Follow the fish: Do Harbour Porpoises (*Phocoena phocoena*) respond to better water quality up rivers?

Mardik F. Leopold, Liliane Solé, Lonneke L. IJsseldijk, Elze Dijkman, Thierry Jauniaux & Jan Haelters

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Abstract

As rivers are being cleaned, life is returning to their estuaries and higher parts. Diadromous fish species are on the increase again in many major rivers discharging into the North Sea. Harbour porpoises (*Phocoena phocoena*), being predators of fish, have been noted to return to North Sea estuaries and rivers as well. Their mere presence in these rivers, however, is no proof that these small cetaceans actually exploit the returning fish. Diet studies of the porpoises found up-river can shed a light on their prey choice and ecological role in the system. Here we show that a major part of the diet of porpoises found in the river Western Scheldt (2007-2014) comprises diadromous fish, particularly juvenile European smelt (*Osmerus eperlanus*). Smelt contributed 46% to porpoise diet (% prey mass) in the Western Scheldt, against 14% in the river mouth and 3% in the North Sea at either side of the river mouth. Even though porpoise numbers are increasing in the river, not all is well, however. Animals found dead on the river banks were generally in a poor nutritional condition and had an elevated probability of being found dead with an empty stomach. Animals swimming very far upstream sometimes braved major water works such as sluices, which might have hindered their return to the sea. Relatively many animals were reported dead later, but to date, too few have been collected for stomach content analysis to make a valid comparison between diets in the lower and higher parts of this river system possible.

Keywords: diet, *Osmerus eperlanus*, river restoration, diadromous fish, habitat quality

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Introduction

Around the North Atlantic, the combination of habitat degradation, pollution and overfishing has stripped major rivers of their diadromous fish populations (de Groot 2002; Lotze 2005; Limburg & Waldman 2009). Conversely, river restoration programmes have resulted in the cautious come-back of several of the impacted fish species. Along the eastern North Sea and Channel seaboard, some species, such as European smelt *Osmerus eperlanus* (Linnaeus, 1758) (further: smelt), shads *Alosa sp.* and several salmonids are slowly returning into several rivers (Raat 2001; Maes *et al.* 2007, 2008; Buysse *et al.* 2008; Rochard *et al.* 2009; Breine & Van Thuyne 2014a,b, 2015). In their wake, predators like the harbour porpoise *Phocoena phocoena* may be expected to follow. Indeed, numbers of sighted porpoises have greatly increased in several estuaries along the eastern North Sea in recent years: in Germany in the rivers Ems, Jade, Weser and Elbe (Wenger & Koschinski 2012; GRD e.V. 2013) and in The Netherlands in the Marsdiep, (western Wadden Sea: Boonstra *et al.* 2013; IJsseldijk *et al.* 2015), the Eastern Scheldt (Zanderink & Osinga 2010; Jansen *et al.* 2013), and the river Scheldt, all the way into its upper parts, in Belgium. Here, Haelters (2013) reported a remarkable influx of harbour porpoises in spring 2013, coinciding with peak catches of smelts (Breine & Van Thuyne 2014a) and speculated that the two phenomena may be linked. If this would be the case, the porpoises should prey on this returning anadromous fish species. Alternatively, the recent incursions into these estuaries may be merely linked to an increased presence of harbour porpoises in the southern North Sea at large (Haelters & Camphuysen 2009; Wenger & Koschinski 2012; Hammond *et al.* 2013). However, in either case the ecological role of porpoises in the estuaries remains to be established. Jansen *et al.* (2013) have shown that porpoises confined to the semi-closed Eastern Scheldt foraged locally, on a more estuarine prey spectrum than their conspecifics in the adjacent North Sea, but porpoise diets in other estuaries and rivers remain unknown. In this study, we report the local increase of harbour porpoises in the river Scheldt and we determine their diet from stomach content analysis, with particular emphasis on the importance of estuarine prey.

Methods

Sightings

Opportunistic sightings data of harbour porpoises in the Scheldt have been used to examine the increased presence of the species in this river. Sightings in the Dutch part of the river, were uploaded by the general public at www.waarneming.nl (2005-2014). Similar data from further upstream the river, in Belgium, were reported to www.waarnemingen.be, to www.zeezoogdieren.org or to the Royal Belgian Institute of Natural Sciences (RBINS), http://www.mumm.ac.be/FR/Management/Nature/search_strandings.php. The river is less wide in Belgium, and therefore harbour porpoises in the Scheldt and its tributaries here have a higher probability of being observed, often by multiple observers along their banks. Multiple reporting made it complicated to assess the exact number of harbour porpoises present in any stretch of the river, especially during 2013 in Belgium, when ≥25 animals swam up river (Haelters 2013). We have analysed the data available at the various platforms, without attempting to identify duplicates and simply plotted all sightings at the reported locations. As a proxy for harbour porpoise density in coastal North Sea waters, from where animals swimming up the river must originate from, we used yearly average numbers seen per hour of observation by Dutch seawatchers, taken from www.trektellen.org.

Collection of stranded animals

Carcasses of harbour porpoises found dead in The Netherlands have been collected since 2006, when logistically possible, within a nation-wide research program which aims to determine their cause of death, body condition and diet (Leopold & Camphuysen 2006). Carcasses were labelled (stranding location, date) and initially stored locally (-20˚C), before transport to IMARES-Texel (2006) or the Department of Pathobiology, Faculty of Veterinary Medicine, Utrecht University (2007-2014), where an necropsy was performed on each carcass. Harbour porpoises stranded in Belgium were reported to the Royal Belgian Institute of Natural Sciences (RBINS), where it was decided at an ad hoc basis if carcasses were to be collected or not. In Belgium, most animals found far inland were badly decomposed, or were reported in locations difficult to reach, leading to the collection of only a small number of carcasses, and only two of these have been necropsied. Carcasses were labelled and initially stored at the RBINS (Ostend), at -20˚C. These necropsies were performed at the University of Liège.

