Estimating diet composition from scat analysis in otariid seals (Otariidae): is it reliable?

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Analysis of teleost sagittal otoliths contained in scats has been widely used to determine the diet of seals. This method is based on the assumption that relative frequencies of otoliths in scats faithfully reflect those of fish in the diet. This assumption has rarely been tested experimentally. We compared the ratios of herring (Clupea harengus) to sprat (Sprattus sprattus) otoliths in faeces (output) of captive California sea lions (Zalophus californianus) and South American fur seals (Arctocephalus australis) with the ratios at feeding (input). Sea lions and fur seals showed no consistent differences in recovery rates and partial digestion of otoliths. Output ratios deviated only slightly from input ratios, the smaller sprat otoliths being underrepresented in the output by 8%. Only about 40% of the otoliths fed to the seals were found in the scats. For both species partial digestion of otoliths led to a 16% underestimation of fish length and a 35% underestimation of fish mass.

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L’analyse des otolithes de téléostéens contenus dans les fèces est une méthode très répandue de détermination du régime alimentaire des phoques. Cette méthode suppose que les fréquences relatives d’otolithes dans les fèces reflètent fidèlement les fréquences relatives des poissons dans le régime. Cette hypothèse n’a pratiquement jamais fait l’objet de vérifications expérimentales. Nous avons mesuré la proportion d’otolithes de harengs (Clupea harengus) et celle d’otolithes de sprats (Sprattus sprattus) dans les fèces (sortie) de Lions de mer californiens, Zalophus californianus, et d’Otaries à fourrure sud-américaines, Arctocephalus australis, gardés en captivité, et comparé ces mesures aux proportions d’otolithes ingérés (entrée). Il n’y avait pas de différence constante entre lions de mer et otaries et les taux de récupération et de digestion partielle d’otolithes étaient les mêmes chez les deux espèces. Les proportions à la sortie différaient seulement un peu des proportions à l’entrée et les otolithes des sprats, plus petits, étaient sous-représentés de 8% à la sortie. Seulement 40% environ des otolithes ingérés ont été retrouvés à la sortie. La digestion partielle des otolithes chez les deux espèces entraîne une sous-estimation de la longueur des poissons consommés, de l’ordre de 16%, et de la masse des poissons consommés, de l’ordre de 35%.

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For 2–8 days before each experiment the animals were fed decapitated fish to ensure that no otoliths remained in their digestive tracts (Table 1). The efficiency of this procedure was insured by collecting and scrutinizing faeces before the experimental feeding. The experimental feeding at the beginning of each series consisted of varying amounts and combinations of herring and sprat with heads. Herring had a mean standard length of 20.9 cm and weighed about 190 g, sprat had a mean length of 12.1 cm and weighed about 18 g. The seals were hand-fed individually and the time of feeding and mass, standard length, and number of fishes fed per animal were recorded. Each seal received about 2.5–3.5 kg of fish at the experimental feeding. When high numbers of herring had to be fed to the seals, some herring were cut in half obliquely from the base of the skull to the anus and only the head parts were given. Other herring had their heads removed and only the body parts were given. The night feeding was rare. Animals were not observed during the night and for the few scats found in the morning the time of defecation was noted. Sometimes an animal squashed a scat with its body. These scats were then strained through three nested sieves with 2.0-, 1.0-, and 0.5-mm mesh sizes. The otoliths were collected from the sieves with a pair of forceps, briefly washed in 98% isopropyl alcohol, air-dried, and stored dry. Otoliths were then identified as belonging to sprat or herring and their lengths were measured to the nearest 0.1 mm from the rostrum to the postrostrum using a microscope (Wild-M7S) at about 30 times magnification.

Otoliths were recovered by immersing scats in water mixed with household detergent to help emulsify the soft constituents of the scats. The scats were then strained through three nested sieves with 2.0-, 1.0-, and 0.5-mm mesh sizes. The otoliths were collected from the sieves with a pair of forceps, briefly washed in 98% isopropyl alcohol, air-dried, and stored dry. Otoliths were then identified as belonging to sprat or herring and their lengths were measured to the nearest 0.1 mm from the rostrum to the postrostrum using a stereomicroscope (Wild-M7S) at about 30 times magnification.

Sagittal otoliths were removed from 22 fresh herring and 22 fresh sprats and their lengths regressed on standard fish lengths and fish body masses. To compare lengths of otoliths before and after passage through the digestive tracts of the experimental animals, expected otolith lengths were estimated from measured standard lengths of fish before feeding. From the measured lengths of otoliths in scats, estimated lengths and body masses of fresh fish in the diet were calculated from regressions.

