Vol. 263: 287–298, 2003 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published November 28

Marine mammals from the southern North Sea: feeding ecology data from $\delta^{13}C$ and $\delta^{15}N$ measurements

K. Das[1,2,*], G. Lepoint[1], Y. Leroy[1], J. M. Bouquegneau[1]

[1]Marine Research Center (MARE), Laboratory for Oceanology, University of Liège, B6c, Sart-Tilman, 4000 Liège, Belgium
[2]Forschung- und Technologiezentrum Westkueste, Werftstrasse 6, 25761 Büsum, Germany

ABSTRACT: The harbour porpoise *Phocoena phocoena*, grey seal *Halichoerus grypus*, harbour seal *Phoca vitulina* and white-beaked dolphin *Lagenorhynchus albirostris* are regularly found stranded along southern North Sea coasts. Occasionally, offshore species such as the fin whale *Balaenoptera physalus*, the white-sided dolphin *L. acutus* and the sperm whale *Physeter macrocephalus* are also found stranded. In order to trace their diet, we measured $\delta^{13}C$ and $\delta^{15}N$ in their muscles as well as in 49 invertebrate and fish species collected from the southern North Sea. The $\delta^{15}N$ data indicate that the harbour seal, grey seal and white-beaked dolphin occupy the highest trophic position, along with ichtyophageous fishes such as the cod *Gadus morhua* (mean muscle values of 18.7, 17.9, 18.8 and 19.2‰ respectively). The harbour porpoise occupies a slightly lower trophic position (mean $\delta^{15}N$ value of 16.2‰), reflecting a higher amount of zooplanktivorous fishes in its diet (mean $\delta^{15}N$ of 14.7‰); 2 suckling harbour porpoises displayed a significant $\delta^{15}N$ enrichment of 2.2‰ compared to adult females. Adult females are $\delta^{15}N$-enriched compared to adult male harbour porpoises. Fin whales, sperm whales and white-sided dolphins are ^{13}C-depleted compared to southern North Sea particulate organic matter and species, suggesting that despite regular sightings, they do not feed within the southern North Sea area.

KEY WORDS: North Sea · Marine mammals · Stable isotopes · Food web

INTRODUCTION

The fertile waters of the North Sea represent a major habitat for at least 4 different marine mammal species: the harbour porpoise *Phocoena phocoena*, harbour seal *Phoca vitulina*, grey seal *Halichoerus grypus* and white-beaked dolphin *Lagenorhynchus albirostris* (Hammond et al. 2002). The harbour porpoise and harbour seal are the most common species in the northeast Atlantic and the North Sea (Boran et al. 1998, Hammond et al. 2002). Their southern distribution seems to be limited to the Dutch Wadden Sea, while white-beaked dolphins are generally concentrated in a band across the North Sea between 55° and 60°N, mostly to the west along the eastern UK coast (De Jong et al. 1999, Hammond et al. 2002). Grey seal hauling and breeding sites are well known and described along the northern UK coast (Nigel Bonner 1989, Reijnders et al. 1995, OSPAR 2000). However, some individuals have already been observed or are regularly found stranded in the southern part of the North Sea, suggesting more extended movements for these species (Haase 1987, Leopold & Couperus 1995, Abt et al. 2002, Jauniaux et al. 2002).

Other species such as fin whale *Balaenoptera physalus*, white-sided dolphin *Lagenorhynchus acutus* and sperm whale *Physeter macrocephalus* are occasionally sighted or found stranded, but are still considered very rare in the southern North Sea (Camphuysen & Winter 1995, Hammond et al. 2002). This area is characterized by intricate systems of sand banks, mudflats, sandy islands and estuaries, and is obviously an unfavourable environment for such oceanic species.

*Email: krishna.das@ulg.ac.be

The distribution of marine mammals is strongly influenced by the distribution of their prey (Gowans & Whitehead 1995, Gannon et al. 1997). However, despite regular and new observations in the southern North Sea, few data dealing with the diets of marine mammals within this area are available (Desportes 1985, Prime & Hammond 1990, Santos 1998, Santos et al. 1999, Santos & Pierce 2003). Strandings offer a good opportunity for scientists to collect biological data but, in most cases, either the stomachs of stranded animal are empty, or digested material is not suitable for dietary research (Santos et al. 1994, Jauniaux et al. 2002). Moreover, strandings can represent potentially biased samples of animals, as sick or injured animals may not be feeding normally prior to death (Sekiguchi et al. 1992, Santos et al. 1994, Santos & Pierce 2003).

The use of naturally occurring carbon and nitrogen stable isotopes has provided complementary data to marine mammal feeding ecology (Hobson & Welch 1992, Abend & Smith 1995, Smith et al. 1996, Hobson et al. 1997, Burns et al. 1998, Hobson & Schell 1998, Das et al. 2000, 2003). Indeed, the carbon and nitrogen isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of a consumer reflect those of its diet, with a slight selective retention of the heavier isotope and excretion of the lighter one. As a result, these ratios (in delta notation $\delta^{13}C$ and $\delta^{15}N$) typically show a trophic enrichment value of 1 and 2 to 5‰ respectively (De Niro & Epstein 1978, 1981, Hobson & Welch 1992, Michener & Schell 1994). Stable nitrogen isotopes can be used to quantitatively assess the trophic level, whereas ^{13}C, rather than being a reliable indicator of trophic level, is generally used to indicate relative contributions to the diet of different potential primary sources in a trophic network, indicating for example the inshore versus offshore, or pelagic versus benthic contribution to food intake (Rau et al. 1992, Hobson et al. 1995, Smith et al. 1996, Lepoint et al. 2000).

Because stable isotope ratios in the tissue of a consumer are derived from assimilated food, the tissue reflects dietary input integrated over time, not just the last meal before stranding, which might be considered as biased.