Necropsies in The Netherlands and Belgium followed the same standardised protocol (Kuiken & Gacia Hartmann, 1991; Jauniaux *et al.* 2002a). Necropsy parameters used for the current analysis were: age, as adult or juvenile, judged from body length with a cut-off point at 130 cm (cf. Lockyer 2003) supplemented by observations on the gonads to determine sexual maturity when possible; gender (male/female); the decomposition code (DCC) of the carcass at necropsy, scored on a 5-point scale from 1 (live stranding) to 5 (mere bones or 'mummified'); and probable cause of death. The most frequent causes of death were drowning by entanglement in fishing gear (by-catch), infectious diseases (such as acute pneumonia, or severe parasitosis), seal attacks and emaciation (Jauniaux *et al.* 2002b; Leopold *et al.* 2015a). For this study we excluded animals that had died from seal attack or by-catch, as these were not encountered among the stranded animals in the Western Scheldt (see under Results). The nutritional body condition (NCC; see also Chapter 3, ES-1) for the Dutch animals was scored on a 6-point scale, from 1 (very fat and muscular) to 6 (emaciated), and for the Belgian animals as good, medium or poor nutritional status, judged from the general appearance of the animal and blubber thickness. Other information used was stranding location and stranding date.

Diet analysis

The main objective of the study was to compare the stomach contents of animals that stranded in the Western Scheldt with those of animals from seaward reference areas: the river mouth, i.e. the North Sea coastline from the Belgian/Dutch border to the western tip of the former island Walcheren; the 'Voordelta' north of the river mouth, from Walcheren to the Maasvlakte off Rotterdam; and the Belgian North Sea coastline south of the river mouth (Figure 1). Animals in the reference areas were selected for comparison, if they 1) had stranded in the same months as the Western Scheldt animals, and 2) had similar nutritional and decomposition conditions, and 3) had similar causes of death. Stomach contents were studied following methods outlined in Leopold *et al.* (2015b). In brief: prey hard parts were collected from stomach contents, identified to the lowest possible taxon, measured, their size corrected for wear and paired if possible. The minimum number of individual prey was determined and prey size and mass for each prey were determined. Prey species were assigned to an estuarine prey group (anchovy *Engraulis encrasicolus* (Linnaeus, 1758), smelt, sand smelt *Atherina presbyter* Cuvier, 1829, Nilsson's pipefish

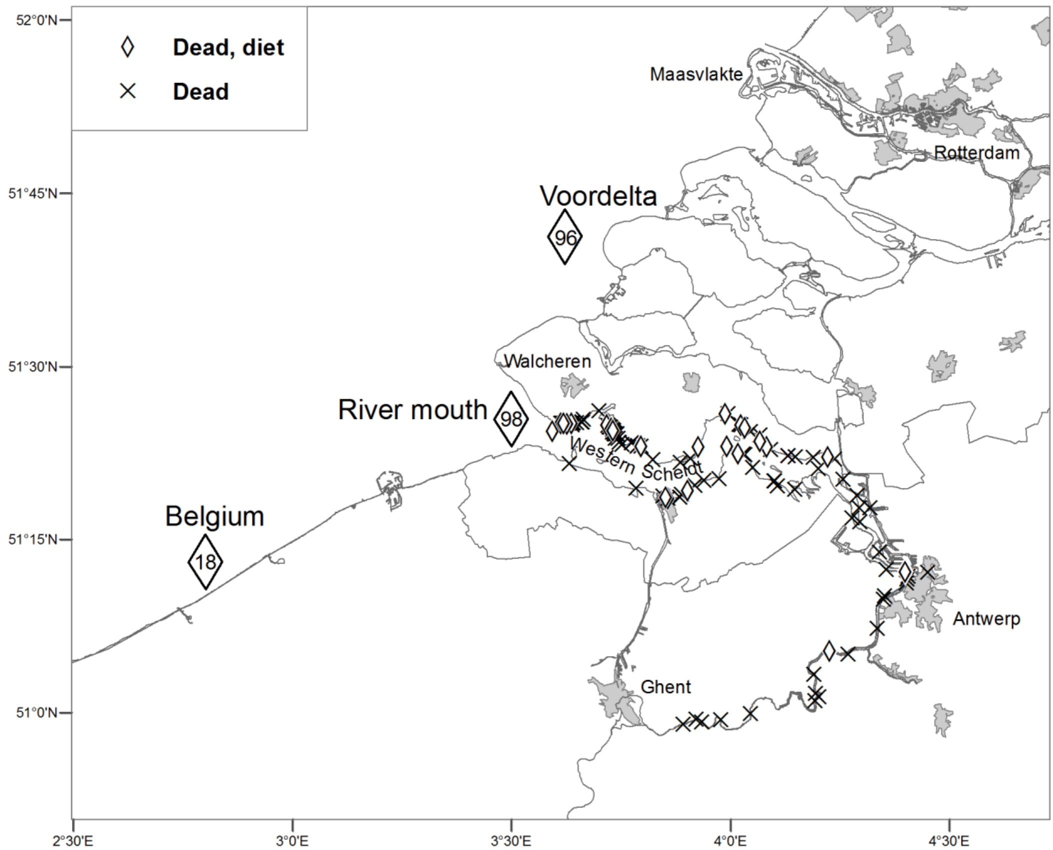

Figure 1. *Locations where carcasses of harbour porpoises were found. Specimens that were used for stomach content analysis are individually marked by small diamonds along the river Scheldt (n=23 in The Netherlands and n=2 in Belgium), and grouped in the reference areas (large diamonds). Outside the Western Scheldt, three reference areas were used: the river mouth: Dutch/Belgian border to the western tip of Walcheren (n=98), the Voordelta: from the tip of Walcheren to the Maasvlakte off Rotterdam (n=96), and the North Sea coastline of Belgium (n=18).*

Syngnathus rostellatus Nilsson, 1855 and European perch *Perca fluviatilis* Linnaeus, 1758), and a North Sea prey group (all other prey species found, see ES-1 for the full list of species found). Summed estimated prey masses per prey group and per harbour porpoise were used to compare diets between the animals found in the Western Scheldt, and in the three reference areas. Some prey remains may have stemmed from secondary prey, e.g. some of the invertebrates and some small fishes, but as this cannot be determined with certainty and because the relative contribution of these small prey is nearly negligible, no distinction was made between supposedly primary and secondary prey.

