Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea

Karl Lundström[1], Olle Hjerne[1], Karin Alexandersson[1] and Olle Karlsson[2]

[1] *Department of Marine Ecology, Göteborg University Tjärnö Marine Biological Laboratory, S-45296 Strömstad, Sweden*
[2] *Swedish Museum of Natural History, Box 50007, S-10405 Stockholm, Sweden*

ABSTRACT

We examined the digestive tract contents from 145 grey seals (*Halichoerus grypus*) collected between 2001 and 2004 in the Baltic Sea. We compensated for biases introduced by erosion of otoliths, both by using additional hard-part structures other than otoliths, and species-specific size and numerical correction factors. In the absence of numerical correction factors based on feeding experiments for some species, we used correction factors based on a relationship between otolith recovery rate and otolith width. A total of 24 prey taxa were identified but only a few species contributed substantially to the diet. The estimated diet composition was, independently of the prey number estimation method and diet composition estimation model used, dominated by herring (*Clupea harengus*), both by numbers and biomass. In addition to herring, common whitefish (*Coregonus lavaretus*) and sprat (*Sprattus sprattus*) were important prey, but cyprinids (*Cyprinidae*), eelpout (*Zoarces viviparus*), flounder (*Platichtys flesus*) and salmon (*Salmo salar*) also contributed significantly. Our results indicated dietary differences between grey seals of different age as well as between seals from the northern (Gulf of Bothnia) and the southern (Baltic Proper) Baltic Sea.

Lundström, K., Hjerne, O., Alexandersson, A. and Karlsson O. 2007. Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea. *NAMMCO Sci. Publ.* 6:177-196.

INTRODUCTION

The grey seal (*Halichoerus grypus*) is the largest and most common of the 3 seal species in the Baltic Sea (Fig. 1), the others being ringed seal (*Phoca hispida*) and harbour seal (*Phoca vitulina*). Grey seals occur over the whole Baltic Sea, but the majority of the seals occur north of latitude 58°. In the early 20th century they were common in the Baltic Sea and the population was estimated to between 88,000 and 100,000 individuals, whereas in the late 1970s the population had declined to less than 4,000 animals (Harding and Härkönen 1999). The dramatic decline was due to extensive hunting and later a disease complex linked to environmental toxins, mainly PCBs and DDTs (Bergman and Olsson 1986). The use of PCBs and DDTs was banned in most countries bordering the Baltic Sea during the 1970s and the health status of Baltic grey seals has slowly improved (Bergman 1999). An estimate of population size based on photo-identification for 2000 (Hiby *et al.* 2007) gave a point estimate of 15,631 with 95% confidence limits from 9,592 to 19,005. Using the growth rate (7.5%) derived from the Swedish grey seal monitoring programme (Karlsson and Helander 2005) gives a point estimate for 2004 of about 21,000 animals. An estimated minimum of 17,640 seals was counted at moulting haul-outs in 2003, which thus provides a lower bound on the population size in that year and represents 84% of the adjusted photo-id point estimate. The increase in population size has led to an escalating conflict with coastal fisheries, and in 1999 the damages caused by seals in Sweden were estimated to be more than 3,500,000 US$ (Westerberg *et al.* 2000).

To assess the role of grey seals in the Baltic Sea ecosystem, and how the seals influence and are influenced by human fisheries, it is im-

Fig. 1. *A grey seal breeding colony on a sandy shoal in the Baltic. Grey seal populations have increased in the Baltic in recent years and conflicts with coastal fisheries have become more common. (Photo: Mart and Ivar Jüssi)*

portant to have information on their diet composition. Previous studies (Söderberg 1972, Tormosov and Rezvov 1978) were carried out during a period (1960s and 1970s) with a different fish community composition in the Baltic Sea. At that time, cod (*Gadus morhua*) were common even as far north as the Gulf of Bothnia, and were one of the major prey species in the earlier studies. Since then the cod stocks have been depleted and stock size estimates and catch statistics indicate that other species, such as sprat (*Sprattus sprattus*) have become more abundant (Thurow 1997, ICES 2004).

This study aims to provide data on food composition of Baltic grey seals, based on otoliths and other skeletal parts recovered from digestive tract contents from hunted and bycaught animals and animals found dead. Partial and complete digestion of otoliths can bias the estimated prey size distribution and diet composition heavily (*e.g.* Harvey 1989, Pierce and Boyle 1991, Tollit *et al.* 1997). Complete digestion of otoliths can introduce errors in the estimated number of prey individuals consumed, and size of the prey can be underestimated when back-calculating fish size from the size of eroded otoliths. We have therefore tried to compensate for differences in recovery rates and stages of erosion of otoliths. In absence of species-specific numerical correction factors (NCFs) for Baltic fish species we developed a relationship between NCF and otolith size based on data from feeding experiments (Bowen 2000).

MATERIALS AND METHODS

We analysed digestive tracts (stomachs and intestines) from hunted and bycaught grey seals and from grey seals carcasses found in the water or washed up on shore. The samples were collected between 2001 and 2004 in cooperation with the Swedish Museum of Natural History in Stockholm that coordinates the collection of tissue samples from seals in Sweden. Stomachs and intestines were separated as a part of the necropsy procedure, placed in plastic bags and stored at -20º C for later examination. Age

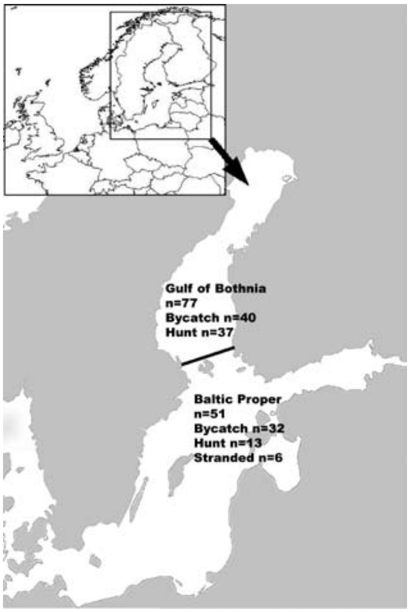


Fig. 2. *Area of origin and cause of death of grey seals containing food remains, collected in the Baltic Sea 2001-2004.*

was determined using longitudinal sections of the canine teeth according to the methodology developed by Hewer (1964). We divided the seals into 3 age groups, in order to examine possible differences in diet composition between weaned pups and yearlings (0-1 group), juveniles (2-4 group) and adults (5+ group). Of 190 seals, 145 contained food remains. Of these 145 seals, 85 were collected from the Gulf of Bothnia (north of lat. 60°), 54 from the Baltic Proper (south of lat. 60°) and 6 were of unknown origin (Fig. 2). For the 2 areas, data on age, sex and sampling season were available for 136, 139 and 132 bycaught and hunted animals respectively (Table 1 and Fig. 3). We used a Chi-square (χ^2) test to analyse the data for differences in composition of sampled seals between areas, causes of death and age groups.

Whole prey items were removed, identified and measured separately. Hard parts from the remaining contents were separated using a series of sieves with the smallest having a mesh size of 0.5 mm. Prey were identified, using sagittal otoliths as well as other structures such as vertebrae, chewing pads and pharyngeal teeth, to the lowest possible taxon, using published guides (Wheeler 1978, Härkönen 1986, Watt *et al.* 1997, Leopold *et al.* 2001) and our own reference material.

Prey number estimation

To assess the number of prey individuals consumed by the seals we used 3 different methods. The first method (A) used only otoliths and whole prey for identification, while the other 2 were different attempts to give a more realistic picture of the actual diet composition at ingestion by (B) using all recovered hard parts for prey identification, or (C) correcting for complete loss of otoliths due to erosion.

Table 1. Age group, as determined from growth layer counts of canine teeth (Hewer 1964), and sex of grey seals containing food remains collected from the Gulf of Bothnia and the Baltic Proper.

Age group	Gulf of Bothnia	Baltic Proper
0	26 (30.6%)	29 (53.7%)
2-4	16 (18.8%)	14 (25.9%)
5+	42 (49.4%)	9 (16.7%)
Unknown	1 (1.2%)	2 (3.7%)
Sex		
Females	39 (45.9%)	23 (42.6%)
Males	46 (54.1%)	31 (57.4%)

A. Otoliths only

The number of individuals per prey species eaten by a seal was the sum of the number of whole prey items, i.e. fish with intact skulls and the count of otoliths divided by 2. In this, the most simplistic method, we did not separate left and right otoliths in order to get a direct comparison with the otoliths corrected numerically method (C).

B. All recovered hard-part structures

The number of whole prey items was added to the number estimated from skeletal remains for each prey species in every seal. The latter was the maximum number obtained from either chewing pads, pharyngeal teeth, other bones, left or right otoliths, or the total otolith number divided by 2.

