Using Simulations to Evaluate Reconstructions of Sea Lion Diet from Scat

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Abstract

Models used to describe pinniped diet can provide very different composition estimates. Occurrence indices as well as biomass reconstruction models (which use estimates of the number and sizes of prey consumed) are commonly used and increasingly utilize a variety of fish hard remains (bones) found in scats. However, the importance of any single fish can be overestimated if its bones are deposited in a succession of scats assumed to be from different fish. Similarly, the importance of a species will be underestimated relative to other species if the bones of one species are more fragile and are completely digested or if bones from different fish of the same species are contained in a single scat and assumed to be from a single fish. Species differences in the proportion of fish bones that survive digestion can be assessed from captive feeding studies where the number and species of prey consumed is known. Numerical correction factors can be calculated to take into account the levels of complete digestion. We performed computer simulations using data from captive feeding studies to investigate levels and sources of error in reconstructing simulated mixed species diets. Our simulations used different combinations of hard remains, were conducted both with and

without the application of numerical correction factors, and compared four different diet indices (1. Modified frequency of occurrence, 2. Split sample frequency of occurrence, 3. Variable biomass reconstruction, 4. Fixed biomass reconstruction). Simulations indicated that levels of error were related to the MNI method of inferring fish numbers from prey remains, prey size, the number of identifiable prey structures used, and the robustness of the remains to digestive processes (recovery rate). The fewer fish fed, the higher the relative probability of counting the fish, particularly when a multiple element structure or all structure techniques are used. If recovery rates were assumed to be consistent across species, then large fish (particularly when fed in small amounts) were overestimated relative to smaller sized prey in all models, but particularly biomass reconstruction models and when using more than one paired structure. When recovery rates of a paired structure (otoliths) were varied across species (as observed in captive feeding studies) then biomass models with no correction factors applied tended, as expected, to overestimate the species with high recovery rates. In contrast, frequency of occurrence models overestimated the contribution of smaller prey (particularly when fed in small amounts). Simulations also indicated correction factors can reduce levels of error in biomass reconstruction models, but cannot solve problems related to counting fish using MNI. Our work shows simulations can form a valuable component in assessing diet indices and the level (and direction) of associated errors in each.

Introduction

Diet composition is increasingly being estimated from prey hard remains (bones) found in pinniped scat (e.g., Browne et al. 2002). A number of different techniques can be used to describe diet and, therefore, it is important to understand the bias and errors associated with each. In the past, otoliths were the most commonly used structure to enumerate and reconstruct diet. However, otoliths from some species are rarely found in scats (e.g., salmonid species) or are difficult to distinguish to the species level (e.g., salmonid and rockfish species). Recently there has been a trend toward using all recovered structures to circumvent problems of high digestibility and non-differentiation of otoliths (Sinclair and Zeppelin 2002, Tollit et al. 2004). However, the bias and error associated with the multi-structure technique have not been fully investigated (Olesiuk et al. 1990, Cottrell and Trites 2002, Laake et al. 2002, Arim and Naya 2003, Tollit et al. 2003).

In scat analysis, it is important not only to determine species presence, but also the proportional contribution of each species. We selected four commonly used indices that are used to describe contributions of prey from hard remains found in scat. There are two methods that use species occurrence data to estimate prey proportions (modified and split-

sample frequency of occurrence), and two variants of a method that use a volumetric technique which combines prey counts and weights to estimate prey biomass proportions (fixed and variable biomass reconstructions; see Laake et al. 2002). However, Laake et al. (2002) found up to a ten-fold difference between consumption estimates using one of each of these models for the smallest and largest prey, highlighting the need for further studies investigating the causes of such differences. Attempts to improve biomass reconstructions include using numerical correction factors, which aim to take into account the different prey species' digestibility (and hence the proportion recovered) or passage probabilities (e.g., Bowen 2000, Browne et al. 2002).

In this paper, we used a computer simulation model that aimed to replicate captive feeding studies. We varied the input parameters of the model to examine the errors associated with methods for enumerating fish, and we investigated the performance of four diet reconstruction indices in assessing a mixed diet (considered a worst case scenario). In particular, we investigated the impact of using different combinations of bones, varying species recovery rates, and applying numerical correction factors to biomass reconstruction indices.

