Marine Mammal Science

Diet of harbor porpoises along the Dutch coast: A combined stable isotope and stomach contents approach

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ABSTRACT

High stranding frequency of porpoises, *Phocoena phocoena*, along the Dutch coast since 2006 has led to increased interest in the ecology of porpoises in the North Sea. Stranded porpoises were collected along the Dutch coast (2006–2008) and their diet was assessed through stomach content and stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of porpoise muscle and prey. Stable isotope analysis (SIAR) was used to estimate the contribution of prey species to the porpoises' diet. This was compared to prey composition from stomach contents, to analyze differences between long- and short-term diet. According to stomach contents, 90.5% of the diet consisted of gobies, whiting, lesser sandeel, herring, cod, and sprat. Stable isotope analysis revealed that 70-83% of the diet consisted of poor cod, mackerel, greater sandeel, lesser sandeel, sprat, and gobies, highlighting a higher importance of pelagic, schooling species in the porpoises' diet compared to stomach contents. This could be due to prey distribution as well as differences in behavior of porpoises and prey between the coastal zone and offshore waters. This study supports the need for multi-method approaches. Future ecological and fishery impact assessment studies and management decisions for porpoise conservation should acknowledge this difference between the long- and short-term diet.

Key words: *Phocoena phocoena*, harbor porpoise, stable isotopes, carbon, nitrogen, SIAR, mixing model.

Strandings of harbor porpoises, *Phocoena phocoena*, along the Dutch coast have become increasingly more frequent since 2006 (Camphuysen *et al.* 2008). Hence, the abundance, distribution, and ecology of porpoises in these waters have become subjects of ecological as well as resource management interest. Understanding their diet can contribute considerably towards the understanding of how the southern North Sea and Dutch coastal waters are supporting the increasing numbers of this species.

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Diets of harbor porpoises have generally been reconstructed from stomach contents of stranded or bycaught animals, and based on identification of undigested prey remains such as otoliths, vertebrae, jaws, and squid beaks (Börjesson *et al.* 2003, Santos and Pierce 2003, Víkingsson *et al.* 2003). Their diet consists mostly of pelagic and demersal species (mainly clupeids (Clupeidae), sandeels (Ammodytidae), and gadoids (Gadidae), although geographical variation in preference of specific prey species has been documented (Santos and Pierce 2003). In Dutch coastal waters, a large variety of prey species have been documented, but here porpoises tend to consume mainly whiting, *Merlangius merlangus*, sandeels, and gobies, *Pomatoschistus* spp. (Santos Vázquez 1998, Santos and Pierce 2003, Santos *et al.* 2005). Christensen and Richardson (2008) analyzed bone tissue of porpoises stranded on the Dutch coast between 1848 and 2002 and found a decrease in $\delta^{15}N$ values over time, suggesting that porpoises have gradually been feeding on lower trophic level prey. They argued that this reflects a change in the food web structure of the North Sea with progressively lower trophic prey available to porpoises.

Stomach content analysis has some inherent biases, *e.g.*, differential recovery rates, degradation, and passage times of prey remains (Prime and Hammond 1987, Bowen 2000). Due to fast digestion rates, stomach contents of stranded animals only provide information on recently ingested prey, possibly over emphasizing the relevance of near shore species (Pierce and Boyle 1991).

To overcome these problems, stable isotope ratios of nitrogen ($^{15}N/^{14}N$ or $\delta^{15}N$) and carbon ($^{13}C/^{12}C$ or $\delta^{13}C$) can be used to analyze past diet composition (Kelly 2000, Crawford *et al.* 2008, Newsome *et al.* 2010). Stable isotope analysis provides insight into feeding ecology over longer time periods and reflects the general diet assimilated over time (Budge *et al.* 2006, Newsome *et al.* 2010). In general, predators are enriched in ^{15}N compared to their prey ($\pm 3.5\%_{oo}$ per trophic level, *e.g.,* Kelly 2000, Michener and Kaufman 2007). In contrast, $\delta^{13}C$ is very similar between predator and prey ($\pm 0.5\%_{oo}$–$1\%_{oo}$ per trophic level, *e.g.,* Post 2002, Michener and Kaufman 2007) but rather reflects geographic differences throughout the food web to indicate foraging location (offshore *vs.* inshore, pelagic *vs.* benthic) (Hobson 1999, Barnes *et al.* 2009). However, factors such as age, type of diet, composition of food, nutritional status, environment, identity of nitrogenous waste product, and taxonomical position can notably influence trophic fractionation (Minagawa and Wada 1984, McCutchan *et al.* 2003, Vanderklift and Ponsard 2003). Depending on their specific turnover time, tissues reflect various time frames, from very short-term (*e.g.,* liver and plasma) to relatively long-term or life-time (*e.g.,* bone tissue and teeth) (Dalerum and Angerbjörn 2005). Muscle tissue, as analyzed in this study, reflects assimilated diet of several months (Tieszen *et al.* 1983, Hobson *et al.* 1996).

Application of stable isotope analysis relies on the fact that stable isotope composition of a consumer is the weighted mixing of the stable isotopic composition of its food sources, modified by isotopic fractionation (Newsome *et al.* 2010). Therefore, several isotopic mixing models have been developed to link isotopic signatures of predators to isotopic signatures of potential prey species, taking into account isotopic fractionation between prey and predator (Phillips 2001; Phillips and Gregg 2001, 2003). *Via* these models, the proportional contribution of each source (prey species) to the isotopic signature (accumulated diet) of the predator is estimated. Simple linear or Euclidean distance-based models are limited in their application, as only few prey species can be included in the model due to the small number of measured isotope ratios (Phillips and Gregg 2001). More recent models are able to deal with more prey species (*e.g.,* IsoSource, Phillips and Gregg 2003) or variability within sources

(*e.g.,* IsoError, Phillips and Gregg 2001). In this study, SIAR (Stable Isotope Analysis in R, Parnell *et al.* 2010) was used. This Bayesian stable isotope mixing model is not only able to deal with more sources than variables, but also includes uncertainties (natural variation and analytical error), producing results as probability distributions with residual errors (Parnell *et al.* 2010).

The primary objective of this study was to estimate the diet composition of harbor porpoises using SIAR on muscle $\delta^{13}C$ and $\delta^{15}N$ values from porpoises stranded on the Dutch coast between 2006 and 2008 (Jansen *et al.* 2012) and using the isotopic composition of their potential prey sources. We then compare the diet as estimated by SIAR with the diet as deduced from stomach contents of the same individuals, enabling a comparison between long- and short-term dietary information.