C. Otoliths corrected numerically

Complete digestion of otoliths can result in

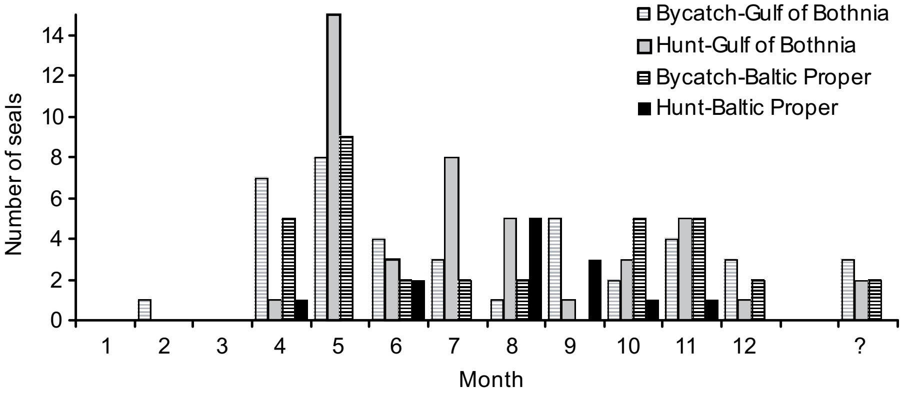


Fig. 3. Monthly distribution of seal samples from bycatch and hunt from the Gulf of Bothnia and Baltic Proper 2001-2004.

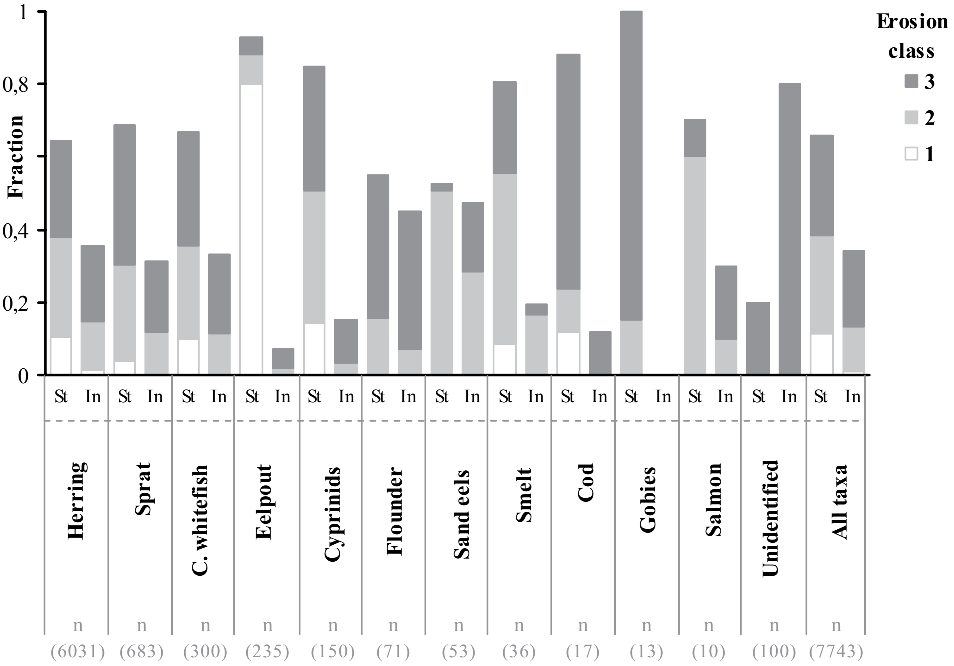


Fig 4. *Fractions of otoliths belonging to the various erosion classes, in stomachs (St) and intestines (In), for prey taxa represented by at least 10 otoliths. The total number of otoliths from each taxon is shown in brackets (n).*

severely biased estimates of the diet composition (*e.g.* Jobling and Breiby 1986, Tollit *et al.* 1997, Bowen 2000, Berg *et al.* 2002). For stomach contents, a straightforward solution to avoid this bias might be to analyse only relatively fresh and non-eroded material to avoid bias caused by digestion of otoliths (Bowen and Harrison 1994). However, since the non-eroded material in our study was only a small part of the entire material (Fig. 4), this approach would have resulted in larger uncertainties around estimates of diet composition, as well as the complete disappearance of prey species represented exclusively by eroded structures. Therefore we used the concept of numerical correction factors (NCFs) based on otolith recovery rates in scats from feeding experiments of captive seals (Tollit *et al.* 1997, Marcus *et al.* 1998, Bowen 2000), to reconstruct the diet composition. All prey added in the numerical correction procedure were assigned the same length and biomass as the specific prey they were reconstructed from.

Numerical correction

Stomach contents might be less affected by bias in recovery rate caused by erosion than scat contents due to the on average shorter exposure time to the environment in the gastrointestinal tract. However, since digestion of otoliths principally occurs in the stomach (Frost and Lowry 1980, Harvey 1989, Pierce and Boyle 1991, Christiansen *et al.* 2005), we applied the NCFs derived from scats for all otoliths found in the intestines. For the stomach contents, we applied the NCFs just for erosion class 3 otoliths, and for erosion class 2 we adjusted the NCFs by adding only half the number predicted by the NCFs. Whole prey and erosion class 1 otoliths in the stomachs were not corrected at all.

Otolith recovery rates vary largely between prey species and are higher for species with large otoliths (*e.g.* da Silva and Neilson 1985, Gales and Cheal 1992, Bowen 2000, Orr and Harvey 2001, Browne *et al.* 2002, Laake *et al.* 2002). Since published NCFs do not exist for most prey species found in our study, we explored the otolith size-recovery rate relationship and used it to generate NCFs. We used recovery rates given in a review by Bowen (2000) but excluded studies in which the seals were not able to swim, since the activity level influences the digestion

Table 2. Average species length and recovery rates from Bowen (2000). Otolith length (OL) and width (OW) calculated from fish length (Leopold *et al.* 2001).

Common name	Scientific name	Fish length (cm)	OL (mm)	OW (mm)	Recovery rate
Cod	*Gadus morhua*	24	9.6	3.8	0.81
Whiting	*Merlangius merlangus*	21	11.4	3.6	0.74
Pout whiting	*Trisopterus luscus*	20	8.5	4.0	0.91
Lemon sole	*Microstomus kitt*	26	3.0	1.9	0.41
Plaice	*Pleuronectes platessa*	20	4.7	3.3	0.61
Dab	*Limanda limanda*	12	2.9	2.0	0.34
Sandeel	*Ammodytes marinus*	14	2.6	1.3	0.27
Herring	*Clupea harengus*	25	4.2	2.0	0.32
Sprat	*Sprattus sprattus*	13	1.9	1.3	0.10

rate (Harvey 1989). Bowen (2000) did not find any differences between NCFs for grey seals and harbour seals (cod and herring investigated), and therefore we use data from both seal species to develop a relationship that could be applied to at least those 2 species. All prey species were included where we either found otolith length (OL) and width (OW) in the original references (Tollit *et al.* 1997, Marcus *et al.* 1998), reviewed by Bowen (2000), or could estimate otolith length and width from fish length in Bowen (2000) based on otolith size-fish size relationships in Leopold *et al.* (2001) (Table 2). Since our focus was differences in recovery rates between fish species, we used species averages of recovery rates and otolith sizes, which gave all species the same weight, independent of how many experimental data points they had.

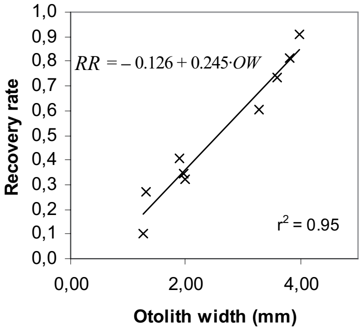
A simple linear regression model with recovery rate as the dependent variable and otolith length and otolith width respectively as independent variables gave a high degree of explanation ($r^2 = 0.78$ and $r^2 = 0.95$ for otolith length and otolith width, respectively, Fig. 5a). To avoid the problem with the linear model of getting negative or very low recovery rates for small otoliths, and recovery rates larger than 1 for large otoliths, we used a sigmoidal model which limits the recovery rate between 0 and 1. The recovery rate, RR, was defined as

$$RR = \frac{1}{1 - e^{\frac{L50-OS}{s}}} + \varepsilon$$

where OS is otolith size (length or width), L50 is the otolith size which gives a recovery rate of 0.5, s is a parameter that determines the slope of the curve, and ε is the normal distributed error. This model gave a similar degree of explanation as the linear model ($r^2 = 0.82$ and $r^2 = 0.93$ for otolith length and otolith width, respectively, Fig. 5b).

We chose the sigmoidal model with otolith width to calculate NCFs (NCF=1/recovery rate) from the average width for all measured otoliths of each species in our data set (Table 3), partly because otolith width gave a higher degree of explanation than otolith length, and partly because otolith width is often possible to measure even if the tip of the otolith is broken.

(a) Linear model



(b) Sigmoidal model

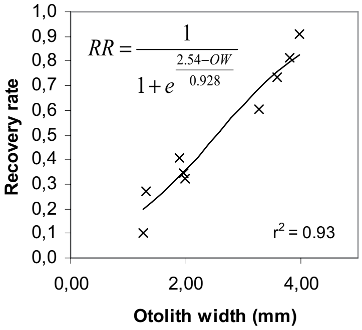


Fig. 5. *Regression models that give high degrees of explanation, with recovery rate as dependent and otolith width as independent.*

Table 3. Numerical correction factors (NCFs) calculated from otolith width for prey species in this study.