### Results

#### Percent otolith recovery

A mean of 38.5 ± 29.5% of otoliths fed during all experiments were recovered in the scats. From fur seal scats, 42.0 ± 23.8% of all sprat otoliths were recovered (n = 8 experiments; 285 of 564 otoliths) and 49.4 ± 26.7% of all herring otoliths were recovered (n = 10; 309 of 590 otoliths). From sea lion scats, we recovered 26.4 ± 33.8% of ingested sprat otoliths (n = 8; 141 of 570) and 34.2 ± 32.7% of ingested herring otoliths (n = 9; 199 of 538). The lower recovery from sea lion scats resulted from very low values for one of the sea lions (3.0 ± 1.9% in four experiments), while recovery for the other sea lion was similar to that of the fur seals (55.3 ± 26.0% in five experiments). Otolith recovery was not significantly different between the two species (Mann–Whitney U-test; n1 = 17, n2 = 18, ns).

For both species together, more of the herring than sprat otoliths were recovered (Wilcoxon signed-ranks test, n = 16, p < 0.05) indicating that the number of the smaller sprats in the diet would be underestimated from scat analysis. However, results of the test were not significant for each seal species separately.

#### Percent glass beads recovered

As glass beads are indigestible they can serve to assess the proportion of otoliths defecated but not recovered. For each seal species glass beads were fed simultaneously with the experimental feeding (four times). The cumulative curve of glass bead recovery reached saturation after about 30 h with little further recovery up to 80 h after the experimental feeding (Fig. 1A). For otoliths saturation was reached after 20–50 h (Fig. 1B) indicating that further defecation of glass beads or otoliths was unlikely after the end of the experiments. A mean of 74.0 ± 37.7% (n = 8 experiments) of glass beads fed with the experimental feedings were recovered in scats. No difference was found between the two seal species (Mann–Whitney U-test; n1 = 4, n2 = 4, ns).

Only 5.8% (68 of 1170) of beads fed 20–25 h before the experimental feeding were found in scats collected after the experimental feeding. Of beads fed > 25 h before the experimental feeding only 0.1% (2 of 1860) were recovered during the experiments.

#### Passage half-times

The time between the experimental feeding and recovery of 50% of all otoliths recovered is here called the passage half-time. It provides an estimate of the average time an otolith was exposed to digestive fluids.

### Table 1. Conditions of the five sets of experiments

| Series No. | Animal No. | Period fed decapitated fish before experimental meal (days) | Time glass beads were fed before experimental meal (h) | Max. time in captivity after experimental meal (h) |
|------------|------------|----------------------------------------------------------|-----------------------------------------------------|--------------------------------------------------|
| 1          | 1, 4, 6    | 3                                                        | —                                                   | 91                                               |
| 2          | 1, 2, 4, 6 | 2                                                        | —                                                   | 94                                               |
| 3          | 1, 2, 3, 4 | 7                                                        | 171, 123, 75, 26                                    | 68                                               |
| 4          | 1, 2, 3, 4 | 8                                                        | 48, 24, 0                                           | 104                                              |
| 5          | 1, 2, 3, 4 | 7                                                        | 48, 25, 22, 0                                       | 69                                               |

**Note:** Animals 1 and 2 are sea lions, animals 3, 4, and 6 are fur seals. A different color of glass beads was given at each time when glass beads were fed several times before the experimental meal. Duration of captivity gives the time after which the last animal of a set of experiments was released.
Half-times ranged between 17.5 and 44 h (median 21.9 h). No difference in half-times was found between herring and sprat otoliths (Wilcoxon signed-ranks test: $T = -0.135$, $n = 14$, ns) or between sea lions and fur seals (Fig. 1; Mann–Whitney $U$-test, $n_1 = 16$, $n_2 = 17$, ns). The correlation between otolith length and half-times was insignificant ($r = 0.03$, $n = 844$), i.e., passage half-times were independent of otolith size, and separation of otoliths according to size did not occur during passage through the intestinal tract.

The glass beads fed in the experimental feedings had half-times similar to those of otoliths (Fig. 1), ranging from 20 to 31 h (median 22 h). Again no difference was found between the seal species. In only two cases did a sea lion retain most of the glass beads beyond the end of the experiment; once the animal produced only two scats, and once it produced very small liquid stools.

Almost all glass beads given before the experimental feeding were eliminated within 25 h, i.e., before the onset of experimental scat collection. This observation implies that passage half-times were shorter for the same individuals when they were moving about and swimming in the pool before the experiment than when they were held in the boxes on dry land during the experiments.

**Reduction in otolith length by digestion**

Distribution of otolith length in scats was significantly different from that estimated by eqs. 1 and 4 in Table 2 for the fishes in the experimental meals (Mann–Whitney $U$-tests: $p < 0.001$; see Fig. 2 for a comparison of the normalized distributions). The estimated length of herring otoliths in the meals was $4.05 \pm 0.25$ mm ($n = 778$), and of sprat otoliths, $1.96 \pm 0.07$ mm ($n = 952$). In the scats, herring otoliths aged 17.4% and sprat otoliths 12.2% shorter than expected from fish size in the meals. The difference in the reduction in otolith size between fish species was not significant (Mann–Whitney $U$-test: $n_1 = n_2 = 9$, ns). No difference was found in reduction in otolith length between the two seal species.

