

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

Scottish Marine and Freshwater Science Report Vol 7 No 23

L J Wilson, K Grellier and P S Hammond

Published by Marine Scotland Science

ISSN: 2043-7722

DOI: 10.7489/1804-1

Marine Scotland is the directorate of the Scottish Government responsible for the integrated management of Scotland's seas. Marine Scotland Science (formerly Fisheries Research Services) provides expert scientific and technical advice on marine and fisheries issues. Scottish Marine and Freshwater Science is a series of reports that publishes results of research and monitoring carried out by Marine Scotland Science. It also publishes the results of marine and freshwater scientific work that has been carried out for Marine Scotland under external commission. These reports are not subject to formal external peer review.

This report represents the results of marine and freshwater scientific work carried out for Marine Scotland under external commission.

© Crown copyright 2016

You may re-use this information (excluding logos and images) free of charge in any format or medium, under the terms of the Open Government Licence. To view this licence, visit: <http://www.nationalarchives.gov.uk/doc/open-governmentlicence/version/3/> or email: psi@nationalarchives.gsi.gov.uk.

Where we have identified any third party copyright information you will need to obtain permission from the copyright holders concerned.

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

Lindsay J. Wilson¹, Kate Grellier² and Philip S. Hammond¹

¹ Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, Fife, KY16 8LB, Scotland

² Natural Power Consultants, McKinven House, George Street, Falkirk, FK2 7EY, Scotland



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 to 2012.

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 to April 2009 (1 adult female) and August 2011 to 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).

Passage rates

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.

Species-specific digestion coefficients

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; $p = 0.125$).

Grade specific digestion coefficients

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.

Application of digestion coefficients to otoliths recovered from scats collected in the wild

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 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 | <i>Limanda limanda</i> | 10.2 | 33 | 585 | 415 | 0.755 | 0.036 | 1.379 | 3 | 5 |
| Lemon sole | <i>Microstomus kitt</i> | 15.6 | 32.1 | 210 | 83 | 0.474 | 0.060 | 2.440 | 2 | 3 |
| Long rough dab | <i>Hippoglossoides platessoides</i> | 8.6 | 23.7 | 438 | 386 | 0.887 | 0.020 | 1.133 | 2 | 2 |
| Plaice | <i>Pleuronectes platessa</i> | 13.9 | 36.4 | 492 | 403 | 0.854 | 0.035 | 1.219 | 6 | 9 |
| Witch | <i>Glyptocephalus cynoglossus</i> | 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 | <i>Gadus morhua</i> | 13 | 60.9 | 232 | 211 | 0.881 | 0.085 | 1.204 | 3 | 11 |
| Haddock | <i>Melanogrammus aeglefinus</i> | 11.5 | 40.6 | 486 | 485 | 1.005 | 0.005 | 0.995 | 3 | 9 |
| Hake | <i>Merluccius merluccius</i> | 45.1 | 54.1 | 26 | 23 | 0.893 | 0.055 | 1.136 | 1 | 2 |
| Pollock | <i>Pollachius pollachius</i> | 43.6 | 55.2 | 8 | 8 | 1.000 | 0.000 | 1.000 | 1 | 1 |
| Whiting | <i>Merlangius merlangus</i> | 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 | <i>Hyperolpus lanceolatus</i> | 18.3 | 33.4 | 544 | 266 | 0.600 | 0.021 | 2.421 | 2 | 2 |
| Sandeel | <i>Ammodytes tobianus</i> | 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 | <i>Trysopterus esmarkii</i> | 9.3 | 19.9 | 3440 | 3477 | 1.026 | 0.003 | 0.980 | 6 | 8 |
| Poor cod | <i>Trysopterus minutus</i> | 7.8 | 23.7 | 1171 | 1186 | 1.008 | 0.002 | 0.993 | 5 | 7 |
| <i>Trisopterus</i> spp | | 7.8 | 23.7 | 4611 | 4663 | 1.017 | 0.002 | 0.986 | 6 | 15 |
| Herring | <i>Clupea harengus</i> | 18.8 | 29.8 | 377 | 140 | 0.428 | 0.071 | 2.697 | 4 | 8 |
| Red gurnard | <i>Chelidonichthys cuculus</i> | 21.6 | 35.2 | 82 | 47 | 0.580 | 0.077 | 1.741 | 1 | 2 |
| Salmon smolt | <i>Salmo salar</i> | 13.8 | 18.9 | 448 | 137 | 0.306 | 0.031 | 3.310 | 2 | 2 |
| Squid | <i>Loligo forbesii</i> | 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 comm |
| 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 |
| <i>Trisopterus</i> 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 |
| <i>Trisopterus</i> 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 |

| | | | | | | |
|------------------------|------|-------|-------|---|----|------|
| Poor cod | 1.14 | 0.018 | 0.016 | 5 | 7 | 1186 |
| <i>Trisopterus</i> 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 |
| <i>Trisopterus</i> 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 |
| <i>Trisopterus</i> 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 |