Common name	Scientific name	NCF
Gobies	*Gobiidae*	6.3
Sprat	*Sprattus sprattus*	5.9
Lumpsucker	*Cyclopterus lumpus*	5.8
Eelpout	*Zoarces viviparus*	5.4
Sandeels	*Ammodytidae*	4.5
Herring	*Clupea harengus*	3.7
Four-bearded rockling	*Enchelyopus cimbrius*	3.0
Trout	*Salmo trutta*	2.8
Salmon or trout	*Salmo spp.*	2.6
Pike perch	*Stizostedion lucioperca*	2.4
Salmon	*Salmo salar*	2.2
Smelt	*Osmerus eperlanus*	1.9
Ruffe	*Gymnocephalus cernuus*	1.8
Perch	*Perca fluviatilis*	1.8
Common whitefish	*Coregonus lavaretus*	1.7
Flounder	*Platichtys flesus*	1.7
Eel	*Anguilla anguilla*	1.7
Sculpins	*Cottidae*	1.6
Plaice	*Pleuronectes platessa*	1.6
Pike	*Esox lucius*	1.4
Cyprinids	*Cyprinidae*	1.3
Cod	*Gadus morhua*	1.2
Burbot	*Lota lota*	1.2

Prey size estimation

We measured length and width of otoliths, as well as chewing pads and pharyngeal teeth from cyprinids (*Cyprinidae*) using a dissecting microscope with an accuracy of 0.04 mm. To calculate fish length and weight from the size of the otoliths we used regression equations valid for the Baltic Proper for the species herring (*Clupea harengus*) and sprat (Table 4). Additional equations, for otoliths, pharyngeal teeth and chewing pads, were taken from Leopold *et al.* (2001) for all other prey species except salmon (*Salmo salar*) and common whitefish for which Härkönen (1986) was used. If more than 50 otoliths of a species were present, a sub sample of 50 otoliths, sampled at random, was measured and classified to assess the size and erosion class distribution, while the remaining otoliths were merely counted. If a prey individual was only identified by diagnostic structures for which we had no regression equations, *i.e.* structures other than otoliths, pharyngeal teeth and chewing pads, the length and weight of the fish was given the averages of all individuals of that species. In cases when skeletal parts could only be determined to a level higher than the species level, the size of the fish was given the average of all individuals belonging to the closest higher taxon (*i.e.* Genus, Family or Order). For cyprinids, all food items we were able to identify to species level belonged to roach (*Rutilus rutilus*). To estimate the size of unknown cyprinids we used the regressions for roach. For gobies (*Gobiidae*) and sandeels (*Ammodytidae*) regressions for sand goby (*Pomatoschistus minutus*) and small sandeel (*Ammodytes tobianus*) were used, respectively.

Size correction

When reconstructing the ingested prey size and biomass from the otolith size it is important to estimate the size of the un-eroded otolith at ingestion, otherwise prey size could be significantly underestimated (*e.g.* da Silva and Neilson 1985, Harvey 1989, Pierce and Boyle 1991, Tollit *et al.* 1997). Following Tollit *et al.* (1997) we classified the otoliths into 3 erosion classes based on otolith morphology and surface topography. Class 1 otoliths were minimally eroded with clear lobations on surfaces, margins and rostrums and had well defined sulcuses. Class 2 otoliths showed obvious signs of erosion with less pronounced lobations, less

Table 4. Relationships between otolith width (OW), total fish length (FL) and fish weight (FW) for herring and sprat collected from ICES subdivision 25, 27 and 29. N equals the number of individuals of each species in the sample on which the equations are based upon. The correlations between otolith width in mm and fish length in mm and fish weight in gram are described by the equations $FL=a+b \cdot OW$ and $FL=c \cdot OW^d$, respectively.

		Fish length			*Fish weight*			*Range*		
Species	**N**	**a**	**b**	**r²**	**c**	**d**	**r²**	**OW**	**FL**	**FW**
Herring	55	-49.294	132.44	0.941	3.994	3.798	0.935	1.12-2.200	105-265	7-111
Sprat	40	-7.516	108.76	0.853	6.600	2.426	0.839	0.68-1.389	70-140	3-15

Table 5. Species and erosion class-specific size correction factors (SFCs) for the prey species herring, sprat and common whitefish and the average for the 3 species. Bold figures indicate the SCFs used in our study.

	Otolith width			**Otolith length**		
	Erosion class			*Erosion class*		
Species	**1**	**2**	**3**	**1**	**2**	**3**
Herring	1.00	1.08	1.32	1.00	1.07	1.23
Sprat	1.00	1.09	1.23	1.00	1.10	1.32
Common whitefish	1.00	1.04	1.26	1.00	1.05	1.33
Average	1.00	1.07	1.27	1.00	1.07	1.29

distinct sulcuses, more rounded rostrums and less pointed ends, whereas class 3 otoliths were highly eroded with altered overall shapes, no lobations or sulcuses and smooth edges. We estimated species- and erosion class-specific size correction factors (SCF) for the most well-represented prey species in our study (herring, sprat and common whitefish). Assuming that class 1 otolith size is minimally affected by digestive erosion, the SCFs are simply the ratio between the average otolith width (and length for common whitefish) in erosion class 1 and erosion class 2 and 3 respectively for each species (Table 5). For all other species the average SCFs of those 3 species were used. No corrections were applied to chewing pads and pharyngeal teeth. However, studies on cyprinid remains in stomach contents from cormorants (*Phalacrocorax carbo*) indicate that at least chewing pads are more resistant to gastric erosion than otoliths (Veldkamp 1995, Nienhuis 2000).

Diet indices

Three different indices have been used to assess the contribution of prey species to the overall grey seal diet. Frequency of occurrence (FO_i) for a prey species was calculated as the number of seals containing the species in relation to the total number of seals containing prey. $FO_i = (s_i/s_t) \times 100$, where si is the number of seals in which taxon *i* occurs and s_t is the total number of seals containing prey remains. We calculated FO_i both using otoliths only (A) and using all hard-part structures (B).

Relative numerical contribution (N_i) for a prey species was calculated as the number of individuals of the prey species in relation to the total number of individuals of all species. $N_i = (n_i/n_t) \times 100$, where n_i is the total number of individuals of taxon *i* and nt is the total number of individuals of all taxa. As described above the number of individuals (n_i and n_t) was estimated by 3 different methods based on otoliths only (A), all recovered hard-part structures (B) and otoliths corrected numerically (C), respectively, resulting in 3 different estimates of the relative numerical contribution.

Relative biomass contribution (B_i) of a prey species was calculated as the total weight of the prey species in relation to the total weight of all species. $B_i = (b_i/b_t) \times 100$, where b_i is the total weight of taxon *i* and b_t is the total weight of all taxa. As for the relative numerical contribution, we estimated 3 different B_i based on the 3 prey number estimation methods.

To describe the diet composition, the 2 latter diet indices (N_i and B_i) were then either calculated by (model 1: all data pooled) adding the biomasses from the entire data set, *i.e.* implicitly weighting each seal in proportion to the total prey biomass in its gastrointestinal tract, or (model 2: seal weighted average) by giving each seal the same weight independently of its total content (*cf.* Laake *et al.* 2002). This resulted in total 6 different (3×2) diet composition estimates for both N_i and B_i, respectively.

Confidence intervals

We used a bootstrap technique to estimate the uncertainty due to random processes in the diet composition (*cf.* Hammond and Rothery 1996, Santos *et al.* 2001). Randomly, n seals were sampled (with replacement) from the original set of n seals and this simulation was repeated 1,000 times. Instead of using the 2.5th and 97.5th percentiles of the diet index for each prey type, we estimated the bias-corrected percentiles to define the 95% confidence limits (Haddon 2001).

The bias in question here is the difference between deterministic diet indices and the bootstrapped estimates from the 1,000 repetitions.

Multivariate analysis of diet composition

To examine multivariate patterns and relate diet composition to the environmental descriptors age group (0-1, 2-4 or 5+), cause of death (bycatch or hunt), area of origin (Gulf of Bothnia or Baltic Proper), quarter of the year (1, 2, 3 or 4) and sex (female or male), we used canonical correspondence analysis (CCA) (ter Braak 1986), implemented in the program CANOCO for Windows 4.5 (available from Microcomputer Power, www.microcomputerpower.com). For this analysis we used only the 123 seals for which the environmental descriptors were known and the 13 prey taxa occurring in at least 3% of the included seals. The dietary data was a matrix consisting of the mean of the biomass consumed from the methods “all recovered hard-part structures” and “otoliths corrected”. The dietary data were log transformed to normalize the data and the categorical environmental descriptors were coded into dummy variables, each of which took a value of either 1 or 0. To investigate whether the observed differences in diet could be accounted for by pure chance, a Monte Carlo permutation test was applied in the CANOCO program with the samples randomly permuted 499 times, and the data were tested for statistically significant differences in diet composition among the environmental descriptors, i.e. if the null hypothesis of independence between diet composition and environmental descriptors could be falsified or not. To examine if an environmental descriptor had a statistically significant effect on the diet we accounted for the effect of the other descriptors by specifying them as covariables. For example, to examine the pure effect of age group we defined the age-group categories 0-1, 2-4 and 5+ as environmental variables and the other descriptors (cause of death, area of origin, quarter of the year and sex) as covariables. In this way we test whether there is still a difference in diet between seals from the different age groups after accounting for the effects of the other environmental descriptors. We then continued analysing the pure effect of the other environmental descriptors (cause of death, area of origin, quarter of the year and sex) in the same way.