In this paper, we used stable-isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) to determine trophic position and relationships among 7 marine mammal species beached along the French, Belgian and Dutch coasts of the southern North Sea between 1994 and 2000: the fin whale, white-sided dolphin, sperm whale, harbour seal, harbour porpoise, grey seal and white-beaked dolphin. Trophic relationships among species were determined by measuring stable nitrogen-isotope abundance in the muscle. Stable carbon isotope analysis was used to investigate species segregation according to source of prey. Stable isotope measurements were also performed for 15 invertebrate and 34 fish species collected in the southern North Sea to delineate trophic relationships between marine mammals and other species from this area. Finally, we also addressed the question of whether more occasional species such as the fin whale, white-sided dolphin or sperm whale actually feed within the Southern Bight of the North Sea.

MATERIALS AND METHODS

Marine mammal sampling. The muscle of 3 fin whales *Balaenoptera physalus*, 2 white-sided dolphins *Lagenorhynchus acutus*, 7 sperm whales *Physeter macrocephalus*, 46 harbour porpoises *Phocoena phocoena*, 6 grey seals *Halichoerus grypus*, 23 harbour seals *Phoca vitulina* and 7 white-beaked dolphins *L. albirostris*, stranded on the French, Belgian and Dutch coasts of the southern North Sea, were sampled between 1994 and 2000 and stored at –20°C until analysis (for necropsy methods see Jauniaux et al. 1998, 2001, 2002).

Invertebrate and fish sampling. We collected 15 invertebrate and 34 fish species (see Table 1) from the southern part of the North Sea (between 51 and 56° N) during 3 cruises of the RV 'Belgica' (Belgium) in September 2000 and in February and May 2001, and during 1 cruise of the RV 'Thalassa' (IFREMER, France) in March 2001. All samples were frozen and stored at –20°C until analysis. Based on their gut-content composition and their lifestyle (Greenstreet et al. 1997, Miller & Loates 1997, Quéro & Vayne 1997) (K.D. pers. obs.) the species were classified into 8 feeding types (see second subsection of 'Results').

Stable isotope measurements. Stable isotope measurements were performed in the muscle of marine mammals, invertebrates and fishes, except for the sea gooseberry *Pleurobrachia pileus*, for which the whole body was ground. Concentrations of lipids may vary in organisms. As the ^{13}C content of lipids has been shown to vary as a function of diet (Tieszen et al. 1983), lipids were extracted from samples using repeated rinses with 2:1 chloroform: methanol prior to analysis. After drying at 50°C (48 h), samples were ground into a homogeneous powder. After grinding, those samples containing inorganic carbonates were acidified with HCl (1 N). As recommended by Pinnegar & Polunin (1999), when samples were acidic, $^{15}N/^{14}N$ ratios were measured before acidification because of significant modifications in these ratios arising from HCl treatment (Bunn et al. 1995).

Stable isotope measurements were performed on a V. G. Optima (Micromass) isotope ratio mass spectrometer coupled to an N-C-S elemental analyser (Carlo

Erba) for automated analyses. Routine measurements were precise to within 0.3‰ for both $\delta^{13}C$ and $\delta^{15}N$. Stable isotope ratios are expressed in delta notation according to

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Carbon and nitrogen ratios are expressed relative to the V-PDB (Vienna Peedee Belemnite) standard and to atmospheric nitrogen, respectively. Reference materials were IAEA CH-6 (sucrose) ($\delta^{13}C = -10.4 \pm 0.2$‰) and IAEA-N1 ($\delta^{15}N = +0.4 \pm 0.2$‰) respectively.

Isotopic model. Muscle $\delta^{15}N$ signatures of harbour porpoise, grey seal, harbour seal and white-beaked dolphin were converted to trophic position (TP) using Eq. (2) (after Hobson & Welch 1992, Lesage et al. 2001):

$$\text{TP} = 2 + (D_m - \text{POM} - \text{TEF}_{\text{mmt}})/\text{TEF} \quad (2)$$

where D_m = $\delta^{15}N$ value in marine mammal muscle, POM = $\delta^{15}N$ value of marine particulate organic matter of the southern North Sea (fixed to 9‰ after Middelburg & Nieuwenhuize 1998) and TEF = trophic enrichment factor in $\delta^{15}N$ for a specific tissue (Hobson & Welch 1992). The latter value was set to a mean of 3.4‰ for all community components (Lesage et al. 2001) except for marine mammals, for which a TEF value (TEF_{mmt}) of 2.4‰ was obtained for the muscles of 2 harbour seals fed on a constant herring diet (Hobson et al. 1996).

Data treatment. Mean isotopic composition values were calculated for each feeding type and compared to marine mammal muscle data. The Kolmogorov-Smirnov test was used to test for data departure from normality. ANOVA followed by post-hoc multiple-comparison tests (least-significant difference test) were used to compare the data between the different species, seasons and feeding types. A Student's *t*-test was used to compare isotopic values between males and females and herring caught in May and September. When the necessary assumptions to realise ANOVA and Student's *t*-test were not gathered (normality of the variables and homogeneity of variances), Kruskal-Wallis tests were used followed by multiple comparisons based on the Kruskal-Wallis rank-sums test for pairwise differences among species. The non-parametric Mann-Whitney *U*-test was performed to compare differences among groups when variances were not homogenous.

RESULTS

The isotopic composition of invertebrates, fishes and marine mammals are summarised in Tables 1 & 2.

Stable isotopic composition of marine mammals

Muscle $\delta^{13}C$ and $\delta^{15}N$ values differed significantly between marine mammal species (ANOVA, $F = 6.7$ and 20.2 respectively, $p < 0.0001$).

Mean $\delta^{13}C$ values did not differ significantly between harbour seals, harbour porpoises, grey seals and white-beaked dolphins (post-hoc test, $p > 0.1$). The mean $\delta^{13}C$ values of fin whales, sperm whales and white-sided dolphins did not differ significantly (post-hoc test, $p > 0.1$), but they were significantly lower than those of other species (post-hoc test, $p < 0.02$).