Results

Increased occurrence in the Scheldt

Opportunistic sightings data show a sharp increase from 2011 in porpoise occurrence in the Western Scheldt (the Dutch part of the river; Figure 2).

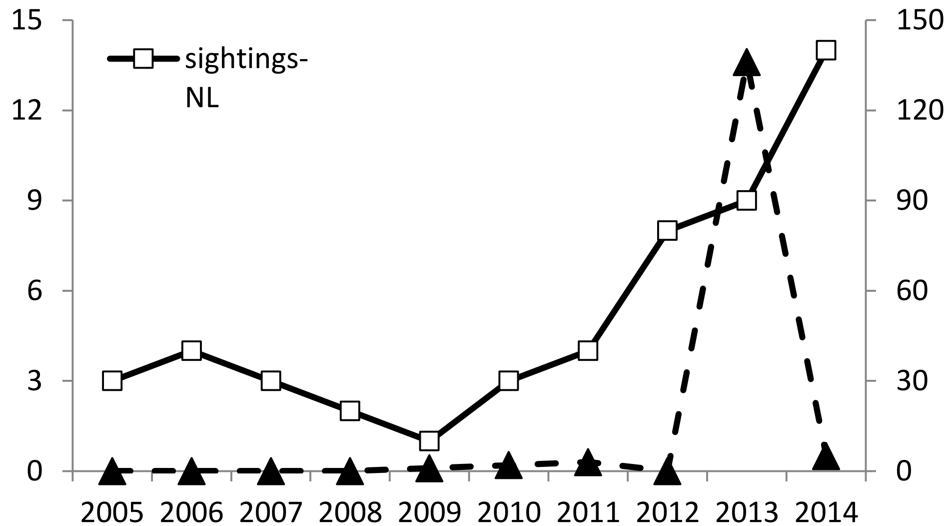

Figure 2. *Reported sightings of live harbour porpoises in the Dutch (open squares) and Belgian (filled triangles) parts of the river, 2005-2014. Note different Y-axis for Belgian sighting at the right. Average group size was 1.6 in The Netherlands and 2.0 in Belgium. Individual porpoises may have been seen and reported several times.*

Further upstream, in Belgium, numbers were lower in most years, but a remarkable number of sightings was reported in spring 2013, peaking on 11 April when at least 25 individuals were supposedly present (Haelters 2013). Many of these animals passed sluices, reaching port areas and stretches of the river system beyond tidal influence (Figure 3). This spring-influx in 2013 may have been a one-time event, with reported numbers of animals ten times those of 2009-2014 combined, while being confined to a few months only, in contrast to other years in which live porpoises were seen year round (Figure 4A). A total of 19 animals, probably the majority of those which took part in the 2013 influx, were reported dead about one month after their peak occurrence was seen (Figure 4B).

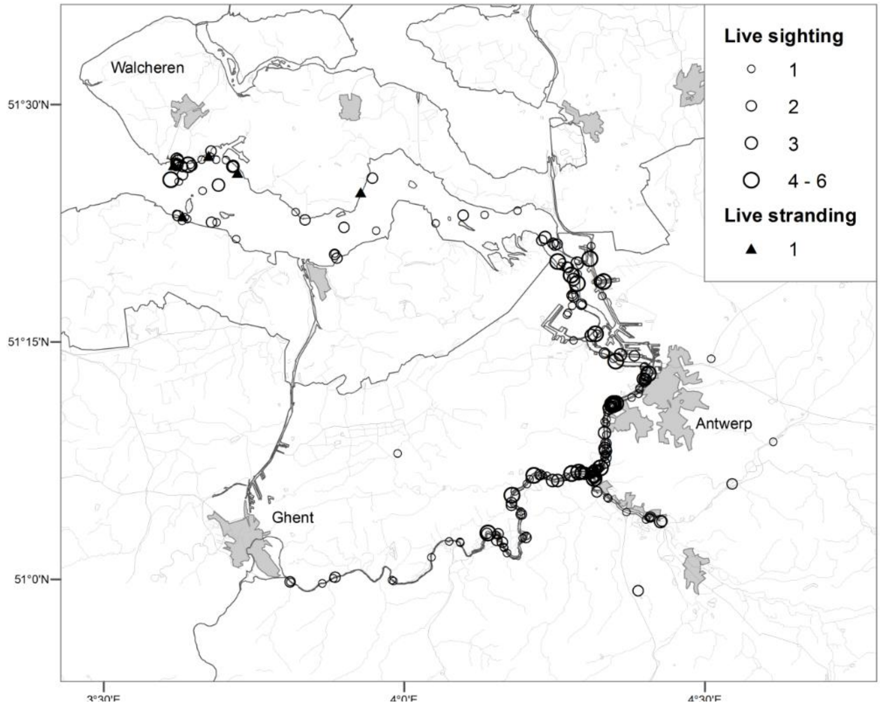

Figure 3. *Locations (circles) where harbour porpoises were seen alive in the river Scheldt or live-stranded (triangles), 2005-2014.*

Only two of these could be collected and necropsied; the others were found very decomposed, or observed in locations difficult to access and were not collected.

A slight spring peak in live sightings is also apparent in the Dutch data, but elevated numbers were also reported in December/January and in September (Figure 5).