RESULTS

Sample composition

Of the 145 seals containing food remains, 85 from the Gulf of Bothnia, 54 from the Baltic Proper and 6 of unknown origin, a total of 7743 otoliths were examined. The majority of the recovered prey remains could be identified to species level and a total of 24 prey groups was recorded (Table 6). A small number of otoliths (n = 100) were too eroded or damaged to be identified and were therefore impossible to classify. For all prey taxa represented by at least 10 otoliths, the relative distributions of the 3 erosion classes found in stomachs and intestines are shown in Fig. 4.

Seals from the 2 areas of origin differed slightly in both age composition and cause of death. The proportion of younger animals was higher in the Baltic Proper whereas there were proportionally more old animals in the Gulf of Bothnia ($\chi^2 = 14.9$, d.f. = 2, $P<0.01$,Table 1). The proportion of hunted animals was higher in the Gulf of Bothnia than in the Baltic Proper ($\chi^2 = 26.5$, d.f. = 1, $P<0.01$, Fig. 2). The age composition also differed among the causes of death ($\chi^2 = 28.9$, d.f. = 2, $P<0.01$) where the bycatch sample was dominated by young individuals (0-1) whereas older animals (5+) dominated the hunt sample. The seals were mainly collected from the last 3 quarters of the year with a peak, both for hunted and bycaught animals, in May (Fig. 3).

Prey occurrence

The most common prey species were herring, sprat and common whitefish, occurring in 81, 27 and 20 percent of the examined seals, respectively. Cyprinids, eelpout, sandeels, flounder (*Platichtys flesus*), smelt (*Osmerus eperlanus*), cod, perch (*Perca fluviatilis*), and salmon occurred in 4 to 10 percent of the seals, while species like trout (*Salmo trutta*), sculpins (*Cottidae*), burbot (*Lota lota*), ruffe (*Gymnocephalus cernuus*), eel (*Anguilla anguilla*), pike (*Esox lucius*) and gobies (*Gobiidae*) occurred in less than 4% of the seals (Table 6). Relatively few species contributed to the diet in individual seals. Thirty-nine percent of the seals had consumed only 1 species while 2 and 3 or more species

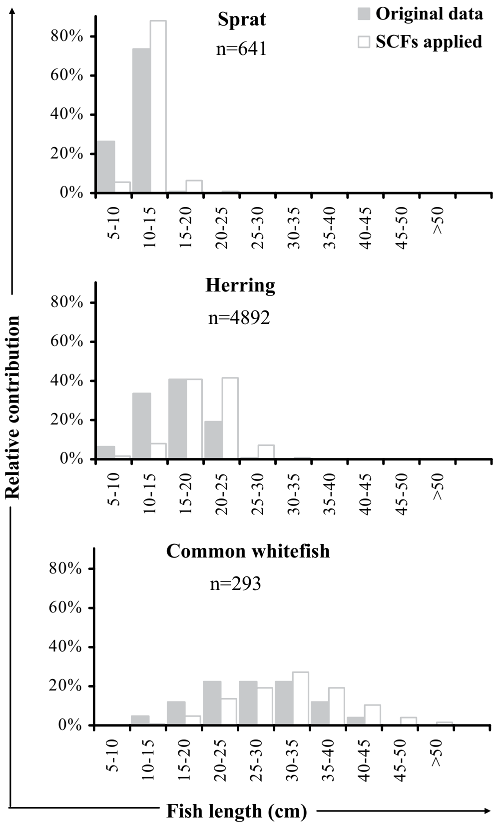


Fig. 6. Length compositions for sprat, herring and common whitefish based on digestive tract prey remains where n equals the number of sagittal otoliths used to estimate the fish lengths. Grey bars indicate length distribution based on original data and white bars indicate length distribution with size correction factors (SCFs) applied.

were consumed by 38% and 23% of the seals respectively. FO_i derived from all hard-part structures was considerably higher for cod, perch, unknown *Salmo spp*. and sculpins compared to FO_i derived from otoliths exclusively. These species were in some cases only identifiable by means of structures other than otoliths.

Prey size

The estimated length of consumed prey ranged from a goby of 2.7 cm to a salmon of 75 cm and an eel of 87 cm (SCFs not applied), with 69.6% of the estimated fish lengths between 10 and 20 cm (median = 16.6 cm). When we applied size correction factors, the estimated length ranged from 3.8 to 114 cm (median = 19.8cm) with 70.4% of the estimated fish lengths between 15 and 25 cm. Length histograms, before and after application of size correction factors, for sprat, herring and common whitefish are presented in Fig. 6.

Diet composition estimation

The diet composition varied both with the diet index, as well as the prey number estimation method and diet composition model used, but there were some general patterns. Herring dominated the diet composition both by numbers and weight independently of diet index, prey number estimation method and diet composition model (Tables 7 and 8). Sprat and common whitefish, in that order, followed by eelpout and cyprinids were numerically important prey species. Depending on the prey number estimation method and diet composition model used, those 5 most numerous species made up between 82% and 96% of the relative numerical contribution (N_i), while no other species or group of species contributed more than 3%. In terms of biomass (B_i) the patterns were more dependent on the prey number method and diet composition model used (further discussed below), but there were some general patterns. Due to its small body size, the importance of sprat decreased in relation to its relative numerical contribution, while the larger common whitefish became the next most important prey after herring (except in 1 case). Other relatively large species that contribute more in terms of biomass are salmon and trout, flatfish and cod, while small species like sandeels, smelt and to some extent eelpout decreased in relation to the relative numerical contribution.

The 2 prey number estimation methods (method B: all hard-part structures, and method C: otoliths corrected) we used to improve and estimate the bias in diet composition based on only otoliths (method A) influenced the relative biomass contribution differently. Using all hard-parts (B) increased the number of identified individuals and biomass proportions of mainly cyprinids, salmon and trout, sculpins and cod. This resulted in decreased biomass contributions mainly by the common species that were not identified in higher numbers with this method, such as common whitefish, sprat and especially herring. Numerical correction, on the other hand, increased the biomass contribution of mainly herring and sprat, both species with relatively small otoliths. The increase in those 2 common

Table 6. Percent frequency of occurrence (FO_i) with upper and lower range of the 95% confidence interval (CI) and minimum number of consumed individuals for prey taxa identified from digestive tract contents. FO_i is based both on all recovered hard-part structures and on otoliths only, where *n* equals the number of seals containing diagnostic structures.

		Diagnostic hard-part structures used					
		All hard parts (n=145)			*Otoliths only (n=138)*		
Common name	**Taxon ($_i$)**	**FO_i**	**No. of consumed ind.**	**95% CI (lower-upper)**	**FO_i**	**No. of consumed ind.**	**95% CI (lower-upper)**
Herring	*Clupea harengus*	80.69	3166	73.79-86.90	84.78	3142	77.54-89.86
Sprat	*Sprattus sprattus*	26.90	355	19.20-33.79	28.26	351	19.57-34.78
Common whitefish	*Coregonus lavaretus*	20.00	167	13.79-25.52	19.57	158	12.32-25.36
Cyprinids	*Cyprinidae*	10.34	120	4.83-15.17	10.14	78	5.07-14.49
Eelpout	*Zoarces viviparus*	6.90	123	2.76-10.34	6.52	120	2.17-10.87
Sandeels	*Ammodytidae*	6.90	32	2.76-11.03	7.25	31	2.90-11.59
Cod	*Gadus morhua*	4.14	14	1.38-7.59	2.90	9	0.00-5.80
Smelt	*Osmerus eperlanus*	4.14	19	0.69-6.90	4.35	18	0.72-7.25
Perch	*Perca fluviatilis*	4.14	8	1.38-6.90	2.90	5	0.00-5.07
Flounder	*Platichtys flesus*	4.14	38	0.69-6.90	3.62	37	0.72-6.52
Salmon	*Salmo salar*	4.14	7	1.38-6.90	3.62	6	0.72-6.52
Trout	*Salmo trutta*	3.45	8	0.69-6.21	2.90	5	0.00-5.07
Salmon or trout	Unknown *Salmo sp.*	4.14	6	0.69-6.90	1.45	2	0.00-2.90
Sculpins	*Cottidae*	2.76	22	0.00-4.83	0.72	1	0.00-1.45
Burbot	*Lota lota*	2.76	4	0.00-4.83	1.45	2	0.00-2.90
Ruffe	*Gymnocephalus cernuus*	2.07	4	0.00-4.14	2.17	4	0.00-4.35
Eel	*Anguilla anguilla*	1.38	2	0.00-2.76	0.72	1	0.00-1.45
Pike	*Esox lucius*	1.38	5	0.00-2.76	0.72	1	0.00-1.45
Gobies	*Gobiidae*	1.38	7	0.00-2.76	1.45	7	0.00-2.90
Unknown flatfish	*Pleuronectiformes*	0.69	1	0.00-2.07			
Lumpsucker	*Cyclopterus lumpus*	0.69	1	0.00-1.38	0.72	1	0.00-1.45
Four-bearded rockling	*Enchelyopus cimbrius*	0.69	4	0.00-1.38	0.72	4	0.00-1.45
Plaice	*Pleuronectes platessa*	0.69	1	0.00-1.38	0.72	1	0.00-1.45
Pike-perch	*Stizostedion lucioperca*	0.69	1	0.00-1.38	0.72	1	0.00-1.45
Unidentified		8.97	53	4.14-13.10	9.42	53	4.35-14.49
Tot. no. of ind.			**4168**			**4038**	

prey species lead to small or negative changes in the biomass contribution of most other species.