Grey seals, harbour seals and white-beaked dolphins displayed similar mean $\delta^{15}N$ values (post-hoc test, $p > 0.1$), that were all significantly higher than those of fin whales, white-sided dolphins, sperm whales and harbour porpoises and (post-hoc test, $p < 0.05$, Table 2, Fig. 1). In turn, the mean $\delta^{15}N$ value of harbour porpoise was significantly higher than that of fin whales, white-sided dolphins, sperm whales and (post-hoc test, $p < 0.05$). $\delta^{15}N$ did not differ significantly between fin whales and white-sided dolphins (post-hoc test, $p > 0.1$).

Based on their muscle $\delta^{15}N$ values, trophic levels were estimated for harbour porpoises, grey seals, harbour seals and white-beaked dolphins (Table 3). The higher trophic position was occupied by the white-beaked dolphin, the lowest by the harbour porpoise. The grey seal and harbour seal displayed a close trophic level of 3.9 and 4.1, respectively. Trophic levels were not estimated for fin whales, white-sided dolphins and sperm whales as their $\delta^{13}C$ depletion strongly suggests that they do not feed in this area (see 'Discussion').

The 2 smallest porpoises (80 and 87 cm) had $\delta^{15}N$ values (19.3 and 18.1‰ respectively) compared to adult females and males (Fig. 2). However, because of the small sample size, no statistical test was performed. Porpoise adult females had higher muscle $\delta^{15}N$ than adult males (Fig. 2, Student *t*-test, $p < 0.05$), while juvenile isotopic values were similar between sexes ($p > 0.5$).

The $\delta^{13}C$ and $\delta^{15}N$ values of harbour porpoises were similar between seasons (ANOVA, $p > 0.5$). Harbour seal $\delta^{13}C$ did not vary between seasons, whereas mean $\delta^{15}N$ measurements were lower in winter than summer (ANOVA, $F = 3.2$, $p < 0.04$, Fig. 3).

Stable isotopic composition of invertebrates and fishes

The lowest mean $\delta^{15}N$ was recorded in the echinoderm *Echinocardium cordatum*, the highest mean $\delta^{15}N$ in the cod *Gadus morhua* and the eel *Anguilla anguilla* (Table 1).

Table 1. Length (cm), δ^{13}C, δ^{15}N content (‰) and feeding type (FT) of selected invertebrates and fishes from the southern North Sea. Data are as mean ± SD ‰ or minimum/maximum values in the case of 2 samples; n: no of individuals; Bif: fish feeding on benthic invertebrate, Bifc: crustaceans feeding on benthic invertebrates, Cf: carnivorous fish, Ct: ctenophore (*: pool of 7 individuals), Gi: grazer invertebrates, Mf: mollusc feeder, Omi: omnivorous invertebrates, Sf: suspension feeders, Zof: fish feeding on zooplankton, nd: not determined. When length not available weight is given in parentheses

Species	Common name	n	Length	δ^{13}C	δ^{15}N	FT
Ctenophores						
Pleurobrachia pileus	Sea gooseberry	1	(7 ind. pooled)	–12.9	16.6	Ct
Molluscs						
Gastropods						
Buccinum undatum	Whelk	2	nd (37–45 g)	–15.2/–15.0	13.0–14.4	Omi
Bivalves						
Solen marginatus	Grooved razor shell	2	10.6–11.2	–16.9/–16.4	11.1–11.3	Sf
Spisula solida	Thick trough shell	2	nd (9–11 g)	–18.0/–17.0	10.2–11.9	Sf
Cephalopods						
Sepia officinalis	Common cuttlefish	5	nd (2.3–3.2 g)	–15.9 ± 0.6	16.1 ± 0.6	Bif
Loligo vulgaris	Common squid	9	nd (2.2–45 g)	–15.9 ± 0.6	17.2 ± 1.3	Bif
Crustaceans						
Crangon crangon	Common shrimp	3	nd (1.6–2.6 g)	–16.8 ± 0.6	17.3 ± 0.2	Bifc
Palaemon cerratus	Common prawn	1	7	–15.8	14.6	Omi
Carcinus maenas	Common shore crab	3	nd (5–11 g)	–17.4 ± 0.3	15.5 ± 0.5	Omi
Liocarcinus holasatus	Swimming crab	2	nd (15–19 g)	–15.1/–15.0	15.8–16.5	Omi
Pagurus berhardus	Hermit crab	2	nd (4.6–7.6 g)	–15.7/–14.8	14.8–15.2	Omi
Echinoderms						
Asteria ruben	Common starfish	3	nd (46–182 g)	–13.8 ± 7	13.3 ± 0.6	Mf
Ophiura ophiura	Sand-star	1	nd (0.8 g)	–15.8	11.7	Sf
Echinorcardium cordatum	Sea potato	1	nd (22.6 g)	–17.4	10.6	Sf
Psammechinus miliaris	Sea urchin	1	nd (14.7 g)	–14.1	12.1	Gi
Elasmobranchs						
Raja clavata	Thornback ray	5	37–94	–15.0 ± 0.6	14.9 ± 0.4	Bif
Raja montagui	Spotted ray	3	56–65	–16.6 ± 1.1	15.3 ± 0.7	Bif
Raja radiata	Starry ray	3	41–49	–16.5 ± 0.6	13.5 ± 0.2	Bif
Scyliorhinus canicula	Small spotted catshark	6	24–70	–15.4 ± 0.4	15.3 ± 1.5	Bif
Mustelus asterias	Stellate smooth-hund	2	70–81	–15.3/–15.1	16.2–16.2	Bif
Clupeiformes						
Clupea harengus	Herring	9	6–29	–17.9 ± 1.9	13.0 ± 1.1	Zof
Engraulis encrasicolus	Anchovy	2	10–12	–18.4/–15.8	14.8–15.2	Zof
Sprattus sprattus	Sprat	5	7–12	–17.3 ± 0.2	16.6 ± 0.5	Zof
Pleuronectiformes						
Buglossidium luteum	Solenette	1	4.5	–16.8	14.8	Bif
Limanda limanda	Dab	7	7–20	–16.6 ± 0.4	16.8 ± 0.4	Bif
Microstomus kitt	Lemon sole	3	16–42	–16.7 ± 0.6	15.2 ± 1.1	Bif
Platichthys flesus	Flounder	4	27–42	–16.9 ± 2.7	17.5 ± 1.9	Bif
Pleuronectes platessa	Plaice	5	19–31	–16.2 ± 0.4	15.8 ± 1.9	Bif
Solea (*Pegusa*) *lascaris*	Sand sole	5	10–12	–15.9 ± 0.2	17.4 ± 0.5	Bif
Solea solea (*vulgaris*)	Common sole	8	9–19	–16.5 ± 0.9	17.4 ± 0.9	Bif
Scorpaeniformes						
Agonus cataphractus	Pogge	5	7–7.5	–15.8 ± 0.5	16.5 ± 0.5	Bif
Aspitriglia cuculus	Red gurnard	6	18–23	–15.8 ± 0.3	16.2 ± 0.6	Bif
Eutriglia gurnardus	Grey gurnard	5	7–21	–15.3 ± 0.7	16.7 ± 0.8	Cf
Liparis liparis	Common seasnail	5	7–9	–15.1 ± 0.4	17.6 ± 0.4	Cf
Trigla lucerna	Tub gurnard	1	26	–15.4	18	Cf
Perciformes						
Scomber scombrus	Mackerel	6	27–42	–16.6 ± 0.4	16.1 ± 0.3	Bif
Ammodytes tobianus	Lesser sandeel	6	15–19	–17.2 ± 0.2	15.6 ± 0.8	Zof
Hyperoplus lanceolatus	Greater sandeel	7	22–24	–16.4 ± 0.4	16.1 ± 1.3	Cf
Callionymus lyra	Common dragonet	5	13–18	–17.3 ± 0.5	17.0 ± 0.3	Bif
Mullus surmuletus	Striped red mullet	3	16–20	–16.3 ± 0.5	17.5 ± 0.3	Bif
Pomatoschistus sp.	Goby	9	5–8	–17.1 ± 0.5	17.8 ± 1.9	Bif
Trachurus trachurus	Atlantic horse mackerel	5	26–29	–16.3 ± 0.5	18.2 ± 0.8	Cf
Echiichtys vipera	Lesser weever	5	12–13	–16.2 ± 0.3	18.7 ± 0.3	Cf
Beloniformes						
Belone belone	Garfish	1	49	–15.9	18.0	Cf
Gadiformes						
Melanogrammus aeglefinus	Haddock	1	40	–16.9	14.8	Zof
Merlangius merlangus	Whiting	8	13–27	–16.3 ± 0.6	19.1 ± 0.7	Cf
Trisopterus luscus	Bib	5	15–17	–16.6 ± 0.4	19.1 ± 0.2	Cf
Gadus morhua	Cod	6	37–95	–16.3 ± 1.3	19.2 ± 1.4	Cf
Anguilliformes						
Anguilla anguilla	Eel	1	38	–17.3	19.6	Cf