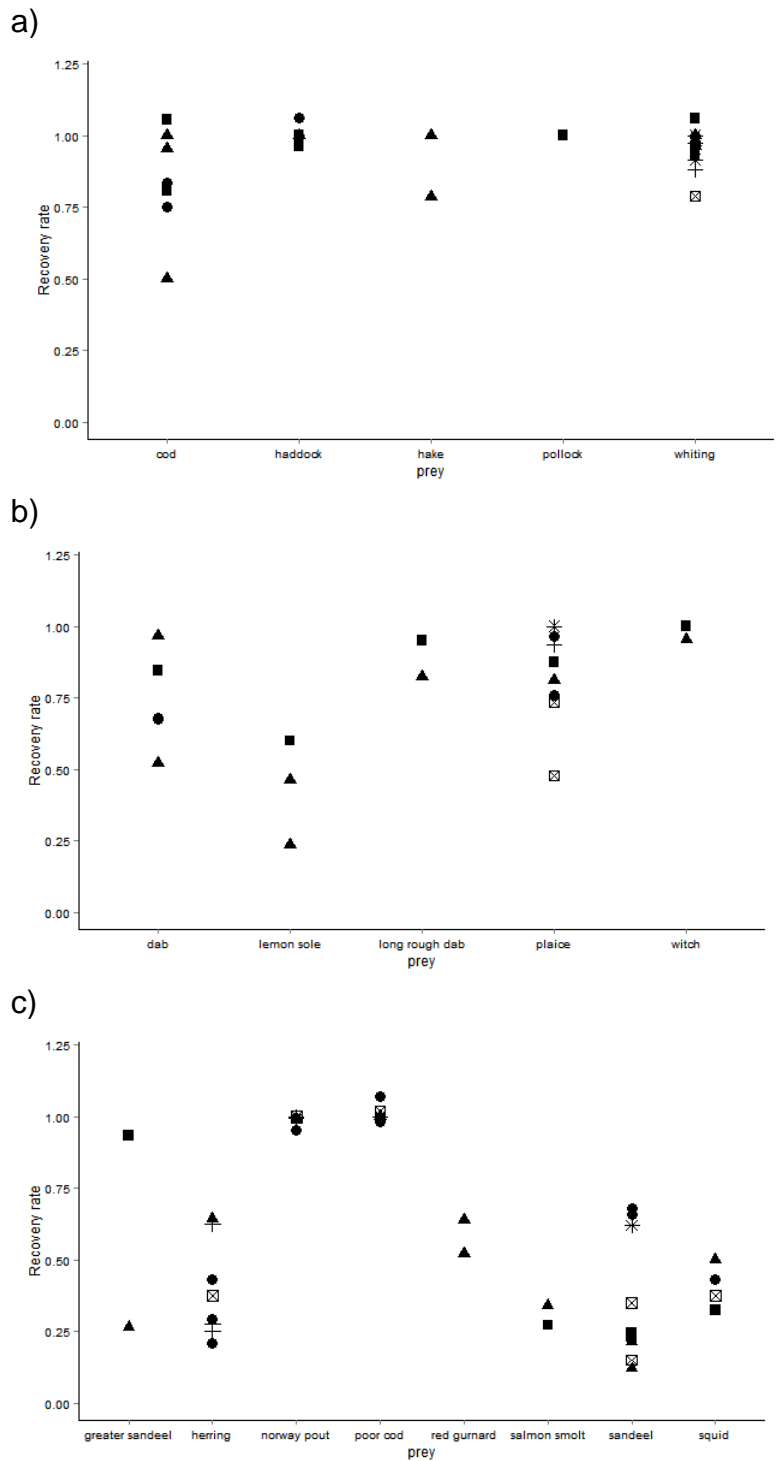


Figure 1: Feeding trial recovery rates showing intra- and inter-individual variability. Each symbol represents a different seal. a) Large gadoids, b) flatfish, c) other species

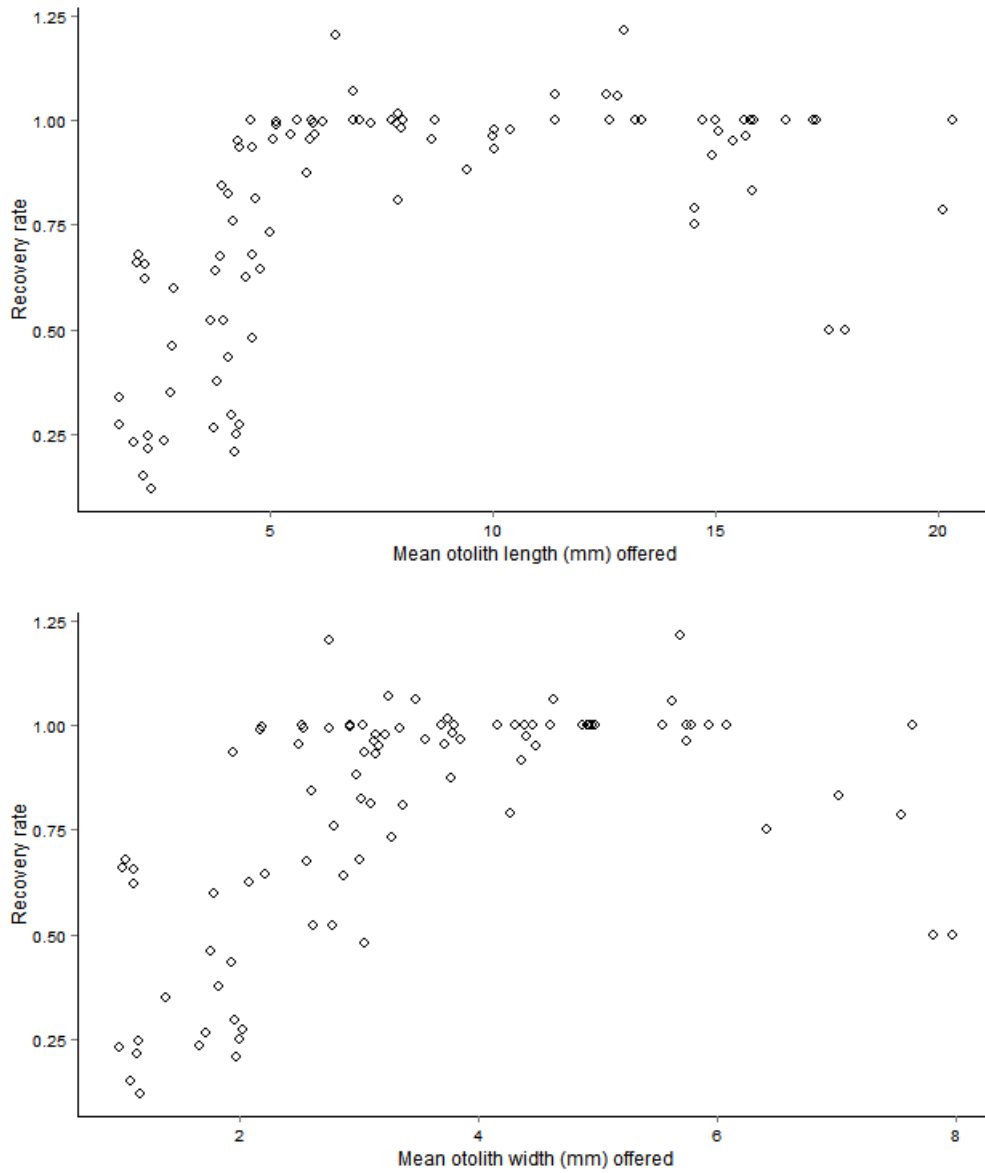
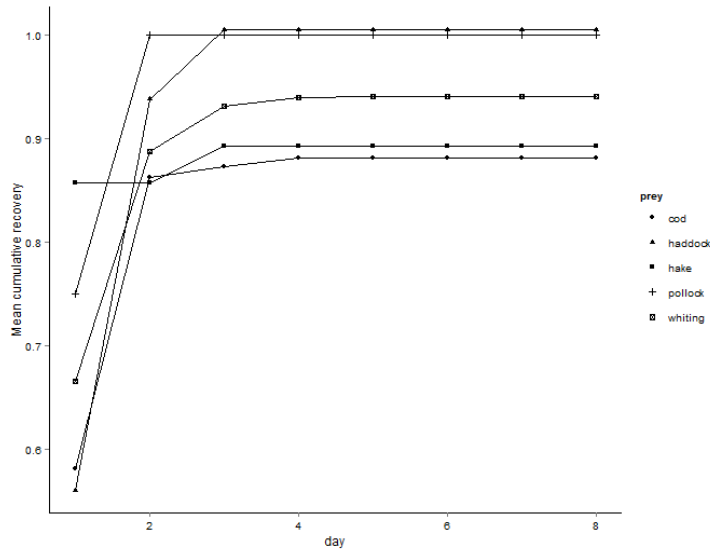
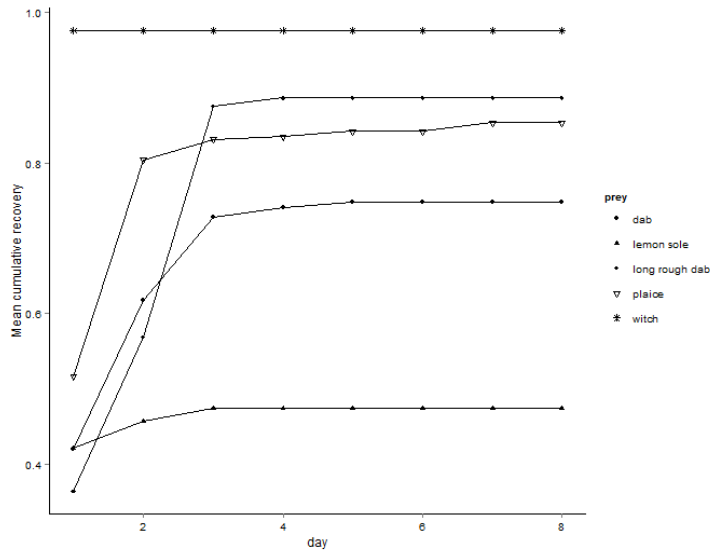