Animals collected for stomach content analysis

All carcasses from the Dutch part of the river Scheldt that were necropsied were collected between 2007 and 2014 (Figure 6) and between March and October (Figure 7A). Five juvenile porpoises collected in the Western Scheldt (The Netherlands) and the two collected in the Belgian part of the river (both adults, in March 2011 and April 2013) had empty stomachs. The other 18 porpoises had prey remains in their stomachs. Four of these were adults and 14 were juveniles;

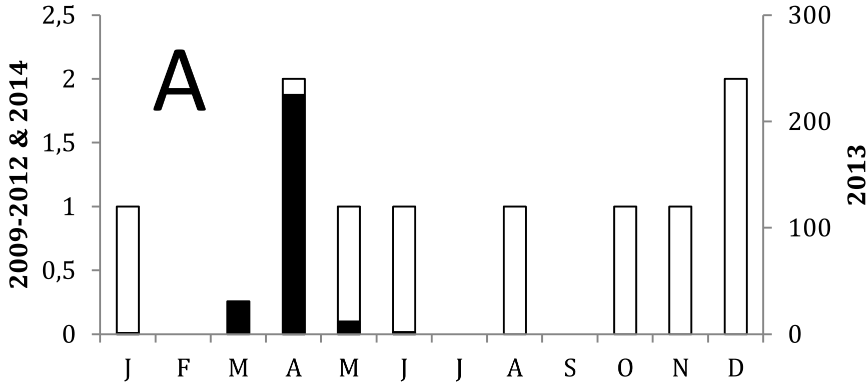

Figure 4A. *Monthly distribution of harbour porpoise sightings in the upper, Belgian parts of the river, summed for 2009-2014 (excluding 2013) as white bars (back), scaled along the left Y-axis, compared to those for 2013 as black bars (front), scaled along the right Y-axis. Note difference in scale.*

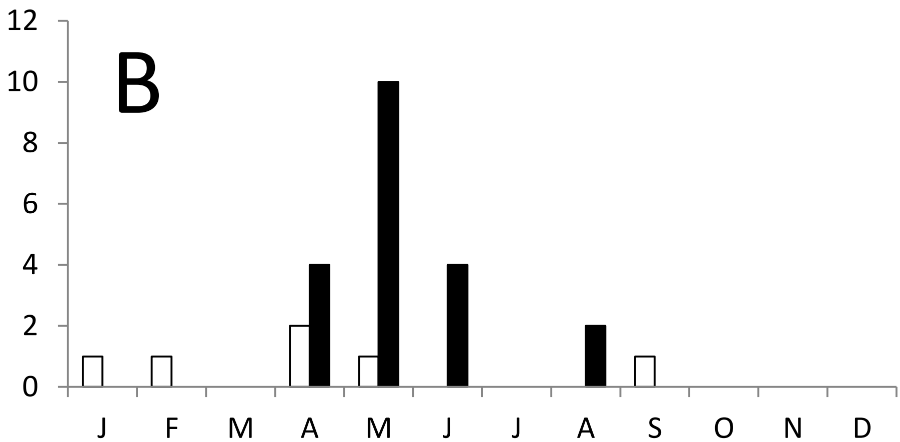

Figure 4B. *Monthly distribution of harbour porpoise strandings in the upper, Belgian parts of the river, summed for 2009-2014 (excluding 2013) as white bars, compared to those for 2013 as black bars. Same scaling for both groups.*

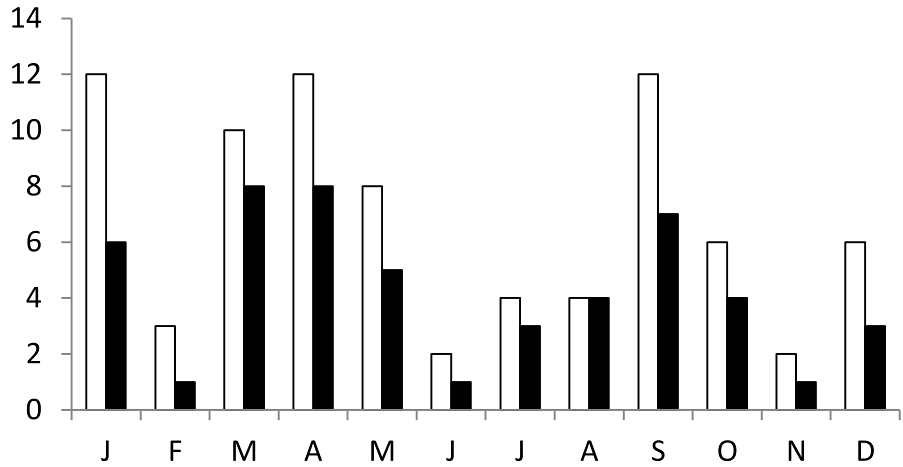

Figure 5. *Monthly distribution of harbour porpoise live sightings (white bars: animals; black bars: sightings) in the Dutch part of the river, summed for 2005-2014.*

six of 17 sexed animals with prey remains in their stomachs were males and eleven were females (versus four females and three males with empty stomachs). The two animals found in Belgium were both adult females, one was found dead emaciated, the other stranded alive (DCC 1) but died shortly afterwards, from an infectious disease. The decomposition codes (DCC) of the other porpoises used for stomach content analysis ranged from 2 to 5 (the full spectrum for animals stranded dead; average DCC with SD = 3.38±1.05, *n*=25). Most were emaciated: NCC ranged from 3 to 6. Probable causes of death included infectious disease (7), emaciation (2) and unknown (16). Importantly, no animals had been found that were clearly victims of grey seal attacks or fishery bycatch, both of which are rather common in the Voordelta (Leopold *et al.* 2015a). In addition, an 86 cm long porpoise was found dying (DCC 1) in the Western Scheldt in August 2013. This animal was a neonate that had not yet eaten solid foods, and was excluded from further analyses.