Table 2. $\delta^{13}C$ and $\delta^{15}N$ values in muscle of marine mammals collected along southern North Sea coasts

Species	n	$\delta^{13}C$	$\delta^{15}N$
Fin whale			
Balaenoptera physalus	3	–18.5 ± 0.9	9.6 ± 1.3
White-sided dolphin			
Lagenorhynchus acutus	2	–19.3/–19.2	10.5–11.0
Sperm whale			
Physeter macrocephalus	7	–19.0 ± 0.9	14.6 ± 0.6
Harbour porpoise			
Phocoena phocoena	46	–16.4 ± 1.6	16.2 ± 1.6
Grey seal			
Halichoerus grypus	6	–15.6 ± 1.6	17.9 ± 2.1
Harbour seal			
Phoca vitulina	23	–16.2 ± 1.3	18.7 ± 2.5
White-beaked dolphin			
Lagenorhynchus albirostris	7	–15.8 ± 0.7	18.8 ± 1.1

The majority of the macro- and megafaunal taxa investigated proved to be either zooplankton-feeding invertebrates such as the ctenophore *Pleurobrachia pileus* (Ct), zooplanktivorous fishes (Zof), suspension-feeders (Sf), omnivorous invertebrates (crustaceans such as common shore crab *Carcinus maenas*), crustaceans feeding on benthic invertebrates (Bifc), mollusc feeders (Mf), grazing invertebrates (Gi, sea urchin *Psammechinus miliaris*), fishes feeding on benthic invertebrates (Bif) or carnivorous fishes (Cf, mainly feeding on fishes or squids: Table 1).

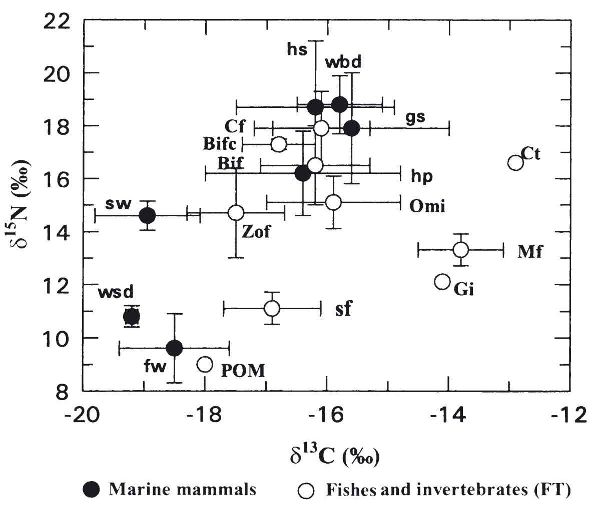

Fig. 1. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ in muscle of selected invertebrates, fishes and marine mammals from southern North Sea. fw: fin whale, wsd: white-sided dolphin, sw: sperm whale, hp: harbour porpoise, gs: grey seal, hs: harbour seal, wbd: white-beaked dolphin, Zof: fish feeding on zooplankton; Omi: omnivorous invertebrates; sf: suspension-feeders; Ct: ctenophores; Gi: grazing invertebrates; Bifc: crustaceans feeding on benthic invertebrates; Mf: mollusc-feeders; Bif: fishes and cephalopods feeding on benthic invertebrates, Cf: carnivorous fishes, POM: particulate organic matter from southern North Sea (data from Middelburg & Nieuwenhuize 1998). Full specific names in Tables 1 & 2

