Improved estimates of digestion correction factors and passage rates for harbour seal (*Phoca vitulina*) prey

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Summary

Diet composition estimates for pinnipeds are widely conducted using prey hard remains recovered from faeces. To estimate the size and number of prey consumed accurately, digestion correction factors must be applied to measurements and counts of fish otoliths and cephalopod beaks. We conducted 101 whole prey feeding trials with six harbour seals (*Phoca vitulina*) and 18 prey species to derive estimates of digestion coefficients (DC; accounting for partial digestion using otolith width (OW) or length (OL)) and recovery rates (RR; accounting for complete digestion). Greater than 98% of otoliths were passed within 3 days of consumption. All otoliths passed were recovered by day 10 and all beaks by day 14. RRs were smallest for Atlantic salmon smolts (*Salmo salar,* RR=0.306; SE=0.031), progressively greater for sandeels, flatfish, squid (*Loligo forbesii*) and large gadoids, and greatest for *Trisopterus* spp (RR=1.017, SE=0.002). Species-specific DCs were greatest for greater sandeel (*Hyperoplus lanceolatus*, DC(OW)=1.75, SE=0.049), then progressively smaller for sandeel, flatfish, large gadoids and *Trisopterus* species (DC(OW)=1.14, SE=0.015). The amount of erosion of each otolith was graded using a scale of 1-4. The majority of otoliths recovered (65.9%) were severely eroded (grade 4). Grade specific DCs were greatest for greater sandeel (DC=1.82, SE=0.047), then progressively smaller for large gadoids, flatfish and *Trisopterus* spp (DC=1.18, SE=0.016). Possible explanations for some results with RR>1 and DC<1 are discussed. In almost all cases the CV was smaller for DCs using OW than using OL. As such, OW DCs (grade-specific) will be used to estimate the diet of harbour seals, where possible. RRs were broadly similar to those for grey seals (*Halichoerus grypus*), but harbour seal species- and grade-specific DCs were generally smaller. Differences in partial and complete digestion rates among prey species and between harbour and grey seals highlight the importance of applying predator- and prey-specific digestion correction factors when reconstructing diet.

Introduction

The recovery of prey hard remains such as fish otoliths and cephalopod beaks from faeces is a widely used method to estimate phocid diet (Hammond *et al.*, 1994a; Hammond *et al.*, 1994b; Bowen and Harrison, 1996; Thompson *et al.*, 1996; Tollit and Thompson, 1996; Hall *et al.*, 1998; Brown *et al.*, 2001; Hammond and Grellier, 2006; Hammond and Harris, 2006). Prey structures which are resistant to digestion can be collected from faeces, regurgitate, stomachs and intestines. Despite providing little information about the source animal, faecal samples are relatively easy and quick to collect and remain the most appropriate method for obtaining information on the diet of seal populations in European waters. Scat analysis is typically representative of recent feeding within 12 - 48 h (Prime and Hammond, 1987; Markussen, 1993; Orr and Harvey, 2001; Grellier and Hammond, 2006; Phillips and Harvey, 2009) and is therefore a useful tool for estimating the diet of primarily coastal species such as the harbour seal (*Phoca vitulina*). The diet composition and prey consumption of harbour seals around Scotland and England will be estimated using >2000 scat samples collected in 2010 - 2012 (MMSS/001/11/CSD3).

Otoliths and beaks are species-specific in their shape. For pristine specimens, this allows accurate identification to species of these structures and there are good allometric relationships between otolith or beak size and fish or cephalopod size that allow the size of ingested prey to be estimated accurately (Clarke, 1986; Härkönen, 1986; Leopold *et al.*, 2001). However, when passing through the gastrointestinal tract of a seal, otoliths and beaks may be partially digested and thus reduced in size. In addition, some otoliths or beaks may be completely digested. Digestion correction factors (DCFs) need to be applied to remove these biases; that is, digestion coefficients and recovery rates (number correction factors) to account for partial and complete digestion, respectively (Prime and Hammond, 1987; Harvey, 1989; Tollit *et al.*, 1997; Bowen, 2000; Tollit *et al.*, 2004; Grellier and Hammond, 2006). Failure to account for the digestion of hard prey remains can lead to estimates of diet composition and prey consumption that are subject to considerable bias.

Captive *in vivo* feeding trials have previously been conducted to quantify the extent of partial and complete digestion of otoliths and beaks consumed by harbour seals (Prime, 1979; Silva and Neilson, 1985; Cottrell *et al.*, 1996; Tollit *et al.*, 1997; Marcus *et al.*, 1998; Phillips and Harvey, 2009). However, available DCFs are limited for NE Atlantic prey species and methodology has varied. As a result, reconstruction of harbour seal diet in European waters has not been conducted consistently. Studies have used harbour seal DCFs for a limited number of prey species (e.g. Brown *et al.*, 2001; Pierce and Santos, 2003), grey seal DCFs (Sharples *et al.*, 2009) or no DCFs (e.g. Wilson *et al.*, 2002).

The aims of this study were (a) to obtain robust estimates of digestion coefficients and recovery rates to use to account for partial and complete digestion of otoliths and beaks of prey species commonly consumed by NE Atlantic harbour seals, and (b) to describe species-specific characteristics of the passage rate through the harbour seal gut of the remains of prey hard parts.

Methods

Feeding experiments were conducted with harbour seals during March - April 2009 (1 adult female) and August 2011 - December 2012 (1 juvenile male and 4 adult males) at the Sea Mammal Research Unit (SMRU), University of St Andrews (Scotland). Seals were captured either in the Eden estuary, St Andrews Bay or at Ardesier, Moray Firth and housed for up to 13 months before being released at the haul-out site from which they were caught. At SMRU, the seals were housed in ambient temperature seawater pools and fed a multi-species diet supplemented with vitamins and iron. This work was carried out under Home Office licences (60/4009 and 60/3303).

For the duration of the feeding experiment, seals were housed individually in an enclosure 6.20m x 4.85m, with access to water (a pool 3 m in diameter and 1.5 m deep) and a dry area. Overflow and outflow water passed through a 250μm filter. The recovery rate of the system was tested using a total of 730 plastic or glass beads which were scattered in the pool enclosure arbitrarily and counted on recovery.

In total, 17 fish and one cephalopod prey species were offered to the seals; prey species and size ranges are given in Table 1. The prey fed included those species most frequently observed in the diet of harbour seals in the UK (Pierce *et al.*, 1991a; Tollit and Thompson, 1996; Brown and Pierce, 1998; Brown *et al.*, 2001; Pierce and Santos, 2003). Prey were obtained commercially or through collaboration with Marine Scotland Science, Aberdeen, the Pittenweem Harbour Fishermen's Mutual Association, or Jack Wright (Fleetwood) Limited. Otoliths and beaks were fed *in situ* in whole or gutted prey (fish obtained commercially had been gutted prior to delivery) because feeding method has been shown to affect digestion in captive seals (Grellier and Hammond, 2005). Differences in prey availability meant that different combinations of prey were offered to each individual seal.

For a minimum of 5 days prior to the start of an experiment, each seal was fed decapitated fish to clear its digestive system of otoliths/beaks. During experiments, seals were offered single-species meals once a day in the late afternoon. Where prey availability allowed, seals were fed the same prey species multiple times. However, multiple meals of the same species were offered only if all otoliths previously fed of that species had been recovered or

if there was a 2 day period when no otoliths of that species were recovered. Meal size was kept constant for individual seals but varied across individuals depending on their size. The total length of fish and the mass of cephalopods fed were measured to the nearest 0.1cm and 0.5g, respectively. The size of otoliths and beaks of the prey fed to the seals was calculated using the relationships given in Table 2.

The pool was drained and cleaned prior to the first experimental meal and then daily within 24h of an experimental meal being fed (average time between feeding and draining was 18:50h). All debris were collected during draining and cleaning, and were washed through a nest of sieves of mesh sizes 2mm, 1mm, 600μm, 335μm and 250μm.

All prey remains were sorted and all otoliths and beaks retained. Otoliths and beaks were identified to species and counted. Broken otoliths and beaks were only included if the widest or longest part of the otolith or the lower rostral length (LRL) of the beak was complete. Otolith length (OL) and width (OW) and cephalopod beak LRL were measured to the nearest 0.01 mm using digital callipers (Mitutoyo) under a binocular microscope (Kyowa optical 2D-2PL and Zeiss Stemi 2000-C). The callipers were zeroed between measurements and were frequently cleaned.

Uneaten prey remains (whole prey or fish heads) were recovered from the pool daily. Lengths of whole fish were measured directly. Otoliths were removed from the heads of damaged fish and lengths and widths measured. The length of the fish that they came from was estimated using the regression equations given in Table 3. Mean uneaten fish length was calculated from whole fish, or whole fish plus fish length estimated from either otolith length or otolith width.

For trials in which greater than 10% of prey was uneaten we used nonparametric bootstrap resampling to determine whether or not the size distribution of fish eaten was representative of the size distribution of prey fed. In each bootstrap resample, the mean length of a randomly selected sample, equal in size to the observed percentage of uneaten fish, was calculated. 95% confidence intervals were calculated from the distribution of 1000 mean lengths using the percentile method. If the observed mean length of uneaten fish, as calculated above, was outwith the 95% confidence interval, the trial was discarded.

Recovery Rate

Recovery rate was calculated as the proportion of otoliths eaten that was recovered at the end of each feeding trial. If all otoliths eaten were recovered, recovery rate = 1, if no otoliths were recovered, recovery rate = 0. The theoretical variance of recovery rate was calculated as $p(1 - p)/n$, where p is the recovery rate and n is the number of otoliths that were eaten. Recovery

rates were averaged across trials to give mean values for each seal for each prey species-size combination, giving each trial equal weight. These values were then averaged across seals to give mean values for each prey species-size combination, giving equal weight to each seal. These values were then averaged to give mean values for each prey species, giving equal weight to each species-size combination.

Passage rates

Cumulative daily recovery rates were calculated for each prey species in each trial and combined as described above to give mean rates for each seal, each prey species-size combination and each prey species. Prey species with similar taxonomy were grouped for presentation purposes. Cumulative daily recovery rates were also calculated for groupings for species: large gadoids (Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, hake *Merluccius merluccius*, pollock *Pollachius pollachius*, whiting *Merlangius merlangus*), *Trisopterus* spp. (Norway pout *Trisopterus esmarkii* and poor cod *Trisopterus minutus*), flatfish, and all sandeels (sandeel *Ammodytes tobianus* and greater sandeel *Hyperoplus lanceolatus*).

Species-specific digestion coefficients

Digestion coefficients (mean otolith or beak size offered divided by mean otolith or beak size recovered) were calculated for fish OL and, OW and squid LRL. The delta method was used to calculate the variance of each digestion coefficient (Seber, 1982; Grellier and Hammond, 2005; Grellier and Hammond, 2006). All trials from which <10 otoliths were recovered were excluded from further analyses, except for large gadoid trials because of the constraints of feeding large fish and maintaining constant meal size. The digestion coefficients from each trial were averaged as described above to give mean values for each seal, each prey species-size combination, each prey species and each prey grouping.

Grade-specific digestion coefficients

All recovered otoliths were examined and the amount by which they had been digested was classified based on external morphological features (Leopold *et al.*, 2001). Pristine otoliths were classified as grade 1, moderately digested otoliths as grade 2, and considerably digested as grade 3. Because of the high number of grade 3 otoliths recovered, and the high level of digestion observed in this and other studies (Tollit *et al.*, 1997; Grellier and Hammond, 2006), a further classification (grade 4, severely digested) was introduced. External morphological features used to classify a grade 4 otolith were: no visible sulcus or lobation or very worn surfaces (see Appendix 1, Figure A1). No attempt was made to classify beak digestion.

Where ≥10 otoliths by grade were recovered from a trial, grade-specific digestion coefficients and variances were calculated and combined in the

same way as for species-specific digestion coefficients. For some species the recovery of specific grades of otoliths was very low and measurements from grade 2 and grade 3 otoliths were pooled.

Results

A total of 23,313 otoliths and beaks of 18 prey species were fed to and eaten by harbour seals during 101 whole prey feeding trials. 61.4% (14,306) of otoliths and beaks were recovered from scats. 98.1% (716/730) of beads were recovered and loss from the system was observed to be though human error. Some beads tossed into the air subsequently bounced out of the enclosure; scattering beads at a low level onto the haulout area and into the water would have avoided this. Prey hard remains could not be lost in this way and therefore we conclude that loss of prey remains from the system was insignificant and can be ignored.