MATERIALS AND METHODS

Porpoise and Prey Samples

$\delta^{13}C$ and $\delta^{15}N$ values analyzed in the muscle of harbor porpoises were extracted from a database ($n = 160$) published by Jansen *et al.* (2012). They have identified suckling neonates by their neonatal enrichment and porpoises stranded within the Eastern Scheldt tidal bay by their distinct isotopic composition. These animals were excluded from this study. They have found no interannual or seasonal variation in isotopic composition but there were differences between juveniles and adults and between males and females. Therefore, the remaining 90 porpoises were analyzed by their age-class and sex.

Details of sample collection, preparation, and isotopic analysis are described in Jansen *et al.* (2012). In short, muscle samples were freeze-dried and homogenized before lipids were extracted in a 2:1 chloroform-methanol solution (Folch *et al.* 1957). Prey samples used for SIAR ($n = 202$) were extracted from a larger database published by Jansen *et al.* (2012). These samples were selected using the following criteria: samples from the southern North Sea (*i.e.*, the Dutch, German, and southeastern UK coastal zone, the English Channel, and the southern Bight), and prey covering the size classes found in stomach contents. Prey samples were either analyzed including lipids, or prey $\delta^{13}C$ values were corrected ($\delta^{13}C'$) using arithmetic lipid normalization as described by McConnaughey and McRoy (1979) where:

$$\text{Lipid}(L) = 93/[1 + (0.246 \, C/N - 0.755)^{-1}]$$

$$\delta^{13}C' = \delta^{13}C + 6 \times [-0.207 + 3.90/(1 + 287/L)]$$

Samples were analyzed for carbon (lipid extracted) and nitrogen (untreated) stable isotope ratios using continuous flow EA-IRMS (Optima, Isoprime, U.K.). Data were expressed in delta (δ) notation (hereafter, noted as $\delta^{15}N$ and $\delta^{13}C$, for nitrogen and carbon stable isotopic composition, respectively) in parts per thousand (‰) using Vienna Pee Dee Belemnite (vPDB) and atmospheric nitrogen as international standard (Coplen 2011). IAEA-C6 and IAEA-N1 were used as certified internal standards. Standard deviations on multibatch replicate measurements of glycine were 0.3‰ and 0.2‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively.

Stomach Content Analysis

Stomach content data were extracted from a wider study on harbor porpoises that stranded along the Dutch coast (Leopold and Camphuysen 2006). Stomach contents were reanalyzed after selection ($n = 76$) using the following criteria: stomachs with identifiable prey remains, stomachs of weaned animals (excluding neonates), and stomachs of animals analyzed for their isotopic composition in this study. All prey remains were identified to the lowest taxonomic level possible, using a reference collection of IMARES and the Royal Netherlands Institute for Sea Research (NIOZ) and guides for otoliths as well as other identifiable remains such as vertebrae, jaw bones, and lenses (Härkönen 1986, Watt *et al.* 1997, Leopold *et al.* 2001). Measurements of otoliths and other identifiable remains were used to reconstruct the length and weight of individual fish using published regressions of fish species (Härkönen 1986, Prime and Hammond 1987, Coull *et al.* 1989, Leopold *et al.* 2001), correcting for wear according to Leopold e*t al.* (1998). Prey composition was described as reconstructed weight (%W), expressed as the mean of the weight of a given prey species as a percentage of the total prey weight in each stomach.

Stable Isotope Mixing Model

The stable isotope mixing model SIAR (Stable Isotope Analysis in R) was used to estimate the relative contribution of different prey species (isotopic sources) to the isotopic composition of porpoises. SIAR (Version 4.1.3) was fitted in R (R 2.9.2, R Development Core Team 2009) including isotopic compositions of the predator, isotopic composition and elemental concentrations of prey species (sources) and trophic enrichment factors (TEFs). In the model, individual porpoise isotope ratios were used while for prey species, means and SDs were entered. Prey species that accounted for more than 1% of the prey composition as determined from stomach contents were included in the SIAR models. Four previously published trophic enrichment factors (TEFs) for carbon ($\Delta^{13}C$) and nitrogen ($\Delta^{15}N$) were tested successively in different model runs, one specifically for seals and other marine mammals (Hobson *et al.* 1996; model run [A]), one as averaged from carnivores (Vander Zanden and Rasmussen 2001; model run [B]), one as averaged from lipid removed muscle samples (McCutchan *et al.* 2003; model run [C]), and one specifically for cetaceans (Caut *et al.* 2011; model run [D]). The TEFs for these four model runs are given in Table 1. As TEFs determined by Caut *et al.* (2011) are based on lipid extracted $\delta^{13}C$ values for predator and prey, lipid corrected prey $\delta^{13}C$ values were used in model run (D). SIAR model outcomes are described as mean percentage (%) with the 95% credibility interval (CI_{95}).

Table 1. Trophic enrichment factors (TEFs) as used in SIAR modeling.

Reference	$\Delta^{13}C$ (‰)		$\Delta^{15}N$ (‰)	
	Mean	SD	Mean	SD
(A) Hobson *et al.* 1996	1.30	0.10	2.40	0.12
(B) Vander Zanden and Rasmussen 2001	0.91	1.04	3.23	0.41
(C) McCutchan *et al.* 2003	1.80	0.29	3.20	0.43
(D) Caut *et al.* 2011	1.26	–	1.23	–

The four resulting relative prey compositions were compared to the prey composition as determined from stomach contents using nonmetric multi-dimensional scaling (NMDS). NMDS based on Bray-Curtis similarity coefficients was applied to the average percentage (SIAR outcomes) and %W (stomach contents) per prey species, using Primer Software (Clarke and Gorley 2006). To limit the influence of dominant prey species on the ordination, data were fourth-root transformed. Subsequently, SIAR was used to separately estimate the diet of porpoises grouped by their age-class and sex.