Methods

Prey enumeration methods

Presence or absence

In frequency of occurrence methods, any number of identifiable structures of a species found in a scat indicates species presence regardless of the number of structures found in the scat. The number of individual fish is not enumerated, but instead mere presence is noted (Croxall 1993). For example, one recovered vertebra in a scat contributes the same "weight" in frequency of occurrence reconstructions as 100 recovered otoliths from a different species found in the same scat regardless of fish size.

Minimum number of individuals (MNI)

MNI is a zooarchaeological quantification method that has been widely used in scat analysis as a building block for diet reconstruction (Allen and Guy 1984). MNI is used in volumetric indices and not in occurrence indices to compute the minimum number of individuals that can be recognized using all identified bones of a species or using a frequently occurring paired bone (e.g., otoliths; Nichol and Wild 1984). The number of bones counted is divided by the number of elements of that type per fish and rounded up to the nearest whole number. For example, if five otoliths are found, then the MNI fish count would be three fish (as otoliths are found as pairs in each fish). When multiple structures are used, the maximum count is typically based on the most frequently occurring identifiable paired structure.

If the MNI technique is biased on its ability to count fish from elements found in scat, then the diet reconstruction based on these numbers will also be biased. We assessed the ability of MNI to determine relative importance of different species in the diet with binomial probabilities. The binomial probability distribution is used in experiments such as this when the outcome of a single trial is either presence or absence, and the probability of a structure occurring in a given scat has a probability (p). Therefore, the number of bones passed in a scat is assumed to follow a binomial distribution, where the probability of x bones passing when n bones were eaten each with a probability of passage (p) is

$$P(X = x) = \binom{n}{x} p^x (1-p)^{(n-x)}.$$

The expected number of fish $E(F)$ counted is computed as

$$E(F) = \sum_{x=0}^{n} g(x) \times P(X = x),$$

where the value $g(x)$ is

$$\frac{x}{\#elements/fish},$$

rounded up to the nearest whole number of fish as in MNI. When T bone types are counted then

$$E(F) = \max\{E(F_1), ..., E(F_T)\}.$$

Here F_j = number of fish derived from x_j or the count of elements from structure j where $j = 1, \ldots, T$.

Diet reconstruction indices

Diet reconstruction indices provide information regarding the relative species contributions to the overall diet. We looked at four commonly used indices. Frequency of occurrence indices are simpler to construct given that no information is needed on prey number or size.

Frequency of occurrence (FO) indices

Modified frequency of occurrence (mFO). This is a version of the most commonly used reconstruction index, which is based on the presence of a species within a scat (Croxall 1993) and does not require a count of prey structures. For direct comparison, we used the modified version of the index such that the sum of all prey contributions totaled 100%.

$$mFO_i = \frac{\sum_{k=1}^{s} I_{ik}}{\sum_{i=1}^{\omega}\sum_{k=1}^{s} I_{ik}}$$

$i = 1, \ldots, \omega$ species of fish prey, I is an indicator function equal to 1 if the ith species is present in the kth scat, and 0 otherwise.

Split sample frequency of occurrence (SSFO). This method is also based on the presence of a species within a scat. It assumes that all prey present in a scat were consumed in equal quantities and that all meals were of equal size (fixed meal size). Olesiuk et al. (1990) investigated the potential impact of these assumptions and highlight the value of this index when sample sizes are relatively large. In summary, each species in the scat is given a value of 1 divided by the number of species detected in the scat (Olesiuk et al. 1990, Laake et al. 2002).

$$SSFO_i = \frac{\sum_{k=1}^{s}\left(\frac{I_{ik}}{\sum_{i=1}^{\omega} I_{ik}}\right)}{s}$$

$i = 1, \ldots, \omega$ species of fish prey, $k = 1, \ldots, s$ scats, I is an indicator function equal to 1 if the ith species is present in the kth scat, and 0 otherwise.