Recovery rates

Variation in prey recovery rates among seals (inter-individual variation) and within seals for prey fed to the same seal multiple times (intra-individual variability) is shown in Figure 1. Recovery rates for *Trisopterus* spp were very high, all trials > 0.95 and mean = 1.017. For large gadoid species, recovery rate was high 0.5 - 1.063 (mean = 0.944, Table 1). Recovery rate was >0.9 in 78% of large gadoid trials, including 18 trials where recovery rate was ≥1. Flatfish recovery rates were lower, mean = 0.789, and more variable ranging from 0.235 to 1 (38% >0.9). Herring (*Clupea harengus*) otolith recovery was low, range 0.210 - 0.643; mean = 0.428, as it was for sandeel (range 0.121 - 0.679, mean = 0.389, n = 10 trials), greater sandeel (range 0.265 - 0.934, mean = 0.600, n = 2 trials), red gurnard (*Chelidonichthys cuculus*, range 0.639 - 0.522, mean = 0.580, n = 2 trials) and Atlantic salmon smolt (*Salmo salar*, range 0.272 - 0.339, mean = 0.306, n = 2 trials). Squid (*Loligo forbesi*) lower beak recovery was high (mean = 0.816, range 0.649 - 1).

The relationship between recovery rate and mean undigested otolith size was positive up to OL = ~5mm and OW = ~3mm but then varied close to 1 for larger otoliths, with some lower values for the largest otoliths (Figure 2; correlation coefficient 0.531 for OL and 0.505 for OW). Recovery rates >1 were calculated for individual trials of cod (n = 2), whiting (n = 2), haddock (n = 1), Norway pout (n = 1) and poor cod (n = 2). Mean recovery rates >1 were calculated for haddock, Norway pout and poor cod. Recovery rates greater than one should be impossible; potential reasons for these anomalous results are discussed below. Although crustaceans were not fed in any experiment, crustacean remains were recovered from two seals during 51 whole fish feeding trials (half of the meals fed).

<u>Passage rates</u>

Greater than 50% of large gadoid and flatfish otoliths and squid beaks consumed were recovered on day 1 (within 16 h, Table 4). By day 2, >90% of large gadoid, sandeel and *Trisopterus* otoliths had been passed (within 40 h). Recovery at day 2 for flatfish was 87.0% and for squid was 79.5%. Greater than 98% of all otoliths were recovered by day 3, for squid by day 9. All otoliths that were going to be recovered had been passed by day 10 (232 h) and all beaks by day 14 (328 h). Variation in passage rate of the remains of individual prey species is shown in Figure 3. The majority of otoliths passed were recovered by the second day of feeding (i.e. within 40 h), regardless of whether final recovery rates were high, medium or low.

<u>Species-specific digestion coefficients</u>

Digestion coefficients varied among individual prey species (Table 5). OL digestion coefficients were greatest for hake, whiting and greater sandeel (1.93, 1.69 and 1.61, respectively), OW digestion coefficients were also greatest for hake and greater sandeel (1.80 and 1.75, respectively). Prey group digestion coefficients were greatest for all sandeels, then all large gadoids, all flatfish and *Trisopterus* spp (Table 5).

Inter- and intra-seal variability in digestion coefficients is shown in Figure 4 and Appendix B, Table B 1. Overall, cross-trial differences were low, but the range was wider for some species than others. Relatively high variability was observed in OL digestion coefficients for whiting, plaice (*Pleuronectes platessa*) and lemon sole (*Microstomus kitt*) and in OW digestion coefficients for lemon sole.

Due to limited prey availability it was not possible to feed multiple size classes of prey. However, there was a slight significant positive relationship between digestion coefficient and mean OL offered (Figure 5, Adj R^2= 0.0523, inverse-variance weighted regression: intercept = 1.117; slope= 0.009; p = 0.015). The relationship between digestion coefficient and mean OW offered was not significant (Figure 5, Adj R^2= 0.0154, inverse-variance weighted regression: intercept = 1.134; slope= 0.0152; p = 0.125).

<u>Grade specific digestion coefficients</u>

Of all otoliths recovered, 1.4% were classified as grade 1 (pristine), 5.0% as grade 2 (moderately digested), 27.8% as grade 3 (considerably digested) and 65.9% as grade 4 (severely digested). Recovery of grade 1 otoliths was very low. Because pristine otoliths have, by definition, not been affected by digestion the grade-specific digestion coefficient was fixed at 1.00. For Atlantic cod, haddock and all large gadoids, measurements from grade 2 and 3 were pooled (Table 6). The majority of the species-specific digestion coefficients are for grades 3 and 4.

As for the species-specific digestion coefficients, there were differences between the grade-specific digestion coefficients based on OL and OW. Standard errors were relatively small for almost all species. There was no overlap of 95% confidence intervals for grade 3 and 4 digestion coefficients for the same species; however, confidence intervals for grades 2 and 3 typically overlapped.

For a number of prey species, including squid, the grade- and species-specific digestion coefficient was <1 (Table 5) which would indicate that mean otolith or beak size increased post-digestion. This should be impossible and this point is discussed below.

<u>Application of digestion coefficients to otoliths recovered from scats collected in the wild</u>

For species-specific digestion coefficients, in almost all cases the coefficient of variation (CV, Table 5) is smaller for OW than for OL. This is also the case for grade-specific digestion coefficients; however, Atlantic cod has markedly smaller CV for OL than for OW (Table 6). Taking all the results into account, we plan to use otolith width as the measurement for correcting the size of otoliths recovered from scats collected in the wild as far as possible. Otolith length must be used for witch (*Glyptocephalus cynoglossus*) and Atlantic salmon (*Salmo salar*) because no suitable regression is available for otolith width. The appropriate measurement to use for Atlantic cod will be explored further.

Discussion

We quantified the passage, recovery and digestion of otoliths and beaks of typical prey of north eastern European harbour seal diet. The six seals used in this study were wild caught and kept in captivity for the duration of the experiments before being released at their capture location. The seals were generally willing to eat a varied diet; however, some individuals were more selective in their feeding choices than others. This suggests that some specialisation in prey selection occurs within what is usually considered to be a generalist predator species.

Several studies report that harbour seals target locally abundant prey species (Pierce *et al.*, 1991b; Thompson *et al.*, 1997; Brown *et al.*, 2001). However, variation in harbour seal foraging behaviour has been shown at a regional level around Britain (Sharples *et al.*, 2012) and there is some evidence for individual variation in foraging strategy. Thompson and Miller (1990) showed that two individuals returned regularly to bathymetrically distinct areas in the Moray Firth and individual harbour seals tagged in the Eden estuary, St Andrews Bay regularly returned to particular foraging sites (SMRU, unpublished telemetry data). Furthermore, Tollit et al. (1998) found that local

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geographical variations in the diet of harbour seals in the Moray Firth were related to local differences in foraging habitats. Specialisation in foraging behaviour has also been observed in grey seals (*Halichoerus grypus*) tracked using Argos satellite relay dataloggers, with individuals showing predictability in foraging trips to localised off-shore areas with characteristic sediment types (McConnell *et al.*, 1999). Individual preferences in the diet of seals have not been studied in wild populations around Britain and preferences exhibited by captive seals must be interpreted with caution.

The method by which seals consumed prey in the experiments varied depending on the size of prey offered to the seals. Small prey were typically ingested underwater while larger prey were brought to the surface and some very large prey were left untouched by the seals. We observed larger prey (Atlantic salmon, Atlantic cod and flatfish) being ripped into small pieces before ingestion and saw seals struggle without success to consume whole the heads of large prey (Atlantic salmon and cod). Some heads were torn into pieces during consumption and otoliths possibly crushed. The non-consumption of very large prey and the breaking up of large or wide prey during feeding is likely a morphological limitation linked to mouth-gape size or, as in odontocetes, the size of the pharynx limiting the largest size of prey that can be consumed (MacLeod *et al.*, 2007).

Whether harbour seals in the wild attempt to consume such large prey is unknown. When diet is estimated from the 2010-12 scat collections, the distribution of fish size estimated from prey remains will provide some information on this. However, if some large prey are eaten in the wild but the heads are not consumed or are broken up, some otoliths will be lost, resulting in some bias in estimates of diet composition and prey consumption. The magnitude of any potential bias will be explored further when the diet composition results are available.

Single-species meals of the major prey of British harbour seals were fed to estimate recovery rates, passage rates and digestion coefficients. Within-species differences in these parameters related to the size of prey consumed have been shown for both harbour and grey seals (Tollit *et al.*, 1997; Grellier and Hammond, 2006); however, prey size-specific digestion parameters have not been calculated in this study because it is not clear how these values might be applied to otoliths recovered from scats collected in the wild. We conducted experiments with a range of prey sizes representative of the diet of wild harbour seals and have minimised potential bias by combining values from trials by individual, then by prey species and finally by prey grouping.

Recovery rates

Complete digestion of fish otoliths and cephalopod beaks can bias diet reconstructions from faecal samples if recovery rate is not taken into account (Bowen, 2000). In this study, recovery rates ranged from 1.02 (Norway pout)

to 0.27 (sandeel). Recovery rates greater than 1 should be impossible. However, the majority of the prey fed to the seals was not gutted and it is likely that the otoliths of some small fish recovered in the scats are actually from the stomachs of the larger fish that were fed; so-called secondary prey/ingestion.

Norway pout, poor cod and haddock had recovery rates slightly greater than 1, reflecting the presence of otoliths in the diet through secondary ingestion. Simple calculations based on the otoliths found in grey seal scats and stomach contents of large gadoids (Atlantic cod, haddock, whiting and saithe *Pollachius virens*) showed that the contribution of secondary prey to the estimates of diet composition is much less than 1% (Hammond and Grellier, 2006). Crustacea are often found in wild scats but there is no evidence that harbour seals target them as prey and we assume that they are secondary prey. This is supported by the result that crustaceans were present in 50% of pool drains although were never specifically fed.

Previous studies have shown that large otoliths are less likely to be completely digested (Tollit *et al.*, 1997; Tollit *et al.*, 2003; Grellier and Hammond, 2005; Grellier and Hammond, 2006) and, as expected, recovery rates for harbour seals were greater for prey species with large, robust otoliths. Species-specific differences in recovery rates are important and if not incorporated into diet composition estimates the estimated contribution of prey species to the diet may be significantly biased and the numerical importance of small fish is likely to be underestimated (Bowen, 2000).

The recovery rate for squid beaks was higher in this study (0.816 SE=0.087) than the 0.437, SD=0.488 and 0.704 recovery rates reported for harbour seals by Harvey (1989) and Tollit et al. (1997), respectively. Recovery rate of beaks from squid (*Loligo opalescens*) fed to Pacific harbour seals *P. vitulina richardii* of 0.895 SD=0.155 (Phillips and Harvey, 2009) and *Loligo forbesii* fed to grey seals of 0.942 SE=0.021 (Grellier and Hammond, 2006) were higher than reported in this study.

Low recovery rate of prey remains was recorded in *Arctocephalus* spp. that were fed mixed species meals and where faecal matter 'at sea' in the enclosure pools was not collected (Casper *et al.*, 2006). Our study does not take into consideration possible differences in defecation rates on land and in the water - all faeces and prey remains were collected daily.

Recovery of otoliths from multiple prey species in harbour seal scats collected in the wild is common and the effect of meal composition warrants further investigation.

Passage rates

Using the results of passage rate studies on captive animals, together with telemetry data and spatial models of prey distribution, simulation studies

suggest that for grey seals the results of scat analysis are not biased by differences in the distribution of prey e.g. offshore vs inshore distributions (Smout 2006). For harbour seals, the majority of otoliths and beaks were passed within 2-3 days and, despite some species-specific differences, these results are comparable with those from studies of grey seals (Grellier and Hammond, 2006) and Pacific harbour seals (Phillips and Harvey, 2009). Harbour seal diet composition estimated using scat analysis is thus likely to be representative of the true diet of this species which has average foraging trip distances between 11 km (Orkney and Shetland) and 100 km (Moray Firth) in Scotland (Sharples et al., 2012).

It is likely that passage rate is affected by food intake rate, meal composition and the activity state of a seal and these are unlikely to be similar in wild and captive seals (Pierce et al., 1991a). Furthermore, grey seals can delay the onset of food processing (digestion) by up to 11 hours, as observed by a delayed increase in metabolic rate (Sparling et al., 2007). Harbour seals face similar competing physiological processes for maximising diving/foraging efficiency and for food processing, so further work for harbour seals that takes into account some of these complexities would be of benefit in checking for any potential bias in the estimation of diet from scat samples.