For comparison with the animals found in the river, we selected 212 animals that had stranded outside the Western Scheldt: 98 from the southern and northern coastlines of the river mouth, 96 from further north, from the adjacent Voordelta, and 18 from the Belgian North Sea coastline, further south (Figure 1). Animals from the years 2007-2014 were selected, that had been found between March and October, had a NCC 3-6 (or were in moderate to poor body condition as scored in Belgium) and had died from disease (27), emaciation (21) or unknown reasons (164).

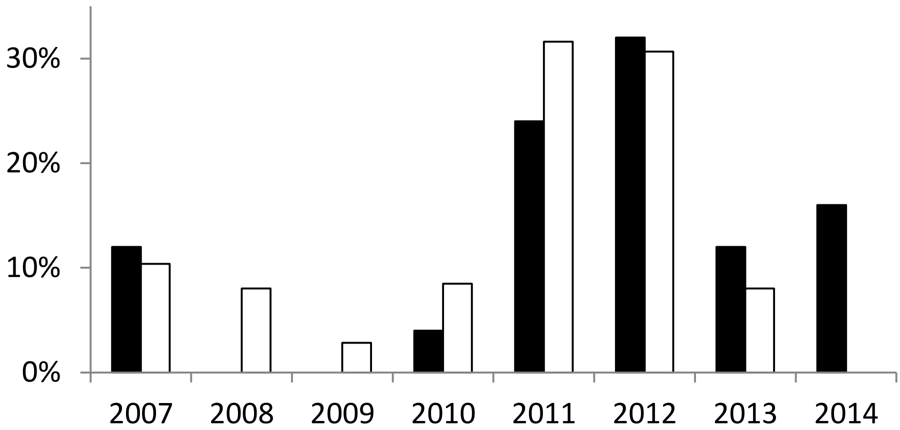

Figure 6. *Frequency distribution of harbour porpoises used for stomach contents analysis (with and without prey remains combined) over the years 2007-2014, compared for the river Scheldt (black bars) and the three reference areas combined (white bars). Monthly numbers are expressed as % of total numbers (25 porpoises from the river Scheldt and 212 from the reference areas).*

This selection yielded temporal distributions that were very similar between animals from the river Scheldt and from the reference areas (combined), both in terms of years (Figure 6) and months (Figures 7A,B).

Among the reference animals with prey remains in their stomachs, 17% (*n*=167 aged animals) were adults, which is rather similar to this percentage for the Western Scheldt (22%, *n*=18), given the low sample size of the latter. However, more males were present among the reference animals: 56% (*n*=165 sexed with prey remains in their stomach), versus 35% (*n*=17) among the animals found in the Western Scheldt with prey. Average DCC among the animals with prey remains in their stomachs from the reference areas (3.6±0.81; *n*=168) and in the river Scheldt (3.4±1.00; *n*=18) were not statistically different (T-test, T=0.82, df=184, p>0.1), but NCC was significantly lower among reference animals with prey remains (4.3±0.94; *n*=95), as compared to animals found in the Western Scheldt (The Netherlands, 5.2±0.75; *n*=11): (T=-3.66, df=104, p<0.001), indicating that animals found in the Western Scheldt had a poorer body condition. The proportion of empty stomachs 7/25 (28%) for the river Scheldt was also slightly higher than in the combined reference areas: 44/212 (21%).

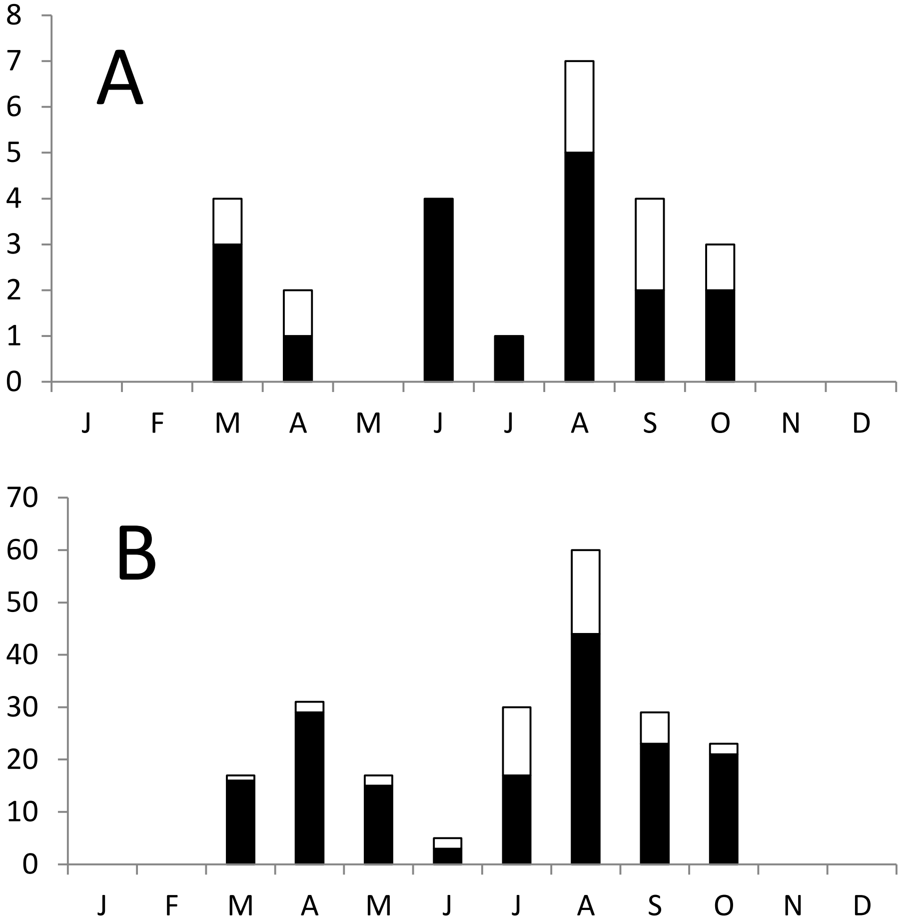

Figure 7A (top). *Monthly numbers porpoises from the river Scheldt used for stomach content analysis (n=18 animals with prey remains in their stomachs (black), and n=7 without (white)).*