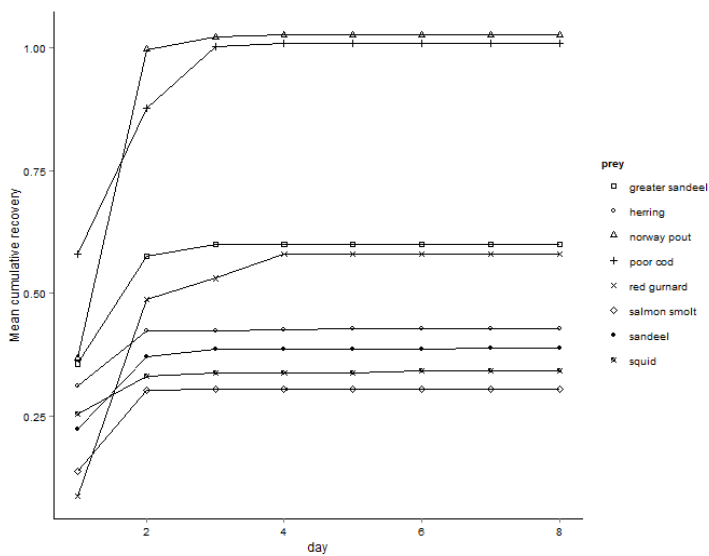
Figure 2: Recovery rate plotted against mean undigested otolith length (top) and width (bottom) for all trials.



a)



b)



c)

Figure 3: Species-specific passage rates for a) large gadoids, b) flatfish, c) all other prey species.

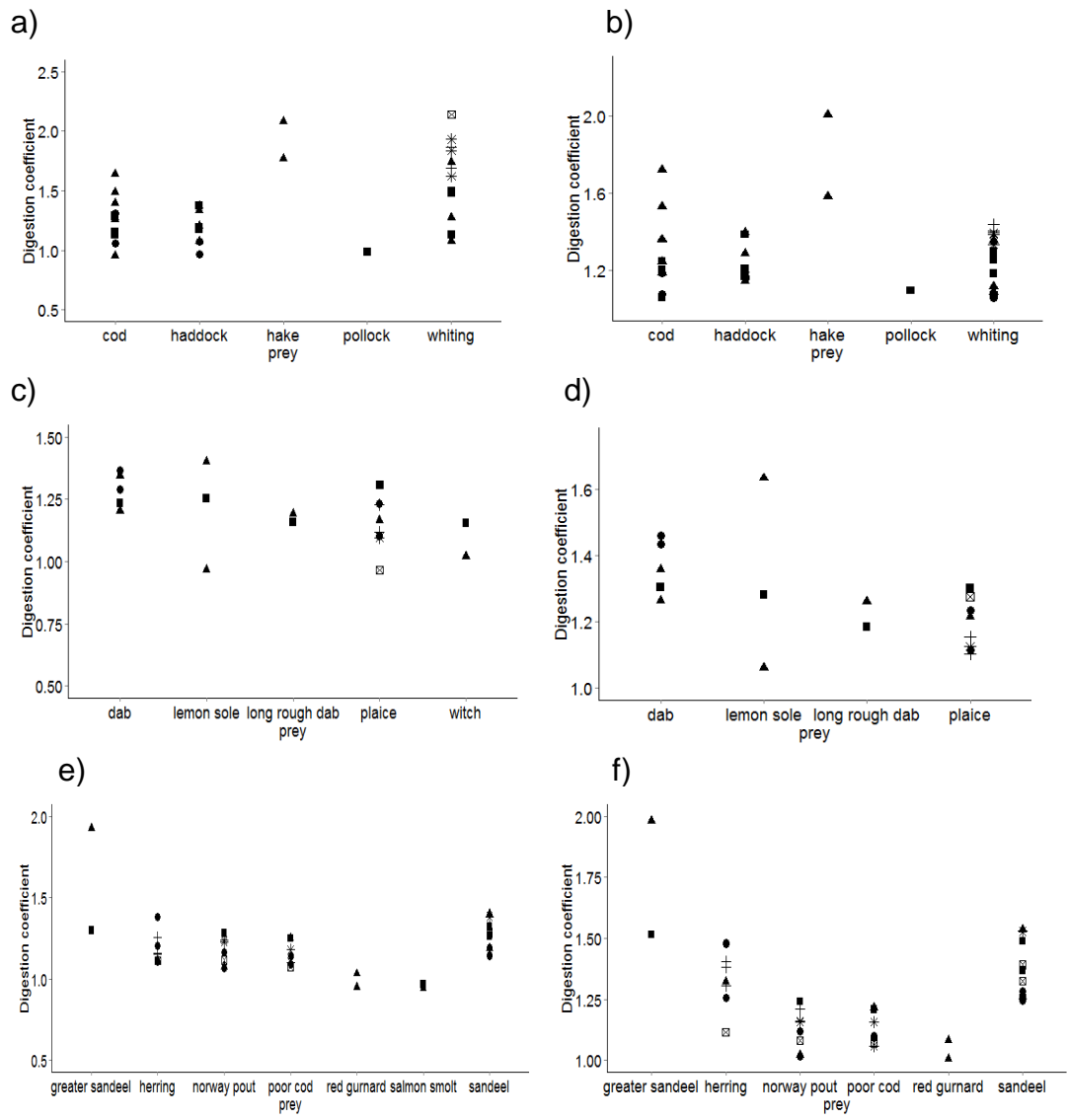
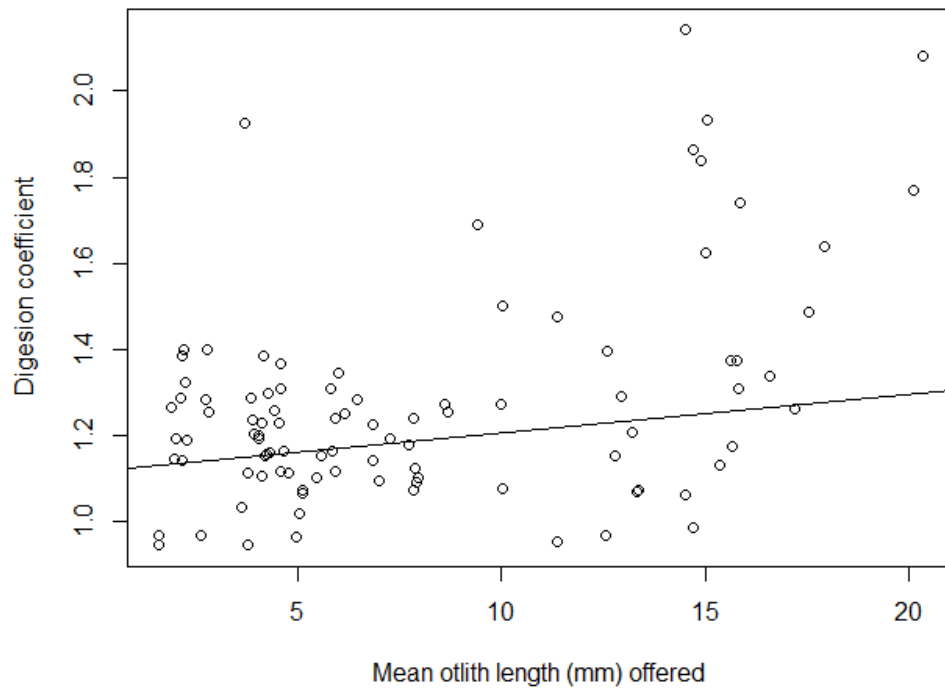