Generally, all differences between methods A, B and C were more pronounced for the all data pooled model (1) than for the seal weighted model (2). The biomass contribution of common whitefish was consistently smaller when all seals were given the same weight (model 2) than when all data were pooled (model 1), indicating that meals containing common whitefish were large. In contrast, the biomass contribution of sprat, cyprinids (except for method B) and eelpout using model 2, as well as for many rare prey species increased, leading to a more even prey distribution and indicating they were consumed in small meals.

Diet composition variation

Herring constituted the principal prey throughout the Baltic Sea, while salmon, trout and sculpins were identified only in seals collected from the Gulf of Bothnia. Cod and flatfish species were found only in seals from Baltic Proper (Fig. 7).

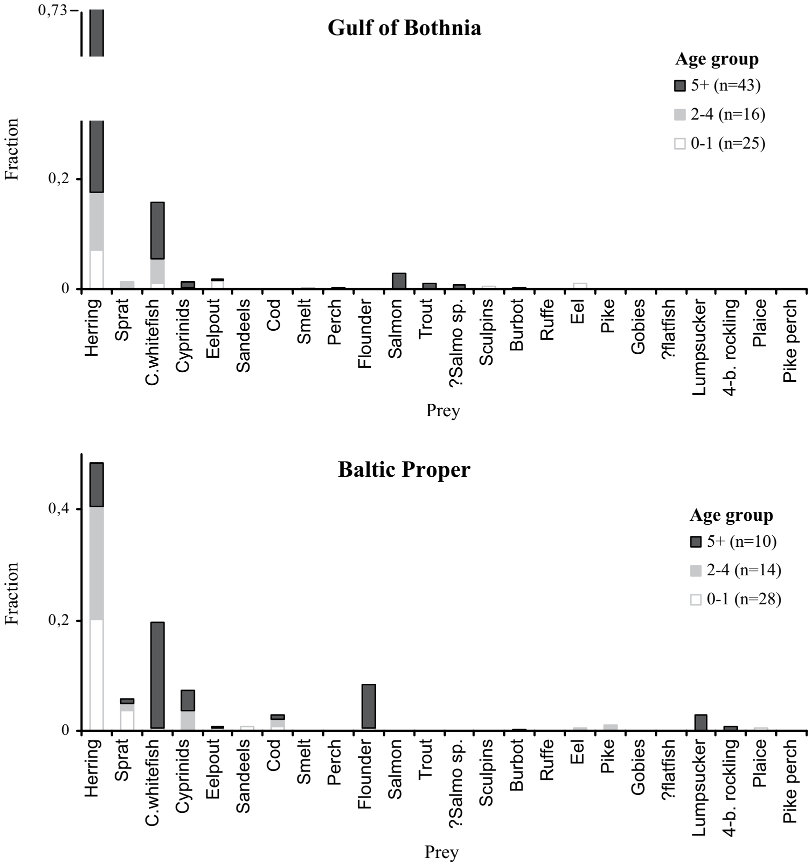


Fig. 7. *Fraction of totally consumed biomass of prey taxa in grey seals belonging to age group 0-1, 2-4 and 5+, in the Gulf of Bothnia and the Baltic Proper, respectively. The consumed biomass of the various prey species has been calculated using the all data pooled model and mean values of consumed biomass of the various prey species, from the methods B (all recovered hard-part structures) and C (otoliths corrected).*

In addition to herring, other important species in the Gulf of Bothnia were common whitefish and salmon, where salmon was only found in seals from the 5+ age group. For the Baltic Proper, the species following herring in importance were common whitefish, cyprinids, flounder and sprat. For the 3 age groups (0-1, 2-4 and 5+), the fraction of totally consumed biomass, represented by the different prey species, in the Gulf of Bothnia and the Baltic Proper is shown in Figure 7. Consumed biomass of the species was calculated using the all data pooled model (1) and mean values from the prey number methods B (all recovered hard-part structures) and C (otoliths corrected).Generally the number of species was higher in samples from the Baltic Proper (19 taxa) compared to the Gulf of Bothnia (14 taxa).

Results from the canonical correspondence analysis in CANOCO showed that the relationship between dietary data and environmental descriptors (age group, cause of death, area of origin, quarter of the year and sex) was statistically significant (P = 0.002, F-ratio = 2.613). The environmental descriptors explained 13.4% of the variance in dietary data. The pure effect of the various environmental descriptors was statistically significant for age group (P = 0.002, F-ratio = 2.545) and area of origin (P = 0.016, F-ratio = 2.836). Age group and area of origin explained 3.9% and 1.8% of the variance in dietary data, respectively. Cause of death, quarter of the year and sex proved not to have a statistically significant effect on diet composition (P = 0.13, P = 0.28 and P = 0.72 for the environmental descriptors cause of death, quarter of the year and sex, respectively).

DISCUSSION

When interpreting the results from analyses of digestive tract contents it is important to remember that all such studies suffer from a number of possible biases. The biases concern both how erosion of hard parts might effect estimations of prey number and prey size, and how the samples are collected.

Sample composition

The diet of bycaught animals might reflect the catch of that particular gear, as would animals hunted close to fishing gear. Animals found dead are in many cases animals previously bycaught in fishing operations that have been lost or discarded during gear recovery. Consequently it is not possible to get an unbiased sample since not even hunted animals can be killed at random. The low number of seals collected during the first quarter of the year can be explained by a ban on hunting during this time and limited fishing activity due to a combination of short days, severe weather and ice conditions. Hunting for grey seals usually begins by mid April, with the majority of animals being taken on the ice in April, May and early June, when seals haul out to moult (Karlsson and Helander 2005). In addition weaned inexperienced pups that start moving around and foraging on their own during spring are vulnerable to fishing gear and are overrepresented in the bycatch. This might explain the high numbers of seals collected during the second quarter. However, results from the CCA indicated no statistically significant effect of quarter of the year on the diet composition, so this sample bias does not seem crucial.

Prey occurrence

In both the Baltic Proper and the Gulf of Bothnia herring dominated the diet. Other important prey species were common whitefish and sprat but also flounder, salmonids, eelpout and cyprinids occur frequently in their diet. The presence of freshwater species, such as cyprinids, perch and pike, makes the diet of Baltic grey seals somewhat different from the north-east Atlantic grey seals where sandeels and gadoids dominate the diet (Prime and Hammond 1990, Hammond *et al.* 1994).

The importance of herring in the diet of Baltic grey seals seems to have increased during the last decades. In a previous Swedish study, consisting of digestive tracts collected between 1968 and 1971 (Söderberg 1972), on average 24% of the consumed food items were herring, compared to 57% (using all recovered hard-part structures and seal weighted average) in the present study. This is despite that herring stock biomass was probably at least as large then in the late 1960s and early 1970s as it is now (Thurow 1997, and ICES 2004). The decreased cod stock size, on the other hand, is reflected by a decreased numerical importance of cod in the diet between Söderberg (19%) and our study (1%). In the seals from the Gulf of Bothnia we did not find any cod remains at all, while Söderberg found cod in 14% of the seals originating from the Gulf of Bothnia. For the increased sprat stock (Thurow 1997, ICES 2004) we also found a corresponding pattern. In Söderberg´s study on average 3% of the consumed prey individuals were sprat compared to 11% in our study. There may however be other reasons for the observed differences, both biological such as changes in seal distribution and differences in sampling procedures. For instance, Söderberg's material was more dominated by hunted seals, younger seals and seals from the Baltic Proper compared to our study.

Prey size

To reduce potential bias in estimates of prey size, some studies have applied correction factors to account for otolith erosion in the digestive tract (*e.g.* Harvey 1989, Prime and Hammond 1990, Tollit *et al.* 1997). Published species-specific otolith size correction factors (SCFs) are available for only a few prey species in our study, and besides SCFs may differ between studies. We estimated SCFs as the ratio between average otolith size of erosion class 1 and erosion class 2 and 3 respectively, from our own dataset, which gave no or small differences in SCFs among our prey species. Since the prey size changed in the same direction and with similar magnitudes for all species the correction did not dramatically change the overall diet composition. However, such correction factors have an important impact on the size distribution of prey consumed, with a shift towards larger, and consequently older, individuals and an increase in size overlap with commercially important fish. The size of the consumed prey varied widely, from a few centimetres to approximately 1 metre, with the majority between 10 and 25 cm. However, since the seals are able to discard the head of larger fish before consumption, evidence of larger fish might be less likely recovered from analyses based on identification of otoliths, and consequently underestimated.