Figure 7B (bottom). *The monthly numbers of reference animals (n=168 with prey (black) and n=44 without (white)).*

Evidence of porpoise births in the river Scheldt

Two of the animals collected for necropsy provided evidence that harbour porpoises might have given birth in the river Scheldt. A freshly dead, lactating female was found in Belgium, near Bornem, on 6 March 2011, circa 100 km up-river. The time of year for this case, however, probably signifies either a very long mother-calf bond, or dysfunctional mammary glands, rather than recent calving. The neonate found in August 2013 stranded near Hoofdplaat, 4.75 km into the Western Scheldt, half an hour after low tide. This timing suggests that this animal originated from the river, rather than having been carried in by a rising tide.

Stomach content analysis

Prey mass

The average reconstructed prey masses for animals with prey remains in their stomachs was 362 g for the Western Scheldt, and 505 g for the reference animals (all subareas combined, Table 1). Due to large standard deviations around these means, average reconstructed prey mass did not differ significantly between the Western Scheldt animals and animals from any of the reference areas, or animals in all reference areas combined.

Table 1. *Average and SD of reconstructed prey mass, per stomach containing prey remains, per sub-area. The value found for the Western Scheldt was tested (T-test) against those of each reference area, and against the value for all reference areas combined.*

	Average (g)	**SD**	***n***	**T**	**df**	***p***
Western Scheldt	**362**	**485**	**18**			
River Mouth	350	1080	73	0.070	89	>0.1
Belgian Coast	960	1411	16	-1.613	32	>0.1
Voordelta	557	1376	79	-1.013	95	>0.1
Total Reference Areas	**505**	**1264**	**168**	**-0.952**	**184**	**>0.1**

Prey species

Smelt comprised 99.2% of all estuarine prey mass, leaving the mass contributions of the 45 Nilsson's pipefishes, the four sand smelts, and the single European perch and anchovy across all studied stomachs (ES-1) insignificant. Among the 18 stomachs from the Western Scheldt with prey remains, nine contained remains of

Table 2. *Numbers of stomachs with prey, and with smelt, per sub-area.*

	Stomachs with prey	Stomachs with smelt	% Stomachs with smelt
Western Scheldt	**18**	**9**	**50**
River Mouth	73	5	6.85
Belgian Coast	16	2	12.50
Voordelta	79	8	10.13
Total Reference Areas	**168**	**15**	**8.93**

smelt (50%). Among the porpoises in the combined reference areas, this proportion was only 9% (Table 2).

The contribution of smelt to the total diet of individual porpoises in terms of reconstructed prey mass varied between 3.5% and 100% in the nine animals from the Western Scheldt that had eaten this prey species, and the average contribution of smelt to the diet (in terms of prey mass) was 46.11% for all 18 Western Scheldt animals combined (Table 3). Among the animals in the various reference areas that had remains of smelt in their stomachs, the contribution to the diet varied from 0.02% to 100% (*n*=15). In animals found in the river mouth, the total contribution of smelt was less than a third of this value for the animals found in the river itself, while in the two reference areas at either side of the river mouth, only circa 3% of the reconstructed prey mass comprised smelt (Table 3).

Table 3. *Summed total reconstructed prey masses (in g), across all animals per sub-area, and the proportions of smelt among these.*

	Summed total prey mass (g)	Summed mass smelt (g)	% smelt
Western Scheldt	**6510**	**3002**	**46.11**
River Mouth	25 518	3660	14.34
Belgian Coast	15365	393	2.56
Voordelta	43 943	1418	3.22
Total REF	**84 862**	**5471**	**6.45**

Table 4. *Minimum, maximum and average (±SD) distance (km) to the river mouth, of stranding locations of harbour porpoises with and without smelt remains in their stomachs.*

	n	min	max	avg	sd
with smelt	9	9.1	49.8	29.5	12.5
without smelt	9	9.1	58.6	23.3	17.8

The probability that smelt was found in a particular stomach from an animal from the Western Scheldt appeared independent from the distance to the river mouth, taken at 03°33'E. The average distance of nine animals with and nine without smelt remains in their stomachs was not statistically different (Table 4: T=0.855, df=16, p>0.1).

Smelt size differed between the stomachs from animals found in the river (n=153 fishes) and in the river mouth and North Sea (n=203). The majority of smelts found in stomachs from animals that stranded in the river were around 8 cm reconstructed total length, with subsequent peaks in the distribution of fish lengths around 10-11 cm and around 14 cm. In the reference areas, reconstructed fish lengths peaked around 12 cm (Figure 8A). Masses of smelts found in river stomachs tended to be lower than in North Sea stomachs (Figure 8B). Most smelts taken were juveniles, but adult fishes, over 20 cm long, were also incidentally found (ES-2).

Discussion

Measures to diminish pollution levels and other ecological restoration measures such as restructuring of river banks have resulted in an ameliorated habitat quality, with some fish species returning to the river Scheldt. Among these are smelts; and monitoring along the upper, Belgian parts of the river system has shown that these are making a spectacular come-back. Smelt catches have greatly increased since 2010 in the river Scheldt and this species has become the most abundant fish species here (Breine & Van Thuyne 2014a,b, 2015). Concurrent with the return of the smelts in the river Scheldt, harbour porpoises have also started to return, but a dietary link between predator and prey was hitherto lacking. The return of the harbour porpoise in the Western Scheldt gained momentum in recent years, with a steady increase of the species in the river. Fike catches of smelt at Zandvliet (Belgium, near the Dutch border) also show an increase that commenced in 2009 (Breine & Van Thuyne 2015).

