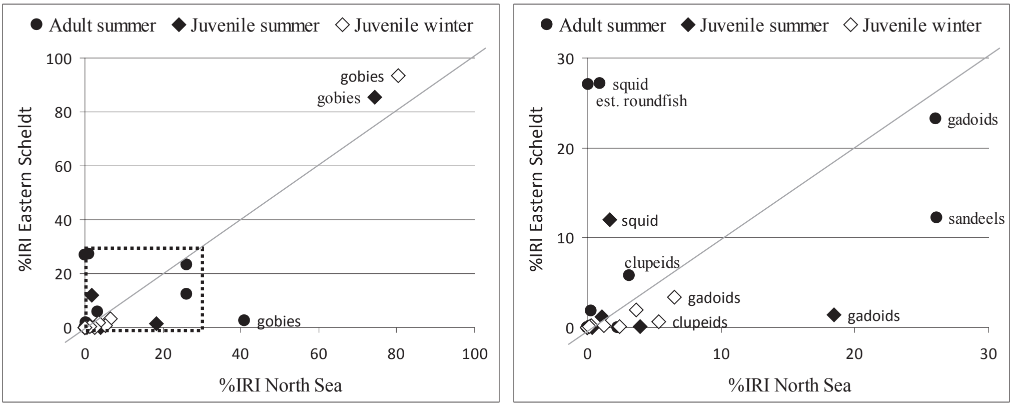

Figure 6. Left panel: percentage index of relative importance (%IRI) per prey group found in porpoises stranded in the North Sea against the %IRI per prey group found in porpoises stranded in the Eastern Scheldt. Right panel: zoomed in on 0-30%IRI.

Table 5. Energy density, %FO, %N and %M for every prey group found in adults stranded during the summer (May-Oct, except July) in the North Sea and the Eastern Scheldt.

Adult summer		North Sea			Eastern Scheldt		
Prey group	Energy density	%FO (25)	%N (3643)	%M (35961)	%FO (7)	%N (349)	%M (2165)
Gobies	low	48.00	68.21	13.21	42.86	4.01	0.61
Gadoids	low	48.00	3.71	48.04	57.14	4.01	25.90
Clupeids	high	20.00	4.09	10.89	28.57	1.15	13.78
Sandeels	high	68.00	20.29	16.36	28.57	6.30	25.32
Estuarine roundfish	high	8.00	0.27	0.50	28.57	44.41	25.39
Pelagic roundfish	high	20.00	0.69	10.17	0.00	0.00	0.00
Other demersal roundfish	low	4.00	0.03	0.14	0.00	0.00	0.00
Flatfish	low	4.00	0.03	0.01	0.00	0.00	0.00
Squid	low	36.00	1.92	0.61	42.86	38.11	8.58
Other invertebrates	low	36.00	0.77	0.07	57.14	2.01	0.42

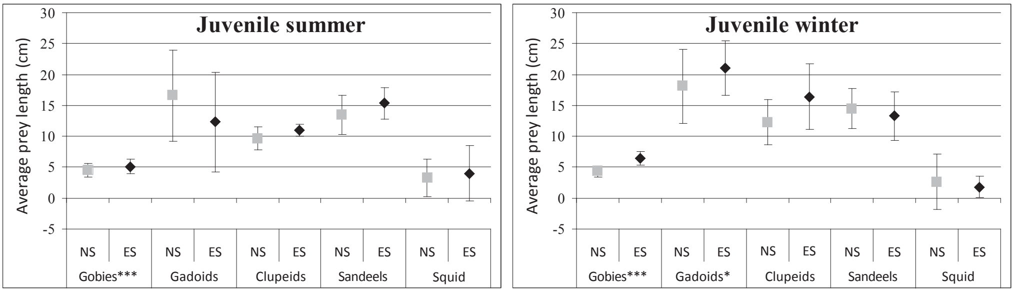

Figure 7. Average prey length (± standard deviation) for the main prey groups eaten by juveniles during the summer (left panel) and winter (right panel), for the North Sea (NS) and the Eastern Scheldt (ES). T-tests; * = *P*<0.05, ** = *P*<0.01, *** = *P*<0.001.

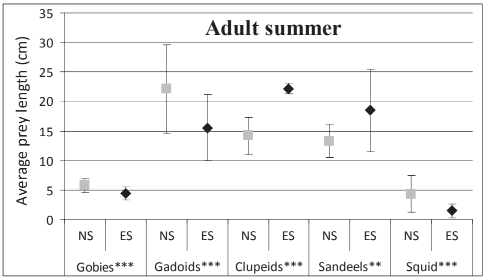

Figure 8. Average prey length (± standard deviation) for the main prey groups eaten by adults during the summer, both for the North Sea (NS) and the Eastern Scheldt (ES). T-tests; * = *P*<0.05, ** = *P*<0.01, *** = *P*<0.001.

high-energy prey, compared to only 5% and 9%, respectively in the Eastern Scheldt.