Diet composition estimation

Complete digestion of otoliths can bias the estimated diet composition because prey species with small and fragile otoliths tend to be underestimated both in faeces (*e.g.* Pierce and Boyle 1991, Tollit *et al.* 1997, Bowen 2000, Berg *et al.* 2002) and stomachs and intestines (Murie and Lavigne 1986). For stomach contents, one solution to avoid this problem would be to analyse only relatively un-eroded material, but that would decrease our sample size, and result in even larger confidence intervals as well as complete loss of several prey species. Published numerical correction factors from feeding experiments are available only for otoliths recovered in faeces and these factors cannot be directly applied to adjust the otolith counts in stomachs. Therefore we applied the faeces-based NCFs only to the material we assume has an equal grade of erosion as in faeces, *i.e.* the most eroded part of the stomach content and all otoliths in the intestine, where gastric acids that erode prey parts are neutralized by sodium bicarbonate (Guyton 1981 in Orr and Harvey 2001). Published NCFs are missing for most prey species found in our study, so we used NCFs generated by the relationship between recovery rate and otolith width. This relationship has a surprisingly high degree of explanation (93%), which confirms its usefulness for generating NCFs. There are, however, other otolith characteristics, like density or shape, which should influence the fragility or susceptibility of otoliths to erosion. In the future, it would be interesting to include such characteristics into the model and important to use more prey species to see if the relationship remains strong.

Besides general experimental conditions, factors that could influence otolith recovery rates are the seal species (Bowen 2000), activity level (Harvey 1989, Bowen 2000), and meal size (Marcus *et al.* 1998). We included results from studies of both grey seals and harbour seals, since Bowen (2000) did not find any differences in NCFs between those 2 species (cod and herring investigated). Low activity levels seem to slow the gastrointesinal evacuation rate, resulting in more complete erosion (Harvey 1989), and therefore we excluded studies where seals were not allowed to swim. Small meals also lead to more complete digestion and lower recovery rates than large meals (Marcus *et al.* 1998). If actual average activity levels in nature are higher, or average meal sizes are larger than in the feeding experiments, there is a possibility that we have overestimated the number of prey with small otoliths and large NCFs.

Other factors that could increase the differences in recovery rates between digestive tracts and scats are e.g. prey fat content (Markussen 1993) and prey size (Tollit *et al.* 1997). Fat prey species reasonably have longer retention times (Markussen 1993) and consequently lower recovery rates in faeces than in stomachs and intestines. If this was an important factor, fat prey species would reasonably turn out as negative residuals in the relationship between recovery rate and otolith width, and have higher NCFs than we predict. If we would use NCFs valid for otoliths found in scats the number of otoliths in stomachs and intestines would be overestimated, but by using the NCFs generated by the relationship between otolith width and recovery rate instead of published species-specific NCFs, we in fact reduce this problem. Large prey with large otoliths have higher recovery rates than small prey, even within species (Tollit *et al.* 1997) and it might be worthwhile to develop NCFs based on otolith characteristics for prey individuals rather than for prey species. Large structures like squid beaks can be retained in the digestive tract at least a day longer than fish otoliths (Bigg and Fawcett 1985). Furthermore, results from feeding studies (*e.g.* Prime and Hammond 1990, Tollit *et al.* 1997) imply that the size reduction of large otoliths is larger than for small otoliths, indicating that large structures are exposed to digestive processes for longer times. This result could, however, at least partly be explained by the methodological artefacts that arise when complete erosion of, especially small otoliths, makes the recovered otolith samples biased towards relatively un-eroded structures. Nevertheless, variation in temporal retention in the gastrointestinal system among prey could result in considerable differences in recovery rates between faeces and gastrointestinal contents. Most likely, the effect of temporal retention would result in an overestimation of large otoliths in the gastrointestinal system in relation to faeces, which imply that NCFs for small otoliths should be even larger for stomach contents. Consequently, the assumption that faeces based NCFs are applicable to stomach

Table 7. Estimated relative numerical contribution in percent (N_i) of consumed prey individuals with upper and lower range of the 95% confidence interval (CI). Indices were calculated using otoliths only (method A), all recovered hard-part structures (method B) and otoliths with numerical and size correction factors applied (method C), for all data pooled (model 1) in Table 7a and seal weighted average (model 2) in Table 7b.

	Otoliths only (1A)		**All hard parts (1B)**		**Otoliths corrected (1C)**	
Prey	N_i	*CI*	N_i	*CI*	N_i	*CI*
Clupea harengus	78.43	69.46-85.81	75.96	66.51-82.97	78.58	69.40-86.53
Sprattus sprattus	8.61	4.72-14.36	8.52	4.91-14.38	14.60	7.93-23.55
Coregonus lavaretus	3.78	1.92-6.61	4.01	2.06-6.81	1.98	1.00-3.52
Cyprinidae	1.89	0.72-3.85	2.88	1.07-5.59	0.74	0.28-1.53
Zoarces viviparus	2.96	0.24-10.64	2.95	0.28-8.91	1.68	0.35-4.35
Ammodytidae	0.67	0.17-1.48	0.77	0.27-1.77	0.80	0.23-1.83
Gadus morhua	0.21	0.02-0.57	0.34	0.06-0.69	0.09	0.01-0.25
Osmerus eperlanus	0.45	0.07-1.25	0.46	0.07-1.18	0.24	0.04-0.70
Perca fluviatilis	0.10	0.01-0.24	0.19	0.05-0.39	0.06	0.01-0.13
Platichtys flesus	0.89	0.05-2.56	0.86	0.09-2.18	0.50	0.02-1.29
Salmo salar	0.13	0.02-0.31	0.17	0.06-0.38	0.08	0.02-0.18
Salmo trutta	0.11	0.02-0.27	0.19	0.05-0.44	0.09	0.01-0.24
Salmo spp.	0.04	0.00-0.11	0.14	0.04-0.30	0.03	0.00-0.11
Cottidae	0.03	0.00-0.10	0.53	0.04-1.47	0.01	0.00-0.05
Lota lota	0.04	0.00-0.11	0.10	0.02-0.22	0.01	0.00-0.04
Gymnocephalus cernuus	0.06	0.00-0.18	0.10	0.00-0.25	0.04	0.00-0.11
Anguilla anguilla	0.01	0.00-0.05	0.05	0.00-0.14	0.01	0.00-0.03
Esox lucius	0.01	0.00-0.05	0.12	0.00-0.45	0.00	0.00-0.01
Gobiidae	0.16	0.00-0.57	0.17	0.00-0.65	0.32	0.00-1.08
Pleuronectiformes			0.07	0.00-0.21		
Cyclopterus lumpus	0.01	0.00-0.05	0.02	0.00-0.08	0.02	0.00-0.09
Enchelyopus cimbrius	0.09	0.00-0.33	0.10	0.00-0.33	0.09	0.00-0.32
Pleuronectes platessa	0.03	0.00-0.10	0.02	0.00-0.09	0.01	0.00-0.05
Stizostedion lucioperca	0.03	0.00-0.10	0.02	0.00-0.10	0.01	0.00-0.03
Unidentified	1.26	0.49-2.40	1.27	0.54-2.32		

and intestinal contents could be a conservative one. Despite all potential bias and uncertainty in using NCFs generated by the relationship between otolith recovery rates in faeces and otolith width on gastrointestinal contents we think that the alternative of ignoring otolith erosion is worse. Furthermore, the harbour seal diet composition in Berg *et al.* (2002) estimated from gastrointestinal contents corresponds much better with the uncorrected than with the numerically corrected diet composition estimated from scats, which highlights the importance of numerical corrections also for stomach contents.