Table 3. Trophic levels of harbour porpoise, grey seal, harbour seal and white-beaked dolphin. Data from Pauly et al. (1998) and this study

Species	Pauly et al. (1998)	This study
Harbour porpoise		
Phocoena phocoena	4.1	3.4
Grey seal		
Halichoerus grypus	4.0	3.9
Harbour seal		
Phoca vitulina	4.0	4.1
White-beaked dolphin		
Lagenorhynchus albirostris	4.2	4.2

$\delta^{13}C$ and $\delta^{15}N$ differed significantly between feeding types (ANOVA, $F = 26.9$ and $F = 12.1$ respectively, $p < 0.001$). Suspension-feeders displayed the lowest mean $\delta^{15}N$ (11.1‰), followed by grazing invertebrates (12.1‰) and mollusc feeders (13.2‰). Carnivorous fishes displayed higher mean $\delta^{15}N$ than fishes (and squids) feeding on benthic invertebrates, fishes feeding on zooplankton and omnivorous invertebrates (Fig. 1, post-hoc test, $p < 0.001$). However, mean values did not differ significantly between carnivorous fishes (17.8‰), crustaceans feeding on benthic invertebrates (17.3‰) or the ctenophore *Pleurobrachia pileus* (16.6‰) (post-hoc tests, $p > 0.1$).

Omnivorous invertebrates were significantly enriched in ^{13}C compared to zooplankton-feeding fishes (post-hoc test, $p < 0.0001$) while $\delta^{15}N$ did not differ significantly between these 2 feeding groups.

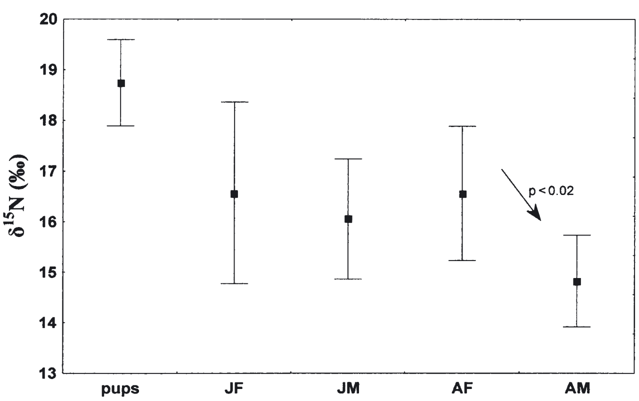

Fig. 2. *Phocoena phocoena*. Mean (±SD) $\delta^{15}N$ in muscle of harbour porpoise pups (pups, n = 2), juvenile females (JF, n = 15), juvenile males (JM, n = 12), adult females (AF, n = 9) and adult males (AM, n = 8)

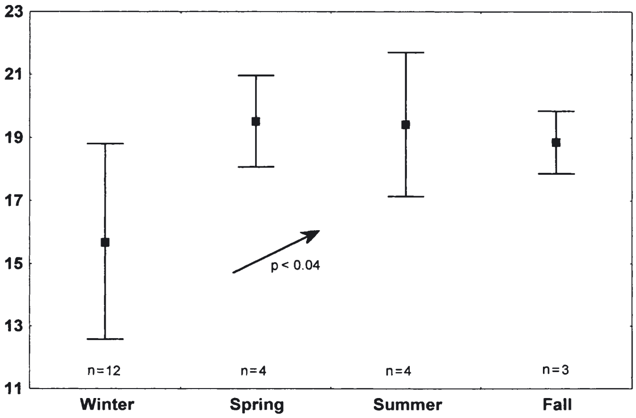

Fig. 3. *Phoca vitulina*. Mean (±SD) δ^{15}N in muscle of harbour seals for each season

The ctenophore *Pleurobrachia pileus*, grazing invertebrate *Psammechinus miliaris* and mollusc feeding *Asteria rubens* were considerably enriched in ^{13}C (mean δ^{13}C value = −12.9, −14.1 and −13.8‰ respectively) compared to other feeding types (Table 1, Fig. 1).

Herring were sampled during 2 cruises, in September 2000 and May 2001. Stable isotope data and length differed significantly between the 2 sampling occasions, with herring caught in May being of significantly greater length and with less ^{13}C and ^{15}N content than herring caught in September (Fig. 4, Student's *t*-test, $p < 0.001$).

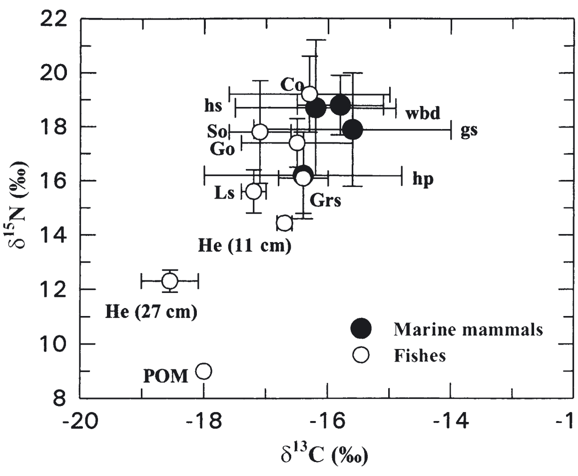

Fig. 4. Mean (±SD) δ^{13}C and δ^{15}N in muscle of marine mammals and selected fishes from southern North Sea. hp: Harbour porpoise, gs: grey seal, hs: harbour seal, wbd: white-beaked dolphin, Co: cod, So: sole, Go: goby, Ls: lesser sandeel, Grs: greater sandeel, He: herring, POM: particulate organic matter from southern North Sea (data from Middelburg & Nieuwenhuize 1998). Full specific names in Tables 1 & 2

Comparison of fishes with marine mammals

The δ^{15}N of carnivorous fishes did not differ significantly from that of grey seals or white-beaked dolphins (Mann-Whitney *U*-test, $p > 0.1$, Fig. 1). However, the δ^{15}N of carnivorous fishes was significantly higher than that of harbour porpoises (Mann-Whitney *U*-test, $p < 0.001$) and lower than that of harbour seals (Mann-Whitney *U*-test, $p < 0.01$). Within the fish species, only zooplankton-feeders such as Clupeiformes or the lesser sandeel *Ammodytes tobianus* displayed lower mean δ^{13}C and δ^{15}N content than harbour porpoises (Mann-Whitney *U*-test test; $p < 0.0001$ and $p < 0.005$ respectively). Fin whales, white-sided dolphins and sperm whales were significantly depleted in ^{13}C compared to other feeding groups or marine mammals from the southern part of the North Sea (Fig. 1; Kruskal-Wallis, $p < 0.001$).