Estimating standard length of fish from otoliths recovered in scats using regression eqs. 2 and 5 in Table 2 resulted in an average underestimate of 16%. Because of the cubic relationship between length and mass, fish mass estimated from otolith length in scats (using eqs. 3 and 6 in Table 2) underestimated actual fish mass by $36 \pm 7\%$ ($n = 9$) for herrings and $33 \pm 11\%$ ($n = 9$) for sprat.

**Proportion of otoliths recovered in scats**

The proportion of herring otoliths (herring/(herring + sprat); H/(H+S)) in scats was compared with the known proportion of herring in the experimental meals. Even for a given experiment this proportion varied noticeably from scat to scat. Regressing all proportions of otoliths found in scats against proportions in the corresponding meals (Fig. 3A, Table 3) resulted in (mostly) significant relationships. Sometimes a seal appeared to be constipated, probably because of the close confinement during the experiment, and only a few otoliths were recovered. Excluding such experiments, in which less than 10% of the otoliths were recovered, a highly significant regression between diet composition and proportion of herring otoliths in scats was found (Fig. 3B, Table 3). To exclude these experiments seems justified since seals in the field are always vigorously exercising and the constipation occurring in a few experiments appeared to be caused by the artificial condition of confinement on dry land.

The difference between regressions for sea lions and fur
seals were never significant (analysis of covariance: slopes $p = 0.56$, intercepts $p = 0.66$). Since most of the regression slopes in Table 3 were close to 1 and intercepts were not far from 0, numerical composition of the diet was usually estimated correctly from scats. A small underestimate of the smaller sprat otoliths still persisted (8.8% from the regression means or 7.7 ± 21.1% from experiment means; $n = 16$).

**Discussion**

**Recovery of otoliths**

The low mean recovery rate of only 38.5% of all otoliths cannot be explained by retention of missing otoliths. Passage half-times were on the order of 22 h for both otoliths and glass beads. Our experiments thus covered usually about four half-times, but hardly any otoliths or glass beads were defecated later than 30 h after the experimental feeding. Missing otoliths either must have been digested completely or were smaller than the smallest mesh size (0.5 mm) and therefore were not recovered. As mean glass bead recovery was only 74%, i.e., 26% somehow got lost, we cannot exclude the possibility that 26% of the otoliths were also lost. Even so, about 35% of all ingested otoliths would have been destroyed by digestion (assuming 39% recovered + 26% lost + 35% dissolved = 100%). However, the main loss of glass beads occurred in one experiment on sea lion No. 2 and in the second experiment with fur seal No. 6 when the animals were obviously not digesting normally.

Nearly complete recovery of otoliths from fish consumed has sometimes been tacitly assumed (Fitch and Brownell 1968; Treacy and Crawford 1981; Ainley et al. 1982) but our data as well as those from previous experiments do not support this assumption (Prime 1979; Hawes 1983; DaSilva and Neilson 1985; Murie and Lavigne 1986). Only Prime and Hammond (1987) reported 78% recovery in an experiment on grey seals (*Halichoerus grypus*). Otherwise, recovery varied from 4% for one common seal, *Phoca vitulina* (DaSilva and Neilson 1985), fed with herring, to 35% for one California sea lion (Hawes 1983) fed with three different fish species. In our own experiments recoveries varied from 1.25 to 87.3% in sea lions and from 3.8 to 80% in fur seals. The latter two values represent the results of two experiments on the same individual under identical conditions. Therefore, high variance in otolith recovery between experiments presently precludes any interpretation of differences in mean recovery rates.

The mechanisms responsible for total or partial recovery have been elucidated by Murie and Lavigne (1985). In the stomachs of grey seals killed at defined times after feeding they found that otoliths remaining in the fish skull case were undigested while others from the same meal, which had fallen out of the skull case, showed strong signs of digestion. They concluded that the probability of digestion of otoliths is highly variable depending on the species and size of fish, the position of a given fish within the stomach content, and the chance of the skull case being broken open. Taken together, the variance of otolith recovery in experiments, the knowledge about the
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1968; Prime 1979; DaSilva and Neilson 1985). Our results support this hypothesis: 8% fewer of the smaller sprat otoliths were recovered relative to the herring otoliths. Hawes (1983), feeding three different fish species sequentially, also found that recovery of anchovy (Engraulis mordax) otoliths was lower than that of the bigger jack mackerel (Trachurus symmetricus) otoliths. Nevertheless, smaller otoliths are not passed more quickly than larger ones. Consequently, the proportion of fish species in the diet (by number, not biomass) will be quite accurately assessed even for animals returning from a long trip at sea, provided that large numbers of scats are analysed and that on their return trip the seals do not fish for food that is different from their diet while far out at sea.

It seems, therefore, that reliable estimation of diet composition in terms of biomass or energy ingested is not possible from scat analysis, while the numerical proportion of different prey species may be estimated correctly from large samples of scats.

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