Species-specific digestion coefficients

In agreement with other studies, we have shown that the amount by which an otolith is digested is related to the species and sometimes the size of the fish fed (Murie and Lavigne, 1986; Tollit *et al.,* 1997; Grellier and Hammond, 2006). Digestion coefficients were calculated based on otolith length and width for all fish species except for witch (*Glyptocephalus cynoglossus*) and Atlantic salmon (*Salmo salar*), for which no suitable OW regression is available. Digestion coefficients for particular size ranges of prey have not been calculated. However, by feeding prey of a size range representative of what seals eat in the wild, we have incorporated prey size variability into the final species-specific digestion coefficients. Although we found a significant positive relationship between digestion coefficient and otolith length, this relationship was not significant exist for otolith width and supports the use of digestion coefficients based on otolith width to correct the size otoliths recovered from scats collected in the wild.

Grade-specific digestion coefficients

The use of grade specific digestion coefficients can help to reduce intra-specific variation and potential bias in correction for partial digestion. Sources of variation include the size, frequency, and species composition of meals and activity level of the seals (Tollit *et al.*, 1997; Marcus *et al.*, 1998). We used standard methods to produce these grade-specific digestion coefficients by

using external morphological features to classify the degree of digestion (Tollit *et al.*, 1997; Grellier and Hammond, 2006). However, we extended the standard range of three grade/wear classes to four in an attempt to reduce variability and bias because average digestion rates may be artificially high in captive seals (Thompson *et al.*, 1991; Tollit *et al.*, 1997; Grellier and Hammond, 2006).

Although the application of grade-specific digestion coefficients should generally reduce bias in estimates of prey size, in an exploration of possible bias in grey seal diet, using overall species-specific rather than grade-specific digestion coefficients resulted in only a small bias in diet in the first quarter of 2002 in Orkney. The amount of sandeels in the diet increased by around 4% and the amount of cod decreased by around 5% (Grellier and Hammond, 2006). Notwithstanding this, use of grade-specific digestion coefficients does improve estimates of diet composition of seals and will be used in analyses of harbour seal diet composition.

Grade-specific digestion coefficients less than 1 were calculated for grade 2 sandeel, Norway pout, poor cod, and Atlantic salmon smolt OL and OW and for grade 3 Norway pout OW. These species are likely to be major components of the diet of wild harbour seals, or of particular interest in the case of Atlantic salmon. The species-specific digestion coefficient for squid LRL was also less than 1; these data will be reanalysed based on regressions developed for mantle length. Because it is not possible for otoliths/beaks to increase in size post digestion, this raises a number of questions in relation to the experiments and analysis.

First, were all otoliths and beaks correctly measured? Some measurement error could have occurred but there is no evidence that this could have led to a tendency for digestion coefficients to be biased in this way.

Second, were the regression equations used to estimate uneaten otolith and/or beak size appropriate for the prey size-range fed? The data used to calculate regressions for fish prey were from fish of a size range similar to those fed in the trials except for Atlantic salmon. Nevertheless, these regressions are from the published literature and not from our studies, and so could potentially have led to bias in some cases.

Third, are certain size ranges of otoliths/beaks eroded and completely digested at different rates? Intuitively, smaller otoliths would be more likely to digest completely more than larger otoliths. Harvey (1989) suggested that otoliths which are small, thin or encased in a thinner cranium or otic capsule may be more susceptible to complete digestion. If smaller otoliths/beaks do have a higher probability of being completely digested, the mean undigested size of those remaining will be larger than the mean size fed and could lead to a bias in digestion coefficient estimation. However, preliminary exploratory analysis has not revealed any evidence that this has led to bias.

Explanations for bias in digestion coefficients and any implications for analysis of diet composition will be explored further.

Comparison with other studies

This study followed the methods of Grellier and Hammond (2006) and therefore direct comparison with grey seal recovery rate, digestion coefficient and passage rate estimates are possible. We also compared our results to those for harbour seals from Tollit et al. (1997) although the experimental feeding method was different and the method of otolith delivery has been shown to affect digestion (Grellier and Hammond, 2005) and, where appropriate, to results for Pacific harbour seals (Phillips and Harvey, 2009).

Species composition of meals is thought to influence passage rates of prey remains through a seal's gut (Prime and Hammond, 1987; Bowen, 2000; Tollit et al., 2004; Casper et al., 2006; Phillips and Harvey, 2009). However, the majority of otoliths and beaks were passed within 2-3 days regardless of prey species composition, which is similar to findings for grey seals (Grellier and Hammond, 2006) and Pacific harbour seals (Phillips and Harvey, 2009).

Recovery rates are comparable with grey seal estimates (Grellier and Hammond, 2006) although a lower proportion of lemon sole otoliths were recovered in this study. Our recovery rates are similar to those for harbour seals for cod but were higher than those previously reported for herring, whiting, lemon sole, plaice, sandeel and squid (Tollit et al., 1997). Although the feeding methods differed between the two harbour seal studies, this is not thought to affect recovery rate in pinnipeds (Grellier and Hammond, 2005).

Digestion coefficients have previously been reported for seven harbour seal prey species (Tollit et al., 1997). Our mean species-specific digestion coefficients were similar to these results for plaice and lemon sole but smaller for cod and whiting (OW) and larger for herring and sandeel (A. marinus, Tollit et al., 1997).

The harbour seal digestion coefficients estimated in our study are generally smaller than those published for grey seals (Grellier and Hammond, 2006). However, those for poor cod, whiting (OW), herring, dab and lemon sole are similar for both species. Digestion coefficient estimates for hake are larger for harbour seals but the sample size is very small compared to the grey seal study.

The grading systems used to classify grade-specific digestion coefficients across harbour and grey seal studies were not identical but they are similar enough to warrant comparison of results. Grade-specific digestion coefficients in this study are smaller than those previously reported for both harbour and grey seals. Differences in feeding method may explain the higher levels of otolith digestion reported by Tollit et al. (1997).

Smaller digestion coefficients than those estimated for grey seals might be expected if the otoliths pass more quickly through the gut of harbour seals; however, we have shown the passage rates of both species to be similar. Grey seals are larger than harbour seals and have been shown to be able to delay food processing in situations where it is physiologically advantageous, such as during active foraging (Sparling *et al.*, 2007). Differences in physiology and food processing strategies between these species may account for differences in rates of otolith erosion.

The potential competition for prey between harbour and grey seals is being investigated as a possible contributing factor to the decline of harbour seals in Scottish waters over the last decade (Lonergan *et al.*, 2007). These digestion correction factors will allow robust estimation of the number and size of prey consumed by harbour seals based on the recovery of otoliths and beaks from scats collected in the wild. They will be used to describe regional and temporal variation in the diet of Scottish harbour seals and investigate evidence for competition for prey between harbour and grey seals.

Table 1: Details of the experimental prey consumed and recovered. Fish length (cm) and squid weight (g) were measured.

Common name	Scientific name	Min	Max	No. eaten	No. recovered	Mean RR	SE	NCF	No. of seals	No. of trials
Dab	*Limanda limanda*	10.2	33	585	415	0.755	0.036	1.379	3	5
Lemon sole	*Microstomus kitt*	15.6	32.1	210	83	0.474	0.060	2.440	2	3
Long rough dab	*Hippoglossoides platessoides*	8.6	23.7	438	386	0.887	0.020	1.133	2	2
Plaice	*Pleuronectes platessa*	13.9	36.4	492	403	0.854	0.035	1.219	6	9
Witch	*Glyptocephalus cynoglossus*	24.6	43.8	68	66	0.976	0.016	1.025	2	2
All flatfish		8.6	43.8	1793	1353	0.789	0.033	1.439	6	21
Atlantic cod	*Gadus morhua*	13	60.9	232	211	0.881	0.085	1.204	3	11
Haddock	*Melanogrammus aeglefinus*	11.5	40.6	486	485	1.005	0.005	0.995	3	9
Hake	*Merluccius merluccius*	45.1	54.1	26	23	0.893	0.055	1.136	1	2
Pollock	*Pollachius pollachius*	43.6	55.2	8	8	1.000	0.000	1.000	1	1
Whiting	*Merlangius merlangus*	11.5	36.7	1229	1180	0.940	0.028	1.071	6	14
All large gadoids		11.5	60.9	1981	1907	0.944	0.034	1.081	6	37
Greater sandeel	*Hyperolpus lanceolatus*	18.3	33.4	544	266	0.600	0.021	2.421	2	2
Sandeel	*Ammodytes tobianus*	7.5	22.1	13235	5692	0.389	0.013	3.704	5	10
All sandeels		7.5	33.4	13779	5958	0.494	0.017	3.062	5	12
Norway pout	*Trysopterus esmarkii*	9.3	19.9	3440	3477	1.026	0.003	0.980	6	8
Poor cod	*Trysopterus minutus*	7.8	23.7	1171	1186	1.008	0.002	0.993	5	7
Trisopterus spp		7.8	23.7	4611	4663	1.017	0.002	0.986	6	15
Herring	*Clupea harengus*	18.8	29.8	377	140	0.428	0.071	2.697	4	8
Red gurnard	*Chelidonichthys cuculus*	21.6	35.2	82	47	0.580	0.077	1.741	1	2
Salmon smolt	*Salmo salar*	13.8	18.9	448	137	0.306	0.031	3.310	2	2
Squid	*Loligo forbesii*	11.5	524.5	121	101	0.816	0.087	1.258	4	4

Table 2: Regressions used to infer the size of otoliths and beaks of the prey items offered

Species	OL or LRL regression	r^2	n	OW regression	r^2	n	Reference
Atlantic cod	OL = 0.266 FL + 2.306	0.93	518	OW = 0.122 FL + 0.811	0.96	547	M. Leopold, pers comm
Haddock	OL = 0.383 FL + 1.560	0.97	450	OW = 0.137 FL + 0.703	0.96	469	M. Leopold, pers comm
Whiting	OL = 0.564 FL - 0.198	0.98	559	OW = 0.142 FL + 0.55	0.96	637	M. Leopold, pers comm
Hake	OL = 0.365 FL + 1.991	0.98	60	OW = 0.131 FL + 1.046	0.96	62	M. Leopold, pers comm
Pollack	OL = 0.243 FL + 2.551	0.97	294	OW = 0.097 FL + 1.066	0.96	304	M. Leopold, pers comm
Norway pout	OL = 0.436 FL + 0.028	0.98	257	OW = 0.186 FL + 0.002	0.98	257	M. Leopold, pers comm
Poor cod	OL = 0.362 FL + 1.718	0.95	267	OW = 0.178 FL + 0.731	0.93	275	M. Leopold, pers comm
Sandeel	OL = 0.185 FL - 0.056	0.93	332	OW = 0.085 FL + 0.079	0.91	337	M. Leopold, pers comm
Greater sandeel	OL = 0.141 FL + 0.510	0.96	399	OW = 0.057 FL + 0.409	0.95	410	M. Leopold, pers comm
Atlantic herring	OL = 0.154 FL + 0.386	0.96	514	OW = 0.061 FL + 0.472	0.93	541	M. Leopold, pers comm
European plaice	OL = 0.203 FL + 0.486	0.99	752	OW = 0.119 FL + 0.641	0.97	787	M. Leopold, pers comm
Common dab	OL = 0.179 FL + 0.734	0.97	508	OW = 0.107 FL + 0.699	0.95	513	M. Leopold, pers comm
Lemon sole	OL = 0.091 FL + 0.624	0.87	240	OW = 0.059 FL + 0.356	0.89	240	M. Leopold, pers comm
Long rough dab	OL = 0.213 FL + 0.477	0.95	322	OW = 0.137 FL + 0.730	0.91	338	M. Leopold, pers comm
Witch	OL = 0.114 FL + 1.602	0.89	81	----	----	----	T. Härkönen, pers comm
Atlantic salmon	OL = 0.008 FL + 1.466	0.66	59	----	----	----	SCOS briefing paper 04/13 (2004)
Gurnard*	OL = 0.111 FL + 0.726	0.94	735	OW = 0.079 FL + 0.697	0.90	741	M. Leopold, pers commu
Squid	LRL = 0.435 $W^{0.347}$	0.77	193	----	----	----	http://www.cephbase.utmb.edu

Note: Otolith length (OL), otolith width (OW) and lower rostral length (LRL) were measured in mm; fish length (FL) was measured in cm; squid weight (W) was measured in g. * The gurnard regression was developed across measurements from both red and grey gurnard species. Original data provided by M. Leopold (Wageningen-IMARES, P.O. Box 167, Landsdiep 4, NRL-1797 SZ Den Hoorn (Texel), The Netherlands) and T. Härkönen (Swedish Museum of Natural History, Box 50007, 104 05 Stockholm, Sweden) are summarised in Leopold et al (2001) and Härkönen (1986), respectively.

