

# Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks

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**Abstract:** The recovery of sagittal fish otoliths and cephalopod beaks from fecal samples is an important source of information about the diets of marine mammals. Nevertheless, diet reconstructions are biased to some extent because of the partial and complete digestion of these prey structures. Although some authors have used correction factors to account for partial digestion of otoliths, none to date have corrected for the number of otoliths and cephalopod beaks that are completely digested, termed number correction factors (NCFs). Data from nine studies of captive pinnipeds show that corrections for the complete digestion of otoliths and cephalopod beaks range from 1.0 to 25.0 in the 28 prey species. Correction factors ranged from 1.0 to 10.0 in cases where seals could exercise by swimming during the experiment. In several species, NCFs vary inversely with prey length. The effect of applying NCFs will depend on the relative proportion of prey species in the diet and the NCFs of these species. Nevertheless, estimates of the species composition of marine mammal diets will benefit from the use of NCFs. Finally, standardization of experimental protocols and attention to the estimation of variability are needed to provide more reliable NCFs.

**Résumé :** La récupération d'otolithes (sagitta) de poissons et de becs de céphalopodes dans des échantillons de fèces de mammifères marins constitue une importante source d'information sur l'alimentation de ces animaux. Toutefois, les reconstitutions sont biaisées dans une certaine mesure du fait que ces structures peuvent être partiellement ou complètement digérées. Bien que certains auteurs aient eu recours à des facteurs de correction pour tenir compte de la digestion partielle des otolithes, aucun n'a pour le moment apporté une correction pour le nombre d'otolithes et de becs de céphalopodes qui sont complètement digérés; nous avons calculé ces facteurs (facteurs de correction numérique ou NCF). Les données fournies par 9 études sur des pinnipèdes en captivité montrent que les corrections pour la digestion complète des otolithes et des becs de céphalopodes va de 1,0 à 25,0 chez les 28 espèces proies. Les facteurs de correction allaient de 1,0 à 10,0 dans des cas où les phoques pouvaient faire de l'exercice en nageant pendant l'expérience. Chez plusieurs espèces, les NCF varient en fonction inverse de la longueur de la proie. L'effet de l'application des NCF dépendra de la proportion relative des espèces proies dans l'alimentation et des NCF de ces espèces. Toutefois, les estimations de la composition spécifique de l'alimentation des mammifères marins tirera profit de l'usage des NCF. Enfin, pour avoir des NCF plus fiables, il faudra normaliser les protocoles expérimentaux et se pencher sur l'estimation de la variabilité.

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## Introduction

Increasing awareness of the value of an ecosystem approach to the management and conservation of marine animals has underscored the importance of understanding trophic relationships. In the case of marine mammals, our knowledge of diet varies considerably among species, and, with few exceptions, indirect methods are used to reconstruct what was eaten. The most common methods rely on the identification of prey structures that are resistant to digestion and can be collected from stomachs, intestines, feces, and spewings. In piscivorous marine mammal species, sagittal otoliths are most commonly used, but other structures such as bones, scales, and lenses also provide a means of prey identification (Fitch and Brownell 1968; Pierce and

Boyle 1991; Pierce et al. 1993). Where cephalopods are eaten, beaks can be used for prey identification (e.g., Clarke 1986). Recovered otoliths and cephalopod beaks can be used to estimate both the number and size of the prey consumed. Stomach contents and fecal samples have been used as the main sources of prey hard parts. However, feces are being increasingly used for this purpose because they are often less expensive to collect, a high proportion of samples contain identifiable prey, and estimates of diet from fecal data are less affected by differential rates of digestion than are estimates from stomachs (Hammond and Prime 1990).

Despite their widespread use, estimates of species composition and the size of prey consumed derived from recovered otoliths and cephalopod beaks may be seriously biased (e.g., Murie and Lavigne 1985; Harvey 1989; Pierce and Boyle 1991). One difficulty is that otoliths and cephalopod beaks erode during digestion, such that the size and number of prey consumed may be underestimated, and, in some cases, prey identification is not possible. A further complication is that the degree of erosion is species specific and is often a function of prey size within species. Otoliths from some spe-

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cies (e.g., Atlantic salmon (*Salmo salar*)) are quickly digested and thus are rarely found in stomach or fecal contents (Boyle et al. 1990). Differential rates of digestion among species may seriously bias stomach content analyses in favor of species with large and robust hard parts.