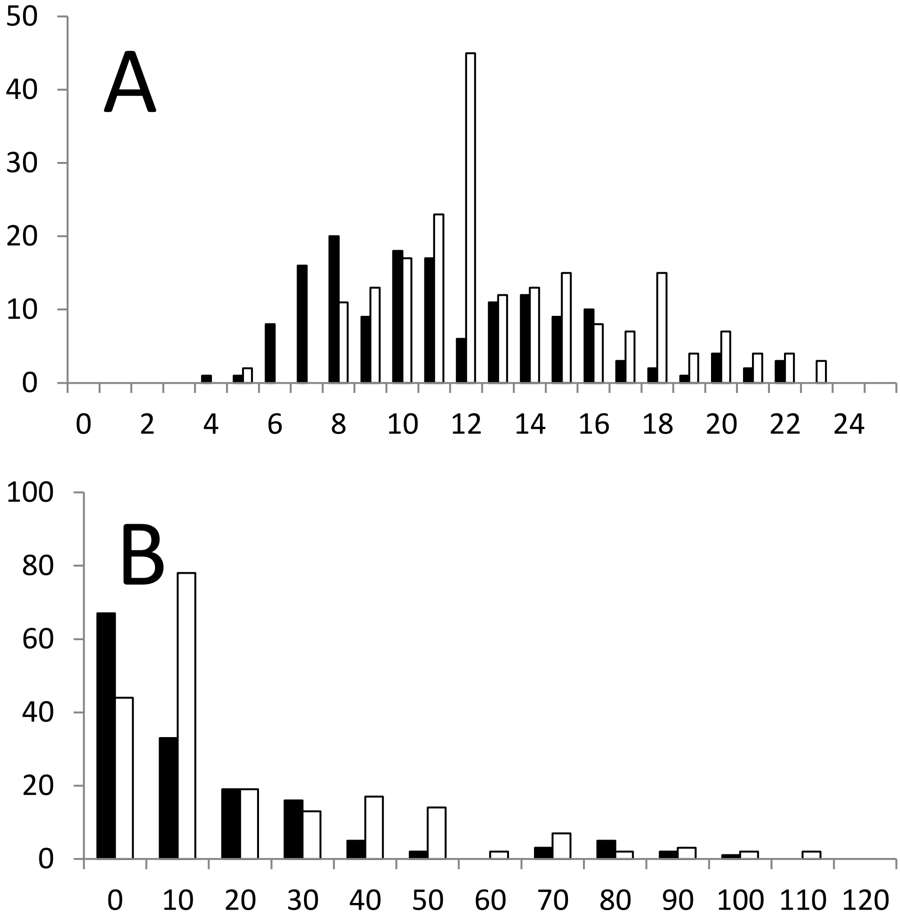

Figure 8A (top). *Length-frequency distribution of smelts (reconstructed total fish lengths in cm) from porpoises found in the river Scheldt (n=153 fishes; black bars) and from porpoises found in the reference areas combined (white bars: n=129, 11, and 63 for river mouth, Belgium and Voordelta, respectively).*

Figure 8B (bottom). *Mass-frequency distribution of the same smelts (g).*

Further upstream in the Belgian part of the river system, smelts were also abundantly caught, but harbour porpoises remained rare until a sudden influx in spring 2013. Whether or ot this mass influx was a one-time phenomenon, future observations will show.

The year 2013 was an anomaly, both in the Dutch and the Belgium part of the river. It might be expected that the numbers of porpoises entering the river are related to the density in the North Sea. The best, long-term trend data for porpoise presence in Dutch coastal waters are provided by seawatchers. Seawatching is primarily aimed at recording the passage of birds, but harbour porpoises are also recorded. The numbers seen per hour of observation show a long-term increase that closely matches yearly numbers of strandings in The Netherlands (Camphuysen & Siemensma 2011). Here, we use the yearly average number of sightings of harbour porpoises per hour of observation, across all seawatching sites in The Netherlands (data: www.trektellen.org). During the current study period, 2005-2014, the increasing trend, as reported by Camphuysen & Siemensma (2011) is near-significant (n=10, R^2=0.3894, 0.05<p<0.1; Figure 9A). The number of animals reported from the Western Scheldt over these years appears to follow the numbers reported by the seawatchers (Figure 9B: n=10, R^2=0.359, 0.05<p<0.1) but the numbers seen in 2013 were much lower than expected, while unprecedented numbers were seen in Belgium. Without this 2013-anomaly, the relationship between numbers reported by seawatchers in the North Sea, and by the general public in the Western Scheldt show a good correlation: n=9, R^2=0.6303, p<0.02), indicating that numbers at sea drive the numbers seen in the river. On the other hand, the increase in porpoise sightings in the Western Scheldt may also be correlated with smelt abundance, but good data from the Western Scheldt are lacking. In Belgian fike catches, numbers of smelts increased from 2009-2014 (Breine & Van Thuyne 2015), as did numbers of porpoises in the Dutch part of the river. Therefore, increasing numbers of porpoises were available for entering the Western Scheldt during the study years, and once in the river, they would have encountered increasing smelt densities, possibly providing better local feeding conditions.

The dietary study was performed on porpoises that were found dead, and had died from infectious disease, emaciation or unknown causes. Stranded animals are probably not representative for the general health status and diet of the animals in the study area. Many of the studied animals were not healthy. This could be explained by the fact that no animals had obviously died a violent, acute death, e.g. due to predation, collisions with ship propellers or fisheries bycatch.