<div align="center">RESULTS</div>

Porpoise Samples Composition and Stable Isotope Analysis

This study included a total of 90 porpoises, of which 31, 13, and 46 animals stranded in 2006, 2007, and 2008, respectively (Fig. 1). The male to female ratio was 1.1 and most animals were juveniles (77%). Juvenile lengths and weights ranged from 87 to 141 cm (111.5 cm ± 12.0) and from 10 to 41 kg (20.4 kg ± 6.1), respectively. Adult lengths and weights ranged from 134 to 165 cm (147.7 cm ± 7.2) and from 33 to 58 kg (41.9 kg ± 7.1), respectively. Samples were available from each month with two distinct stranding periods, one from January to May with a distinct peak of strandings in March and a second stranding period from June until December, comparable with the seasonal pattern of all recorded strandings along the Dutch coast (Jansen *et al.* 2012). $\delta^{13}C$ and $\delta^{15}N$ values measured in the selected 90 porpoises ranged from –19.7‰ to –16.8‰ (–18.3‰ ± 0.5‰) for $\delta^{13}C$ and from 13.4‰ to 18.7‰ (16.2‰ ± 1.3‰) for $\delta^{15}N$. $\delta^{13}C$ and $\delta^{15}N$ values per age-class are given in Table 2.

Stomach Content Analysis

In total, 27 prey species were identified (Table 3), of which 10 species each accounted for more than 1%W in overall diet composition (indicated with an asterisk in Table 3). These 10 prey species together accounted for 97.4% of the total ingested prey weight. Gobies were the most important prey species (36.6%), followed by whiting (25.4%) and lesser sandeel, *Ammodytes tobianus* (13.2%). Herring, *Clupea harengus*, cod, *Gadus morhua*, and sprat, *Sprattus sprattus*, accounted for 5.9%, 5.2%, and 4.1%, respectively. For SIAR, gobies were included in the model separately as sand goby, *Pomatoschistus microps*, and common goby, *Pomatoschistus minutus*. The isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of the resulting 11 prey species is given in Table 4.

SIAR Modeling

The estimated relative contribution of the 11 prey species to the diet of porpoises differed slightly between model runs using different TEFs (Table 5). In all model runs poor cod, *Trisopterus minutus* (17.1%–40.2%) and mackerel, *Scomber scombrus* (15.9%–35.3%) were the most important prey species. In model run A and C, lesser sandeel, greater sandeel, *Hyperoplus lanceolatus*, and sprat accounted for 25.4% or 21.5% of the diet,
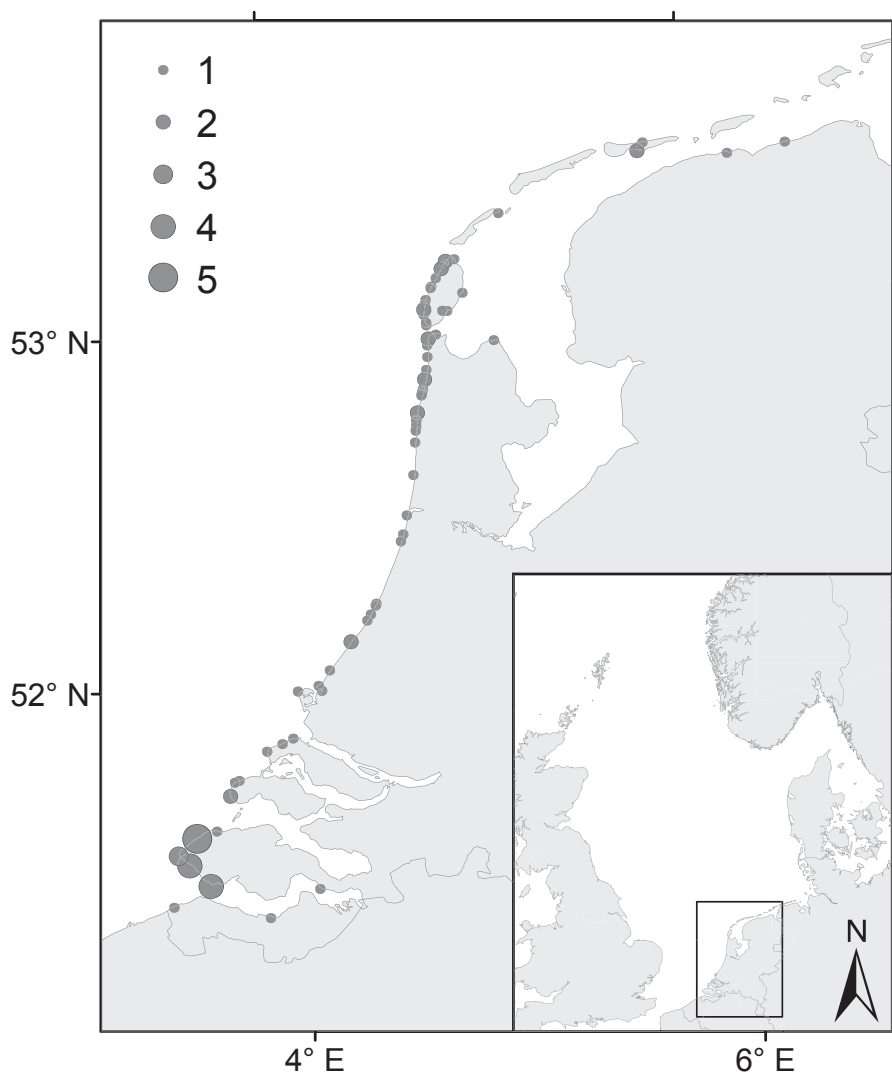
Figure 1. Porpoise *Phocoena phocoena* stranding locations and numbers (*n* = 90) along the Dutch coast analyzed in this study (2006–2008).

respectively. In model run B, lesser sandeel*,* greater sandeel, and sprat accounted for 37.1% of the diet. In model run D, greater sandeel, sprat, lesser sandeel, gobies, and herring accounted for 57.8% of the diet. Outcomes of these four different model runs show similarity coefficients (*s*) ranging between 90.9% and 97.7% (Table 6). Prey composition using TEFs as published by Caut *et al.* (2011) most closely resembled the prey composition as determined from stomach contents (*s* = 83.9, Fig. 2) as it estimated the highest importance of gobies and the lowest importance of poor cod out of all the models.

Table 2. Isotopic composition (δ^{13}C and δ^{15}N) of porpoises ($n = 90$) stranded on the Dutch coast between 2006 and 2008 and analyzed in this study.

| Age class | Sex | *n* | C:N | δ^{13}C (‰) | | | δ^{15}N (‰) | | | |
				Mean	SD	Minimum	Maximum	Mean	SD	Minimum	Maximum
Juvenile	Female	32	3.33	−18.21	0.49	−19.31	−17.26	16.57	1.21	14.18	18.71
	Male	37	3.37	−18.37	0.45	−19.69	−17.21	16.23	1.26	13.92	18.48
Adult	Female	10	3.37	−18.07	0.62	−19.09	−16.82	16.25	1.39	13.68	17.65
	Male	11	3.29	−18.32	0.57	−19.21	−17.02	15.15	1.34	13.45	17.52

Table 3. Diet composition as determined by stomach content analysis ($n = 76$). Species with a %W > 1% and included in the SIAR modeling are indicated with an asterisk.