Using these methods, there is generally little that can be done about the potential biases caused by nonrepresentative sample collection and the consumption of species without hard parts. However, a number of studies have attempted to experimentally measure in vivo the reduction in the size of otoliths that occurs during digestion and to apply correction factors to estimates of diet composition (e.g., Bigg and Fawcett 1985; Harvey 1989; Tollit et al. 1997). Although this is desirable, a correction for the complete digestion of ingested otoliths should also be made (Jobling 1987). Estimates of these prey-number correction factors (NCFs) come from the same studies in which partial-erosion correction factors have been derived. Nevertheless, corrections for the complete digestion of otoliths have not been routinely used. The purpose of this paper is to show that these correction factors usually exceed 1.0, to briefly illustrate their effect on estimates of marine mammal diets, and to encourage well-designed experimental studies to better determine the magnitude of these factors.

## Methods

The data were obtained from nine papers (Table 1). An experiment by Gales and Cheal (1992) on two captive Australian sea lion (*Neophoca cinerea*) were not included in Table 1, as the number of otoliths of each prey species fed and recovered was not provided and thus correction factors could only be approximated from percentages in their fig. 2. Furthermore, the recovery rate was based on otoliths recovered from an aggregate of meals over a period of 4–7 days rather than from individual meals as in the other studies. Given this experimental design, it was not clear that the recovery rate calculated by Gales and Cheal (1992) were comparable with the other studies. Nevertheless, their results do help to shed light on some of the factors that may affect correction factors (see Discussion).

Otoliths not recovered from experimental meals may have been lost because they were completely digested or because the method used to recover otoliths was ineffective. Ineffective otolith recovery will introduce a positive bias in estimates of the number of otoliths lost to digestion. Thus, prior to analyses, I evaluated the quality and comparability of the data from each of these nine studies. The effectiveness of otolith recovery was tested in only five of the nine studies (Table 2.) Testing was done by distributing in the pool or feeding to the animals glass beads or by distributing marked otoliths of various sizes in the tank before draining the water and feces. The rate of recovery of these glass beads or otoliths was then used to infer the recovery of otoliths and cephalopod beaks from experimental meals. Essentially all test glass beads or otoliths were recovered in three of the five studies, indicating that all otoliths that survived digestion were likely recovered. In the study by Tollit et al. (1997), all test English whiting otoliths were recovered, but only 70–73% of sand eel otoliths were recovered. As the Atlantic cod fed in the Tollit et al. (1997) study were of similar size to the English whiting, I assumed that all Atlantic cod and English whiting otoliths were recovered. However, I corrected the number of otoliths recovered from other prey, with smaller otoliths, by applying the reciprocal of the mean sand eel otolith recovery test results (i.e., 1.40) to these species. Similarly, Dellinger and Trillmich (1988) recovered on average only 74% of test glass beads. Thus, I corrected their data by a factor of 1.35.

Four studies did not test the effectiveness of otolith recovery. In three of these, however, the conditions in which the animals were held suggested that few otoliths would have been missed. However, in the study by Prime and Hammond (1987), the authors noted that some fecal material could have been lost and thus the effect of digestion on otolith disappearance was confounded by effectiveness of otolith recovery. Thus, data from this study may overestimate the effect of digestion on otolith recovery rate.

NCFs were calculated as the inverse of the proportion of the number of sagittal otoliths/beaks fed that were recovered in fecal samples. Some of the NCFs from Tollit et al. (1997) were recalculated from the data given in the paper, as the reported NCFs did not agree with the data. However, in all but one case (i.e., Atlantic herring), the differences between the recalculated factors and those presented in Table 3 were insignificant. NCFs were calculated from the data in Harvey and Antonelis (1994) by combining feeding trials across the two seals before calculating the proportion recovered.

Approximate 95% confidence limits of the NCFs were calculated assuming a binomial distribution with otoliths as the sampling unit. In most cases, these limits are too small, as they assume that each otolith was involved in an independent trial. In reality, groups of otoliths were fed together to an individual seal or, in some cases, to a group of seals.

To examine the effect of prey size on NCFs, I used only values for each of the size-classes of prey fed to seals, excluding the overall average values from studies that fed more than one size-class. For example, there are nine estimates of NCFs for Atlantic cod in Table 1. Excluding the two average values left seven estimates to be used to examine the effect of prey size on NCFs.

One- and two-way ANOVAs were used to test for differences in NCFs among species and for the effect of pinniped species and prey type on NCFs of Atlantic herring. A Mann–Whitney test was used to test the effect of experimental housing (i.e., wet versus dry) on NCFs. An alpha level of 0.05 was used to establish statistical significance. Statistical analyses were performed using SPSS version 8.0. The standard error is given as a measure of variability about the mean.