Biomass reconstruction indices

Variable biomass reconstruction (VBR). This index uses MNI counts of structure elements and weights estimated from the mean species weight to provide relative biomass estimates. Optimally, an estimate of prey size is derived from each structure by back-calculating from bone measurements and considering the degree of partial digestion (see Tollit et al. 2004). The index divides the biomass estimated for each species by the total biomass estimated for all species in all scats. The rationale for this index is that it allows the contributions in scats to be different (variable) sizes, such that biomass is proportional to the actual number of individuals of each prey species consumed (i.e., scats represent an unweighted cross-section of meals eaten). Thus the variable biomass reconstruction index for the ith species is:

$$FBR_i = \frac{f_i \bar{w}_i}{\sum_{i=1}^{\omega} f_i \bar{w}_i}$$

where f_i is the number of fish of species i, $\bar{w}_i$ is the average weight of a fish of species i, and the summation is taken over the number of prey species $i, \ldots, \omega$ (Laake et al. 2002).

Fixed biomass construction (FBR)

This index also uses MNI enumeration from structures, and prey weights to compute the proportion of biomass by species per scat. The FBR index is the average of species proportions across scats. Similar to SSFO, it assumes that a scat represents a fixed quantity of food consumed, such

that the prey proportions within each scat are equally weighted. The fixed biomass reconstruction index for the *i*th species is:

$$VBR_i = \frac{\sum_{k=1}^{s}\left(\frac{f_{ik}\bar{w}_i}{\sum_{i=1}^{\omega} f_{ik}\bar{w}_i}\right)}{s}$$

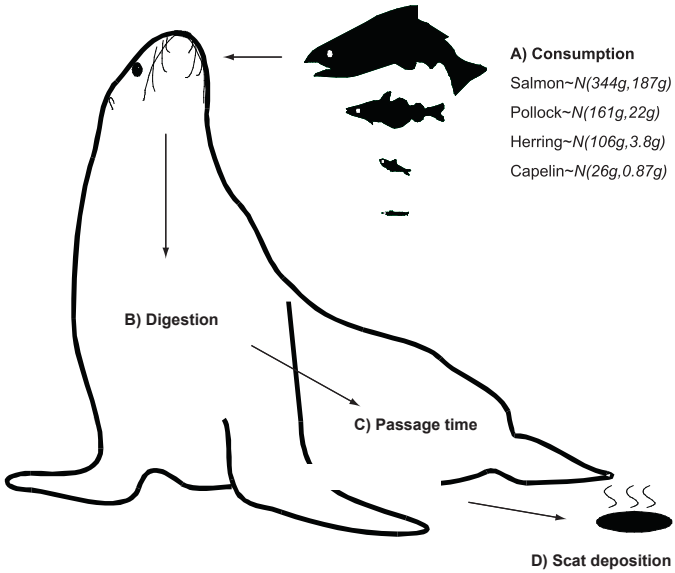
where f_{ik} is the number of fish of species i in scat k, $\bar{w}_i$ is the average weight of species i, s is the number of scats (Laake et al. 2002).

Correction factors

To date, numerical correction factors have typically been calculated only at the species level and for a single paired structure (e.g., otoliths; Bowen 2000). More recently, data on recovery of multiple structures has become available (Cottrell and Trites 2002, Tollit et al. 2003), providing additional information with which to assess diet. In our simulations, we applied numerical correction factors that were unique to each structure and species, and applied them to each structure prior to calculating MNI, and not at the species level after counting the fish. In the first simulation, the recovery rate (passage probability) of all structures was standardized, such that numerical correction factors were identical across species. By setting a constant recovery probability across species, this parameter did not contribute additional error from introducing bias to the results, therefore allowing us to better assess error associated with fish enumeration and biomass reconstruction methods. In the second simulation, experimentally derived numerical correction factors were applied to each species. In both simulations, correction factors were calculated as the inverse of the passage probability and hence can be considered "true" values. This approach, while ignoring the potential error of incorrect values, permitted us to focus on errors in diet reconstruction methodology by omitting error from passage rate variability due to, for example, differences between animals or activity levels.