In contrast, adult diet (summer only) had a much higher energy density in the Eastern Scheldt than in the North Sea, as in the latter overall prey mass has relatively high contributions of both low-energy gobies and gadoids. Sandeels and estuarine roundfish (particularly sand smelt), and to a lesser extent, clupeids, together contributed much more to the overall prey mass in the Eastern Scheldt than in the North Sea, but note that sample sizes are small (7 animals from the Eastern Scheldt and 25 from the North Sea). Like for the juveniles, squid was a relatively important prey for adults in the Eastern Scheldt.

Within-group variation in prey found in individual porpoises was large, and the diets between the North Sea and the Eastern Scheldt did not differ significantly between any age or seasonal groups (table 6).

However, comparing the %IRI of North Sea and Eastern Scheldt diets (figure 6) shows that gobies are by far the most important prey for juveniles, in both regions. Gobies are also important to adults in the North Sea in summer, even though the total contribution to prey mass was not very large (table 5). Zooming in on the less important prey (figure 6, right panel), we find that gadoids are relatively important to juveniles in the North Sea (particularly in summer), while squids are more important in the Eastern Scheldt. Gadoids are almost equally important to adults in both regions, but North Sea adults had eaten comparatively many sandeels, while adults in the Eastern Scheldt relied more on squid and sand smelt.

Prey size

Juveniles tended to eat slightly larger gobies in the Eastern Scheldt, as compared to the North Sea (figure 7). Sizes of gadoids ingested by juveniles in the Eastern Scheldt in winter were larger than in the North Sea, whereas the difference in summer was not significant. Sizes of other prey did not differ significantly between the two regions, in any season.

Among adult porpoises, between-region prey sizes were different in all main prey groups

A harbour porpoise in the Eastern Scheldt with, in the background, the storm surge barrier. *Photo: W.J. Strietman.*

Table 6. Permanova table of results, on the data for all harbour porpoise stomachs with prey remains stranded in the devised seasons.

Age	Season	Variable	df	Pseudo-F	*P* (perm)	Unique perms
Juvenile	Summer	Region	154	1.0364	0.375	998
Juvenile	Winter	Region	129	0.59984	0.725	998
Adult	Summer	Region	31	1.6876	0.119	999

(only summer tested). Gobies, gadoids, and squids eaten in the Eastern Scheldt were smaller than in the North Sea, while energy-rich clupeids and sandeels were larger (figure 8).

Conclusion and discussion

The Eastern Scheldt has an impoverished fish fauna. Extensive surveys (2006-2015, Tulp 2015) showed that the biomass per surface area of the most import prey groups for harbour porpoises, i.e. gobies, gadoids, clupeids and sandeels in the Eastern Scheldt, were only 7.5%, 9.9%, 13.8% and 36.8%, respectively, of the biomass in the adjacent North Sea. Sprat was almost completely lacking from the Eastern Scheldt (figure 2). On the other hand, estuarine species like sand smelt and black goby were much more abundant in the Eastern Scheldt, and, based on prey remains found in the harbour porpoises, so were small sepiolids (squid). The latter, however, may also have been taken relatively often by porpoises in the Eastern Scheldt, for want of other prey.

Even though there is apparently less fish available in the Eastern Scheldt, the harbour porpoises that had stranded here did not differ from those found along the North Sea shorelines in terms of their average nutritional condition and length, gender and age ratios and causes of death. Porpoises in the Eastern Scheldt were thus remarkably similar to those sampled from the North Sea in these respects. It should be noted, however, that stomach contents of dead stranded animals were studied, which may present a biased view of the food intake of healthy animals. However, given that the porpoises in our two samples had largely the same characteristics, any bias would likely apply to both groups.

No differences were found in average reconstructed prey masses per stomach and the percentage empty stomachs between the

North Sea and the Eastern Scheldt. However, prey composition differed to some extent. Juvenile porpoises in the Eastern Scheldt took relatively less gadoids and clupeids than their conspecifics in the North Sea. In summer this was (partly?) compensated by a higher importance of squid in the diet. Overall, diet of juveniles in the Eastern Scheldt was dominated by small, lean prey, i.e. gobies and small squid. This resulted in a much leaner diet in the Eastern Scheldt, where most prey taken was both small and low in energy content.

In contrast, relatively few goby remains were found in stomachs of adult porpoises in the Eastern Scheldt. Sandeels were also rarely taken here, but this was compensated by a comparatively high importance of energy-rich sand smelts (estuarine roundfish). Like in juveniles, adults had also taken rather large quantities of squid in the Eastern Scheldt. With similar proportions of gadoids in the diets, adults in the Eastern Scheldt had a diet that was comparable to, or even of a higher quality (higher overall energy density of prey) than, the diet in the North Sea. Note, however, that numbers of adults available for study in the Eastern Scheldt were small. Tentative differences in diets of adults in the Eastern Scheldt as compared to diets in the North Sea may thus have been due to a low sample size, and more adults, particularly from the Eastern Scheldt need to be studied to resolve the question whether such differences are real.