## Results

NCFs were available for 24 fish and four invertebrate species (Table 1). Although five species of pinnipeds (three phocids and two otariids) have been used in experiments to estimate these NCFs, most of the data were derived from experiments with harbour seals (*Phoca vitulina*) and to a lesser extent on grey seals (*Halichoerus grypus*). NCFs differed greatly among prey species, ranging from 1.0 to 25.0 (Table 1). For the subset of prey species with three or more estimates, NCFs varied significantly among species (one-way ANOVA on inverse transformed data,  $F_{4,27} = 13.4$ ,  $p < 0.001$ ) (Table 3). NCFs for Atlantic cod and English whiting did not differ significantly; however, these factors were significantly lower than the NCFs for Atlantic herring, sprat, and sand eel, which also did not differ from one another (Table 3). In 58 of 66 cases, the estimated confidence limits on the NCFs did not include 1.0 (Table 1). Marcus et al. (1998) found the NCF for Atlantic cod (mean length 25 cm) was 1.0 ( $n = 120$  otoliths fed). However, in most cases where the 95% confidence limits included 1.0, sample size was small (i.e., 20–54 otoliths fed).

Some of the variation in NCFs among species may be an artifact of experimental housing conditions, namely whether the seals could exercise by swimming or not during the feeding trial. In three of the studies, the seals were held in dry

**Table 1.** Prey size (cm), pinniped species and age-class (ad, adults; juv, juveniles), and experimental condition (wet or dry, see text) used to estimate NCFs for fish and invertebrates.