Table 3: Regressions used to infer prey size from otoliths and beaks that were not eaten

Species	OL or LRL regression	r^2	n	OW regression	r^2	n
Atlantic cod	FL = 3.49 OL - 6.64	0.88	268	FL = 7.84 OW - 5.51	0.86	275
Haddock	FL = 2.53 OL -3.27	0.90	236	FL = 6.99 OW - 4.00	0.90	240
Whiting	FL = 1.73 OL + 0.81	0.79	303	FL = 6.74 OW - 2.97	0.86	315
Poor cod	FL = 2.61 OL -3.84	0.96	144	FL = 5.22 OW - 2.98	0.94	144
Sandeel	FL = 5.00 OL + 1.16	0.86	170	FL = 10.92 OW	-	172
Dab	FL = 5.43 OL - 3.49	0.88	261	FL = 8.88 OW - 5.40	0.9	261
Plaice	FL = 4.85 OL - 2.07	0.76	405	FL = 8.15 OW - 4.70	0.79	405

Note: Otolith length (OL), otolith width (OW) and lower rostral length (LRL) were measured in mm; fish length (FL) was measured in cm; squid weight (W) was measured in g.

Table 4: Percentage of the total number of otoliths and beaks recovered, calculated per day. The approximate number of hours after feeding is 16 h for day one then + 24 h for each subsequent day.

Prey	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10	Day 11	Day 12	Day 13	Day 14
Flatfish	67.56	87.00	98.56	99.18	99.51	99.51	99.81	99.81	99.87	100	100	100	100	100
Large gadoids	73.19	96.21	99.68	99.98	100	100	100	100	100	100	100	100	100	100
Sandeels	46.16	91.65	99.55	99.70	99.80	99.85	99.94	99.96	99.99	100	100	100	100	100
Trisopterus spp	47.45	92.16	99.51	99.96	99.99	100	100	100	100	100	100	100	100	100
All fish	56.12	92.14	98.81	99.73	99.86	99.87	99.95	99.95	99.97	100	100	100	100	100
Squid	56.71	79.51	81.60	81.60	81.60	82.29	82.29	82.29	98.96	98.96	98.96	98.96	98.96	100

Table 5: Species-specific digestion coefficients (dc) calculated for harbour seals (*Phoca vitulina*)

Prey species	dc	SE	CV	No. of seals	No. of trials	No. of otoliths recovered
Otolith length or lower rostral length						
Dab	1.28	0.035	0.028	3	5	383
Lemon sole	1.22	0.112	0.092	2	3	57
Long rough dab	1.18	0.023	0.020	2	2	367
Plaice	1.17	0.048	0.041	6	9	358
Witch	1.09	0.033	0.030	2	2	61
All flatfish	1.19	0.050	0.042	6	21	1226
Atlantic cod	1.24	0.066	0.053	3	11	150
Haddock	1.17	0.038	0.032	3	9	376
Hake	1.93	0.172	0.089	1	2	14
Pollock	0.98	0.028	0.028	1	1	5
Whiting	1.69	0.090	0.053	5	12	537
All large gadoids	1.40	0.079	0.056	6	35	1082
Greater sandeel	1.61	0.048	0.030	2	2	213
Sandeel	1.28	0.020	0.016	5	10	5097
All sandeels	1.45	0.034	0.024	5	12	5310
Norway pout	1.18	0.013	0.011	6	8	3364
Poor cod	1.17	0.018	0.016	5	7	1138
Trisopterus spp	1.17	0.016	0.013	6	15	4502
Herring	1.16	0.051	0.044	4	8	87
Red gurnard	0.99	0.034	0.034	1	2	30
Salmon smolt	0.96	0.028	0.029	2	2	112
Squid	0.88	0.047	0.053	4	4	101
Otolith width						
Dab	1.35	0.035	0.026	3	5	414
Lemon sole	1.32	0.081	0.062	2	3	80
Long rough dab	1.22	0.024	0.019	2	2	385
Plaice	1.18	0.041	0.035	6	9	395
All flatfish	1.27	0.045	0.036	6	21	1340
Atlantic cod	1.23	0.063	0.051	3	11	210
Haddock	1.23	0.024	0.020	3	9	485
Hake	1.80	0.144	0.080	1	2	23
Pollock	1.10	0.071	0.065	1	1	8
Whiting	1.25	0.033	0.027	6	14	1180
All large gadoids	1.32	0.067	0.051	6	37	1906
Greater sandeel	1.75	0.049	0.028	2	2	266
Sandeel	1.40	0.022	0.015	5	10	5687
All sandeels	1.57	0.035	0.023	5	12	5953
Norway pout	1.13	0.012	0.011	6	8	3476

Prey species	dc	SE	CV	No. of seals	No. of trials	No. of otoliths recovered
Poor cod	1.14	0.018	0.016	5	7	1186
Trisopterus spp	1.14	0.015	0.013	6	15	4662
Herring	1.30	0.058	0.044	4	8	139
Red gurnard	1.04	0.037	0.036	1	2	42

Table 6: Grade-specific digestion coefficients (dc) calculated for harbour seals (*Phoca vitulina*)

Prey species	Grade	dc	SE	CV	No. of seals	No. of trials	No. of otoliths recovered
Otolith length							
Dab	2	1.09	0.052	0.048	1	2	28
	3	1.18	0.033	0.028	3	5	143
	4	1.45	0.075	0.052	3	4	205
Lemon sole	3	1.12	0.076	0.068	1	1	16
	4	1.45	0.137	0.095	2	3	37
Long rough dab	3	1.07	0.019	0.018	2	2	246
	4	1.48	0.047	0.032	2	2	119
Plaice	2	1.03	0.019	0.019	1	1	27
	3	1.02	0.052	0.051	2	3	85
	4	1.32	0.070	0.053	3	3	94
Witch	3	1.00	0.032	0.032	1	1	13
	4	1.10	0.036	0.032	2	2	46
All flatfish	2	1.06	0.036	0.034	2	3	55
	3	1.08	0.042	0.039	3	12	503
	4	1.36	0.073	0.054	3	14	501
Atlantic cod	2+3	1.15	0.053	0.046	3	7	30
	4	1.31	0.046	0.035	3	9	115
Haddock	2+3	1.05	0.033	0.031	3	6	25
	4	1.21	0.023	0.019	3	8	351
Hake	4	1.93	0.134	0.070	1	2	14
Whiting	2	1.07	0.034	0.031	2	2	15
	3	1.12	0.018	0.016	2	3	39
	4	1.39	0.033	0.023	2	6	403
All large gadoids	2+3	1.10	0.043	0.039	3	13	55
	4	1.46	0.059	0.040	3	25	883
Greater sandeel	4	1.68	0.043	0.026	2	2	199
Sandeel	2	0.93	0.020	0.022	2	4	344
	3	1.02	0.032	0.031	4	7	1275
	4	1.40	0.026	0.018	4	8	2526
All sandeels	2	0.93	0.020	0.022	2	4	344
	3	1.02	0.032	0.031	4	7	1275
	4	1.54	0.034	0.022	4	10	2725
Norway pout	2	0.91	0.018	0.020	2	3	60
	3	1.01	0.018	0.018	3	4	915

	4	1.22	0.011	0.009	3	4	1609
Poor cod	2	0.99	0.045	0.045	1	1	11
	3	1.11	0.024	0.022	2	3	135
	4	1.23	0.021	0.018	3	4	748
Trisopterus spp	2	0.95	0.031	0.033	2	4	71
	3	1.06	0.021	0.020	3	7	1050
	4	1.22	0.016	0.013	3	8	2357
Red gurnard	3	1.01	0.034	0.034	1	2	23
Salmon smolt	3	0.85	0.017	0.020	2	2	35
	4	1.04	0.038	0.037	2	2	73

Otolith width

Dab	2	1.14	0.045	0.040	1	2	30
	3	1.23	0.031	0.026	3	5	148
	4	1.53	0.060	0.039	3	4	229
Lemon sole	3	1.13	0.070	0.062	1	1	16
	4	1.49	0.116	0.077	2	3	55
Long rough dab	3	1.10	0.020	0.018	2	2	251
	4	1.54	0.047	0.031	2	2	132
Plaice	2	1.03	0.014	0.014	1	1	27
	3	1.08	0.046	0.043	2	3	94
	4	1.29	0.074	0.057	3	3	100
All flatfish	2	1.09	0.030	0.027	2	3	57
	3	1.14	0.042	0.037	3	12	523
	4	1.46	0.074	0.051	3	14	566
Atlantic cod	2+3	1.16	0.059	0.051	3	7	34
	4	1.32	0.068	0.052	3	10	169
Haddock	2+3	1.07	0.035	0.033	3	6	40
	4	1.25	0.023	0.018	3	9	445
Hake	4	1.80	0.144	0.080	1	2	23
Whiting	2	1.02	0.017	0.016	3	4	29
	3	1.03	0.011	0.011	3	4	89
	4	1.22	0.021	0.017	3	8	791
All large gadoids	2+3	1.12	0.047	0.042	3	13	74
	4	1.39	0.061	0.044	3	30	1431
Greater sandeel	4	1.82	0.047	0.026	2	2	252
Sandeel	2	0.95	0.021	0.022	2	4	359
	3	1.07	0.035	0.033	4	7	1375
	4	1.54	0.028	0.018	4	8	2914
All sandeels	2	0.95	0.021	0.022	2	4	359
	3	1.11	0.060	0.054	4	9	1387
	4	1.68	0.038	0.022	4	10	3166
Norway pout	2	0.90	0.019	0.022	2	3	61
	3	0.98	0.014	0.014	3	4	944
	4	1.16	0.010	0.009	3	4	1636
Poor cod	2	0.97	0.043	0.045	1	1	11

	3	1.09	0.023	0.021	2	3	141
	4	1.19	0.021	0.018	3	4	773
Trisopterus spp	2	0.93	0.031	0.034	2	4	72
	3	1.03	0.018	0.018	3	7	1085
	4	1.18	0.016	0.013	3	8	2409
Herring	3	1.28	0.038	0.030	1	1	18
Red gurnard	3	1.02	0.029	0.028	1	2	25
	4	1.22	0.064	0.052	1	1	10

a)

b)