Figure 4: Inter and intra-individual variation in digestion coefficients for each trial. Each symbol represents a different seal. Species-specific digestion coefficients by individual feeding trial are displayed for a) large gadoid otolith length b) large gadoid otolith width, c) flatfish otolith length, d) flatfish otolith width, e) other species otolith length f) other species otolith width

a)



b)

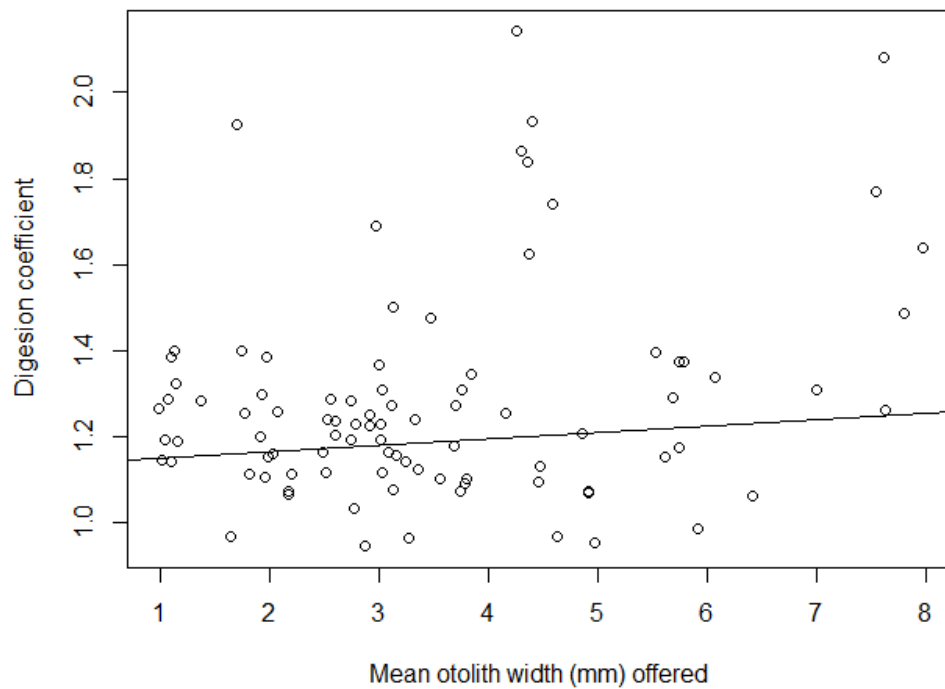


Figure 5: Inverse-variance weighted linear regression of digestion coefficient on mean estimated length (a) and width (b) of otoliths fed for all trials of all size ranges of prey.

Acknowledgements

We thank Iain Gibb and Craig Davis (Marine Scotland Science, Aberdeen), Pittenweem Harbour Fishermen's Mutual Association and Jack Wright (Fleetwood) Ltd. for their help in obtaining fish; Mardik Leopold (Wageningen-IMARES) and Tero Härkönen (Swedish Museum of Natural History) for providing the otolith and fish size data used to construct some of the regressions; John Watkins (Conservation Research Ltd.), Caya Sievers, Mel Froude, Mia Kent and Chris McKnight for assistance with otolith and beak analysis and Ryan Milne, Alicia Widmer, Simon Moss, Donald Malone and the diet team volunteers for assistance with experimental work. This work was carried out with support from Marine Scotland and Scottish Natural Heritage.

References

- Bowen, W. D. (2000). Reconstruction of pinniped diets: Accounting for complete digestion of otoliths and cephalopod beaks. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 898-905.
- Bowen, W. D. & Harrison, G. D. (1996). Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology* **74**, 125-135.
- Brown, E. G. & Pierce, G. J. (1998). Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Marine Ecology Progress Series* **167**, 275-289.
- Brown, E. G., Pierce, G. J., Hislop, J. R. G. & Santos, M. B. (2001). Interannual variation in the summer diets of harbour seals *Phoca vitulina* at Mousa, Shetland (UK). *Journal of the Marine Biological Association of the United Kingdom* **81**, 325-337.
- Casper, R. M., Gales, N. J., Hindell, M. A. & Robinson, S. M. (2006). Diet estimation based on an integrated mixed prey feeding experiment using *Arctocephalus* seals. *Journal of Experimental Marine Biology and Ecology* **328**, 228-239.
- Clarke, M. R. (1986). *A handbook for the identification of Cephalopod beaks*: Clarendon Press, Oxford.
- Cottrell, P. E., Trites, A. W. & Miller, E. H. (1996). Assessing the use of hard parts in faeces to identify harbour seal prey: results of captive-feeding trials. *Canadian Journal of Zoology* **74**, 875-880.
- Grellier, K. & Hammond, P. S. (2005). Feeding method affects otolith digestion in captive gray seals: implications for diet composition estimation. *Marine Mammal Science* **21**, 296-306.
- Grellier, K. & Hammond, P. S. (2006). Robust digestion and passage rate estimates for hard parts of grey seal (*Halichoerus grypus*) prey. *Canadian Journal of Fisheries and Aquatic Science* **63**, 1982-1998.
- Hall, A. J., Watkins, J. & Hammond, P. S. (1998). Seasonal variation in the diet of harbour seals in the south-western North Sea. *Marine Ecology Progress Series* **170**, 269-281.
- Hammond, P. S. & Grellier, K. (2006). Grey seal diet composition and prey consumption in the North Sea. In *Final Report* (Department for Environment, F. a. R. A. u. p. M., ed.), pp. 1-54.
- Hammond, P. S., Hall, A. J. & Prime, J. H. (1994a). The diet of grey seals around Orkney and other islands and mainland sites in north-eastern Scotland. *Journal of Applied Ecology* **31**.