Species		Meal size	Prey		NCF		Pinniped species and age-class	No.	Condition
Common name	Scientific name		Length	Structures <sup>a</sup>	Mean <sup>b</sup>	95% CL			
<b>Fish</b>									
Atlantic cod <sup>e</sup>	<i>Gadus morhua</i>	Average	17	54	1.1	1.0–1.3	Harbour, ad/juv	7	Wet
Atlantic cod <sup>e</sup>	<i>Gadus morhua</i>	Average <sup>c</sup>	22	148	1.2	1.1–1.4	Harbour, ad/juv	7	Wet
Atlantic cod <sup>e</sup>	<i>Gadus morhua</i>	Average	23	60	1.5	1.2–1.8	Harbour, ad/juv	7	Wet
Atlantic cod <sup>f</sup>	<i>Gadus morhua</i>	Average <sup>c</sup>	25	190	1.2	1.1–1.3	Grey, juv	8	Wet
Atlantic cod <sup>f</sup>	<i>Gadus morhua</i>	Half	25	70	1.5	1.3–1.8	Grey, juv	8	Wet
Atlantic cod <sup>f</sup>	<i>Gadus morhua</i>	1.5	25	120	1.0		Grey, juv	4	Wet
Atlantic cod <sup>g</sup>	<i>Gadus morhua</i>	Average	25	70	1.2	1.1–1.3	Grey, ad	2	Wet
Atlantic cod <sup>e</sup>	<i>Gadus morhua</i>	Average	27	34	1.1	1.0–1.4	Harbour, ad/juv	7	Wet
Atlantic cod <sup>h</sup>	<i>Gadus morhua</i>	Average	29	52	1.2	1.1–1.4	Harbour, juv	1	Dry
Haddock <sup>h</sup>	<i>Melanogrammus aeglefinus</i>	Average	24	20	1.1	1.0–1.5	Harbour, juv	1	Dry
Walleye pollock <sup>i</sup>	<i>Theragra chalcogramma</i>	Average	29	238	1.3	1.2–1.4	Harbour, ad/juv	4	Wet
Atlantic tomcod <sup>j</sup>	<i>Microgadus proximus</i>	Average	21	92	6.6	4.1–11.7	NES, <sup>d</sup> juv	2	Dry
Atlantic tomcod <sup>k</sup>	<i>Microgadus proximus</i>	Average	—	98	1.4	1.3–1.6	Harbour, ad/juv	6	Wet
English whiting <sup>e</sup>	<i>Merlangius merlangus</i>	Average	10	242	1.7	1.5–1.9	Harbour, ad/juv	7	Wet
English whiting <sup>e</sup>	<i>Merlangius merlangus</i>	Average	18	234	1.4	1.3–1.5	Harbour, ad/juv	7	Wet
English whiting <sup>e</sup>	<i>Merlangius merlangus</i>	Average <sup>c</sup>	18	744	1.4	1.3–1.5	Harbour, ad/juv	7	Wet
English whiting <sup>e</sup>	<i>Merlangius merlangus</i>	Average	22	102	1.3	1.2–1.5	Harbour, ad/juv	7	Wet
English whiting <sup>h</sup>	<i>Merlangius merlangus</i>	Average	25	23	1.2	1.1–1.6	Harbour, juv	1	Dry
English whiting <sup>e</sup>	<i>Merlangius merlangus</i>	Average	26	166	1.2	1.1–1.3	Harbour, ad/juv	7	Wet
English whiting <sup>g</sup>	<i>Merlangius merlangus</i>	Average	31	136	1.2	1.1–1.2	Grey, ad	2	Wet
Pout whiting <sup>g</sup>	<i>Trisopterus luscus</i>	Average	20	112	1.1	1.1–1.2	Grey, ad	2	Wet
Pacific hake <sup>j</sup>	<i>Merluccius productus</i>	Average	25	154	3.7	2.8–5.0	NES, <sup>d</sup> juv	2	Dry
Pacific hake <sup>i</sup>	<i>Merluccius productus</i>	Average	33	290	1.4	1.3–1.5	Harbour, ad/juv	4	Wet
Dover sole <sup>k</sup>	<i>Microstomus pacificus</i>	Average	—	24	1.2	1.0–1.6	Harbour, ad/juv	6	Wet
English sole <sup>k</sup>	<i>Pleuronectes vetulus</i>	Average	—	88	4.1	2.9–6.4	Harbour, ad/juv	6	Wet
Lemon sole <sup>e</sup>	<i>Microstomus kitt</i>	Average	19	76	3.8 (5.4)	2.6–6.0	Harbour, ad/juv	7	Wet
Lemon sole <sup>e</sup>	<i>Microstomus kitt</i>	Average <sup>c</sup>	23	108	2.3 (3.2)	1.9–3.0	Harbour, ad/juv	7	Wet
Lemon sole <sup>e</sup>	<i>Microstomus kitt</i>	Average	33	32	1.1 (1.6)	1.0–1.3	Harbour, ad/juv	7	Wet
Rex sole <sup>k</sup>	<i>Errex zachirus</i>	Average	—	188	1.3	1.2–1.4	Harbour, ad/juv	6	Wet
European plaice <sup>e</sup>	<i>Pleuronectes platessa</i>	Average	23	48	1.7 (2.4)	1.4–2.3	Harbour, ad/juv	7	Wet
European plaice <sup>g</sup>	<i>Pleuronectes platessa</i>	Average	17	134	1.6	1.4–1.9	Grey, ad	2	Wet
Dab <sup>g</sup>	<i>Limanda limanda</i>	Average	12	28	2.2	1.5–3.6	Grey, ad	2	Wet
Eulachon <sup>k</sup>	<i>Thaleichthys pacificus</i>	Average	—	152	2.9	2.3–3.7	Harbour, ad/juv	6	Wet
Sand eel <sup>e</sup>	<i>Ammodytes marinus</i>	Average	9	114	5.2 (7.1)	3.6–8.0	Harbour, ad/juv	7	Wet