c)
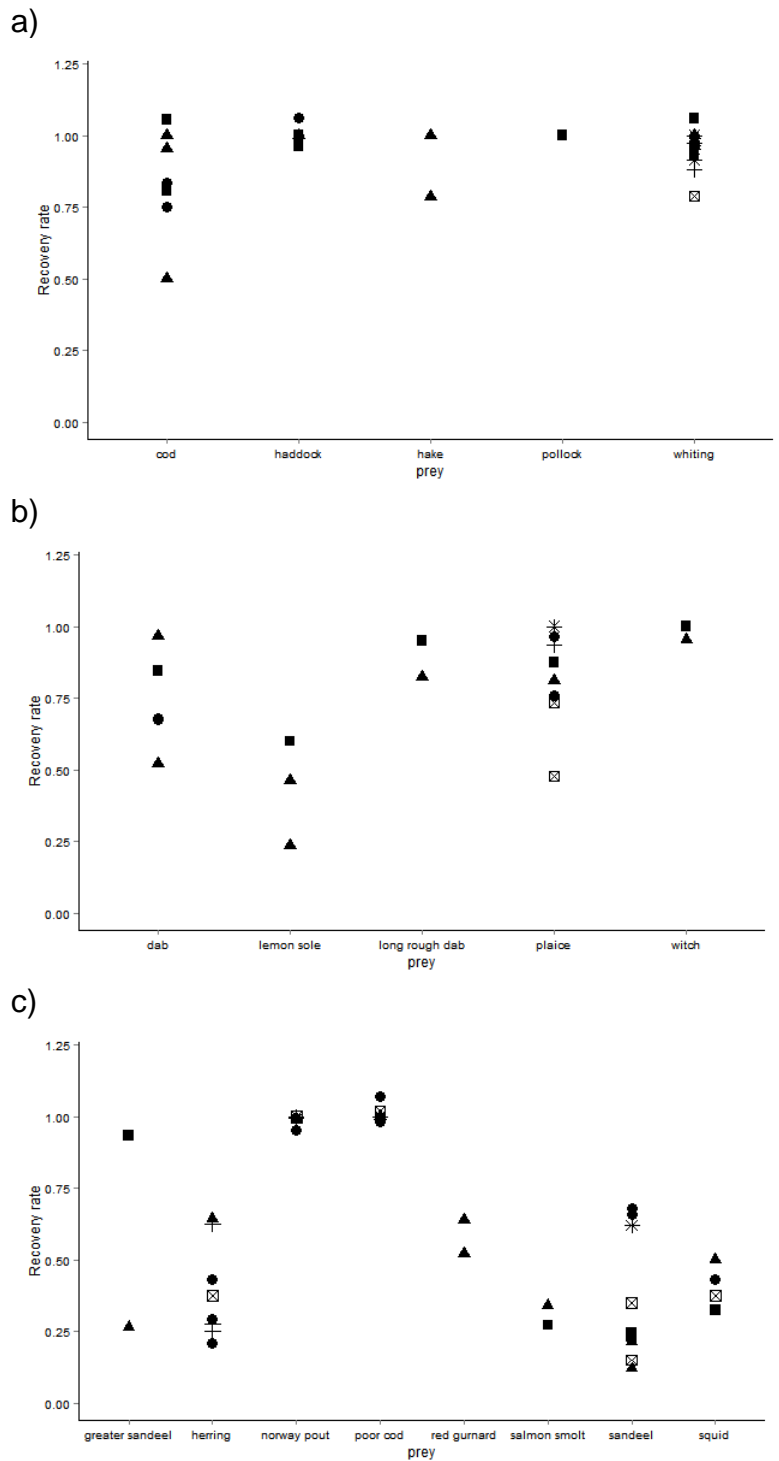
Figure 1: Feeding trial recovery rates showing intra- and inter-individual variability. Each symbol represents a different seal. a) Large gadoids, b) flatfish, c) other species
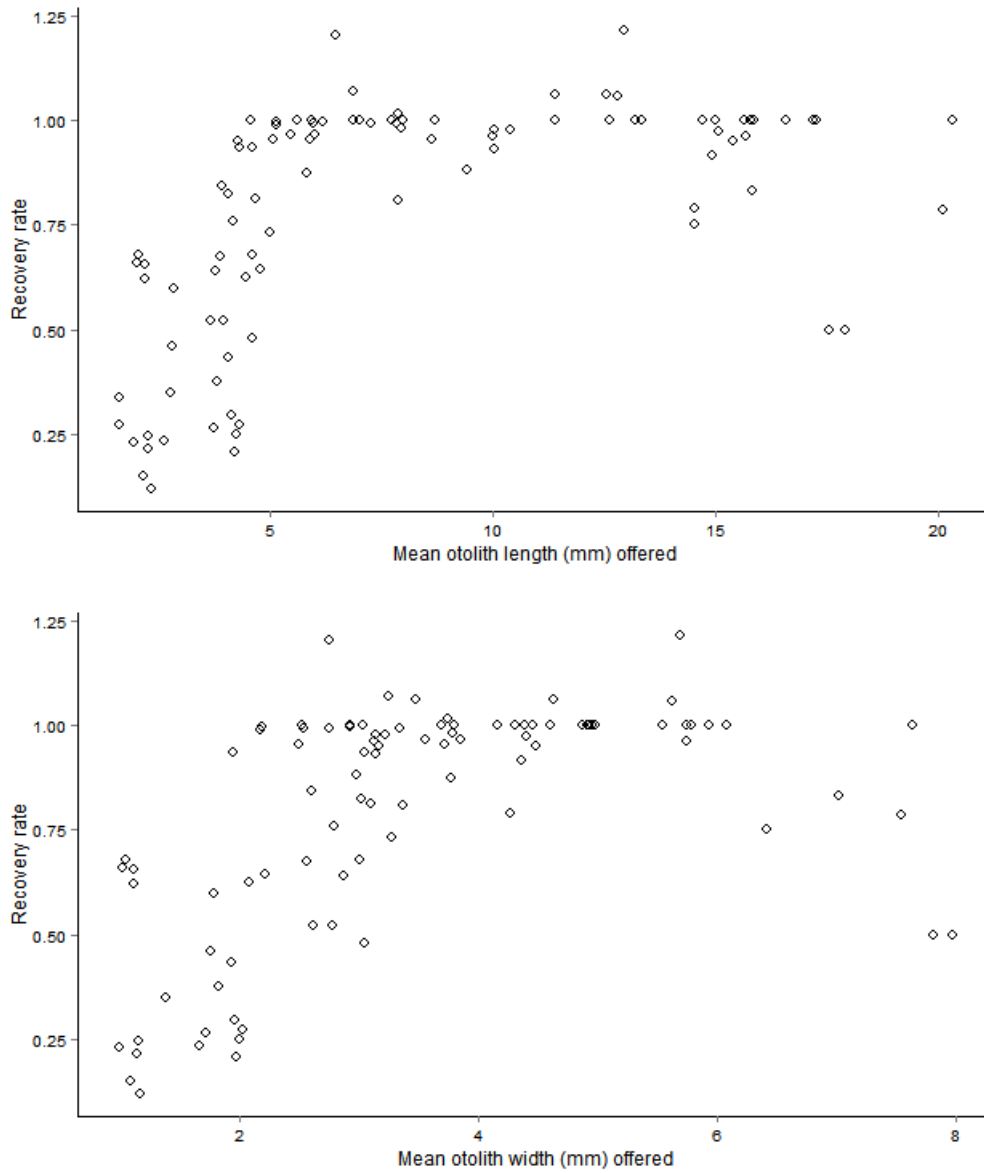
Figure 2: Recovery rate plotted against mean undigested otolith length (top) and width (bottom) for all trials.
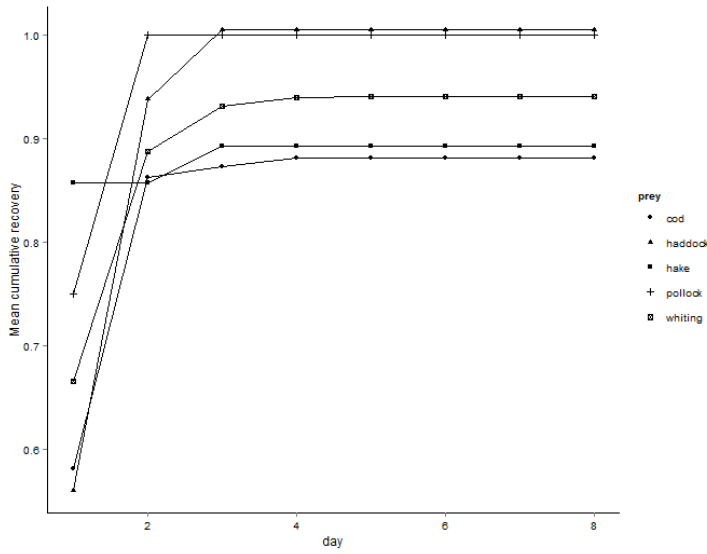
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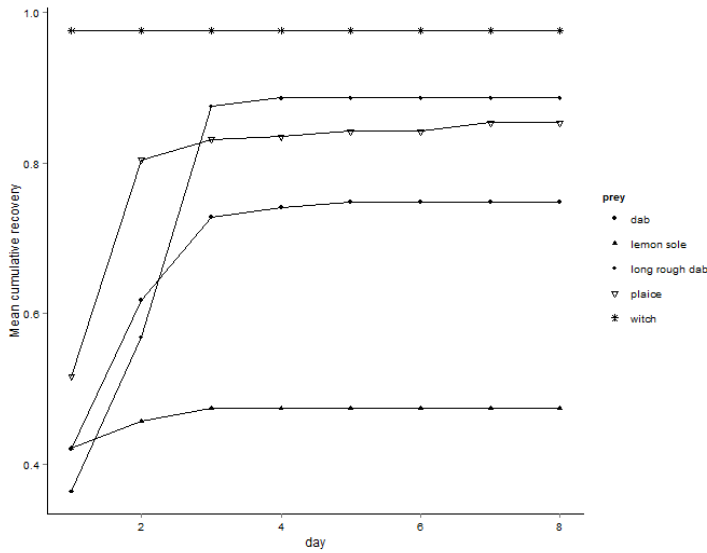
b)
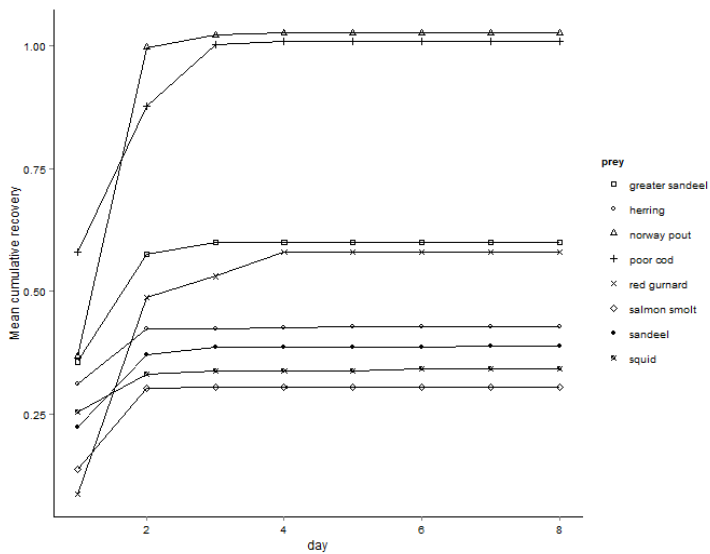
c)
Figure 3: Species-specific passage rates for a) large gadoids, b) flatfish, c) all other prey species.
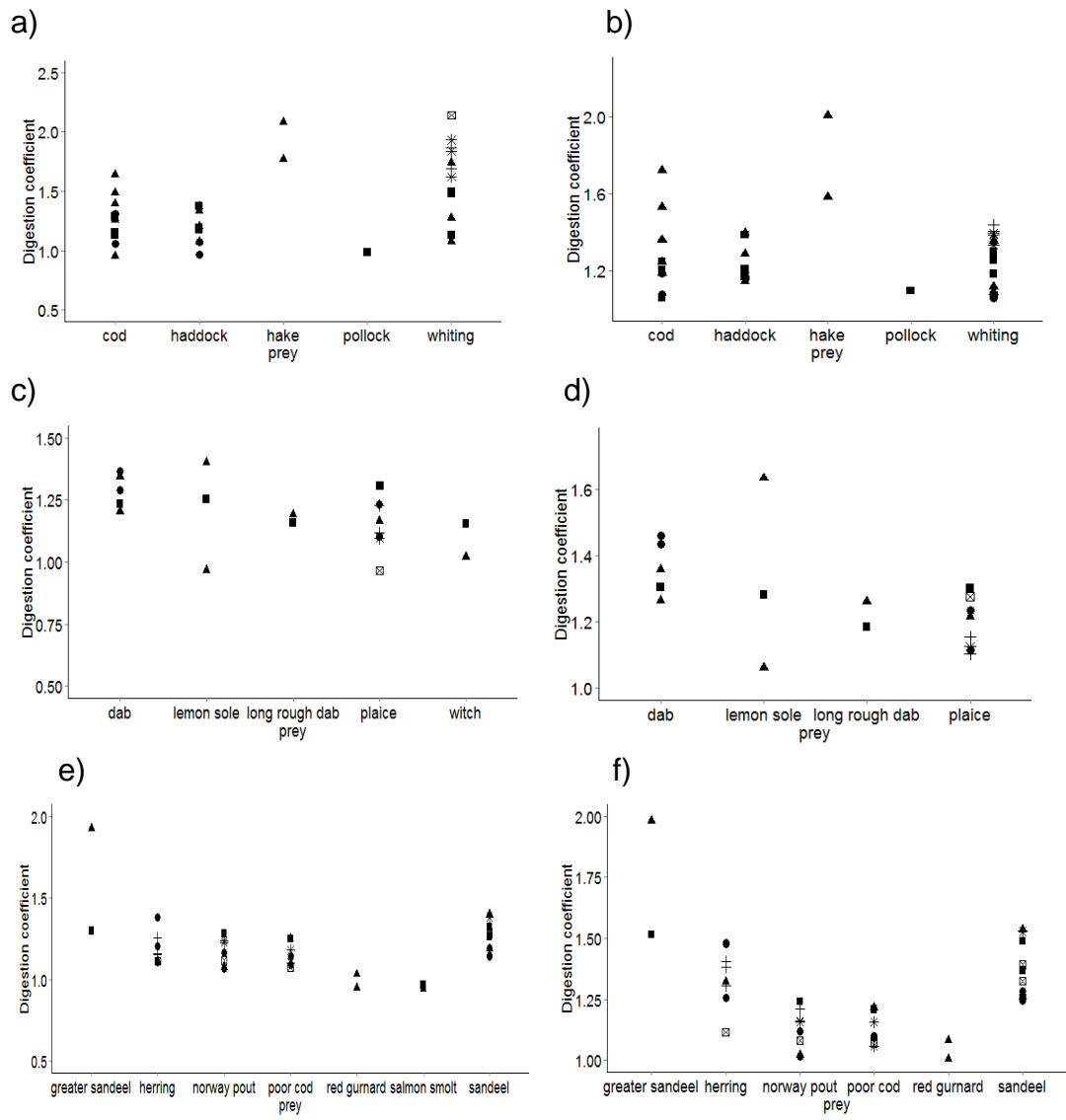
Figure 4: Inter and intra-individual variation in digestion coefficients for each trial. Each symbol represents a different seal. Species-specific digestion coefficients by individual feeding trial are displayed for a) large gadoid otolith length b) large gadoid otolith width, c) flatfish otolith length, d) flatfish otolith width, e) other species otolith length f) other species otolith width