The results from other diet studies (*e.g.* Murie and Lavigne 1986, Tollit *et al.* 1997, Bowen 2000), as well as the large range of NCFs in our investigation (between 1.2 and 6.3, Table 5) suggest that numerical correction is crucial for good diet composition estimates. However, in this study, the difference in diet composition between estimates with and without numerical correction is relatively small. Generally the proportion of prey species with small otoliths and large number correction factors (*e.g.* herring and sprat) increased, while species such as common whitefish decreased, but since herring was already the dominant prey item in the diet before the correction factors were applied and species with large otoliths constitute only a relatively small proportion of the diet, the differences between corrected and uncorrected composition

Table 7b

	Otoliths only (2A)		All hard parts (2B)		Otoliths corrected (2C)	
Prey	*N_i*	*CI*	*Ni*	*CI*	*Ni*	*CI*
Clupea harengus	62.89	57.02-68.99	57.23	50.24-63.00	64.48	57.47-70.71
Sprattus sprattus	11.18	7.50-15.89	10.81	7.09-14.96	13.24	9.22-18.63
Coregonus lavaretus	6.46	3.58-10.42	6.41	3.49-10.03	6.05	3.00-9.64
Cyprinidae	5.25	2.39-8.55	5.40	2.85-8.94	4.46	2.10-8.08
Zoarces viviparus	4.12	1.60-7.42	4.06	1.54-7.51	4.29	1.79-7.88
Ammodytidae	2.40	0.91-4.90	1.87	0.63-3.87	2.70	0.91-5.52
Gadus morhua	0.72	0.03-2.03	1.13	0.16-2.46	0.35	0.01-0.96
Osmerus eperlanus	1.14	0.21-2.86	1.05	0.22-2.57	0.98	0.11-2.80
Perca fluviatilis	0.41	0.03-1.21	1.20	0.13-3.27	0.30	0.03-0.88
Platichtys flesus	1.90	0.20-4.17	1.98	0.52-4.18	1.67	0.21-3.95
Salmo salar	0.18	0.04-0.39	0.88	0.09-2.85	0.14	0.03-0.32
Salmo trutta	0.10	0.02-0.22	0.31	0.06-0.82	0.09	0.01-0.21
Salmo sp.	0.16	0.00-0.47	1.79	0.23-4.32	0.18	0.00-0.50
Cottidae	0.16	0.00-0.32	2.02	0.14-4.70	0.09	0.00-0.19
Lota lota	0.27	0.00-0.78	0.32	0.04-0.85	0.10	0.00-0.32
Gymnocephalus cernuus	0.11	0.01-0.38	0.14	0.01-0.42	0.11	0.00-0.37
Anguilla anguilla	0.14	0.00-0.29	0.28	0.00-0.83	0.21	0.00-0.60
Esox lucius	0.36	0.00-0.72	0.57	0.00-1.70	0.22	0.00-0.43
Gobiidae	0.13	0.00-0.38	0.13	0.00-0.38	0.20	0.00-0.58
Pleuronectiformes			0.69	0.00-1.38		
Cyclopterus lumpus	0.01	0.00-0.01	0.01	0.00-0.02	0.01	0.00-0.02
Enchelyopus cimbrius	0.05	0.00-0.09	0.05	0.00-0.10	0.04	0.00-0.08
Pleuronectes platessa	0.12	0.00-0.24	0.10	0.00-0.30	0.07	0.00-0.14
Stizostedion lucioperca	0.02	0.00-0.04	0.02	0.00-0.04	0.01	0.00-0.02
Unidentified	1.71	0.75-3.07	1.56	0.65-2.57	0.00	

were moderate. However, in the perspective of the individual prey species, the changes can still be important. For example, when comparing the biomass index from method A to the index from method C using the all data pooled model, sprat increases by a factor 1.7 while common whitefish and cyprinids decrease by a factor 0.65 and 0.41 respectively. An exception to the general pattern is eelpout, which had a lower biomass contribution, using the all data pooled model, despite its large correction factor (5.4). The reason for this is that most eelpout otoliths were found relatively un-eroded in the stomachs (Fig. 4) and therefore were not numerically corrected. If the absence of eroded otoliths in the intestines is due to rapid complete erosion, resulting in a low recovery rate, eelpouts are probably heavily underestimated. Use of all hard parts, not only otoliths, reduces the bias associated with pinniped diet reconstructions (Browne *et al.* 2002). Including additional structures increased the number of identifiable prey items, and resulted in higher biomass contributions from cyprinids, salmonids and sculpins. For large individuals and species (*e.g.* salmon), if the seals do not eat the head of the fish, using other structures than otoliths will improve the estimated diet composition. This seems to be a fact for the thorny sculpins as well, for which mostly bones and no otoliths were found. However, the number of cyprinids, on the other hand, may have been overestimated because they have robust and easily identifiable structures that other species lack (*i.e.* chewing pads and pharyngeal teeth). Another potential bias in inferring seal diet from digestive tract analyses is that seals in some cases only eat

Table 8. Estimated relative contribution in percent to estimated biomass (Bi) of consumed prey individuals with upper and lower range of the 95% confidence interval (CI). Indices were calculated using otoliths only (method A), all recovered hard-part structures (method B) and otoliths with numerical and size correction factors applied (method C), for all data pooled (model 1) in Table 8a and seal weighted average (model 2) in Table 8b.

	Otoliths only (1A)		**All hard parts (1B)**		**Otoliths corrected (1C)**	
Prey	B_i	*CI*	B_i	*CI*	B_i	*CI*
Clupea harengus	58.51	47.21-71.09	50.65	39.13-62.18	70.13	58.37-80.38
Sprattus sprattus	1.89	0.96-3.26	1.68	0.95-2.95	3.24	1.76-5.81
Coregonus lavaretus	23.08	12.13-34.89	21.39	11.63-31.94	15.10	6.96-26.46
Cyprinidae	4.51	1.40-8.96	7.22	3.04-14.67	1.90	0.69-4.05
Zoarces viviparus	2.31	0.20-8.28	2.07	0.22-6.22	1.35	0.35-3.01
Ammodytidae	0.20	0.05-0.45	0.21	0.06-0.46	0.24	0.07-0.59
Gadus morhua	1.15	0.13-3.46	1.51	0.33-3.48	0.62	0.01-1.73
Osmerus eperlanus	0.36	0.07-1.04	0.32	0.06-0.86	0.21	0.04-0.67
Perca fluviatilis	0.19	0.03-0.51	0.34	0.08-0.80	0.12	0.02-0.33
Platichtys flesus	2.72	0.10-7.23	2.51	0.20-6.30	2.35	0.07-5.97
Salmo salar	2.34	0.39-5.04	4.52	0.96-10.58	1.32	0.24-2.91
Salmo trutta	0.56	0.10-1.38	0.81	0.17-1.95	0.71	0.08-2.23
Salmo spp.	0.31	0.00-0.96	1.03	0.33-2.07	0.42	0.00-1.31
Cottidae	0.07	0.00-0.28	1.29	0.15-3.46	0.03	0.00-0.11
Lota lota	0.45	0.00-1.58	0.89	0.17-1.96	0.13	0.00-0.41
Gymnocephalus cernuus	0.03	0.00-0.08	0.05	0.00-0.13	0.02	0.00-0.05
Anguilla anguilla	0.62	0.00-2.23	1.56	0.00-4.65	0.70	0.00-2.62
Esox lucius	0.19	0.00-0.72	1.27	0.00-4.70	0.04	0.00-0.15
Gobiidae	0.00	0.00-0.01	0.00	0.00-0.01	0.01	0.00-0.02
Pleuronectiformes			0.10	0.00-0.38		
Cyclopterus lumpus	0.16	0.00-0.61	0.27	0.00-1.11	0.93	0.00-3.31
Enchelyopus cimbrius	0.14	0.00-0.53	0.11	0.00-0.47	0.26	0.00-0.93
Pleuronectes platessa	0.18	0.00-0.68	0.15	0.00-0.60	0.14	0.00-0.57
Stizostedion lucioperca	0.04	0.00-0.14	0.03	0.00-0.12	0.01	0.00-0.04

the soft parts of the fish, discarding the head and skeleton. To be able to control for this behaviour complementary analyses of seal diet are needed, using other methods than analyses of hard parts in digestive tracts and faeces.

The differences between the prey number estimation methods (A-C: otoliths only, all recovered hard-part structures and otoliths corrected) decreased when the diet composition was estimated by the seal weighted model (2) compared to the all data pooled model (1). The probable reason is that since each seal often contains only 1 or a few prey species, the higher number of identified prey individuals when the methods all hard-part structures (B) and otoliths corrected (C) are used will have no or a limited effect on the relative contribution (N_i and B_i) for each seal. In the all data pooled model (1) the diet composition will be dominated by seals containing large quantities of consumed prey, whereas in the seal weighted model (2) each seal contributes equally which seems to smooth out the diet composition, making rare species more important. The probable explanation is that rare species occur in relatively empty stomachs, but we cannot say if this reflects a more realistic diet composition or not. If the lower food content in seals containing rare species reflects a lower consumption of those species, the all data pooled model would be preferable, but if the lower content has other explanations, e.g. higher digestion rates or a more continuous food intake in smaller portions, the seal weighted model is probably better. Also, to be able to study variations in food composition among individual seals the seal weighted model should be preferred.

Diet composition variation

It is likely that the differences in diet composition between the Gulf of Bothnia and the Baltic Proper are explained by different prey availability in the 2 areas. It is also possible that the differences between the areas are explained partially by differences in age composition of the sampled seals between the 2 areas. Canonical correspondence analysis indicated that both age group and area of origin had significant effects on the diet composition, indicating an actual difference in diet composition between areas as well as between age groups. Differences in sampling regimes are the most likely cause of the differences in age composition between the 2 areas. There is a strong correlation between the age composition and the cause of death with more young seals bycaught, while hunting seems to target older seals. We also found that the cause of death differed significantly between the areas of origin, with a higher proportion of hunted animals in the Gulf of Bothnia and a higher proportion of bycaught animals in the Baltic Proper.