**Table 1** (concluded).

Species		Meal size	Prey		NCF		Pinniped species and age-class	No.	Condition
Common name	Scientific name		Length	Structures <sup>a</sup>	Mean <sup>b</sup>	95% CL			
Sand eel <sup>e</sup>	<i>Ammodytes marinus</i>	Average	14	314	4.7 (6.5)	3.8–5.8	Harbour, ad/juv	7	Wet
Sand eel <sup>e</sup>	<i>Ammodytes marinus</i>	Average <sup>c</sup>	15	1118	2.8 (4.0)	2.7–2.9	Harbour, ad/juv	7	Wet
Sand eel <sup>e</sup>	<i>Ammodytes marinus</i>	Average	16	400	2.1 (2.9)	2.0–2.3	Harbour, ad/juv	7	Wet
Sand eel <sup>e</sup>	<i>Ammodytes marinus</i>	Average	18	290	2.6 (3.6)	2.2–3.0	Harbour, ad/juv	7	Wet
Pacific herring <sup>i</sup>	<i>Clupea pallasii</i>	Average	18	3956	3.4	3.2–3.5	Harbour, ad/juv	4	Wet
Pacific herring <sup>j</sup>	<i>Clupea pallasii</i>	Average	20	126	21.0	9.9–56.7	NES, <sup>d</sup> juv	2	Dry
Pacific herring <sup>k</sup>	<i>Clupea pallasii</i>	Average	—	64	3.1	2.2–4.8	Harbour, ad/juv	6	Wet
Atlantic herring <sup>l</sup>	<i>Clupea harengus</i>	Average	21	590	1.4 (2.0)	1.4–1.5	Northern fur, ad	3	Dry
Atlantic herring <sup>l</sup>	<i>Clupea harengus</i>	Average	21	538	2.0 (2.9)	1.9–2.1	Sea lion, ad	2	Dry
Atlantic herring <sup>f</sup>	<i>Clupea harengus</i>	Average <sup>c</sup>	25	120	2.3	1.9–2.9	Harbour, juv	1	Wet
Atlantic herring <sup>f</sup>	<i>Clupea harengus</i>	Average <sup>c</sup>	25	334	4.1	3.4–5.0	Grey, juv	8	Wet
Atlantic herring <sup>f</sup>	<i>Clupea harengus</i>	Half	25	24	4.0	2.1–10.2	Harbour, juv	1	Wet
Atlantic herring <sup>f</sup>	<i>Clupea harengus</i>	Half	25	94	5.9	3.8–10.2	Grey, juv	8	Wet
Atlantic herring <sup>f</sup>	<i>Clupea harengus</i>	Double	25	96	1.6	1.4–1.9	Harbour, juv	1	Wet
Atlantic herring <sup>f</sup>	<i>Clupea harengus</i>	1.5	25	120	1.6	1.4–1.9	Grey, juv	4	Wet
Atlantic herring <sup>f</sup>	<i>Clupea harengus</i>	Double	25	120	2.1	1.8–2.6	Grey, juv	3	Wet
Atlantic herring <sup>e</sup>	<i>Clupea harengus</i>	Average	26	8732	3.3 (4.6)	4.4–4.8	Harbour	7	Wet
Atlantic herring <sup>m</sup>	<i>Clupea harengus</i>	Average	26	54	25.0	7.5–204	Harbour, ad	1	Dry
Sprat <sup>l</sup>	<i>Sprattus sprattus</i>	Average	12	564	1.5 (2.4)	1.4–1.6	Northern fur, ad	3	Dry
Sprat <sup>l</sup>	<i>Sprattus sprattus</i>	Average	12	570	3.0 (4.0)	2.9–3.3	Sea lion, ad	2	Dry
Sprat <sup>e</sup>	<i>Sprattus sprattus</i>	Average	13	252	10.0 (14.0)	6.9–15.0	Harbour, ad/juv	7	Wet
Rainbow trout <sup>k</sup>	<i>Oncorhynchus mykiss</i>	Average	—	146	1.6	1.4–1.8	Harbour, ad/juv	6	Wet
Chinook salmon <sup>i</sup>	<i>Oncorhynchus tshawytscha</i>	Average	14	148	1.6	1.4–1.9	Harbour, ad/juv	4	Wet
Shiner perch <sup>k</sup>	<i>Cymatogaster aggregata</i>	Average	—	240	1.7	1.5–1.9	Harbour, ad/juv	6	Wet
Surf smelt <sup>i</sup>	<i>Hypomesus pretiosus</i>	Average	17	3060	4.3	4.2–4.3	Harbour, ad/juv	4	Wet
Pacific staghorn sculpin <sup>k</sup>	<i>Leptocottus armatus</i>	Average	—	174	2.1	1.8–2.5	Harbour, ad/juv	6	Wet
Shortspine thornyhead <sup>k</sup>	<i>Sebastolobus alascanus</i>	Average	—	90	1.1	1.0–1.2	Harbour, ad/juv	6	Wet
<b>Invertebrates</b>									
Squid <sup>e</sup>	<i>Loligo forbesi</i>	Average	—	27	1.4	1.1–1.9	Harbour, ad/juv	7	Wet
Berryteuthis <sup>j</sup>	<i>Berryteuthis magister</i>	Average	17	33	1.1	1.0–1.4	NES, <sup>d</sup> juv	2	Dry
Loligo <sup>j</sup>	<i>Loligo opalescens</i>	Average	12	55	1.2	1.1–1.5	NES, <sup>d</sup> juv	2	Dry
Loligo <sup>k</sup>	<i>Loligo</i> sp.	Average	—	35	2.3	1.6–3.7	Harbour, ad/juv	6	Wet
Octopus <sup>e</sup>	<i>Eledone cirrhosa</i>	Average	—	36	1.2	1.1–1.5	Harbour, ad/juv	7	Wet