We conclude that juvenile porpoises that find themselves in the Eastern Scheldt must survive here on a lean diet. With time, they may get a very good knowledge of local prey hotspots within the Eastern Scheldt and this may help them to cope with the available prey. Adults did not have an average diet that was inferior to that in the adjacent North Sea. A photo identification study in the Eastern Scheldt has shown that some individual porpoises survived here over a range of years, with one individual recorded over a period of eight years (Bakkers et al. 2016). Once settled in the Eastern Scheldt, harbour porpoises may become specialists, that can deal with the local feeding conditions. They take advantage of local specialties, like abundant small squid and sand smelts, while still being able to find enough gadoids to sustain themselves. The latter may seem remarkable, as gadoid abundance was found to be only 9.9% of that in the adjacent North Sea. Therefore, adult porpoises might be very good in catching these gadoids in the Eastern Scheldt, e.g. around artificial hard structures such as bridge piles, which are not sampled in the fishery surveys. Alternatively, a 90% reduction in gadoid presence has no effect on the abilities of porpoises to catch them, i.e. gadoids are just superabundant in the North Sea, from a porpoise perspective.

Juveniles may have less access to gadoid prey in the Eastern Scheldt, possibly because these fishes are too hard for them to catch, or because of competition with adult porpoises. Although juveniles in the Eastern Scheldt may thus face a prey base consisting mainly of small and lean prey, and possibly competition with adults, their average body condition did not differ from that of animals stranded along the North Sea coastline, suggesting that also the juveniles are able to cope with the prevailing conditions in the Eastern Scheldt.

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Samenvatting

De Oosterschelde: een bruinviswalhalla of bruinvisgevangenis?

Bruinvissen (*Phocoena phocoena*) zijn de kleinste walvisachtigen. Vanwege hun geringe formaat en koude leefomgeving hebben ze circa 10% van hun eigen lichaamsgewicht aan voedsel per dag nodig om te overleven. Bruinvissen eten vooral kleine vissen, maar hun stapelvoedsel varieert per regio. In het Kattegat en Skagerrak eten ze bijvoorbeeld veel vette haringachtigen, terwijl bruinvissen in de Noordzee voornamelijk relatief magere grondels en kabeljauwachtigen eten. Van bruinvissen die de Oosterschelde binnen zwemmen via de openingen in de Oosterscheldekering is bekend dat zij langere tijd (weken, maanden of zelfs jaren) in de Oosterschelde blijven en dus overleven op het lokale prooiaanbod. De visstand in de Oosterschelde is echter ongeveer tien keer lager dan in de aangrenzende Noordzee, wat de vragen oproept waarom bruinvissen niet terug zwemmen naar de Noordzee, of ze wel voldoende te eten kunnen vinden in de Oosterschelde en wat hier de belangrijkste prooisoorten zijn. Daarom wordt in dit onderzoek gekeken wat het dieet van de bruinvissen in de Oosterschelde is, in vergelijking met het dieet van bruinvissen in de Voordelta (Hoek van Holland tot de Belgische kust).

Drie-en-veertig dode bruinvissen, gestrand tussen 2006 en 2015 in de Oosterschelde, zijn onderzocht, waarvan er 37 (28 juveniele en 9 volwassen dieren) visresten in hun maag hadden. Uit dezelfde periode zijn 421 (276 juveniele en 56 volwassen dieren met prooiresten) gestrande bruinvissen uit de Voordelta onderzocht. De bruinvissen uit de Oosterschelde en de Voordelta hadden een overeenkomstige leeftijdssamenstelling, geslachtverhouding, conditie en doodsoorzaken, maar vertoonden wel kleine verschillen in hun dieet. Ondanks de relatief lage visstand in de Oosterschelde is er geen bewijs gevonden van massale verhongering onder de gestrande bruinvissen in deze voormalige zeearm. Zowel in de Oosterschelde als in de Voordelta waren grondels en kabeljauwachtigen de belangrijkste prooien voor bruinvissen. Wel werden er verschillende soorten gegeten. In de Noordzee was wijting de favoriete kabeljauwachtige prooi; in de Oosterschelde waren dit bolken (steenbolk en/of dwergbolk). Sprot en zandspiering (vette vis) werden in de Oosterschelde nauwelijks gegeten, maar hier stonden wel een aantal estuariene soorten op het menu, zoals zwarte grondel en grote koornaarvis. Ook werden in de Oosterschelde relatief veel kleine inktvissen gegeten. Onze analyse laat zien dat bruinvissen die langere tijd in de Oosterschelde overleven hun dieet enigszins aanpassen om genoeg prooien van voldoende kwaliteit te kunnen vangen in deze relatief prooi-arme omgeving. Juveniele bruinvissen daarentegen, eten vooral magere en kleine prooien en zijn wellicht in competitie met volwassen bruinvissen.

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