Species		n	Weight (g)	W% Mean	SD
Agonus cataphractus	Hooknose	1	14.3	0.1	0.0
Alloteuthis subulata	Common squid	1	3.6	0.0	0.0
Alosa fallax	Twaite shad	1	151.1	0.3	0.0
Ammodytes marinus	Lesser sandeel	12	91.0	0.2	0.0
Ammodytes tobianus[*]	Small sandeel	364	2,375.8	13.2	0.3
Atherina presbyter	Sand smelt	12	52.0	0.1	0.0
Callionymus lyra	Dragonet	6	45.7	0.1	0.0
Clupea harengus[*]	Herring	51	1,567.2	5.9	0.2
Dicentrarchus labrax	Seabass	65	574.9	0.4	0.0
Gadus morhua[*]	Cod	24	5,803.3	5.2	0.2
Hyperoplus lanceolatus[*]	Greater sandeel	48	1,948.6	1.8	0.1
Limanda limanda	Dab	7	30.6	0.1	0.0
Merlangius merlangus[*]	Whiting	176	15,975.9	25.4	0.4
Osmerus eperlanus[*]	Smelt	707	1,699.7	1.0	0.1
Perca fluviatilis	Perch	4	47.4	0.1	0.0
Platichthys flesus	Flounder	5	17.9	0.0	0.0
Pleuronectes platessa	Plaice	3	14.1	0.1	0.0
Pomatoschistus spp.[*]	Gobies	7,883	8,247.4	36.6	0.4
Scomber scombrus[*]	Mackerel	4	1,147.4	1.3	0.1
Sepiola atlantica	Bobtail	6	6.9	0.0	0.0
Solea solea	Sole	32	263.8	0.7	0.1
Sprattus sprattus[*]	Sprat	64	907.6	4.1	0.1
Syngnathus rostellatus	Nilsson's pipefish	14	7.9	0.3	0.0
Trachurus trachurus	Scad	4	161.9	0.1	0.0
Trisopterus luscus	Bib	1	8.9	0.0	0.0
Trisopterus minutus[*]	Poor cod	22	706.8	2.9	0.2
Zoarces viviparus	Viviparous blenny	1	34.7	0.0	0.0

[*]Species with a %W > 1% and included in the SIAR modeling.

Using TEFs as published by Caut *et al.* (2011), we found slight differences in diet between porpoises grouped by their age-class and sex (Table 7, Fig. 3). For all groups, mackerel was the most important prey species (11.0%–17.9%). Mackerel is followed by poor cod (10.6%–14.9%), sprat (10.2%–13.0%), greater sandeel (10.1%–13.9%), and small sandeel (10.1%–11.2%). The remaining prey species all accounted for less than 10% of the estimated diet. For juvenile porpoises, greater sandeel, mackerel, and poor cod were more important than for adults, especially for juvenile females. On the other hand, juvenile females fed less on herring compared to the other groups. Cod, whiting, and smelt, *Osmerus eperlanus,* were less important for juvenile porpoises than for adults, being of lowest importance for female juveniles. Sprat and small sandeel were only slightly less important for adult porpoises compared to juveniles, this difference in importance being smaller for adult females. Herring was less important for juvenile females compared to the other groups while gobies were more important for adult females compared to the other groups. Gobies, both common goby and sand goby, were more important for adult females than for the other groups.

Table 4. Isotopic composition (δ^{13}C and δ^{15}N) of prey species analyzed in this study.

Species		n	C:N	δ^{13}C Mean	SD	δ^{15}N Mean	SD
Ammodytes tobianus	Lesser sandeel	10	3.25	–18.76	0.80	15.08	1.02
Clupea harengus	Herring	20	3.22	–18.59	0.37	15.82	1.18
Gadus morhua	Cod	18	3.16	–17.94	1.10	17.61	0.70
Hyperoplus lanceolatus	Greater sandeel	20	3.24	–18.07	0.95	15.19	0.63
Merlangius merlangus	Whiting	19	3.16	–17.91	0.76	17.38	0.96
Osmerus eperlanus	Smelt	14	3.36	–18.50	0.97	18.48	0.28
Pomatoschistus microps	Common goby	20	3.50	–15.66	0.72	16.73	0.48
Pomatoschistus minutus	Sand goby	20	3.27	–16.61	1.00	16.96	0.41
Scomber scombrus	Mackerel	17	6.48	–22.35	0.61	13.70	1.36
Sprattus sprattus	Sprat	19	4.36	–20.57	0.89	14.96	0.71
Trisopterus minutus	Poor cod	25	3.12	–18.54	0.63	14.58	0.77

Table 5. Diet composition as modeled by SIAR, using TEFs from A: Hobson *et al.* (1996), B: Vander Zanden and Rasmussen (2001), C: McCutchan *et al.* (2003), and D: Caut *et al.* (2011).

Model	A Mean	CI_{95}	B Mean	CI_{95}	C Mean	CI_{95}	D Mean	CI_{95}
A. tobianus	9.4	0.0–22.2	14.2	1.2–26.5	7.6	0.0–19.7	9.7	0.0–23.6
C. harengus	3.2	0.0–9.1	6.1	0.0–14.8	2.8	0.0–8.6	5.6	0.0–14.6
G. morhua	1.2	0.0–3.4	1.7	0.0–4.6	1.0	0.0–2.9	2.3	0.0–6.4
H. lanceolatus	8.9	0.0–22.9	13.7	1.9–25.4	6.8	0.0–17.6	15.5	0.0–32.4
M. merlangus	1.3	0.0–3.6	1.9	0.0–5.1	1.2	0.0–3.3	2.4	0.0–6.3
O. eperlanus	0.8	0.0–2.4	1.1	0.0–3.1	0.8	0.0–2.3	1.8	0.0–5.2
P. microps	2.4	0.0–6.8	4.4	0.0–10.5	2.0	0.0–5.9	9.5	0.5–18.3
P. minutus	1.7	0.0–4.8	2.8	0.0–7.9	1.4	0.0–4.2	5.7	0.0–14.7
S. scombrus	23.7	16.3–30.3	15.9	8.6–23.3	35.3	28.3–41.6	18.6	1.7–34.7
S. sprattus	7.1	0.0–19.3	9.2	0.0–19.0	7.1	0.0–19.9	11.8	0.0–25.8
T. minutus	40.2	18.8–60.5	29.0	15.3–43.0	34.0	15.3–51.9	17.1	0.1–34.1

Table 6. Bray-Curtis similarities (%) between prey compositions deduced from stomach contents (SC) and as estimated by SIAR modeling using different TEFs (1–4).