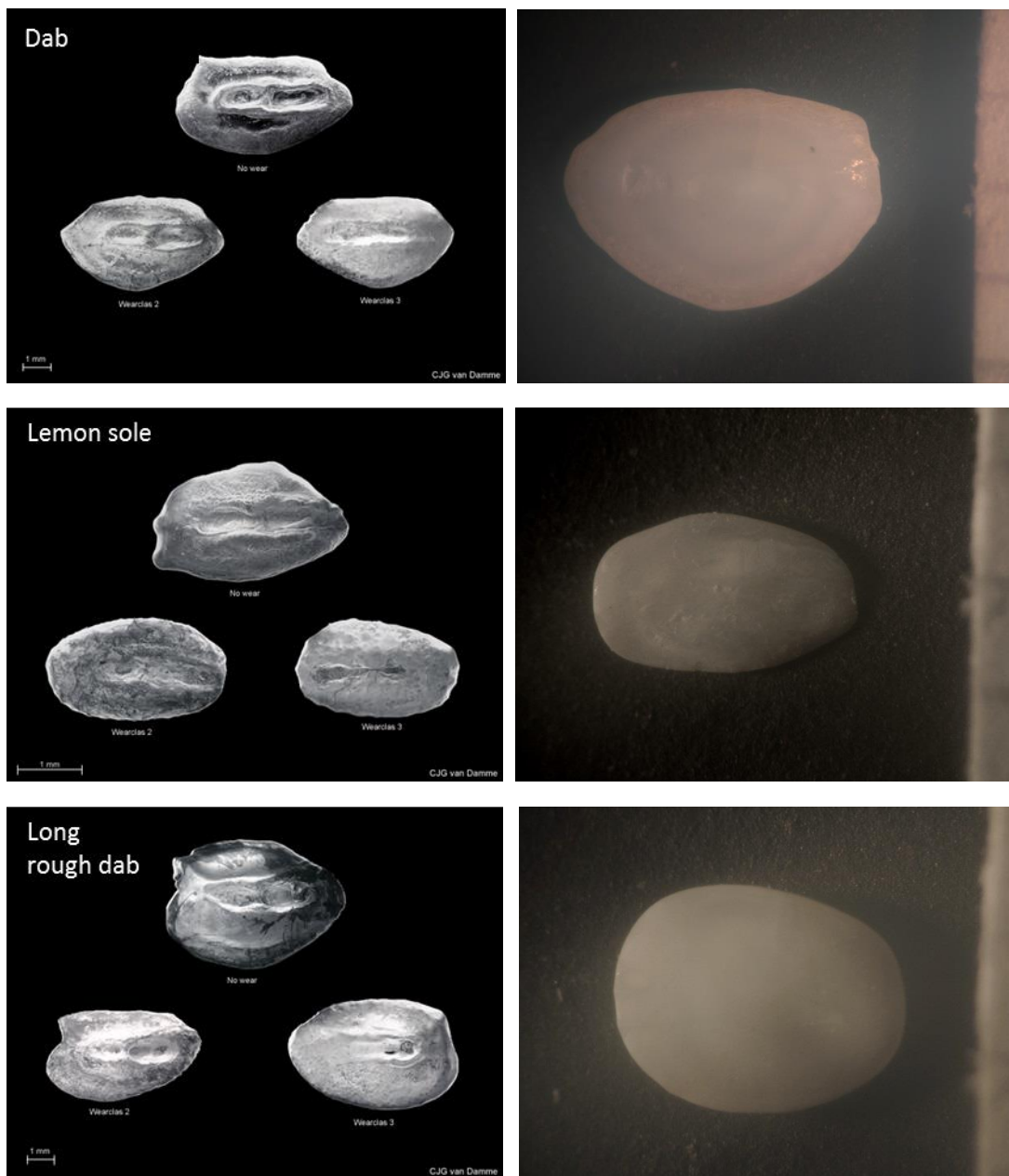
- Hammond, P. S., Hall, A. J. & Prime, J. H. (1994b). The diet of grey seals in the Inner and Outer Hebrides. *The Journal of Applied Ecology* **31**, 737-746.
- Hammond, P. S. & Harris, R. N. (2006). Grey seal diet composition and prey consumption off western Scotland and Shetland. In *Final report to Scottish Executive Environment and Rural Affairs Department and Scottish Natural Heritage*, p. 41.
- Härkönen, T. (1986). *Guide to the otoliths of the bony fishes of the northeast Atlantic*. Hellrup, Denmark: Danbiu ApS. Biological Consultants.
- Harvey, J. (1989). Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. *Journal of Zoology* **219**, 101-111.
- Leopold, M. F., van Damme, C. J. D., Philipart, C. J. M. & Winter, C. J. N. (2001). Otoliths of North Sea fish - fish identification key by means of otoliths and other hard parts. In *CD ROM. Version 1.0. ETI (Expert Centre for Taxonomic Identification)*. University of Amsterdam, Amsterdam, The Netherlands.
- Lonergan, M., Duck, C., Thompson, P. M., Mackey, B. L., Cunningham, L. & Boyd, I. L. (2007). Using sparse survey data to investigate the declining abundance of British harbour seals. *Journal of Zoology* **271**, 261-269.
- MacLeod, C. D., Reidenberg, J. S., Weller, M., Santos, M. B., Herman, J., Goold, J. & Pierce, G. J. (2007). Breaking symmetry: the marine environment, prey size and the evolution of asymmetry in cetacean skulls. *The Anatomical Record* **290**, 539-545.
- Marcus, J., Bowen, W. D. & Eddington, J. (1998). Effects of meal size on otolith recovery from fecal samples of gray and harbor seal pups. *Marine Mammal Science* **14**, 789-802.
- Markussen, N. H. (1993). Transit time of digesta in captive harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology* **71**, 1071-1073.
- McConnell, B. J., Fedak, M. A., Lovell, P. & Hammond, P. S. (1999). Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology* **36**, 573-590.
- MMSS/001/11/CSD3 Marine Mammal Scientific Support Research Programme: Common Seal Decline. In *The diet of harbour seals in Scotland*. Scottish Government.
- Murie, D. J. & Lavigne, D. M. (1986). Interpretation of otoliths in stomach content analysis of phocid seals: quantifying fish consumption. *Canadian Journal of Zoology* **64**, 1152-1157.
- Orr, A. J. & Harvey, J. T. (2001). Quantifying errors associated with using faecal samples to determine the diet of California sea lion (*Zalophus californianus*). *Canadian Journal of Zoology* **79**, 1080-1087.