DISCUSSION

Pattern of carbon-isotope signatures

δ^{13}C signatures varied widely (ranging up to 9.4‰) among the organisms collected from the southern North Sea (Fig. 1). Fin whales, white-sided dolphins and sperm whales were highly ^{13}C-depleted relative to the particulate organic matter (POM), invertebrate, fish and other marine mammal species (Tables 1 & 2, Fig. 1). This low δ^{13}C in the muscle and liver of fin whales, white-sided dolphins and sperm whales could be related to a mainly oceanic feeding regime. Stable carbon isotope ratios have proved most useful in identifying the feeding grounds of particular organisms, as δ^{13}C values are typically higher in species from coastal or benthic food webs than in those of offshore food webs (Hobson 1999, Lesage et al. 2001). No food was found in the digestive tract of the sperm whales, which seems to indicate that they had not been feeding within the southern North Sea prior to stranding (Jauniaux et al. 1998, Santos et al. 1999).

Male sperm whales are recorded as including significant proportion of squids and fishes in their diet in the deep waters of North Atlantic and Arctic waters (Santos et al. 1999). In the Northern hemisphere, they leave warm waters at the beginning of the summer to migrate to feeding grounds on the perimeter of the polar zone, returning again in winter (Santos et al. 1999). From our isotopic data, it appears that despite regular sightings of sperm whales within the southern North Sea, they do not feed mainly within this area, not even on local cephalopods. Indeed, the squid species sampled in the southern North sea (*Loligo vulgaris* or *Sepia officinalis*) had higher δ^{13}C (and δ^{15}N) than sperm whales (Tables 1 & 2). Oceanic or abyssal cephalopods have a quite different isotopic signature, more similar to that of sperm whales (Ostrom et al. 1993, Abend & Smith 1995, Iken et al. 2001). Similar conclusions can be drawn for fin whales and white-sided dolphins stranded along the Belgian and Dutch coasts. The depletion in ^{13}C observed for the 2 white-sided dolphins might also be linked to a mainly off-shore feeding. The $\delta^{13}C$ of these dolphins was similar to that recorded in other parts of the Northeast Atlantic (Das et al. 2003).

White-sided and white-beaked dolphins have been sighted in mixed-species aggregations in the southern North Sea (Haase 1987). Such temporary associations are not likely to be diet-related, as the $\delta^{13}C$ content strongly differs between these 2 species, suggesting 2 different feeding habits. The white-beaked dolphin has a more coastal feeding habit, as suggested by its ^{13}C-enrichment (Fig. 1). Similar isotopic observations have been recorded for white-sided and white-beaked dolphins collected along the Irish coasts (Das et al. 2003).

The $\delta^{13}C$ range observed for grey seals is likely to reflect a mixed sample of resident seals from the southern North Sea (probably the Wadden Sea colonies) and temporary or seasonal immigrants from the UK coasts (Abt et al. 2002). The 6 grey seals in this study were collected along the Belgian and French coasts of the English Channel in 2000 and 2001. No stranding had been recorded previously for the Belgian coast. This apparent increase in stranding events could be related to a dispersal of the eastern UK stock into the southeastern North Sea, as observed seasonally in other areas (Abt et al. 2002). Indeed, long-distance travel outside the breeding season is not uncommon for grey seals (McConnell et al. 1999). Some grey seals within the southeastern North Sea during the spring (after their moult) are assumed to have come from more northern haul-out sites such as Scotland, Faroe Islands or from the Humber estuary, i.e. along the UK coasts (Abt et al. 2002). Resident grey seals have also been observed increasingly during the last decade along the Wadden Sea coasts (Reijnders et al. 1995, Abt et al. 2002).

Invertebrates and fishes were more enriched in ^{13}C compared to marine POM data previously recorded for the southern North Sea (Middelburg & Nieuwenhuize 1998). Considerable overlap between species was observed (Figs. 1 & 4). Since the $\delta^{13}C$ of an animal is largely determined by the $\delta^{13}C$ of its diet, inter-taxa overlaps in isotope abundance indicate isotopic similarity among the respective diets of many of these species. As expected, suspension-feeders are ^{13}C-enriched compared to POM. Among the different feeding types, the grazing invertebrates, the mollusc-feeders and (strikingly) the ctenophores are strongly ^{13}C-enriched. Deposit-feeders have been shown to be more enriched in $\delta^{13}C$ than suspension-feeders, suggesting 2 different isotopic carbon signatures for suspended particulate matter and a mixture of suspended and sedimentary organic matter respectively (Dauby et al. 1998). Coastal or continental inputs are important in this area, leading to ^{13}C-enrichment of the particulate matter of the Channel and the North Sea compared to the Bay of Biscay (Dauby et al. 1994). However, the reason of for high enrichment of the ctenophore *Pleurobrachia pileus* is unclear. This species differs strongly from other zooplanktivorous animals such as the herring or the lesser sandeel (Table 1, Fig. 1).

$\delta^{13}C$ and $\delta^{15}N$ differed also between herring sampled in September 2000 and May 2001 (Fig. 4). The herring caught in May were ^{13}C- and ^{15}N-depleted compared to herring caught in September. Moreover, the mean length of these fish was higher in May than in September. The structure of the herring stock in the northeast Atlantic is complex, with different subpopulations, age-classes and feeding-types (Jennings et al. 2001). The herring captured in May were adults displaying an oceanic carbon signature, while those collected in September were juveniles with a typical coastal $\delta^{13}C$ enrichment compared to POM.