	(SC)	(A)	(B)	(C)	(D)
(SC) Stomach contents					
(A) Hobson *et al.* 1996	79.578				
(B) Vander Zanden and Rasmussen 2001	82.880	94.979			
(C) McCutchan *et al.* 2003	78.473	97.674	93.327		
(D) Caut *et al.* 2011	83.927	92.577	95.842	90.925	

Stable Isotopes vs. *Stomach Contents*

Using SIAR, mackerel was found to be the most important prey species (11.0%–17.9%) while in stomach contents, it is only of minor importance (1.3%). Poor cod,
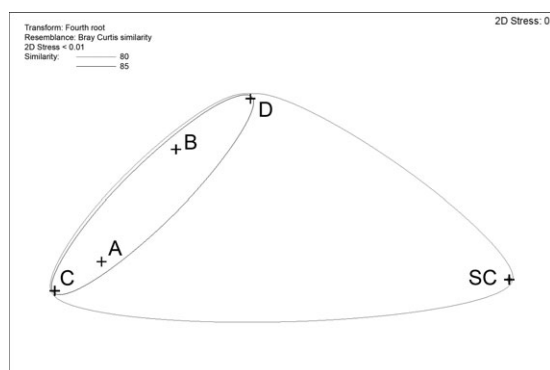
Figure 2. Nonmetric multi-dimensional scaling (NMDS) graph, comparing relative prey composition in the diet of porpoises, *Phocoena phocoena*, as deduced from stomach content analysis [SC] and as modeled by SIAR using eleven prey species and four Trophic Enrichment Factors (TEFs): (A) by Hobson *et al.* (1996), (B) by Vander Zanden and Rasmussen (2001), (C) by McCutchan *et al.* 2003, and (D) by Caut *et al.* (2011).

Table 7. Diet composition of porpoises as modeled by SIAR, using TEFs from Caut *et al.* (2011), A: juvenile males, B: juvenile females, C: adult males, and D: adult females.

Model	A		B		C		D	
	Mean	CI_{95}	Mean	CI_{95}	Mean	CI_{95}	Mean	CI_{95}
A. tobianus	11.2	0.0–23.7	11.1	0.0–24.4	10.5	0.0–21.0	10.1	0.0–19.8
C. harengus	8.6	0.0–19.6	7.2	0.0–18.8	9.2	0.0–19.1	9.0	0.0–18.6
G. morhua	4.9	0.0–12.7	3.3	0.0–9.1	7.4	0.0–17.3	7.4	0.0–16.6
H. lanceolatus	12.0	0.0–24.8	13.9	0.0–29.8	10.5	0.0–20.8	10.1	0.0–19.7
M. merlangus	4.8	0.0–13.0	3.4	0.0–9.8	7.1	0.0–16.5	7.4	0.0–16.4
O. eperlanus	3.9	0.0–10.3	2.7	0.0–7.5	6.6	0.0–15.7	6.6	0.0–15.8
P. microps	6.8	0.0–14.1	7.1	0.0–14.7	6.4	0.0–14.1	8.9	0.0–17.1
P. minutus	7.0	0.0–16.2	5.9	0.0–14.5	7.2	0.0–15.8	8.7	0.0–18.2
S. scombrus	14.4	1.2–27.4	17.9	1.6–33.1	12.2	0.3–22.5	11.0	0.0–20.9
S. sprattus	13.0	0.0–26.3	12.7	0.0–27.2	11.7	0.2–22.6	10.2	0.1–19.6
T. minutus	13.4	0.1–26.4	14.9	0.0–30.1	11.2	0.0–21.6	10.6	0.1–20.6

sprat, and greater sandeel, which are among the most important prey species as estimated by SIAR (together accounting for 30.9%–41.8%), are only of minor importance in stomach contents (8.0%). In stomach contents, gobies were found to be the most important prey species (39.5%) followed by whiting (25.5%), while using SIAR, their importance was estimated to be much lower, between 12.9% and 17.6% for gobies and between 3.4% and 7.4% for whiting.

DISCUSSION

Using stable isotope analysis allows the estimation of past prey composition over a longer term than stomach content analysis (Newsome *et al.* 2010). Using the same
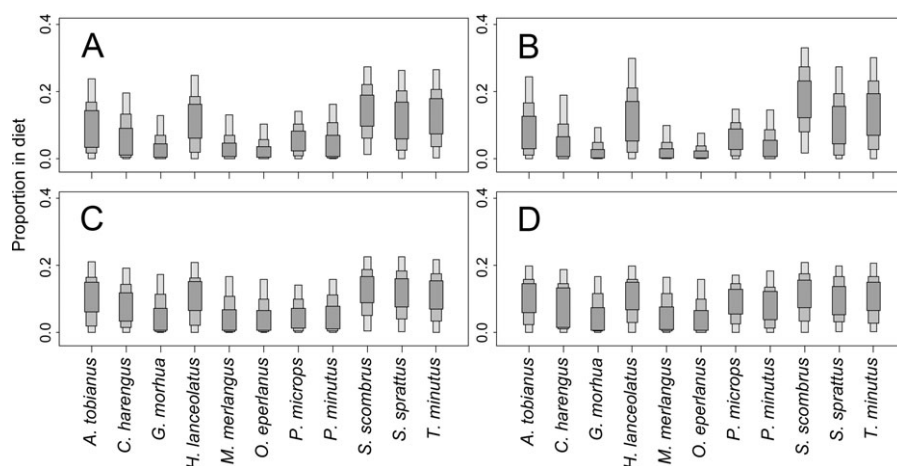
Figure 3. Boxplots of the relative contribution of prey sources to the diet of porpoises, *Phocoena phocoena*, as modeled by SIAR using TEFs by Caut *et al.* (2011). A: juvenile males, B: juvenile females, C: adult males and D: adult females. Credibility intervals (CI): CI_{50} = dark gray, CI_{75} = medium gray, CI_{95} = light gray.

individuals for both analyses, we have found profound differences in the dietary composition estimated by the two techniques, reflecting a genuine difference between the long- and short-term diet of harbor porpoises. The long-term diet outcome reveals that porpoises feed offshore on pelagic, schooling species (*e.g.,* poor cod, mackerel, greater sandeel, and sprat) whereas the short-term diet outcome indicates that they feed closer to shore on more benthic and demersal species (*e.g.,* gobies, whiting, herring, and cod).