Simulation experiments

The computer simulation model was designed to replicate captive feeding studies by simulating sea lion consumption, scat deposition, fish enumeration, and biomass reconstruction (Fig. 1.). Simulated meals were composed of four major prey species of the Steller sea lion (walleye pollock, *Theragra chalcogramma*; coho salmon, *Oncorhynchus kisutch*; Pacific herring, *Clupea harengus pallasii*; capelin, *Mallotus villosus*; e.g., Sinclair and Zeppelin 2002); these species also have been used in feeding trials at the Vancouver Aquarium Marine Science Centre and therefore structural passage probabilities were available (Tollit et al. 2003). Meals consumed by individuals were randomized for size (for both total meal size and fish size). The simulated diet was fed for 18 days and scats collected throughout.



A) Consumption: Meals were consumed *(~Exp [24 hr])* for 18 days. The median meal size was 8 kg *(~Unif [0 kg,16 kg])*, or the typical captive meal size for a female Steller sea lion. Prey species weights were normally distributed, proportion biomass was prechosen and reflected a fixed captive diet. Thus the number of individuals eaten in a given meal was a Poisson variable with mean and variance = λ, and λ = *biomass proportion* × *meal size/species weight*. Each fish consumed contained countable structures such as otoliths and vertebrae.

B) Digestion: Probability of structures surviving digestion and being recovered was 0.4 *(~Bin [x_{ij};n_{ij},p])* in simulation 1, and differed by species and structure in simulation 2 *(~Bin [x_{ij};n_{ij},p_{ij}])*, where n_{ij} is the number of structures consumed, and x_{ij} is the number of structures recovered.

C) Passage time: Time it took for a structure to pass through a sea lion *(~Gamma[α,β])*.

D) Scat deposition: Once a structure has passed through the sea lion, structures accumulated until they were expelled in scat at discrete times points *~Exp (24 hrs)*.

One animal consumes a series of random meals for 18 days, all scats were collected, all structures enumerated, correction factors either were or were not applied, and four diet biomass indices were estimated. This whole procedure was replicated 1,000 times, with the four indices reconstructed each time. 95% confidence intervals were empirically derived.

Figure 1. Diagram with details of simulation study that estimated fish biomass in sea lion diet from prey remains found in scat.

In the first set of simulations, we standardized certain variables in an attempt to isolate sources of error. We used the following parameters for the first simulation: the four prey species were fed to a sea lion for 18 days; passage (or recovery) probabilities and passage times of structures were set as equal across all prey species; passage probability for all structures was 0.40; and passage times were set to the value observed in captive feeding trials (passage time~Gamma [$\hat{\mu}$ = 33.3 hours, s = 21.9 hours]). Meal size was a random amount with a median meal size of 8,000 g (~Uniform [min = 0 g; max = 16,000 g]), the typical meal size in captive trials. Average mass of the four prey species matched those fed in the captive experiments (salmon = N~($\hat{\mu}$ = 344 g, s = 186.57), walleye pollock = N~[$\hat{\mu}$ = 161 g, s = 21.9], herring = N~[$\hat{\mu}$ = 106 g, s = 3.78], and capelin = N~[$\hat{\mu}$ = 26 g, s = 0.87]) and were fed as 2.5, 7.5, 22.5, and 67.5% of the biomass, respectively. In short, the number of individual fish fed in a simulated meal, was a random Poisson variable with the mean number (λ) a function of a series of random variables derived elsewhere such that λ = biomass proportion x meal size per species weight.

The biomass proportions were selected specifically to assess the general perception that small prey are underestimated and larger prey are overestimated (Bowen 2000). Thus, in this first selected diet scenario, the larger fish were fed in small amounts and the small fish in large amounts. It should be noted that, the largest fish species contribution was pre-set to a small proportion of biomass (salmon = 2.5%) and therefore might not occur in all meals, but over the length of an 18 day feeding trial would comprise the 2.5% pre-set composition.

To assess the effectiveness of using multiple structures, repeated simulations were conducted (i) using one paired structure (e.g., paired otoliths), (ii) using one structure with 66 elements (e.g., vertebrae), and (iii) using "all structures" in which 10 different paired structures were used to enumerate and estimate biomass.