a)
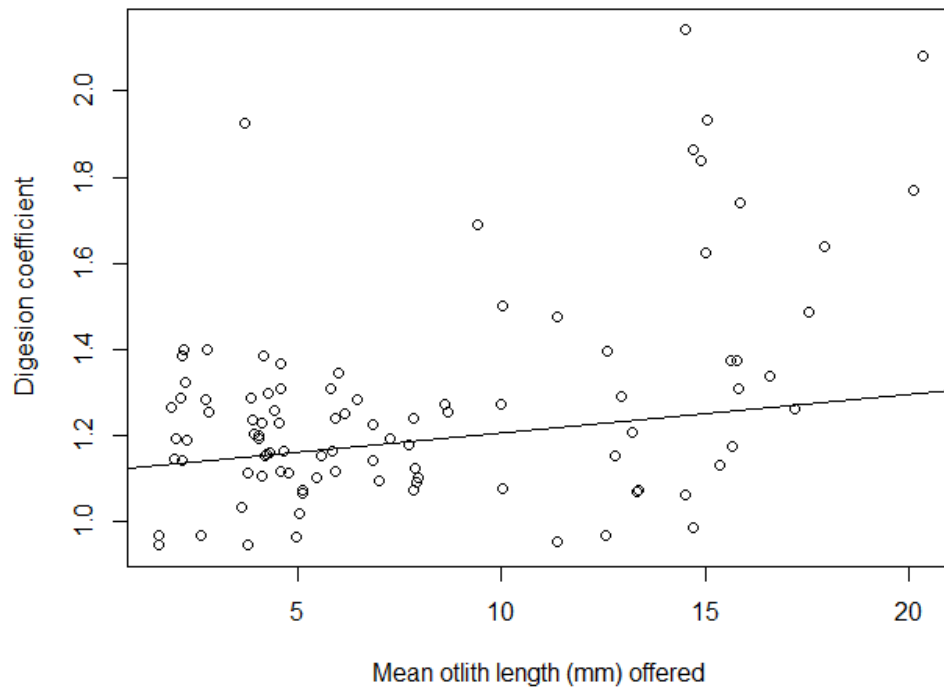
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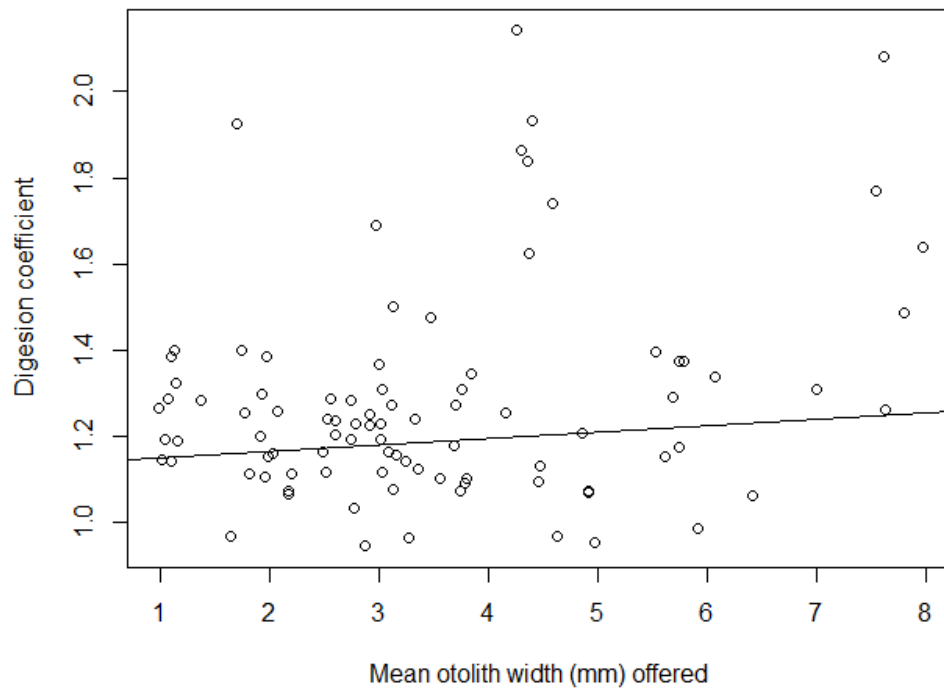
Figure 5: Inverse-variance weighted linear regression of digestion coefficient on mean estimated length (a) and width (b) of otoliths fed for all trials of all size ranges of prey.

Acknowledgements

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Appendix A

Figure A1: Images in the left column of pristine (grade 1, upper image), moderately digested (grade 2, lower left image) and considerably digested (grade 3, lower right image) otoliths and in the right column severely digested (grade 4) otoliths. These images were used as a guide to classify otoliths by the level of digestion. No wear classes were listed for witch, hake, greater sandeel or Atlantic salmon and for these species we used wear classes for species with similar otoliths (long rough dab, whiting, sandeel and brown trout, respectively). Images of grade 1, 2 and 3 otoliths taken from Leopold et al. (2001).