Stable Isotope Analysis

There are three possible methodological sources of variation that can influence the resulting diet estimate: (1) the number of prey sources included in the model (Phillips and Gregg 2003), (2) the TEFs used (Gannes *et al.* 1997, Bond and Diamond 2011), and (3) isotopic representation of sources (Parnell *et al.* 2010).

Number of prey sources—From stomach contents it has been shown that porpoises feed on a wide variety of prey species. Even though SIAR modeling can cope with more sources than isotopes (Parnell *et al.* 2010), reliably entangling the contribution of as many as 30 prey sources to the isotopic composition of the predator using just two stable isotopes (δ^{13}C and δ^{15}N) is impossible. In our study we have only included prey species that have been shown to be of major importance to the diet of porpoises as deduced from stomach contents. Concentrating on only few species or grouping species with similar isotopic values will improve source differentiation but will also reduce distinction in quantitative diet estimation

Trophic enrichment factors—TEFs are thought to be, *i.a.*, species-, tissue- and diet-specific (DeNiro and Epstein 1981, Vanderklift and Ponsard 2003). It is common practice to use TEFs of other species or tissues when TEFs for the species analyzed are not available yet (Bond and Diamond 2011). It has been shown that stable isotope mixing mod-

els are sensitive to variation in discrimination factors and can lead to misinterpretation when species- and tissue-specific TEFs are unknown and general ones are applied instead (Martínez del Rio *et al.* 2009, Bond and Diamond 2011). Unfortunately, species- and diet-specific TEFs for porpoises are not available. We have therefore used several different published TEFs as calculated from seals (Hobson *et al.* 1996), as averaged for carnivores (Vander Zanden and Rasmussen 2001), averaged for lipid extracted muscle (McCutchan *et al.* 2003), and as derived from killer whales (Caut *et al.* 2011). Our study showed that for the porpoise, model outcomes using the different TEFs were in general very similar (Fig. 2, Table 6). The model using TEFs as deduced from cetaceans (*i.e.,* killer whales, Caut *et al.* 2011) was most similar to the results from stomach contents. The fact that the cetacean derived TEFs show the highest similarity with stomach contents supports the need for the use and development of species-specific TEFs. The influence of diet-specific TEFs on the predictive power of SIAR is hard to evaluate. This issue would probably concern mostly mackerel and sprat, as other food items have similar C:N ratios, and therefore presumably similar nutritional quality. However, even prey showing similar C:N ratios can have different biochemical composition, leading to variability in trophic enrichment (Aberle and Malzahn 2007). Experimental measurements of species- and diet-specific TEFs would likely improve the accuracy of SIAR outputs, and efforts to produce these are desirable in this field of research.

Isotopic representation of sources—SIAR modeling is most useful when few prey species with distinct isotopic composition are used (Parnell *et al.* 2010). The isotopic composition of prey species, however, showed great spatial variation and large overlap between species. When dealing with a highly mobile predator that feeds on a multitude of species, sampling sufficient characteristic and representative prey is challenging, time consuming and expensive. Porpoises stranded along the Dutch coast are considered to have fed mainly in Dutch coastal waters, but satellite tracking has shown that they can range over considerable distances (Read and Westgate 1997, Johnston *et al.* 2005). Prey samples were therefore collected from the southern North Sea, with the majority of samples from Dutch coastal waters, covering size classes that were identified in stomach contents (Leopold and Camphuysen 2006). Spatial variation in isotopic composition among prey from the southern North Sea has been shown to be low (Jansen *et al.* 2012). In order to improve species differentiation, a reduced set of prey sources (%W > 1) was used, but there was still some overlap in δ^{13}C and δ^{15}N values between species.

Stomach Content Analysis

Stomach content analysis provides insight into the diet shortly before the stranding and may be biased towards species with large, robust hard parts (Hyslop 1980, da Silva and Neilson 1985). The otoliths of whiting and cod are large, robust and very distinct (Härkönen 1986), which makes them easy to identify, even in very digested or decomposed stomach samples. Otoliths of mackerel and sprat, however, are fragile (Härkönen 1986), and so may be less recognizable due to digestion and decomposition. This bias may lead to an overrepresentation of whiting and cod and an underrepresentation of species like mackerel and sprat in stomach contents (Bowen 2000). A second bias of stomach content analysis is the confusion between fish species that are closely related and therefore have very similar otoliths, *e.g.,* poor cod and bib, *Trisopterus luscus*, lesser and small sandeel, or different goby species. Including prey remains other than otoliths (Watt *et al.* 1997, Cottrell and Trites 2002) and correct-

ing for wear (Jobling and Breiby 1986, Leopold *et al.* 1998) as we did, reduces this bias in stomach content analysis.

Ecological Implications

Fish species identified in stomachs and by SIAR modeling are all very abundant in the North Sea, including pelagic, schooling species (*e.g.,* mackerel, herring, and sprat), demersal species (*e.g.,* whiting, poor cod, and sole) and typical coastal species (*e.g.,* gobies, smelt, and bass). However, as stomach contents are likely biased towards nearshore species that are ingested shortly before the stranding, it is not surprising that gobies dominate the diet when only stomach contents are used (Knijn *et al.* 1993). It has been suggested that gobies are mainly prey of juvenile porpoises (Addink *et al.* 1995), however, this was not the case for animals included in this study (Leopold and Camphuysen 2006).

Although SIAR is limited to the number and quality of prey sources included in the model, it covers a longer term diet, thus raising the chance to include prey taken during foraging trips further offshore. It is also able to recognize species with fragile hard prey remains and distinguishes between species with similar otoliths. Using SIAR resulted in a significant reduction in the importance of small benthic fish *i.e.,* gobies while pelagic, schooling species such as mackerel became more important.