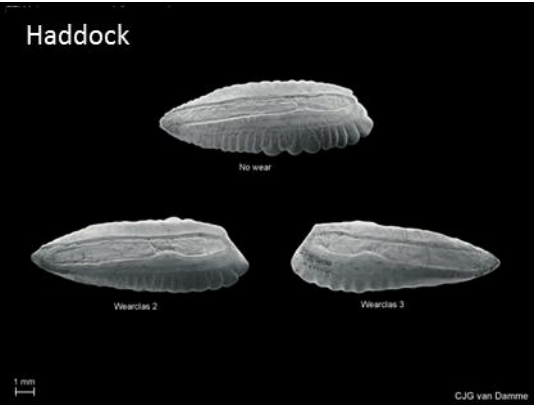
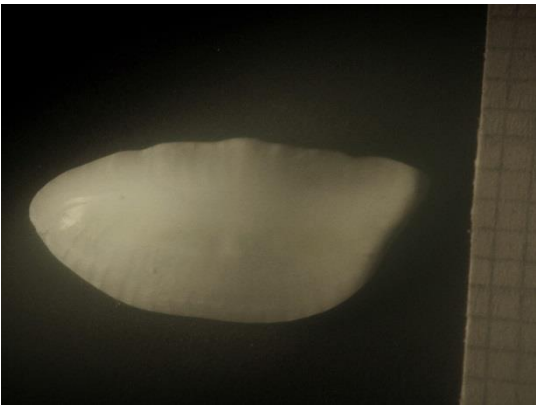
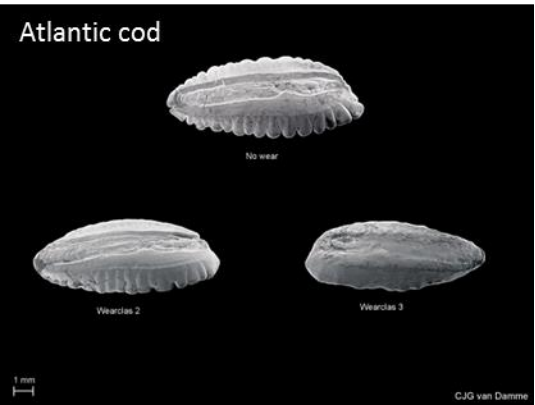
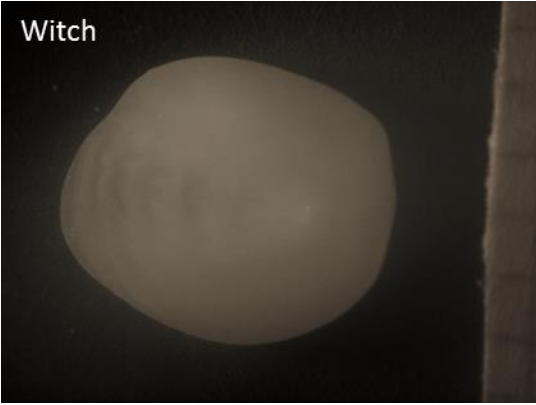
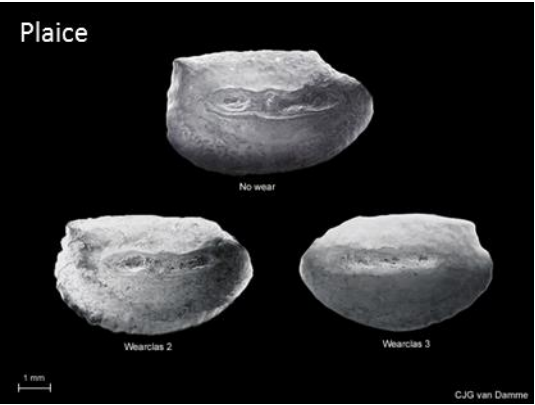
- Phillips, E. M. & Harvey, J. T. (2009). A captive feeding study with the Pacific harbor seal (*Phoca vitulina richardii*): Implications for scat analysis. *Marine Mammal Science* **25**, 373-391.
- Pierce, G. J., Boyle, P. R. & Diack, J. S. W. (1991a). Identification of fish otoliths and bones in faeces and digestive tracts of seals. *Journal of Zoology* **224**, 320-328.
- Pierce, G. J. & Santos, M. B. (2003). Diet of harbour seals (*Phoca vitulina*) in Mull and Skye (Inner hebrides, western Scotland). *Journal of the Marine Biological Association of the United Kingdom* **83**, 647-650.
- Pierce, G. J., Thompson, P. M., Miller, A., Diack, J. S. W., Miller, D. & Boyle, P. R. (1991b). Seasonal variation in the diet of common seals (*Phoca vitulina*) in the Moray Firth area of Scotland. *Journal of Zoology* **223**, 641-652.
- Prime, J. H. (1979). Observations on the digestion of some gadoid fish otoliths by a young common seal. In *ICES CM 1979/N:14*. Copenhagen, Denmark: International Council for the Exploration of the Sea.
- Prime, J. H. & Hammond, P. S. (1987). Quantitative assessment of grey seal diet from faecal analysis. In *Approaches to marine mammal energetics* (Huntley, A. C., Costa, D. P., Worthy, G. A. J. & Castellini, M. A., eds.). Lawrence, KS 66044, USA: Allen Press.
- Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters*. London, UK: Charles Griffin and Company.
- Sharples, R. J., Arrizabalaga, B. & Hammond, P. S. (2009). Seals, sandeels and salmon: diet of harbour seals in St Andrews Bay and the Tay Estuary, southeast Scotland. *Marine Ecology Progress Series* **390**, 265-276.
- Sharples, R. J., Moss, S. E., Patterson, T. A. & Hammond, P. S. (2012). Spatial Variation in Foraging Behaviour of a Marine Top Predator (*Phoca vitulina*) Determined by a Large-Scale Satellite Tagging Program. *PLoS ONE* **7**, e37216.
- Silva, J. d. & Neilson, J. D. (1985). Limitations of Using Otoliths Recovered in Scats to Estimate Prey Consumption in Seals. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1439-1442.
- Sparling, C. E., Fedak, M. A. & Thompson, D. (2007). Eat now, pay later? Evidence of deferred food-processing costs in diving seals *Biology Letters* **3**, 95-99.
- Thompson, P. M., Mcconnell, B. J., Tollit, D. J., Mackay, A., Hunter, C. & Racey, P. A. (1996). Comparative distribution, movements and diet of harbour seals and grey seals from Moray Firth, N.E. Scotland. *Journal of Applied Ecology* **33**, 1572-1584.