<sup>a</sup>Sagittal otoliths or squid beaks.<sup>b</sup>Original values in parentheses (see Methods).<sup>c</sup>Average NCF calculated over all length-classes or meal sizes fed.<sup>d</sup>Northern elephant seal.<sup>e</sup>Tollit et al. (1997).<sup>f</sup>Marcus et al. (1998).<sup>g</sup>Prime and Hammond (1987).<sup>h</sup>Prime (1979).<sup>i</sup>Cottrell et al. (1996).<sup>j</sup>Harvey and Antonelis (1994).<sup>k</sup>Harvey (1989).<sup>l</sup>Dellinger and Trillmich (1988).<sup>m</sup>da Silva and Neilson (1985).

**Table 2.** Methods used to test the effectiveness of otolith recovery and to feed test prey in experiments on captive pinnipeds.

Effectiveness of recovery	Method to feed prey	Comments	% recovery	Source
Not tested	Atlantic herring as carrier	Animal held in dry compound; all feces recovered		Prime 1979
Not tested	1 otolith removed	Animal held in raised dry pen with mesh bottom; 95% of each fecal sample recovered based on visual estimate		da Silva and Neilson 1985
Not tested	Whole	Animals in water; not possible to distinguish loss during recovery from complete digestion		Prime and Hammond 1987
90 glass beads fed in 11 trials	Whole	Animals in dry room but given time each day to interact with other pinnipeds	74.0±37.7	Dellinger and Trillmich 1988
34 otoliths scattered in tank on 3 days	Whole	Pairs of seals held in water during feeding trial	97	Harvey 1989
Not tested	Whole	Animals held in dry cage; all fecal material collected twice daily		Harvey and Antonellis 1994
20–25 marked otoliths	Whole	Seals housed individually in water during feeding trials	100	Cotrell et al. 1996
36 marked otoliths on two occasions	Atlantic herring used as carrier	All seals held in same pool in water during the feeding trials	100	Tollit et al. 1997
60 glass beads at each of 42 fecal collections	Atlantic herring whole; Atlantic cod heads in Atlantic herring	Seals housed individually in water during feeding trials	70–73 sand eel 99.1±1.3	Marcus et al. 1998

surroundings for the duration of a feeding trial and were therefore relatively inactive, whereas in the other studies, the seals were able to swim during the feeding trials. Level of activity is known to affect the rate of digestion in mammals (see Harvey 1989), and thus, experimental condition might have effected estimates of NCFs. I examined the hypothesis that this difference might account for some of the variation in NCFs by comparing the NCFs for the same prey species using both the wet and dry protocols. In the case of Atlantic herring, the mean NCF from dry feeding trials was higher (12.5,  $n = 4$ ) and more variable (CV = 94.5%) than those from wet feeding trials (mean = 3.3, CV = 40%,  $n = 7$ ). However, this difference was not significant (Mann–Whitney test,  $p = 0.65$ ). The dry protocol estimate of the NCF for Atlantic tomcod was about five times higher than the wet protocol estimate. However, this result is confounded by the fact that different seal species were used in the two studies. In species with more robust otoliths (e.g., Atlantic cod and English whiting), the data suggest that there is little difference among NCFs estimated in experiments using the wet or dry feeding protocol (Table 1). The data on sprat are unusual in this regard, as the estimate from Tollit et al. (1997) using the wet protocol was much higher than the two estimates using the dry protocol (Table 1). However, these results are further confounded, as three species of pinnipeds were used in these experiments.

Data were available for several prey species to examine the influence of prey size on NCFs. In English whiting, NCFs appear to vary inversely with prey length ( $r = -0.96$ ,  $p = 0.002$ ,  $n = 6$ ); however, in Atlantic cod ( $r = 0.06$ ,  $p = 0.89$ ,  $n = 7$ ) and Atlantic herring ( $r = -0.31$ ,  $p = 0.42$ ,  $n = 10$ ), there was no correlation between prey length and NCF.