Gadoids are found to be the main prey in many studies, with regional differences in specific species (Santos and Pierce 2003). Poor cod can be found throughout the entire North Sea, although densities are generally lower in deeper parts (Knijn *et al.* 1993). Poor cod was identified among the most important prey species in Scottish and Irish waters (Rogan and Berrow 1996, Santos *et al.* 2004). Mackerel has also been identified in other studies (Santos and Pierce 2003); however, only in the coastal waters of Eastern Canada were they identified among the most important prey species (Smith and Gaskin 1974). Gadoids such as whiting and cod are more important in stomach contents than in the diet estimated by SIAR. They are both abundant and widely distributed species throughout the North Sea (Knijn *et al.* 1993). In almost all studies on porpoise diet, sandeels are found to be important prey species (Santos and Pierce 2003), also in our study, irrespective of the method used. The decline of sandeel stocks has been suggested as a reason for starvation and a southern migration of porpoises from Scottish waters (MacLeod *et al.* 2007*a*, *b*), underlining the impact that declines of certain fish stocks can have on the distribution of porpoises throughout the North Sea. Clupeids are among the most important prey species, using both SIAR (*i.e.,* sprat) and stomach contents (*i.e.,* herring). These energy-rich prey species seem to have become less important in the diet of porpoises over the years. It has been suggested that this is due to declines in their respective stocks (Santos and Pierce 2003).

The difference between the results of stomach contents and SIAR is not necessarily a result of the horizontal distribution of prey species but may also be caused by differences in the behavior of fish species and porpoises in the turbid coastal waters compared to the clearer offshore waters. Pelagic fish tend to school during the day, while these aggregations become more dispersed in dark or turbid conditions (Glass *et al.* 1986, Turesson and Brönmark 2007). Dutch coastal waters are very turbid due to the outflow of big rivers (Eisma and Kalf 1979, Fettweis and Van den Ende 2003). Pelagic fish are therefore highly dispersed in the coastal zone, rendering them less easy to catch. This could explain the higher occurrence of pelagic schooling prey species (*e.g.,* mackerel) using SIAR compared to stomach content analysis. The comparison between the two methods suggests that porpoises are not limited to preying on

demersal species in the coastal zone, but also prey on pelagic schooling species in off-shore waters. A future step in the interpretation of differences between diets as deduced from stable isotopes and from stomach contents should be the inclusion of age, seasonality in strandings, and/or prey availability.

Conclusion

Profound differences were found in the diet of harbor porpoises as estimated by SIAR and the diet as deduced from stomach content analysis. This points towards an ecological and not a methodological difference, because the prey species used in the isotope estimate were chosen on the basis of being most important in the stomach contents. This may indicate a difference between long-term diet where porpoises feed also offshore on pelagic, schooling species and their short-term diet where they feed closer to shore on more benthic and demersal species. This could be due to the distribution of prey species as well as differences in behavior of porpoises and their prey between the coastal zone and offshore waters.

This difference between long- and short-term diet as deduced from applying two techniques, is of relevance for *e.g.,* ecological impact assessment studies, fishery impact assessments, and management decisions for the conservation of porpoises. When only one technique is used, key prey species in the predator-prey relation may be missed or underestimated, highlighting the need for multi-method approaches in diet reconstruction.

LITERATURE CITED

Aberle, N., and A. M. Malzahn. 2007. Interspecific and nutrient dependent variations in stable isotope fractionation: Experimental studies simulating pelagic multitrophic systems. Oecologia 154:291–303.

Addink, M. J., M. García Hartman and C. Smeenk. 1995. The harbour porpoise *Phocoena phocoena* in Dutch waters: Life history, pathology and historical records. IWC Scientific Committee Document SC/47/SM5. 13 pp.

Barnes, C., S. Jennings and J. T. Barry. 2009. Environmental correlates of large-scale spatial variation in the $\delta^{13}C$ of marine animals. Estuarine Coastal and Shelf Science 81:368–374.

Bond, A. L., and A. W. Diamond. 2011. Recent Bayesian stable-isotope models are highly sensitive to variation in discrimination factors. Ecological Applications 21:1017–1023.

Börjesson, P., P. Berggren and B. Ganning. 2003. Diet of harbor porpoises in the Kattegat and Skagerrak seas: Accounting for individual variation and sample size. Marine Mammal Science 19:38–58.

Bowen, W. D. 2000. Reconstruction of pinniped diets: Accounting for complete digestion of otoliths and cephalopod beaks. Canadian Journal of Fisheries and Aquatic Sciences 57:898–905.

Budge, S. M., S. J. Iverson and H. N. Koopman. 2006. Studying trophic ecology in marine ecosystems using fatty acids: A primer on analysis and interpretation. Marine Mammal Science 22:759–801.

Camphuysen, C. J., C. Smeenk, M. Addink, H. Van Grouw and O. E. Jansen. 2008. Cetaceans stranded in the Netherlands from 1998 to 2007. Lutra 51:87–122.

Caut, S., S. Laran, E. García-Hartmann and K. Das. 2011. Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). Journal of Experimental Biology 214:538–545.

Christensen, J. T., and K. Richardson. 2008. Stable isotope evidence of long-term changes in the North Sea food web structure. Marine Ecology Progress Series 368:1–8.

Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6.1.13: Multivariate statistics for ecologists. PRIMER-E Ltd., Ivybridge, U.K.

Coplen, T. B. 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. Rapid Communications in Mass Spectrometry 25:2538–2560.

Cottrell, P. E., and A. W. Trites. 2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). Marine Mammal Science 18:525–539.

Coull, K. A., A. S. Jermyn, A. W. Newton, G. I. Henderson and W. B. Hall. 1989. Length/weight relationships for 88 species of fish encountered in the North East Atlantic. Scottish Fisheries Research Report. 81 pp.

Crawford, K., R. A. Mcdonald and S. Bearhop. 2008. Applications of stable isotope techniques to the ecology of mammals. Mammal Review 38:87–107.

da Silva, J., and J. D. Neilson. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Canadian Journal of Fisheries and Aquatic Sciences 42:1439–1446.

Dalerum, F., and A. Angerbjörn. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658.

DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341–351.

Eisma, D., and J. Kalf. 1979. Distribution and particle size of suspended matter in the southern bight of the North Sea and the eastern Channel. Netherlands Journal of Sea Research 13:298–324.

Fettweis, M., and D. Van den Ende. 2003. The mud deposits and the high turbidity in the Belgian-Dutch coastal zone, southern bight of the North Sea. Continental Shelf Research 23:669–691.

Folch, J., M. Lees and G. H. S. Stanley. 1957. A simple method for the isolation and purification of total lipides from animal tissues. Journal of Biological Chemistry 226: 497–509.

Gannes, L. Z., D. M. O'Brien and C. M. Del Rio. 1997. Stable isotopes in animal ecology: Assumptions, caveats, and a call for more laboratory experiments. Ecology 78:1271–1276.