In the second set of simulations, we used a single paired structure (otoliths) to assess the impact of varying species' passage probabilities (recovery rates) on the performance of the biomass indices. Biomass of salmon, pollock, herring and capelin was pre-set at 3%, 66%, 23%, and 8% respectively. In this scenario, pollock was selected to dominate the diet, a species found in other studies to be overrepresented when estimating numbers using MNI (Tollit et al. 2003). In contrast to simulation 1, capelin only contributed a small proportion. For these species, otolith passage probabilities were 0.10, 0.62, 0.18, and 0.15 respectively and reflected probabilities observed in captive feeding studies (Tollit et al. 2003, D. Tollit unpubl. data).

In both simulations, animals consumed a series of random meals for 18 days and all recovered elements in every scat produced were counted and the four diet indices were calculated both with and without species/structure-specific correction factors. This procedure was replicated 1,000

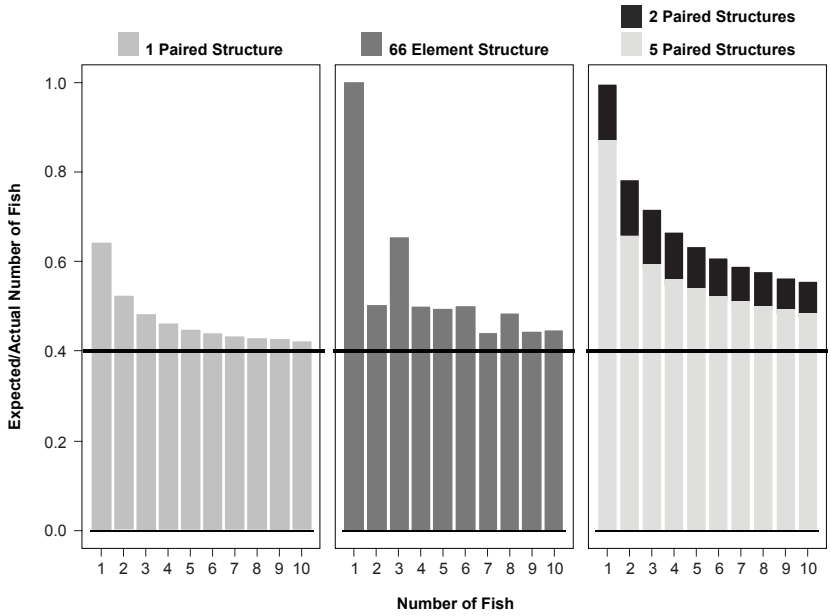


Figure 2. Ratio of fish counted using the minimum number of individuals (MNI) method to actual numbers of fish fed when the passage probability for elements was 0.40. The fewer fish fed, the higher the relative probability of counting the fish, particularly when a multiple element structure (such as vertebrae; middle graph) or all structure techniques (right-most graph) are used. For there to be no enumeration bias, the ratio of expected to actual numbers would be constant for any number of fish eaten (i.e., the bars would all be the same height).

times as if there were 1,000 animals involved in the captive feeding trial. Ninety-five percent confidence intervals were empirically derived as the 25th and 975th ordered observations from 1,000 estimates.

We recognize there are many other sources of error that future simulations need to address, particularly with respect to composition and addressing the significant sampling issues associated with collecting scat from the wild. However, the intention of this simulation study was to look at some of the basic error and bias errors inherent to diet reconstruction in a captive feeding environment. In future simulations, scats could be selected randomly or at one particular time to replicate a scat collection.