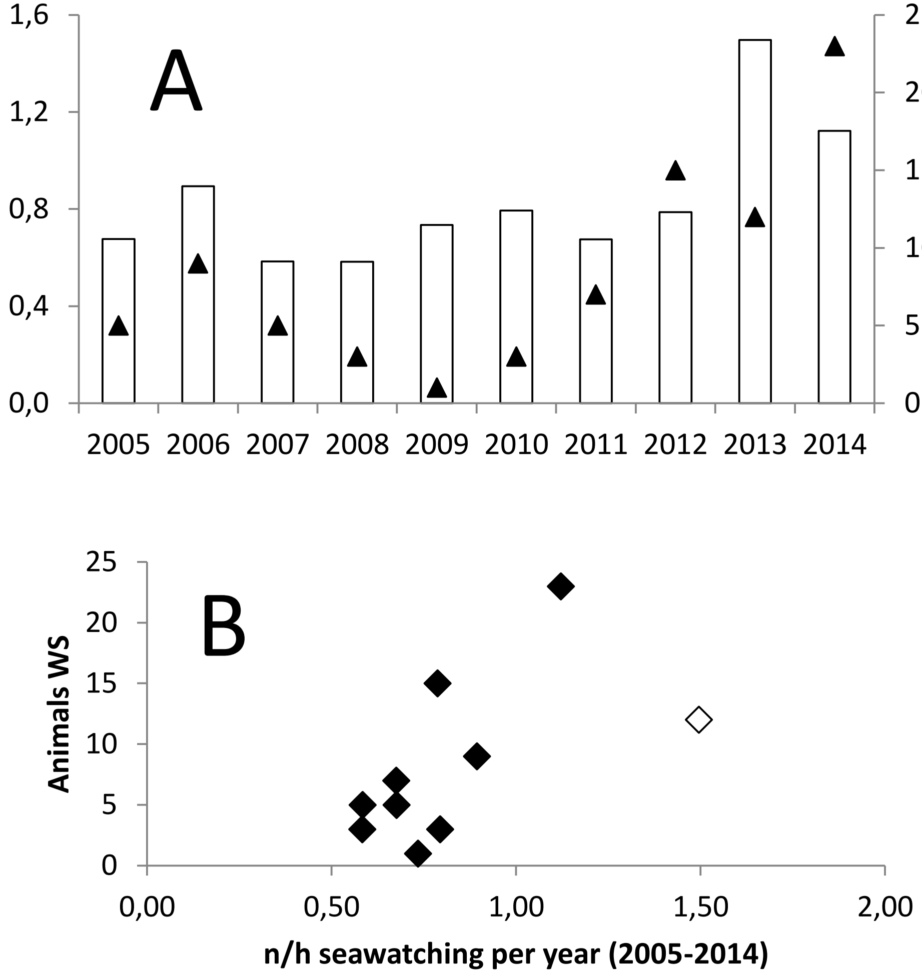

Figure 9A (top). *Numbers of harbour porpoises recorded per hour of observation per year, by Dutch seawatchers (www.trektellen.org, accessed 22 March 2015; all seawatching stations combined): bars and left Y-axis, and numbers of porpoises reported from the Western Scheldt per year, 2005-2014: filled triangles, right Y-axis.*

Figure 9B (bottom). *The relationship between the yearly seawatching average, as a proxy for porpoise density in North Sea nearshore waters, and numbers of porpoises reported per year in the Western Scheldt (2005-2014). Open symbol represents the year 2013.*

The peak in strandings along the Belgian, upper parts of the river, one month after the peak in live sightings in 2013 and the presumably high proportion of casualties here, suggests that most porpoises had wasted away here. The rather high NCC scores in general also indicated that most animals had probably died from infectious disease or from emaciation, although many such animals were also found along the shores of the river mouth and further away from the river, along Dutch and Belgian North Sea coastlines. From the animals stranded in the reference areas, we selected study subjects that were similarly emaciated or sick as the study animals in the Western Scheldt, to enable comparison of diets between these groups.

Relative to conspecifics from stretches of North Sea coastline at either side of the river mouth, harbour porpoises found up-river had similar reconstructed prey masses in their stomachs. However, porpoises found in the river tended to be in poorer body condition and had a slightly higher percentage of empty stomachs. The main difference between the two groups was that much more smelt had been consumed by animals in the Western Scheldt. Smelt was the most important single prey species in the Western Scheldt in terms of biomass (46.11% smelt), but was only of marginal importance in the adjacent North Sea (ca. 3%). Animals stranded along the river mouth had an elevated proportion of reconstructed smelt biomass in their diet (14.34%), as compared to animals found further away from the river. As the river is subject to tidal movements, river water will mostly flow into the North Sea during the ebb tide. With the riverine water mass, fishes may also move from the river into the river mouth, and so might carcasses of porpoises that died in the Western Scheldt. From the various reference areas, the river mouth should thus be most similar to the Western Scheldt as we found in the stomach contents from the various locations.

This study cannot resolve the question whether harbour porpoises in the Western Scheldt had purposefully swam up-river to feed on smelt. However, once in the river system, they clearly had been feeding on this anadromous fish, which was an important contribution of their diet here. Diets further upstream, e.g. in the Belgian part of the river, remain unknown as yet, but monitoring of fish has shown that smelts are common here (Breine & Van Thuyne 2014a,b, 2015). Very far upstream, other fishes, such as fresh water cyprinids, will become more dominant among the fish fauna. It would therefore be very interesting to study more stomach contents of animals found dead in the Belgian parts of the river system, and in other, similar river systems in the southern North Sea, to investigate if such fish species are, and in which quantities, taken by porpoises venturing far upstream.

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Supporting information has been requested by Marine Biology Research: Tables ES-1 & ES-2, and can be found on line, after publication of this paper.

Table ES-1. Prey list for the porpoises considered in this study, per sub-region. Total numbers of prey (and summed prey masses) were: Western Scheldt n=1119 (6510 gram); River Mouth n=11 062 (25 526 gram); Belgium n=5094 (15 364 gram); Voordelta n=11 582 (43 980 gram).

Table ES-2. Length and mass frequency distributions for smelts, per sub-region. Total fish lengths (cm) and prey mass (gram) were back-calculated from otolith sizes.