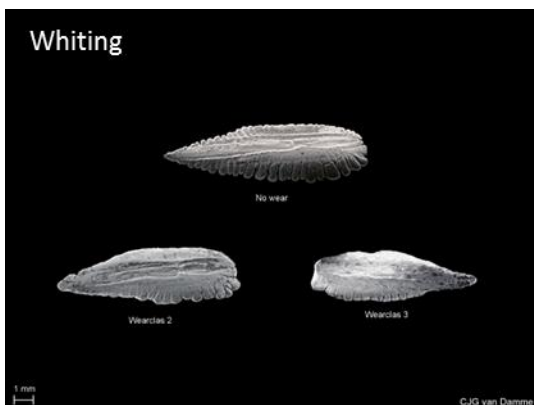
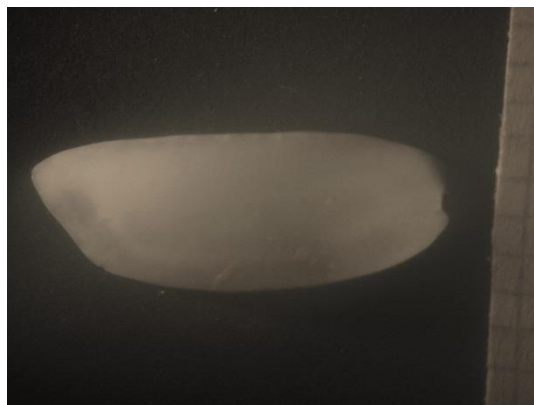
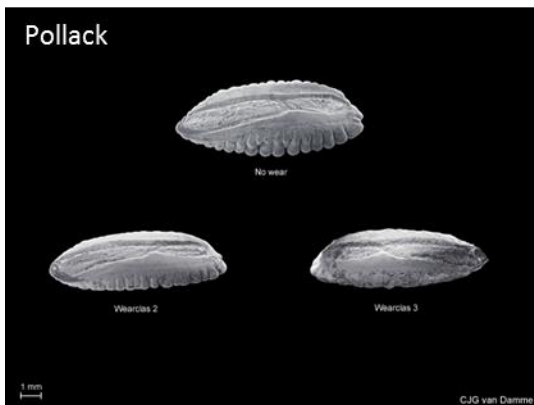
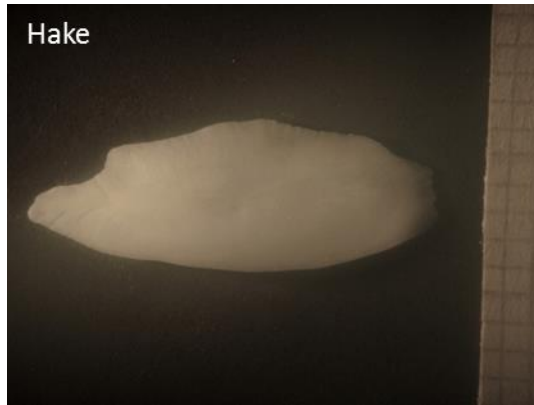
- Thompson, P. M. & Miller, D. (1990). Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina*) in the Moray Firth, Scotland. *Journal of Applied Ecology* **27**, 492-501.
- Thompson, P. M., Pierce, G. J., Hislop, J. R. G., Miller, D. & Diack, J. S. W. (1991). Winter foraging by common seals (*Phoca vitulina*) in relation to food availability in the inner Moray Firth, N.E. Scotland. *Journal of Animal Ecology* **60**, 283-294.
- Thompson, P. M., Tollit, D. J., Corpe, H. M., Reid, R. J. & Ross, H. M. (1997). Changes in haematological parameters in relation to prey switching in a wild population of harbour seals. *Functional Ecology* **11**, 743-750.
- Tollit, D. J., Black, A. D., Thompson, P. M., Mackay, A., Corpe, H. M., Wilson, B., Van Parijs, S. M., Grellier, K. & Parlane, S. (1998). Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology* **244**, 209-222.
- Tollit, D. J., Heaslip, S. G., Zeppelin, T. G., Joy, R., Call, K. A. & Trites, A. W. (2004). A method to improve size estimates of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monoterygius*) consumed by pinnipeds: digestion correction factors applied to bones and otoliths recovered in scats. *Fishery Bulletin* . **102**, 498-508.
- Tollit, D. J., Steward, M. J., Thompson, P. M., Pierce, G. J., Santos, M. B. & Hughes, S. (1997). Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Canadian Journal of Fisheries and Aquatic Science* **54**, 105-119.
- Tollit, D. J. & Thompson, P. M. (1996). Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Canadian Journal of Zoology* **74**, 1110-1121.
- Tollit, D. J., Wong, M., Winship, A. J., Rosen, D. A. & Trites, A. W. (2003). Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller's sea lion (*Eumetopias jubatus*). *Marine Mammal Science* **19**, 724-744.
- Wilson, S. C., Pierce, G. J., Higgins, C. M. & Armstrong, M. J. (2002). Diet of the harbour seals *Phoca vitulina* of Dundrum Bay, north-east Ireland. *Journal of the Marine Biological Association of the United Kingdom* **82**, 1009-1018.

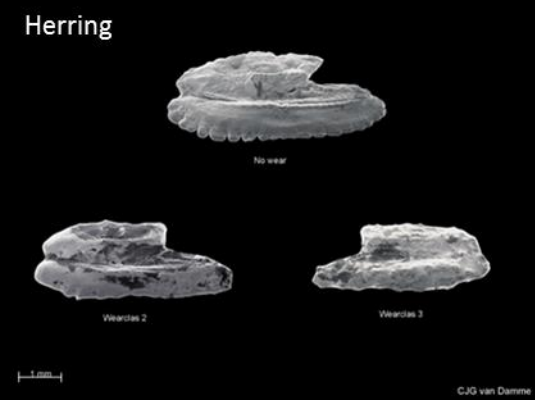
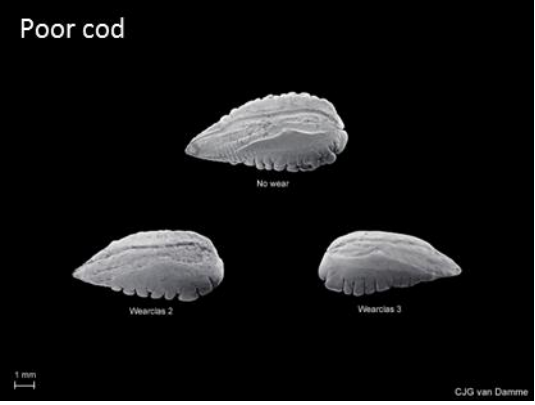
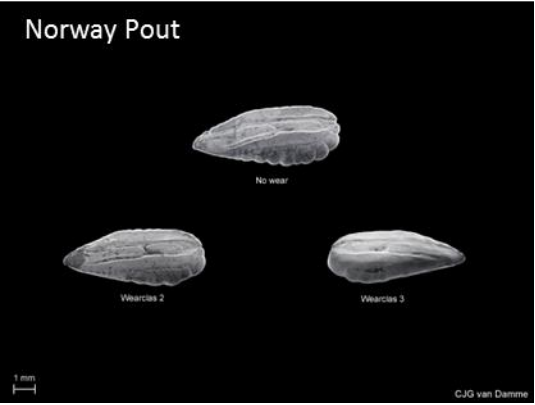
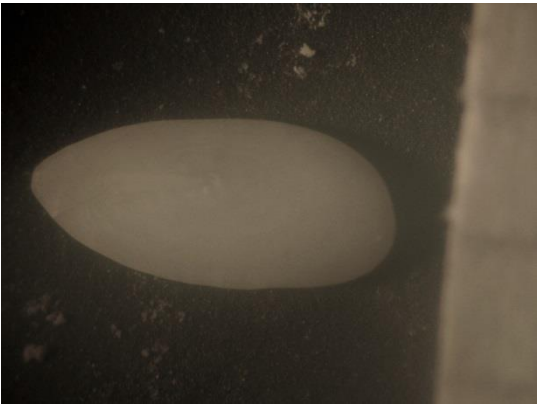
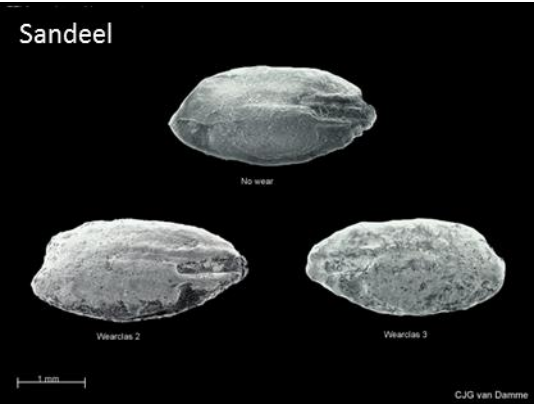
Appendix A