Pattern of nitrogen-isotope signatures

Trophic levels of marine mammals

Trophic positions were estimated according to the model of Lesage et al. (2001) for harbour porpoises, harbour seals, grey seals and white-beaked dolphins. Trophic positions were not evaluated for fin whales, white-sided dolphins and sperm whales. Indeed, their ^{13}C-depletion strongly suggests that they do not feed in the southern North Sea (Fig. 1). A consumer isotopic signature is determined initially by the isotopic composition of the baseline phyto- and zooplankton sources, which may vary widely as a function of sampling area (Middelburg & Nieuwenhuize 1998, Riera et al. 1999, Lesage et al. 2001). Southern North Sea POM values cannot be extrapolated to such oceanic species.

$\delta^{15}N$ values might also increase in starving animals as they might use their proteins for survival (Gannes et al. 1998), and this raises the question of the suitability of stranded marine mammals for isotopic studies as they might have poor body condition (Jauniaux et al. 1998, 2001, 2002). In birds, nutritional stress led to a substantial increase in diet-fractionation values (Hobson & Clark 1992, Gannes et al 1998). In contrast, Arctic ground squirrels *Spermophilus parryii plesius* in poor and excellent body condition had similar $\delta^{15}N$ values (Ben-David et al. 1999). Similarly, muscle $\delta^{15}N$ and $\delta^{13}C$ values did not differ between porpoises from the North Sea displaying poor, moderate and good body condition, allowing the use of muscle tissue of stranded animals for stable isotope studies (Das 2002, Das et al. unpubl.).

Within the North Sea, grey seals, harbour seals and white-beaked dolphins seem to occupy a similar trophic position at the top of the food web, as suggested by the high $\delta^{15}N$ content of both muscle and liver (Tables 2 & 3, Fig. 1).

The trophic levels estimated by Pauly et al. (1998), based on stomach-contents data, indicate that the trophic levels of harbour porpoises, grey seals, harbour seals and white-beaked dolphins are similar, ranging between 4.0 and 4.2 (Table 3). Pauly et al. (1998) calculated a mean trophic level for each of 97 marine mammal species, and emphasized the tentative nature of the modelling. The trophic positions estimated from $\delta^{15}N$ values in the present study are in agreement with the data of Pauly et al. (1998), except for harbour porpoises, which displayed a lower trophic position than the other 3 species (Table 3). This discrepancy reflects the high proportion of low trophic level prey (such as zooplanktivorous fishes) in the diet of harbour porpoises from the southern North Sea. Furthermore, porpoises and dolphins are opportunist feeders, taking advantage of local abundance of prey (Lick 1991, Rogan & Berrow 1996, Couperus 1997, Hassani et al. 1997).

Adult female porpoises fed at a higher trophic level than adult males, while juveniles displayed no differences as a function of sex (Fig. 2). The male porpoises were also slightly ^{13}C-depleted compared to females (–16.6 vs –16.1‰ respectively). Previous studies have reported that pregnant or lactating females may have a higher consumption, feed on larger prey or forage on different prey species (studies cited in Aarefjord et al. 1995). Segregation of harbour porpoises into groups of different sex and/or age has been proposed by several authors (Tomilin 1957, Kinze 1994, Santos & Pierce 2003). For instance, females with calves tend to be associated with shallow waters (Smith & Gaskin 1983, Kinze 1994). The low $\delta^{15}N$ signature (and $\delta^{13}C$) of the males suggested that they fed on more offshore prey with a low $\delta^{15}N$ signature (around 12.4‰ if we assume a mean enrichment of 2.4‰ from prey to predator) such as adult herring (Fig. 4), while females and juveniles stayed closer to shallow waters. Difference in diet between sexes has also been suggested as a mechanism to reduce competition (Santos & Pierce 2003). The high $\delta^{15}N$ value recorded for the 2 harbour porpoise pups might be due to their reliance on their mother for subsistence, i.e. milk or nutrition via the placenta (Hobson et al. 1997). Indeed, the length range of these 2 pups corresponded to the suckling period just after their birth (Aarefjord et al. 1995). A mean enrichment of 2.2‰ was observed between these 2 pups and adult females, which is in agreement with previous studies on northern fur seals (Hobson et al. 1997) and black bears (Hobson et al. 2000); Mobson et al. (1997, 2000) reported a mean $\delta^{15}N$ enrichment of 1.9 and 2.5‰ between suckling juveniles and adult females for fur seals and black bears, respectively. However, this trophic enrichment between pup and mother is strongly specific and needs further investigation before stable isotopes can be used to quantify weaning or other lactation processes (Jenkins et al. 2001).

Harbour porpoises displayed no isotopic differences between seasons, while harbour seals collected in winter had a lower mean $\delta^{15}N$ values than seals collected in summer (Fig. 3). This $\delta^{15}N$ depletion indicates that the difference in the mean trophic level between porpoises and seals is not apparent all year round.

Trophic relationships

Within the North Atlantic, herring, cod, sandeels, whiting, gobies and sole represent the major prey for marine mammals, with large intraspecific variations. Indeed, the marine mammal diet has been shown to vary according to the age of the individuals and the abundance of prey species, or as a function of season or geographic location (Evans 1987, Lick 1991, Pierce et al. 1991b, Aarefjord et al. 1995, Tollit et al. 1997, 1998).

In the North Sea, the harbour porpoise is known to feed on a wide range of pelagic and demersal fish species such as cod, herring, sole, gobies or dabs (Lick 1991). Expressed as fish biomass, sole and cod comprised 41 and 25% respectively of the stomach contents of harbour porpoises from German waters. In contrast, in the Baltic Sea, cod can represent 70% of the harbour porpoise diet biomass. In young porpoises, gobies are the main prey by number and weight (Lick 1991). Harbour seals usually feed on clupeids, gadoids, cephalopods or sandeels depending on prey availability (North Sea Task Force 1993, Tollit et al. 1998). A large proportion (~70%) of the grey seal diet includes sandeels (Ammodytidae), depending on location and season (Prime & Hammond 1990, Pierce et al. 1991a, Hammond et al. 1994).