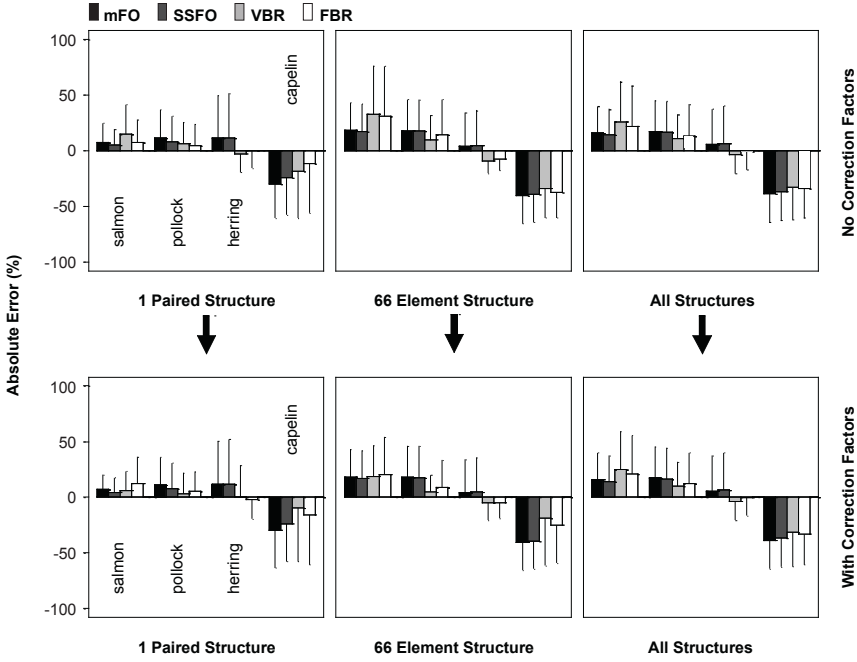


Figure 3a. Results of a simulation experiment in which sea lions were fed a diet of 2.5% salmon, 7.5% pollock, 22.5% herring, and 66.5% capelin. In the left-most graphs, a paired structure such as otoliths was used to infer proportion of fish eaten or relative biomass. In the middle graphs a multiple element structure such as vertebrae was used, and in the right-most graphs all structure techniques (here 10 paired structures) were used. In this simulation the passage probability for all structures was the same (0.40). Fish eaten is represented as four different diet reconstruction indices; for 3a, the y axis denotes the amount of absolute error in these indices, given we know what the animals were fed. The upper graphs are without correction factors applied to the structures found in the scat; the lower graphs are with correction factors applied only to BR indices. The bars represent 95% confidence intervals on the reconstruction indices. In 3b the same data is plotted with the y axis representing the difference between fed and predicted, as a percentage of the amount fed.

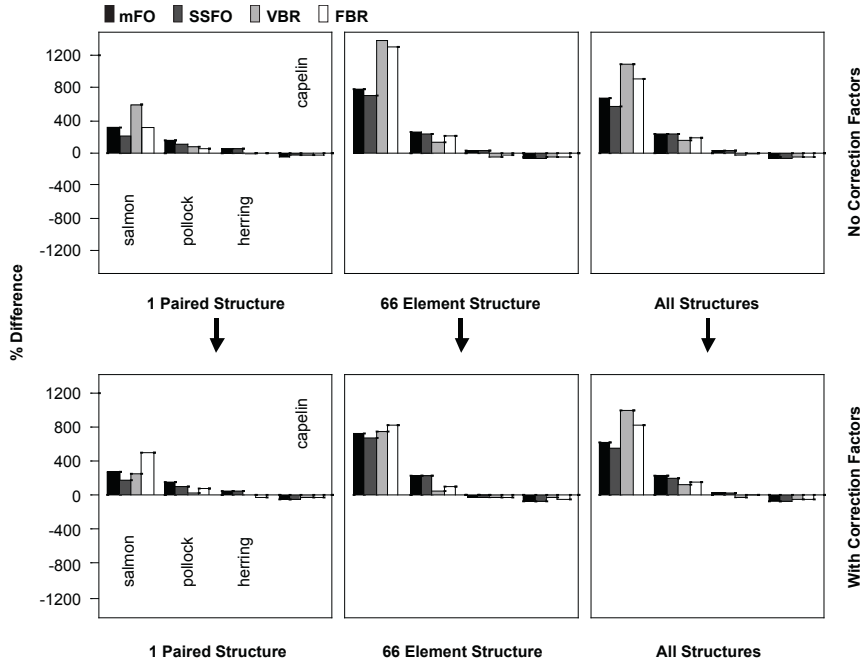


Figure 3b.