Differences in digestive efficiency among pinniped species might result in different NCFs within prey species. To examine this, I compared the NCFs of Atlantic cod and Atlantic and Pacific herring fed to grey seals and harbour seals. There was no difference in the NCFs of either prey species between seal species (Table 4). However, the mean NCF of Atlantic tomcod fed to two northern elephant seals (*Mirounga angustirostris*) (6.6, 95% CI = 4.1–11.7) was higher than that found in six harbour seals (1.4, 95% CI = 1.3–1.6), suggesting a predator digestion effect on NCF (Table 1). This conclusion is somewhat confounded, as the northern elephant seals were held in dry conditions during the feeding experiment, whereas the harbour seals were held in water. The mean NCFs for sprat also differed among three pinniped species, as the 95% confidence intervals did not overlap: northern fur seal (*Callorhinus ursinus*), 1.4–1.6; California sea lion (*Zalophus californianus*), 2.9–3.3; harbour seal, 6.9–15.0. Here again, different holding conditions were used with the northern fur seals and sea lions during the feeding experiment compared with the harbour seal. However, the direction of the effect (i.e., lower NCF in dry conditions) appears to be the reverse of that expected if experimental conditions were the source of the difference (Table 1).

## Discussion

It has been known for some time (e.g., Prime 1979; Frost and Lowry 1980) that prey hard structures, used to both

**Table 3.** NCFs for prey species with three or more observations from captive feeding experiments with several species of pinnipeds (see Table 1).

	Atlantic cod	English whiting	Atlantic herring	Sprat	Sand eel
Mean	1.2 <i>a</i>	1.3 <i>a</i>	6.6 <i>b</i>	4.8 <i>b</i>	3.5 <i>b</i>
SE	0.07	0.08	2.48	2.62	0.62
<i>n</i>	7	6	11	3	5

**Note:** One-way ANOVA:  $F_{4,27} = 13.4$ ,  $p < 0.001$ . Means followed by the same letter are not significantly different at the 5% level (Sidak multiple-comparisons test).

**Table 4.** NCFs of Atlantic cod and Atlantic and Pacific herring fed to grey and harbour seals.

	Atlantic cod		Atlantic and Pacific herring	
	Grey seal	Harbour seal	Grey seal	Harbour seal
Mean	1.2	1.2	4.0	6.1
SE	0.26	0.16	1.90	8.37
<i>n</i>	3	4	3	7

**Note:** Two-way ANOVA, main effects: prey species,  $p = 0.22$ ; seal species,  $p = 0.73$ .

identify and determine the size and number of prey consumed by marine mammals, are eroded and in some cases completely dissolved during digestion. Thus, in most cases, the number of recovered otoliths underestimates the number of ingested otoliths and therefore the number of ingested prey. The biases produced by the complete and partial digestion of otoliths/beaks also have been appreciated for some time (e.g., Jobling and Breiby 1986). As a result, a growing number of studies have attempted to estimate prey-specific factors to correct for these two biases (see Introduction). However, in practice, authors have corrected only for partial erosion of otoliths in the reconstruction of marine mammal diets. Given the results presented in Tables 1 and 5, there can be little doubt that the use of NCFs to account for the complete digestion of otoliths and cephalopod beaks could have a significant effect on estimates of the number of prey consumed by marine mammals.

The implications of complete digestion of otoliths for estimates of marine mammal diet have been previously explored (Jobling 1987). For example, if equal numbers of haddock and herring were ingested, Jobling (1987) showed that one would conclude that the marine mammal consumed 3.6 times as many haddock as herring, based on recovered otoliths. In the case of grey seals on Sable Island, sand lance dominate the number of prey eaten (Bowen and Harrison 1994). Application of NCFs to the July 1991 sample of otoliths resulted in an increase in the estimated number of sand lance eaten to 95.3% from 88.1% with a corresponding decrease in the percentage of other prey. Clearly, the impact of NCFs on estimates of diet composition will vary with the mixture of prey species consumed and their relative NCFs. In general, however, the use of NCFs will tend to decrease the importance of gadoids in the diets of pinnipeds. As such, their use could have implications with respect to the importance of pinniped predation on the dynamics of many

**Table 5.** Mean NCFs for fish and invertebrates.

Prey species	Prey length range (cm)	Mean NCF
Atlantic cod	16–33	1.2
Haddock	22–32	1.1
Walleye pollock	20–38 <sup>a</sup>	1.3
Atlantic tomcod	na	1.4
English whiting	9–31	1.3
Pout whiting	na	1.1
Pacific hake	27–39 <sup>a</sup>	1.4
Dover sole	na	1.2
English sole	na	4.1
Lemon sole	16–35	2.1
Rex sole	na	1.3
European plaice	21–24	1.6
Dab	na	2.2
Eulachon	na	2.9
Sand eel	8–19	3.6
Atlantic herring	13–28 <sup>b</sup>	3.0
Sprat	12–14	4.8
Rainbow trout	na	1.6
Chinook salmon	12–17 <sup>a</sup>	1.6
Shiner perch	na	1.7
Surf smelt	14–20 <sup>a</sup>	4.3
Pacific staghorn sculpin	na	2.1
Shortspine thornyhead	na	1.1
<i>Berryteuthis</i>	14–20	1.1
<i>Loligo forbesi</i>	na	1.4
<i>Loligo opalescens</i>	9–15	1.3
<i>Loligo</i> sp.	na	2.3
Octopus	401–1025 <sup>c</sup>	1.2

**Note:** na, not available.

<sup>a</sup>Range estimated as  $\pm 3$  SD.