Hake

Pollack

Whiting

Greater sandeel
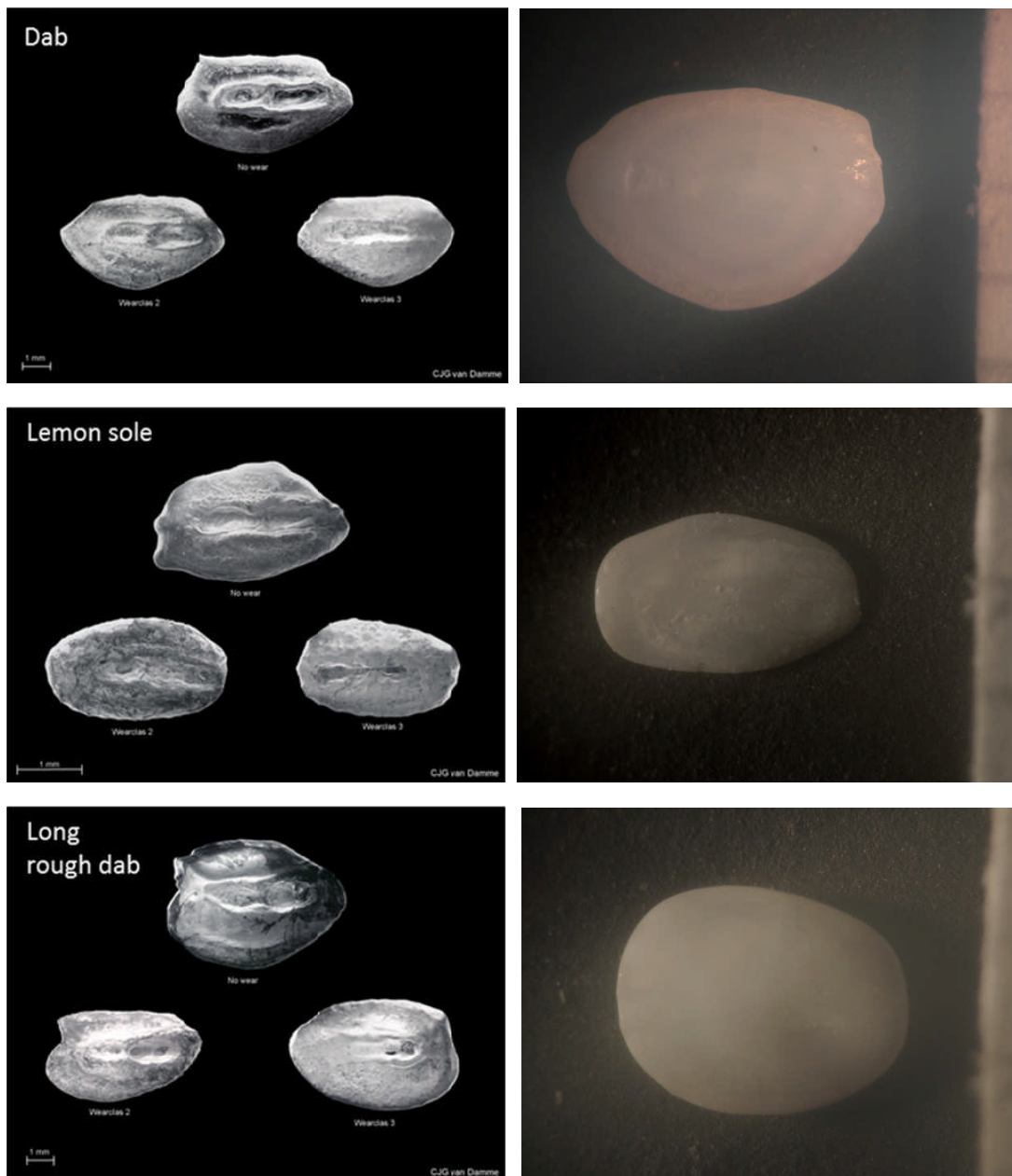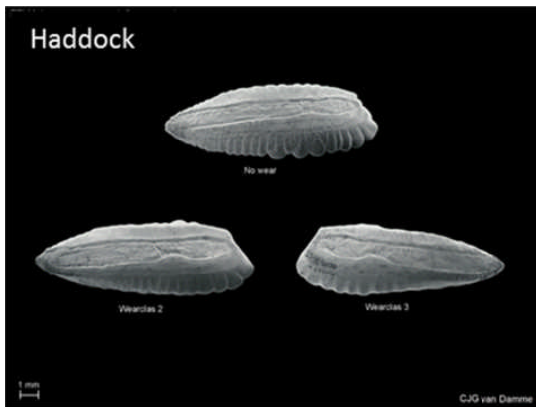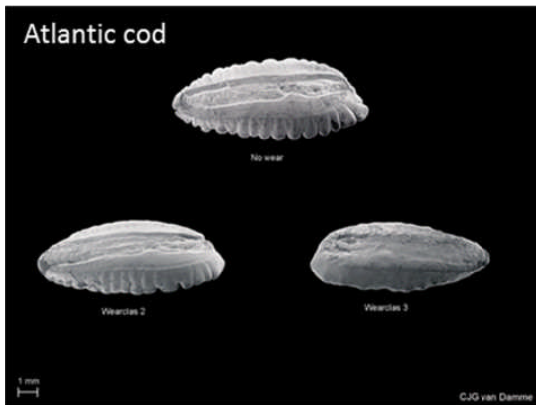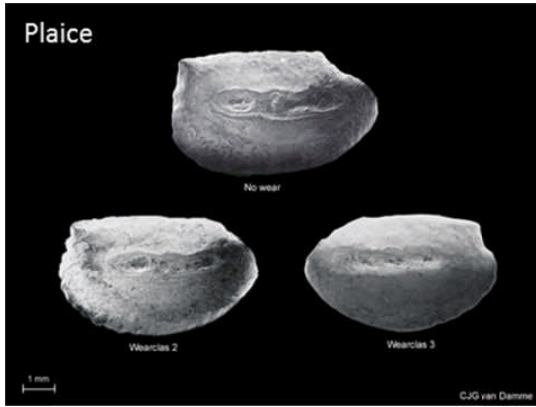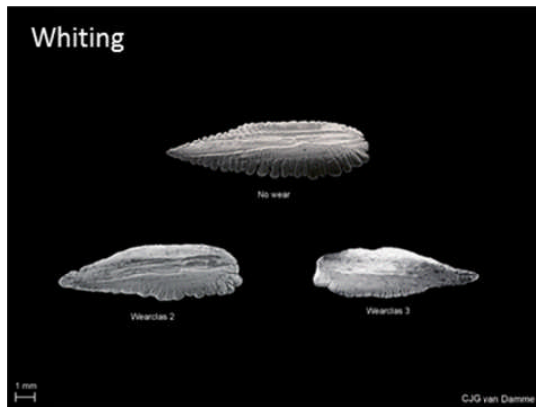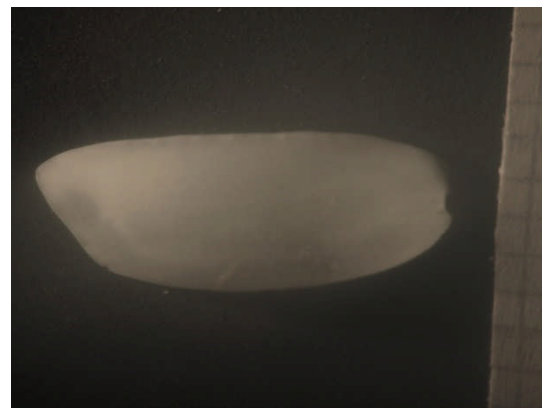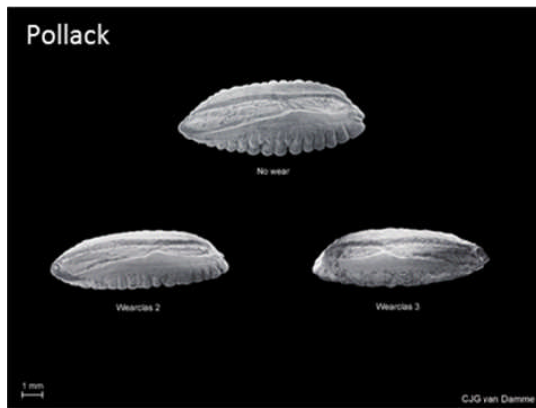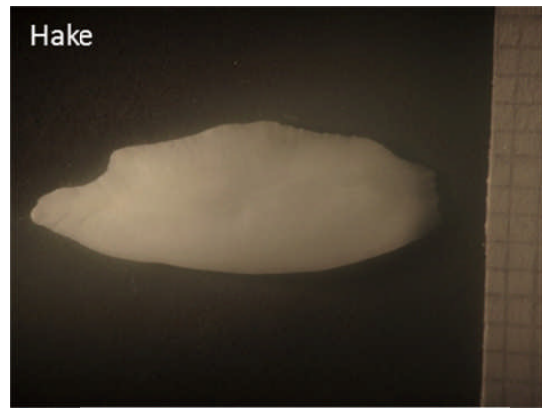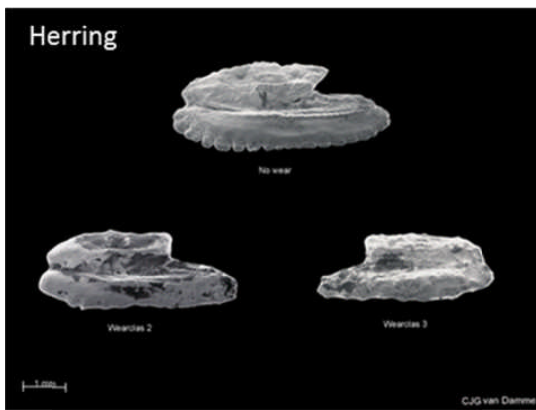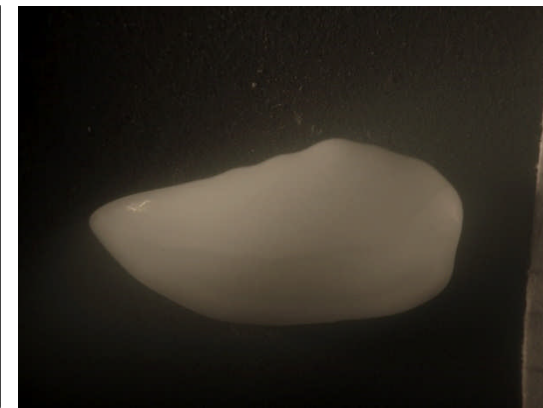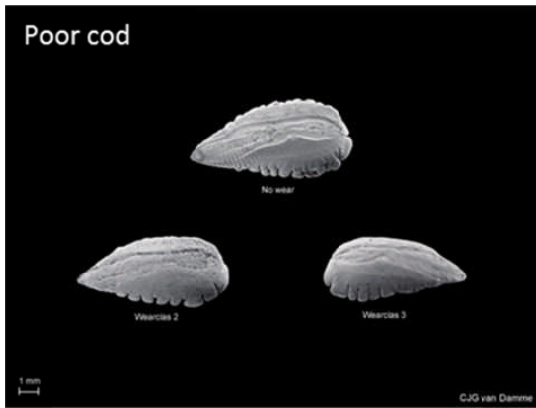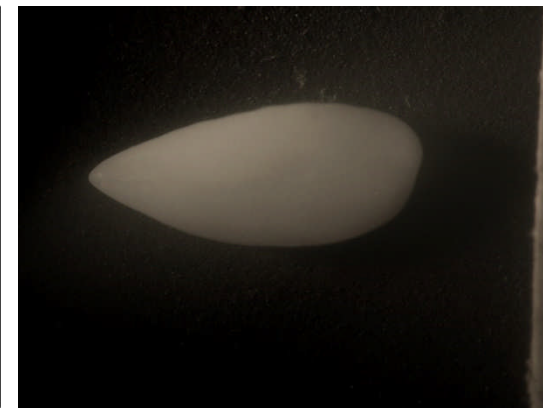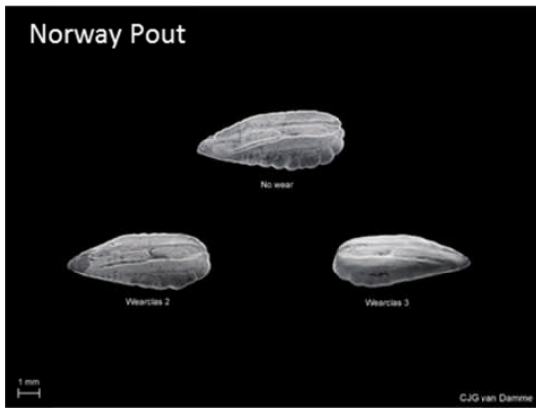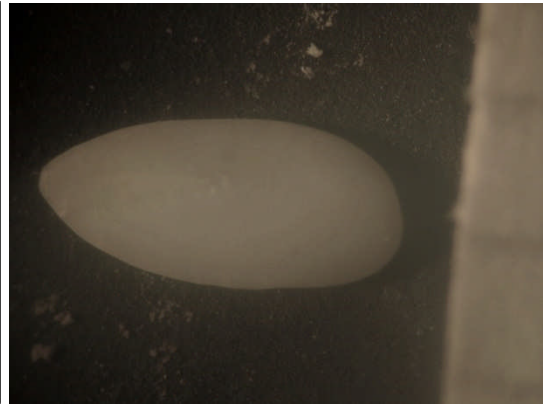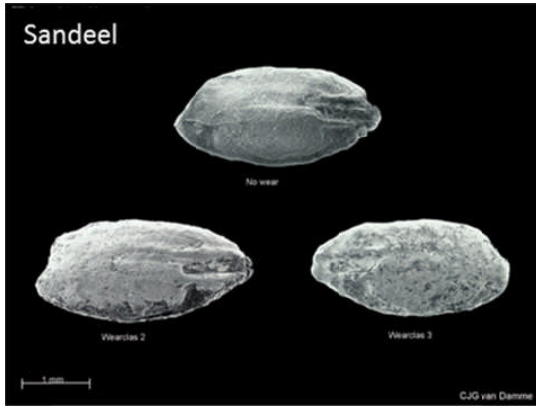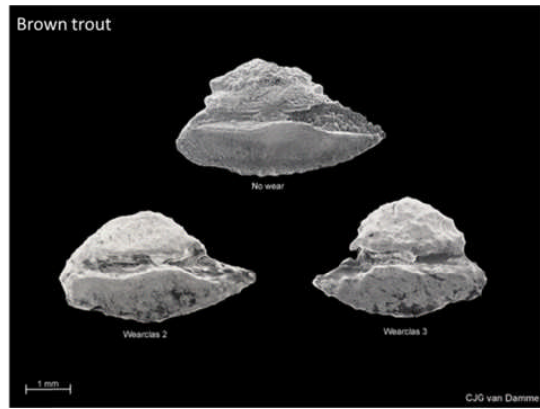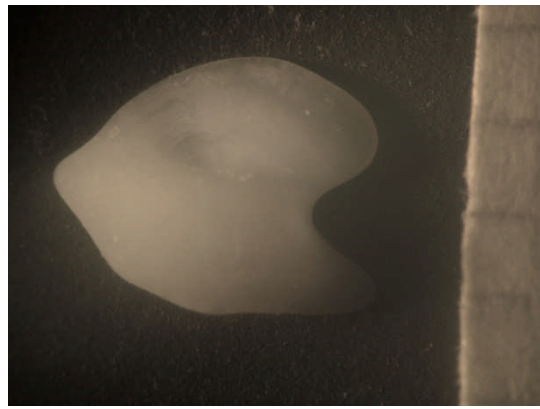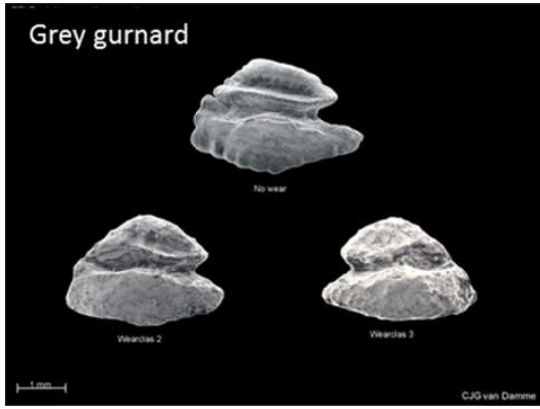
Appendix B

Table B 1: Prey-specific digestion coefficients (DC) and standard errors (SE) from each trial were averaged to give mean values for each seal, averaged across seals to give mean values for each prey species and averaged across prey species to give mean values for each prey group (fl = flatfish, lg = large gadoid, oth = other spp., se = sandeels, tc = *Trisopterus* spp.) for otolith length, width and lower rostral length.

| Trial | | | | | | Seal | | | Prey & Group | | |
seal	prey	Gp	trial	DC	SE	prey	DC	SE	prey	DC	SE
Otolith length or lower rostral length											
D	dab	fl	48	1.29	0.03	dab	1.33	0.05	dab	1.28	0.04
D	dab	fl	59	1.37	0.06	plaice	1.17	0.06	lemon sole	1.22	0.11
D	plaice	fl	41	1.23	0.07	cod	1.18	0.08	LR dab	1.18	0.02
D	plaice	fl	54	1.10	0.04	haddock	1.02	0.05	plaice	1.17	0.05
D	cod	lg	50	1.31	0.03	whiting	NA	NA	witch	1.09	0.03
D	cod	lg	55	1.06	0.14	herring	1.23	0.10	cod	1.24	0.07
D	haddock	lg	43	0.97	0.08	sandeel	1.16	0.01	haddock	1.17	0.04
D	haddock	lg	60	1.07	0.03	norway pout	1.11	0.01	hake	1.93	0.17
D	whiting	lg	47	NA	NA	poor cod	1.12	0.02	pollock	0.98	0.03
D	whiting	lg	53	NA	NA				whiting	1.69	0.09
D	herring	oth	46	1.38	0.11				herring	1.16	0.05
D	herring	oth	52	1.20	0.06				red gurnard	0.99	0.03
D	herring	oth	57	1.11	0.12				salmon smolt	0.96	0.03
D	squid	oth	44	1.04	0.04				squid	0.88	0.05
D	sandeel	se	42	1.14	0.01				G. sandeel	1.61	0.05
D	sandeel	se	49	1.15	0.01				sandeel	1.28	0.02
D	sandeel	se	56	1.19	0.01				norway pout	1.18	0.01
D	norway pout	tc	40	1.17	0.02				poor cod	1.17	0.02
D	norway pout	tc	58	1.06	0.01						
D	poor cod	tc	45	1.09	0.01				**Group**	**DC**	**SE**
D	poor cod	tc	51	1.14	0.02				Flatfish	1.19	0.05
E	dab	fl	61	1.35	0.04	dab	1.27	0.03	Lg. gadoids	1.40	0.08
E	dab	fl	88	1.20	0.02	lemon sole	1.18	0.14	Other	1.04	0.04
E	lemon sole	fl	80	1.40	0.17	LR dab	1.19	0.03	Sandeels	1.45	0.03
E	lemon sole	fl	124	0.97	0.11	plaice	1.16	0.05	Trisopterus	1.17	0.02
E	LR dab	fl	83	1.19	0.03	witch	1.02	0.02			
E	plaice	fl	91	1.16	0.05	cod	1.33	0.05			
E	witch	fl	76	1.02	0.02	haddock	1.25	0.03			
E	cod	lg	69	1.64	0.04	hake	1.93	0.17			
E	cod	lg	74	1.49	0.03	whiting	1.36	0.06			
E	cod	lg	77	0.95	0.09	herring	1.11	0.02			
E	cod	lg	89	1.26	0.03	red gurnard	0.99	0.03			
E	cod	lg	120	1.27	0.07	salmon smolt	0.94	0.03			
E	cod	lg	125	1.40	0.04	G. sandeel	1.92	0.08			
E	haddock	lg	71	1.34	0.06	sandeel	1.30	0.03			