Carnivorous fishes, such as gadids, display similar $\delta^{15}N$ to grey seals, harbour seals and white-beaked dolphins, suggesting that they occupy a similar trophic level at the top of the food web (Fig. 1). Moreover, the mean $\delta^{15}N$ value of fish species usually described as potential prey for North Sea marine mammals is high compared to that of harbour porpoises, grey seals, harbour seals and white beaked dolphins (Fig. 4). As a $\delta^{15}N$ trophic enrichment of 2.4‰ is expected between potential prey and marine mammals (Hobson et al. 1996), the usual prey such as cod, other gadids, gobies or sole are not likely to form the bulk of their diet. Indeed, the $\delta^{15}N$ data of gobies, sole or cod is higher than that of harbour porpoises. Gadids, gobies and sole constituted a significant part of the diet of the German North Sea harbour porpoise (Lick 1991), but the isotopic data indicate that they are not likely to constitute the main part of its diet within the southern North Sea. Cod $\delta^{15}N$ value is even higher than that of the 2 seal and white-beaked dolphin species (Fig. 4). However, a relationship between body size and $\delta^{15}N$ value has been shown for several marine species (Jennings et al. 2002), complicating data interpretation. Even though the range of fish lengths is similar to that described for marine mammal prey (Aarefjord et al. 1995, Gannon et al. 1997, Hall et al. 1998), it cannot be excluded that smaller fish individuals with lower $\delta^{15}N$ values could be preyed by marine mammals.

In contrast, zooplanktivorous fishes such as herring, lesser sandeels, or anchovies have lower $\delta^{15}N$ (and $\delta^{13}C$) values of about 2 to 4‰, and are likely to represent a major link between the basis of the food web, which includes various bacterio-, phyto- and zooplankton, and marine mammals or carnivorous fishes (Fig. 1). The lesser sandeel is one of the most common fish species on the continental shelf of northwest Europe, comprising 10 to 15 % of the total fish biomass in the North Sea, and is currently the target of the largest single-species industrial fishery in the North Sea (Rindorf et al. 2000). Sandeel availability has been shown to have major effects on the breeding success of other marine predators, such as seabirds (Rindorf et al. 2000).

Harbour and grey seals have higher trophic positions than harbour porpoises, suggesting that some prey with a higher $\delta^{15}N$ signature than herring or lesser sandeels might also be included in their diet (Fig. 4). The diet of harbour seals from the southwestern North Sea included whiting and sole and, to a lesser extent, other flatfish and gadoid species as well as sandeels (Hall et al. 1998). Mean $\delta^{13}C$ and $\delta^{15}N$ signatures were similar between grey and harbour seals confirming that the foraging range of these 2 species overlap in this part of the North Sea (Pierce et al. 1991a,b). Similar observations based on faecal samples have been made in the southwestern North Sea along the coast of The Wash (east England) (Hall et al. 1998). Harbour seals are known to travel 10 km to feed (Thompson & Miller 1990), and grey seals may travel far greater distances (McConnell et al. 1999). Additional partition of resources may result from differential foraging in offshore and coastal areas.

Our isotopic data clearly suggest that pleuronectiformes, cod and other gadids comprise a minor contribution to the diet of southern North Sea marine mammals. Why these high trophic-level fishes do not represent a major part of the marine mammal diet is unclear. The range of species preyed upon by marine mammals can be wide, since >30 fish prey species have been identified in the diet of some marine mammals (e.g. Lick 1991, Hall et al. 1998). However, diet preferences seem to be oriented towards lower trophic level prey, such as clupeids or sandeels. Previous studies have indicated that during the last few decades, intensive and size-selective fishing has changed the size-structure of the North Sea fish community, resulting in a general decrease in body size. Smaller and early-maturing species have increased in relative abundance (North Sea Secretariat 2002).

In summary, despite occasional sightings of fin whales, white-sided dolphins and sperm whales in the Southern Bight of the North Sea, they mainly feed offshore e.g. within the North Atlantic. In contrast, harbour porpoises, grey seals, harbour seals and white-beaked dolphins belong to the southern North Sea food web. Grey seals, harbour seals and white-beaked dolphins feed on prey of a higher trophic level than harbour porpoises but dietary overlap occurs between these species. Some intraspecific variations associated with sex and season have been observed in harbour porpoises and harbour seals respectively, indicating that trophic segregation does not occur all year round.

Acknowledgements. We are grateful to T. Jauniaux (Marine Animal Research and Intervention Network) who necropsied the marine mammals for this study. Thanks to J. Tavernier and J. Haelters (Management Unit of the North Sea Mathematical Models, Belgium) for logistical coordination. Thanks to R. Bouhy, D. Vangeluwe and R. Biondo (Oceanology Laboratory, Liège, Belgium) for their valuable technical assistance and help. The authors are grateful to K. Cooreman and his team of scientists and fishermen (Centrum voor Landbouwkundig Onderzoek, Oostende, Belgium) for their continuous support in sample collection and species determination. We are also grateful to the crews of the RV 'Belgica' and RV 'Thalassa' (IFREMER, Boulognes, France) for satisfying cruises. This study was funded by the Belgian Office for Scientific, Technical and Cultural Affairs (contract MN/DD/50). G.L. and K.D. received grants from the Fonds pour la Recherche dans l'Agriculture et l'Industrie (FRIA). K.D. received a grant from the Marie-Curie Fellowship. Thanks to A. Gilles (FTZ, Germany) for her useful remarks. This manuscript was greatly improved by the comments of 4 anonymous reviewers. Thanks also to K. A. Hobson for useful discussion and remarks on isotopic fractionation. This paper is MARE publication 026.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: March 21, 2003; Accepted: August 5, 2003
Proofs received from author(s): November 13, 2003