Glass, C. W., C. S. Wardle and W. R. Mojsiewicz. 1986. A light intensity threshold for schooling in the Atlantic mackerel, *Scomber scombrus*. Journal of Fish Biology 29:71–81.

Härkönen, T. 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic. Danbiu ApS, Hellerup, Netherlands.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: A review. Oecologia 120:314–326.

Hobson, K. A., D. M. Schell, D. Renouf and E. Noseworthy. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: Implications for dietary reconstructions involving marine mammals. Canadian Journal of Fisheries and Aquatic Sciences 53:528–533.

Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their application. Journal of Fish Biology 17:411–429.

Jansen, O. E., G. M. Aarts, K. Das, G. Lepoint, L. Michel and P. J. H. Reijnders. 2012. Feeding ecology of harbour porpoises: Stable isotope analysis of carbon and nitrogen in muscle and bone. Marine Biology Research 8:829–841.

Jobling, M., and A. Breiby. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia 71:265–274.

Johnston, D. W., A. J. Westgate and A. J. Read. 2005. Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. Marine ecology Progress Series 295:279–293.

Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1–27.

Knijn, R. J., T. W. Boon, H. J. L. Heessen and J. R. G. Hislop. 1993. Atlas of North Sea fishes based on bottom-trawl survey data for the years 1985–1987. ICES Cooperative Research Report, Copenhagen, Denmark. 268 pp.

Leopold, M., and C. J. Camphuysen. 2006. Bruinvisstrandingen in Nederland in 2006: Achtergronden, leeftijdsverdeling, sexratio, voedselkeuze en mogelijke oorzaken [Porpoise strandings in the Netherlands in 2006: Backgrounds, age distribution, sex ratio, prey choice and possible causes]. Wageningen IMARES, Texel en Koninklijk Nederlands Instituut voor Onderzoek der Zee, Texel, Netherlands. 136 pp.

Leopold, M. F., C. J. G. van Damme and H. W. van der Veer. 1998. Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. Journal of Sea Research 40:93–107.

Leopold, M. F., C. J. G. Van Damme, C. J. M. Phillippart and C. J. N. Winter. 2001. Otoliths of North Sea fish: Interactive guide of identification of fish from the SE North Sea, Wadden Sea and adjacent fresh waters by means of otoliths and other hard parts. ETI BioInformatics, Amsterdam, Netherlands.

MacLeod, C. D., G. J. Pierce and M. B. Santos. 2007a. Starvation and sandeel consumption in harbour porpoises in the Scottish North Sea. Biology Letters 3:535–536.

MacLeod, C. D., M. B. A. Santos, R. J. Reid, B. E. Scott and G. J. Pierce. 2007b. Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: Could climate change mean more starving porpoises? Biology Letters 3:185–188.

Martínez del Rio, C., N. Wolf, S. A. Carleton and L. Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews 84:91–111.

McConnaughey, T., and C. P. McRoy. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Marine Biology 53:257–262.

McCutchan, J. H., W. M. Lewis, C. Kendall and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390.

Michener, R. H., and L. Kaufman. 2007. Stable isotope ratios as tracers in marine food webs: An update. Chapter 9. Pages 238–282 *in* R. H. Michener and K. Lajtha, eds. Stable Isotopes in ecology and environmental science. Blackwell Publishing, Boston, MA.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between δ^{15}N and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.

Newsome, S. D., M. T. Clementz and P. L. Koch. 2010. Using stable isotope biogeochemistry to study marine mammal ecology. Marine Mammal Science 26:509–572.

Parnell, A. C., R. Inger, S. Bearhop and A. L. Jackson. 2010. Source partitioning using stable isotopes: Coping with too much variation. PLoS ONE 5:1–5.

Phillips, D. L. 2001. Mixing models in analyses of diet using multiple stable isotopes: A critique. Oecologia 127:166–170.

Phillips, D. L., and J. W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127:171–179.

Phillips, D. L., and J. W. Gregg. 2003. Source partitioning using stable isotopes: Coping with too many sources. Oecologia 136:261–269.

Pierce, G. J., and P. R. Boyle. 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanography and Marine Biology 29:409–486.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83:703–718.

Prime, J. H., and P. S. Hammond. 1987. Quantitative assessment of gray seal diet from fecal analysis. Pages 165–181 *in* A. C. Huntley, D. P. Costa, G. A. J. Worthy and M. A. Castellini, eds. Approaches to marine mammal energetics. Special Publication Number 1. The Society for Marine Mammology.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Read, A. J., and A. J. Westgate. 1997. Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. Marine Biology 130:315–322.

Rogan, E., and S. D. Berrow. 1996. A Review of Harbour Porpoises, *Phocoena phocoena*, in Irish Waters. Report of the International Whaling Commission 46:595–605.

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

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

Santos, M. B., G. J. Pierce, E. N. Ieno, M. Addink, C. Smeenk, C. C. Kinze and M. Sacau. 2005. Harbour porpoise (*Phocoena phocoena*) feeding ecology in the eastern North Sea. ICES CM 2005/Theme Session R:15 (Marine Mammals: Monitoring Techniques, Abundance Estimation, and Interactions with Fisheries). 19 pp. Available at http://www.ices.dk/products/CMdocs/2005/R/R1505.pdf.

Santos Vázquez, M. B. 1998. Feeding ecology of harbour porpoises, common and bottlenose dolphins and sperm whales in the Northeast Atlantic. Ph.D. thesis, University of Aberdeen, Aberdeen, U.K. 284 pp.

Smith, G. J. D., and D. E. Gaskin. 1974. The diet of harbor porpoises (*Phocoena Phocoena* (L)) in coastal waters of Eastern Canada, with special reference to Bay of Fundy. Canadian Journal of Zoology 52:777–782.

Tieszen, L. L., T. W. Boutton, K. G. Tesdahl and N. A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. Oecologia 57:32–37.

Turesson, H., and C. Brönmark. 2007. Predator-prey encounter rates in freshwater piscivores: Effects of prey density and water transparancy. Oecologia 153:281–290.

Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography 46:2061–2066.

Vanderklift, M. A., and S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: A meta-analysis. Oecologia 136:169–182.

Víkingsson, G. A., D. Olafsdottir and J. Sigurjonsson. 2003. Geographical and seasonal variation in the diet of harbour porpoises (*Phocoena phocoena*) in Icelandic waters. NAMMCO Scientific Publication 5:243–270.

Watt, J., G. J. Pierce and P. R. Boyle. 1997. Guide to the identification of North Sea fish using premaxilla and vertebrae. ICES Cooperative Research Report. 231 pp.