Results

Enumeration methods

The first source of error we assessed was the error that arises from estimating fish number using the MNI technique (Fig. 2). For there to be a relative measure of "no error" in fish enumeration, the ratio of expected to observed counts would be constant for any number of fish eaten. Counting fish from structures found in scat using MNI is most problematic when few fish are consumed (Fig. 2). This is true when a paired structure, a 66-element structure, or all structures are used to enumerate fish from structures recovered from scat, but is least for a paired structure. This enumeration problem becomes less important when the number of fish consumed exceeds eight (Fig. 2). The MNI enumeration error observed will contribute to error in biomass reconstruction diet indices (see following sections).

Simulations

It is important to note that simulation results are based on just two mixed diet scenarios, with the aim of taking advantage of computer simulations

to understand underlying causes of error due to prey enumeration as well due to the incorporated variability in consumption, digestion rates, passage times, and deposition. Additionally, all scats are collected in these simulations, which is unlikely to be the case in the wild.

We present error using two different measures. Absolute error is defined as the difference in percentage biomass between the estimated and the actual percentages of fish fed. For example if we fed 2.5% salmon and the diet prediction was 5%, then the absolute error would be +2.5%; if the diet prediction was 1.5% then the absolute error would be –1%. An alternative method to describe error is in terms of percent difference. In this case the difference between that fed and that predicted is calculated as a percentage of the amount fed. For example, if salmon is fed at 2.5% and the diet prediction is 5%, then the percent difference would be calculated as +100%.

Frequency of occurrence indices

Frequency of occurrence indices are affected by errors associated with presence/absence data as well as variability in other parameters. In both simulations, absolute error was largest for species fed in the largest amounts (capelin in Fig. 3a and pollock in Fig. 4b). In both simulations, the proportion of a species consumed in large amounts (>65%) was underestimated (by 22-37%) with little difference between the two FO indices. Predictions of the dominant species were poorer (higher absolute error) when using more than one structure or element, as the more structures used to indicate presence increases the chances of detecting minor prey species. Those species eaten in minor amounts are typically overestimated (Figs. 3 and 4), with the exception being where a large prey item has a low recovery rate (i.e., salmon in the second simulation, Fig. 4b).

Biomass reconstruction indices

Because of the MNI enumeration biases observed (Fig. 2), both VBR and FBR indices estimate less biomass contribution from those species eaten in greater numbers than those eaten in smaller numbers. Per unit mass, larger fish will be eaten in fewer numbers, relative to small fish. Therefore, in the simulation in which passage probabilities were set to 0.40 independent of species or structure, the smaller fish (herring and particularly capelin) were underrepresented while larger fish (pollock and particularly salmon) were overrepresented (Fig. 3). Despite the controlled settings of the simulations, absolute error in the BR indices ranged from zero to <40%, but were least when a single paired structure was used. Ninety-five percent confidence limits remained large across different structures used to enumerate, and across species (Fig. 3a). In the second simulation when recovery rates varied by species but no correction factors were applied, the smaller prey (herring and capelin) with relatively low recovery rates were underestimated and pollock (the