<sup>b</sup>Excluding values from dry condition experiments.

<sup>c</sup>Mass in grams.

groundfish species. Given these implications, it would be unwise to continue to assume that NCFs are not required.

There is little evidence from the recent literature that investigators are aware of this bias. Part of the reason why NCFs have not been regularly used may stem from the fact that, until recently, too few prey species and marine mammals had been studied to provide much confidence in their use. However, recent studies (Cottrell et al. 1996; Tollit et al. 1997; Marcus et al. 1998) combined with earlier work provide a firmer empirical basis for the use of NCFs. A broad range of prey species, representing those with small, fragile otoliths and those with large, robust otoliths, now have been used in feeding studies. Thus, as a first approximation, authors will generally be able to find NCFs from an analogous prey species to fill gaps.

Although I would argue that the use of NCFs will improve estimates of the species composition of marine mammal diets, the existing estimates of NCFs are not satisfactory in several respects. There is evidence that at least five factors affect NCFs within a prey species: meal size (Marcus et al. 1998), the condition in which the animal is held (i.e., in water versus dry; see Results), the size of prey used (Tollit et

al. 1997), the species of pinniped, and the effectiveness of hard part recovery. Yet for none of these factors have experiments been conducted across a range of prey types and pinnipeds species under standardized experimental conditions. Although data on the effect of experimental housing on NCFs are conflicting, exercise likely affects digestive efficiency in pinnipeds, and thus, it would seem prudent to provide pinnipeds with the opportunity to exercise during feeding trials. The length-specific NCFs for English whiting and lemon sole are quite convincing. However, despite the evidence that NCFs in some prey species may vary as a function of length, there is not enough data at this time to use size-specific NCFs in most cases. The influence of pinniped species on NCFs within prey species is also unclear. There appears to be little difference in the NCFs of prey consumed by harbour and grey seals, but the northern elephant seal data suggests that even within phocids, there may be pinniped species effects. Although not included in Table 1, the high NCFs (i.e., >25) in six prey species fed to the otariid *N. cinerea* (Gales and Cheal 1992) differ from the results of Dellinger and Trillmich (1988) for two other otariids, again suggesting pinniped species effects on NCFs. Lack of standardization also applies to the method of feeding otoliths and cephalopod beaks to pinnipeds (Table 2). Whole prey should be used in these experiments. Although this may not be possible in all cases, we need to understand the effect on NCFs of using a carrier species, such as Atlantic herring, to present otoliths of other prey species to pinnipeds. Until this is done, comparisons among studies will be problematic.

Recent developments in the use of telemetry and animal-borne video to determine feeding frequency, meal size, and the size of prey eaten by free-ranging marine mammals suggest that it may be possible to greatly improve estimates of diet composition by using NCFs that account for these variables. Thus, future experimental studies should systematically investigate the relationships between NCFs, meal size, and prey size for a range of species differing in otolith architecture. It is also important to obtain estimates of the variability of NCFs such that this variability can be used to estimate confidence limits associated with diet composition (Hammond and Rothery 1996).

There is also the issue of whether to use NCFs derived from hard parts recovered in feces on hard parts recovered from stomach contents. Murie and Lavigne (1985) showed that the proportion of Atlantic herring otoliths recovered from the stomachs of harp (*Phoca groenlandica*) and grey seals decreased inversely with time since feeding. Up to 3 h postfeeding, 100% of the otoliths were recovered from the stomachs, indicating an NCF of 1.0. However, beyond 3 h, the percentage of otoliths recovered in the stomach decreased rapidly, reaching 0% after 12 h. The clearance and digestion rate will undoubtedly differ among prey species. Thus, it would not seem possible to apply the NCFs derived from recovery of otoliths and cephalopod beaks in feces to hard parts recovered from stomach contents. However, Murie and Lavigne's (1985) work does indicate that, with the exception of quite recently ingested meals, the number of recovered otoliths from stomach contents will not accurately estimate the number of prey consumed.

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