Conclusions

We stress the importance of being aware of the possible biases present in estimates of prey number and prey size when assessing seal diet from hard-part prey remains. A way to deal with the problem of biases due to digestive erosion of otoliths is to use other structures in addition to otoliths and to apply species-specific numerical and size correction factors. Although the results differ among prey number methods and diet composition models, the general conclusion remains that herring is the dominant prey followed by common whitefish and sprat. Cyprinids, salmonids, eelpout and flounder were also common prey for grey seals in the Baltic Sea. Our results indicate differences in the diet of Baltic grey seals both between age groups and between the Gulf of Bothnia and the Baltic Proper.

ACKNOWLEDGEMENTS

The study is financed by the EU project FRAP (Framework of biodiversity reconciliation action plans), a project funded by the European Union under the fifth framework programme (www.frap-project.net). Herring and sprat otoliths from the Baltic Sea were kindly provided by M. Casini (Institute of Marine Research, Swedish Board of Fisheries, Lysekil, Sweden). We also thank 2 anonymous reviewers for constructive comments on the manuscript.

REFERENCES

Berg, I., Haug, T. and Nilssen, K.T. 2002. Harbour seal (*Phoca vitulina*) diet in Vesterålen, north Norway. *Sarsia* 87:451-461.

Bergman, A. 1999. Health condition of the Baltic grey seal (*Halichoerus grypus*) during two decades. Gynaecological health improvement but increased prevalence of colonic ulcers. *APMIS* 107:270-282.

Bergman, A. and Olsson, M. 1986. Pathology of Baltic Grey Seal and Ringed Seal females with special reference to adrenocortical hyperplasia: Is environmental pollution the cause of a widely distributed disease syndrome? Proc. from the Symposium on the Seals in the Baltic and Eurasian Lakes. Savonlinna, 1984-06-05--08. *Finnish Game Research* 44:47-62.

Bigg, M.A. and Fawcett, I. 1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). In: Beddington, J.R., Beverton, R.J.H. and Lavigne, D.M. (eds.); *Marine mammals and fisheries.* George Allen and Unwin Ltd, London, 284-291.

Bowen, W.D. 2000. Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. *Can. J. Fish. Aquat. Sci.* 57:898-905.

Bowen, W.D. and Harrison, G.D. 1994. Offshore diet of grey seals, *Halichoerus grypus*, near Sable Island, Canada. *Mar. Ecol. Prog. Ser.* 112:1-12.

Browne, P., Laake, J.L. and DeLong, R.L. 2002. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. *Fish. Bull*. 100:423-433.

Christiansen, J.S., Gamst Moen, A.-G., Hansen, T.H. and Nilssen, K.T. 2005. Digestion of capelin, *Mallotus villosus* (Muller), herring, *Clupea harengus* L., and polar cod, *Boreogadus saida* (Lepechin), otoliths in a simulated seal stomach. *ICES J. Mar. Sci.* 62:86-92.

da Silva, J. and Neilson, J.D. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. *Can. J. Fish. Aquat. Sci*. 42:1439-1442.

Frost, K.J. and Lowry, L.F. 1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. *Can. J. Zool*. 58:1601-1607.

Gales, N.J. and Cheal, A.J. 1992. Estimating diet composition of the Australian sea-lion (*Neophoca cinerea*) from scat analysis: an unreliable technique. *Wildl. Res*. 19:447-456.

Haddon, M. 2001. *Modelling and quantitative methods in fisheries*. Chapman & Hall/CRC. Boca Raton, Florida.

Hammond, P.S. and Rothery, P. 1996. Application of computer sampling in the estimation of seal diet. *J. Appl. Stat*. 23:525-533.

Hammond, P.S., Hall, A.J. and Prime, J.H. 1994. The Diet of grey seals around Orkney and other island and mainland sites in the North-Eastern Scotland. *J. Appl. Ecol*. 31:340-350.

Harding, K.C. and Härkönen, T.J. 1999. Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during the 20th century. *Ambio* 28:619-625.

Härkönen, T. 1986. *Guide to the otoliths of the bony fishes of the northeast Atlantic.* Danbiu ApS., Hellerup, 256 pp.

Harvey, J.T. 1989. Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. *J. Zool*. 219:101-111.

Hewer, H.R. 1964. The determination of age, sexual maturity, longevity and a life-table in the grey seal (*Halichoerus grypus*). *Proc. Zool. Soc. Lond*. 4:593-624.

Hiby, L., Lundberg, T., Karlsson, O., Watkins, J., Jüssi, M., Jüssi, J. and Helander, B. 2007. Estimates of the size of the Baltic grey seal population based on photo-identification data. *NAMMCO Sci. Publ*. 6:163-175.

[ICES] International Council for the Exploration of the Sea. 2004. Report of the Baltic fisheries assessment working group. *ICES CM 2004/ACFM*:22.

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

Karlsson, O. and Helander, B. 2005. Gråsäl (Grey seal). In: Wiklund, K. (ed.) *Bottniska viken 2004*. Årsrapport från den marina miljöövervakningen. Umeå Marina Forskningscentrum (UMF). (Yearly report from the monitoring of the marine environment of the Gulf of Bothnia. Umeå Marine Research Centre),27-28. (In Swedish with English legends).

Laake, J.L., Browne, P., DeLong, R.L. and Huber, H.R. 2002. Pinniped diet composition: a comparison of estimation models. *Fish. Bull.* 100(3):434-447.

Leopold, M.F., Van Damme, C.J.G., Philippart, C.J.M. and Winter, C.J.N. 2001. *Otoliths of North Sea fish: fish identification key by means of otoliths and other hard parts*. World Biodiversity Database CD-ROM Series. Expert Center for Taxonomic Identification (ETI): Amsterdam, The Netherlands. ISBN 90-75000-22-7.

Marcus, J., Bowen, W.D. and Eddington, J.D. 1998. Effects of meal size on otolith recovery from fecal samples of gray and harbour seal pups. *Mar. Mamm. Sci.* 14:789-802.

Markussen, N.H. 1993. Transit time of digesta in captive harbour seals (*Phoca vitulina*). *Can. J. Zool.* 71:1071-1073.

Murie, D.J. and Lavigne, D.M. 1986. Interpretation of otoliths in stomach content alalyses of phocid seals: quantifying fish consumption. *Can. J. Zool*. 64:1152-1157.

Nienhuis, J. 2000. The use of chewing pads and otoliths of cyprinids for estimating food intake of cormorants *Phalacrocorax carbo*. *Wetlands International Cormorant Research Group Bulletin* 4:40-42.

Orr, A.J. and Harvey, J.T. 2001. Quantifying errors associated with using fecal samples to determine the diet of the California sea lion (*Zalophus californianus*). *Can. J. Zool*. 79:1080-1087.

Pierce, G.J. and Boyle, P.R. 1991. A review of methods for diet analysis in piscivorous marine mammals. *Oceanogr. Mar. Biol. Ann. Rev.* 29:409-486.

Prime, J.H. and Hammond, P.S. 1990. The diet of grey seals from the South-Western North Sea assessed from analyses of hard parts found in faeces. *J. Appl. Ecol.* 27:435-447.

Santos, M.B., Clarke, M.R. and Pierce, G.J. 2001. Assessing the importance of cephalopods in the diets of marine mammals and other top predators: problems and solutions. *Fish. Res.* 52:121-139.

Söderberg, S. 1972. Sälens födoval och skadegörelse på laxfisket i Östersjön (The seals food choice and damage to the salmon fishery in the Baltic Sea). Undersökning utförd på uppdrag av Svenska Ostkustfiskarenas Centralförbund (Report to the federation of Swedish East Coast fishermen), 60 pp. (In Swedish).

ter Braak C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167-1179.

Thurow, F. 1997. Estimation of total fish biomass in the Baltic Sea during the 20th century. *ICES J. Mar. Sci.* 54:444-461.

Tollit, D.J., Steward, M.J., Thompson, P.M., Pierce, G.J., Santos, M.B. and Hughes, S. 1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Can. J. Fish. Aquat. Sci.* 54:105-119.

Tormosov, D.D. and Rezvov, G.V. 1978. Information on the distribution, number and feeding habits of ringed and grey seals in the gulfs of Finland and Riga in the Baltic Sea. *Finnish Game Research* 37:14-17.

Veldkamp, R. 1995. The use of chewing pads for estimating the consumption of cyprinids by cormorants *Phalacrocorax carbo. Ardea* 83(1):135-138.

Watt, J., Pierce, G.J. and Boyle, P.R. 1997. Guide to the identification of North Sea fish using premaxillae and Vertebrae. *ICES Coop. Res. Rep*. 220: 231 pp.

Westerberg, H., Fjälling, A. and Martinsson, A. 2000. Sälskador i det svenska fisket. Beskrivning och kostnadsberäkning baserad på loggboksstatistik och journalföring 1996-1997. (Seal-fisheries interaction in the Swedish fishery). *Fiskeriverket Rapport* 2000:3:3-38. (In Swedish with English summary).

Wheeler, A. 1978. *Key to the fishes of northern Europe*. Frederick Warne Ltd., London, England.