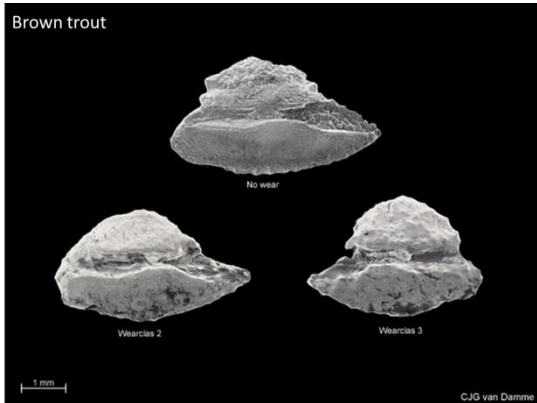
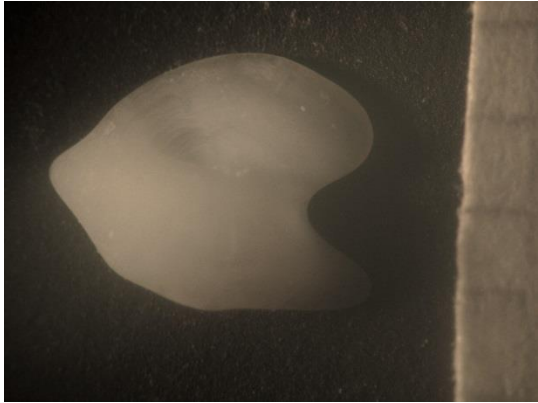
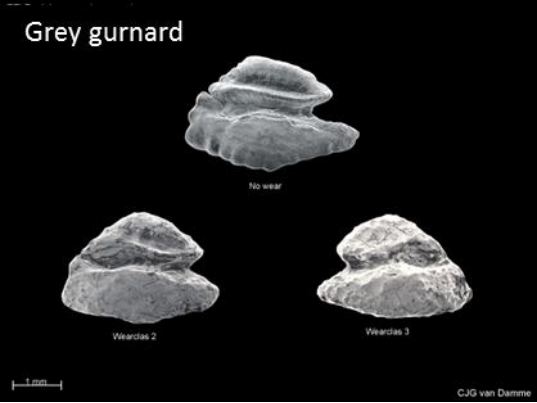
Figure A1: Images in the left column of pristine (grade 1, upper image), moderately digested (grade 2, lower left image) and considerably digested (grade 3, lower right image) otoliths and in the right column severely digested (grade 4) otoliths. These images were used as a guide to classify otoliths 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).











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 | | | | | | |
| D | poor cod | tc | 51 | 1.14 | 0.02 | | | | | | |
| E | dab | fl | 61 | 1.35 | 0.04 | dab | 1.27 | 0.03 | | | |
| E | dab | fl | 88 | 1.20 | 0.02 | lemon sole | 1.18 | 0.14 | | | |
| E | lemon sole | fl | 80 | 1.40 | 0.17 | LR dab | 1.19 | 0.03 | | | |
| E | lemon sole | fl | 124 | 0.97 | 0.11 | plaice | 1.16 | 0.05 | | | |
| 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 | | | |
| | | | | | | | | | Group | DC | SE |
| | | | | | | | | | Flatfish | 1.19 | 0.05 |
| | | | | | | | | | Lg. gadoids | 1.40 | 0.08 |
| | | | | | | | | | Other | 1.04 | 0.04 |
| | | | | | | | | | Sandeels | 1.45 | 0.03 |
| | | | | | | | | | Trisopterus | 1.17 | 0.02 |

| | | | | | | | | |
|---|--------------|-----|-----|------|------|--------------|------|------|
| 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 | | | |

| | | | | | | | | | | | |
|---|-------------|-----|----|------|------|-------------|------|------|--|--|--|
| 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 | | | | | | |

| Seal | prey | Trial | | | | prey | Seal | | | Prey & Group | | |
|----------------------|-------------|-------|-------|------|------|-------------|------|------|--------------|--------------|-----------|--|
| | | Gp | trial | DC | SE | | 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 | | | | |

| | | | | | | | | |
|---|--------------|-----|-----|------|------|--------------|------|------|
| E | plaice | fl | 91 | 1.22 | 0.04 | herring | 1.32 | 0.04 |
| E | witch | fl | 76 | NA | NA | lemon sole | 1.35 | 0.08 |
| E | cod | lg | 120 | 1.53 | 0.09 | LR dab | 1.26 | 0.03 |
| E | cod | lg | 125 | 1.36 | 0.03 | norway pout | 1.02 | 0.01 |
| E | cod | lg | 69 | 1.72 | 0.05 | plaice | 1.22 | 0.04 |
| E | cod | lg | 74 | 1.36 | 0.04 | poor cod | 1.22 | 0.02 |
| E | cod | lg | 77 | 1.19 | 0.11 | red gurnard | 1.04 | 0.04 |
| E | cod | lg | 89 | 1.25 | 0.02 | salmon smolt | NA | NA |
| E | haddock | lg | 126 | 1.40 | 0.03 | sandeel | 1.40 | 0.03 |
| E | haddock | lg | 71 | 1.29 | 0.03 | whiting | 1.19 | 0.02 |
| E | haddock | lg | 81 | 1.14 | 0.02 | witch | NA | NA |
| 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 | cod | 1.17 | 0.07 |
| F | lemon sole | fl | 92 | 1.28 | 0.08 | dab | 1.30 | 0.03 |
| F | LR dab | fl | 107 | 1.18 | 0.02 | G. sandeel | 1.52 | 0.02 |
| F | plaice | fl | 116 | 1.30 | 0.04 | haddock | 1.26 | 0.02 |
| F | witch | fl | 97 | NA | NA | lemon sole | 1.28 | 0.08 |
| F | cod | lg | 104 | 1.06 | 0.03 | LR dab | 1.18 | 0.02 |
| F | cod | lg | 110 | 1.20 | 0.08 | norway pout | 1.24 | 0.01 |
| F | cod | lg | 93 | 1.25 | 0.09 | plaice | 1.30 | 0.04 |
| F | haddock | lg | 108 | 1.39 | 0.03 | pollock | 1.09 | 0.07 |
| F | haddock | lg | 117 | 1.21 | 0.01 | poor cod | 1.21 | 0.02 |
| F | haddock | lg | 98 | 1.17 | 0.03 | salmon smolt | NA | NA |
| F | pollock | lg | 119 | 1.09 | 0.07 | sandeel | 1.43 | 0.02 |
| F | whiting | lg | 100 | 1.30 | 0.02 | whiting | 1.25 | 0.02 |
| F | whiting | lg | 105 | 1.26 | 0.02 | witch | NA | NA |
| 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 | herring | 1.36 | 0.07 |
| Q | plaice | fl | 37 | 1.10 | 0.02 | norway pout | 1.21 | 0.01 |
| Q | whiting | lg | 32 | 1.41 | 0.05 | plaice | 1.13 | 0.03 |
| Q | whiting | lg | 38 | 1.44 | 0.03 | whiting | 1.42 | 0.04 |
| Q | herring | oth | 31 | 1.40 | 0.04 | | | |
| Q | herring | oth | 34 | 1.38 | 0.08 | | | |
| Q | herring | oth | 39 | 1.31 | 0.09 | | | |

| | | | | | | | | |
|---|-------------|-----|----|------|------|-------------|------|------|
| 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 | | | |