E	haddock	lg	81	1.07	0.02	norway pout	1.07	0.01
E	haddock	lg	90	1.21	0.03	poor cod	1.25	0.02
E	haddock	lg	126	1.38	0.03			
E	hake	lg	84	2.08	0.18			
E	hake	lg	123	1.77	0.16			
E	whiting	lg	66	1.08	0.03			
E	whiting	lg	75	1.27	0.02			
E	whiting	lg	86	1.74	0.14			
E	herring	oth	78	1.11	0.02			
E	red gurnard	oth	79	0.95	0.04			
E	red gurnard	oth	85	1.03	0.03			
E	salmon smolt	oth	122	0.94	0.03			
E	squid	oth	63	1.06	0.04			
E	G. sandeel	se	121	1.92	0.08			
E	sandeel	se	65	1.19	0.03			
E	sandeel	se	73	1.40	0.04			
E	norway pout	tc	64	1.07	0.01			
E	poor cod	tc	72	1.25	0.02			
F	dab	fl	111	1.23	0.02	dab	1.23	0.02
F	lemon sole	fl	92	1.25	0.09	lemon sole	1.25	0.09
F	LR dab	fl	107	1.16	0.02	LR dab	1.16	0.02
F	plaice	fl	116	1.31	0.05	plaice	1.31	0.05
F	witch	fl	97	1.15	0.04	witch	1.15	0.04
F	cod	lg	93	1.29	0.08	cod	1.19	0.06
F	cod	lg	104	1.15	0.05	haddock	1.25	0.03
F	cod	lg	110	1.13	0.07	pollock	0.98	0.03
F	haddock	lg	98	1.17	0.03	whiting	1.37	0.07
F	haddock	lg	108	1.37	0.04	salmon smolt	0.97	0.03
F	haddock	lg	117	1.19	0.01	G. sandeel	1.30	0.02
F	pollock	lg	119	0.98	0.03	sandeel	1.29	0.02
F	whiting	lg	100	1.50	0.02	norway pout	1.28	0.01
F	whiting	lg	105	1.48	0.03	poor cod	1.25	0.02
F	whiting	lg	114	1.13	0.15			
F	salmon smolt	oth	118	0.97	0.03			
F	squid	oth	94	0.98	0.09			
F	G. sandeel	se	113	1.30	0.02			
F	sandeel	se	99	1.32	0.02			
F	sandeel	se	106	1.26	0.02			
F	norway pout	tc	95	1.28	0.01			
F	poor cod	tc	103	1.25	0.02			
Q	plaice	fl	33	1.23	0.07	plaice	1.17	0.04
Q	plaice	fl	37	1.12	0.02	whiting	1.78	0.08
Q	whiting	lg	32	1.86	0.10	herring	1.19	0.04
Q	whiting	lg	38	1.69	0.06	norway pout	1.24	0.01
Q	herring	oth	31	1.26	0.04			
Q	herring	oth	34	1.16	0.03			

Seal	prey	Gp	trial	DC	SE	prey	DC	SE
Q	herring	oth	39	1.15	0.05			
Q	norway pout	tc	35	1.24	0.01			
V	plaice	fl	11	0.97	0.04	plaice	1.14	0.04
V	plaice	fl	17	1.31	0.04	whiting	2.14	NA
V	whiting	lg	18	2.14	NA	herring	1.11	0.04
V	herring	oth	14	1.11	0.04	sandeel	1.28	0.03
V	squid	oth	15	0.45	0.02	norway pout	1.12	0.02
V	sandeel	se	10	1.29	0.03	poor cod	1.07	0.02
V	sandeel	se	16	1.28	0.03			
V	norway pout	tc	9	1.12	0.02			
V	poor cod	tc	13	1.07	0.02			
X	plaice	fl	25	1.10	0.05	plaice	1.10	0.05
X	whiting	lg	1	1.84	0.34	whiting	1.80	0.15
X	whiting	lg	8	1.62	0.02	sandeel	1.38	0.01
X	whiting	lg	24	1.93	0.09	norway pout	1.23	0.02
X	sandeel	se	27	1.38	0.01	poor cod	1.14	0.02
X	norway pout	tc	7	1.23	0.02			
X	norway pout	tc	26	1.24	0.02			
X	poor cod	tc	4	1.10	0.02			
X	poor cod	tc	21	1.18	0.01			

		Trial				**Seal**			**Prey & Group**		
Seal	prey	Gp	trial	DC	SE	prey	DC	SE	prey	DC	SE
Otolith width											
D	dab	fl	48	1.44	0.04	cod	1.13	0.06	dab	1.35	0.03
D	dab	fl	59	1.46	0.06	dab	1.45	0.05	lemon sole	1.32	0.08
D	plaice	fl	41	1.24	0.06	haddock	1.16	0.03	LR dab	1.22	0.02
D	plaice	fl	54	1.12	0.04	herring	1.41	0.08	plaice	1.18	0.04
D	cod	lg	50	1.19	0.01	norway pout	1.07	0.01	cod	1.23	0.06
D	cod	lg	55	1.08	0.11	plaice	1.18	0.05	haddock	1.23	0.02
D	haddock	lg	43	1.17	0.03	poor cod	1.10	0.02	hake	1.80	0.14
D	haddock	lg	60	1.16	0.02	sandeel	1.26	0.01	pollock	1.09	0.07
D	whiting	lg	47	1.35	0.03	whiting	1.20	0.02	whiting	1.25	0.03
D	whiting	lg	53	1.06	0.01				herring	1.30	0.06
D	herring	oth	46	1.48	0.11				red gurnard	1.04	0.04
D	herring	oth	52	1.26	0.05				G. sandeel	1.75	0.05
D	herring	oth	57	1.48	0.10				sandeel	1.40	0.02
D	sandeel	se	42	1.28	0.01				norway pout	1.13	0.01
D	sandeel	se	49	1.24	0.01				poor cod	1.14	0.02
D	sandeel	se	56	1.27	0.01						
D	norway pout	tc	40	1.12	0.02				**Group**	**DC**	**SE**
D	norway pout	tc	58	1.02	0.01				Flatfish	1.27	0.05
D	poor cod	tc	45	1.09	0.01				Lg. gadoids	1.32	0.07
D	poor cod	tc	51	1.10	0.02				Other	1.17	0.05
E	dab	fl	61	1.36	0.03	cod	1.40	0.06	Sandeels	1.57	0.04
E	dab	fl	88	1.26	0.03	dab	1.31	0.03	Trisopterus	1.13	0.02
E	lemon sole	fl	124	1.06	0.10	G. sandeel	1.98	0.07			
E	lemon sole	fl	80	1.63	0.07	haddock	1.26	0.02			
E	LR dab	fl	83	1.26	0.03	hake	1.80	0.14			

	Species	Gear	Num		
E	plaice	fl	91	1.22	0.04
E	witch	fl	76	NA	NA
E	cod	lg	120	1.53	0.09
E	cod	lg	125	1.36	0.03
E	cod	lg	69	1.72	0.05
E	cod	lg	74	1.36	0.04
E	cod	lg	77	1.19	0.11
E	cod	lg	89	1.25	0.02
E	haddock	lg	126	1.40	0.03
E	haddock	lg	71	1.29	0.03
E	haddock	lg	81	1.14	0.02
E	haddock	lg	90	1.20	0.02
E	hake	lg	123	1.58	0.14
E	hake	lg	84	2.01	0.15
E	whiting	lg	66	1.09	0.01
E	whiting	lg	75	1.12	0.01
E	whiting	lg	86	1.36	0.04
E	herring	oth	78	1.32	0.04
E	red gurnard	oth	79	1.01	0.04
E	red gurnard	oth	85	1.08	0.04
E	salmon smolt	oth	122	NA	NA
E	G. sandeel	se	121	1.98	0.07
E	sandeel	se	65	1.26	0.03
E	sandeel	se	73	1.54	0.04
E	norway pout	tc	64	1.02	0.01
E	poor cod	tc	72	1.22	0.02
F	dab	fl	111	1.30	0.03
F	lemon sole	fl	92	1.28	0.08
F	LR dab	fl	107	1.18	0.02
F	plaice	fl	116	1.30	0.04
F	witch	fl	97	NA	NA
F	cod	lg	104	1.06	0.03
F	cod	lg	110	1.20	0.08
F	cod	lg	93	1.25	0.09
F	haddock	lg	108	1.39	0.03
F	haddock	lg	117	1.21	0.01
F	haddock	lg	98	1.17	0.03
F	pollock	lg	119	1.09	0.07
F	whiting	lg	100	1.30	0.02
F	whiting	lg	105	1.26	0.02
F	whiting	lg	114	1.18	0.02
F	salmon smolt	oth	118	NA	NA
F	G. sandeel	se	113	1.52	0.02
F	sandeel	se	106	1.37	0.02
F	sandeel	se	99	1.49	0.02
F	norway pout	tc	95	1.24	0.01
F	poor cod	tc	103	1.21	0.02
Q	plaice	fl	33	1.16	0.04
Q	plaice	fl	37	1.10	0.02
Q	whiting	lg	32	1.41	0.05
Q	whiting	lg	38	1.44	0.03
Q	herring	oth	31	1.40	0.04
Q	herring	oth	34	1.38	0.08
Q	herring	oth	39	1.31	0.09

Right-hand column:

E

Species		
herring	1.32	0.04
lemon sole	1.35	0.08
LR dab	1.26	0.03
norway pout	1.02	0.01
plaice	1.22	0.04
poor cod	1.22	0.02
red gurnard	1.04	0.04
salmon smolt	NA	NA
sandeel	1.40	0.03
whiting	1.19	0.02
witch	NA	NA

F

Species		
cod	1.17	0.07
dab	1.30	0.03
G. sandeel	1.52	0.02
haddock	1.26	0.02
lemon sole	1.28	0.08
LR dab	1.18	0.02
norway pout	1.24	0.01
plaice	1.30	0.04
pollock	1.09	0.07
poor cod	1.21	0.02
salmon smolt	NA	NA
sandeel	1.43	0.02
whiting	1.25	0.02
witch	NA	NA

Q

Species		
herring	1.36	0.07
norway pout	1.21	0.01
plaice	1.13	0.03
whiting	1.42	0.04

Q	norway pout	tc	35	1.21	0.01			
V	plaice	fl	11	0.98	0.04	herring	1.12	0.04
V	plaice	fl	17	1.28	0.05	norway pout	1.08	0.02
V	whiting	lg	18	1.07	0.06	plaice	1.13	0.04
V	herring	oth	14	1.12	0.04	poor cod	1.07	0.02
V	sandeel	se	10	1.39	0.03	sandeel	1.36	0.03
V	sandeel	se	16	1.32	0.03	whiting	1.07	0.06
V	norway pout	tc	9	1.08	0.02			
V	poor cod	tc	13	1.07	0.02			
X	plaice	fl	25	1.13	0.04	norway pout	1.16	0.02
X	whiting	lg	1	1.33	0.06	plaice	1.13	0.04
X	whiting	lg	24	1.39	0.03	poor cod	1.11	0.02
X	whiting	lg	8	1.39	0.03	sandeel	1.53	0.01
X	sandeel	se	27	1.53	0.01	whiting	1.37	0.04
X	norway pout	tc	26	1.16	0.02			
X	norway pout	tc	7	1.16	0.02			
X	poor cod	tc	21	1.16	0.01			
X	poor cod	tc	4	1.06	0.02			