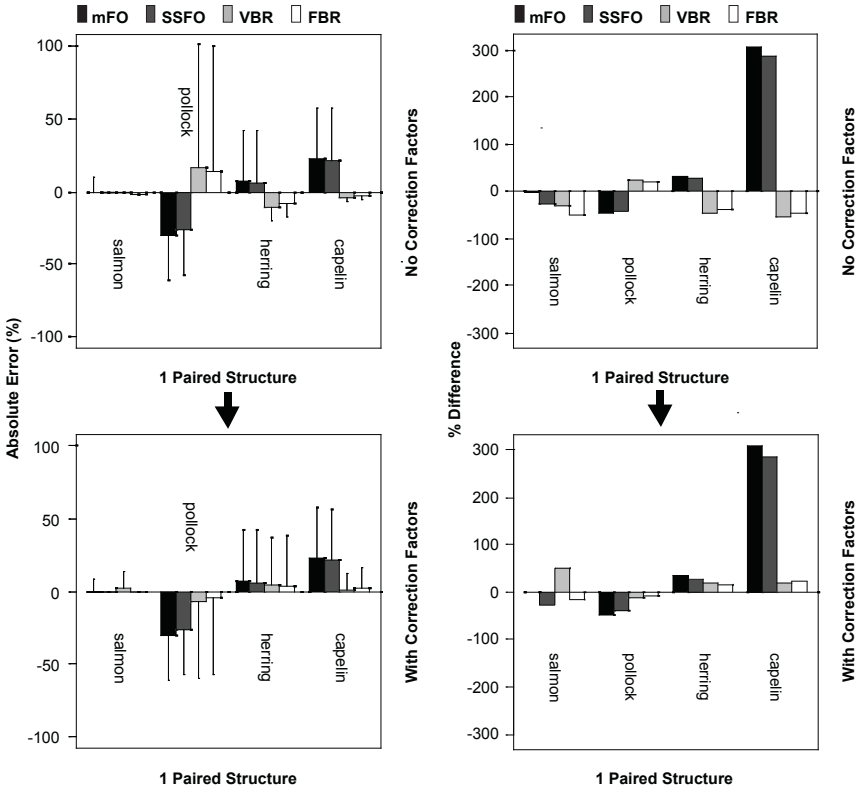


Figure 4. (Left) Results of a second simulation experiment in which sea lions were fed on a diet of 3% salmon, 66% pollock, 23% herring, and 8% capelin. Passage probabilities for a paired structure such as otoliths were varied by species and reflect those of captive feeding trials. Proportion of prey consumed is shown as four different diet reconstruction indices, where the y axis denotes the amount of absolute error in these indices given we know what the animals were fed. The upper graph is without correction factors applied to the structures found in the scat, and the lower graph is with species and structure specific correction factors applied. The bars represent 95% confidence intervals on the reconstruction indices. (Right) The same data is plotted with the y axis representing the difference between fed and predicted as a percentage of the amount fed.

species with the highest recovery rate) overestimated. In stark contrast to simulation 1, salmon was slightly underestimated, highlighting the influence of recovery rates to diet predictions (Fig. 4). When correction factors were applied, absolute error decreased, but did not disappear. In the first simulation where recovery rates were held constant (Fig. 3), the correction factor applied did not vary and therefore no change in the direction of error was observed for any species. Conversely, when species-specific correction factors were applied (Fig. 4), the direction of error changed. Prior to application, pollock is overestimated relative to herring and capelin because of its higher passage probability (0.62 vs. 0.18 and 0.15 respectively; i.e., more large robust pollock otoliths are recovered than fragile otoliths of herring and capelin). When correction factors were applied in the second simulation, pollock was slightly underestimated and herring and capelin slightly overestimated. Despite the application of perfect correction factors, error did not disappear completely due to prey enumeration problems, but was low for all species (Fig. 4). In the case of salmon, VBR and FBR indices after the application of correction factors provided contrasting estimates, highlighting the potential effect of using different BR methods to combine compositional data from a collection of scats.

Discussion

A key finding of this study is that the MNI technique can lead to an underestimate in the relative importance of smaller prey and an overestimate in the importance of larger prey in diet biomass reconstructions. We have shown that this bias is closely related to the number of prey consumed (Fig. 2), where smaller prey are consumed in greater numbers than larger prey per unit mass. However, we also demonstrate that this error is strongly influenced by recovery rate (Fig. 4). For example, the low recovery rate of salmon otoliths in the second simulation tends to diminish the impact of the MNI enumeration bias.

Enumeration using a structure with multiple elements brings additional problems. It takes just one structure out of two (with otoliths for example) or just one out of 66 (with vertebrae) for an entire fish to be counted. If a structure with two elements is used for enumeration, it is possible to count two fish if the structures are deposited in different scats. If vertebrae are counted instead, it is possible, although unlikely, to count as many as 66 fish if elements are deposited in different scats over time. When all structures are used to enumerate fish, there are similar problems in that it becomes easier to detect just one fish. Overall, paired structures with reasonable passage probabilities provide the best estimate of diet and using a 66 element structure the worst. In captive feeding experiments, overcounting of large fish from single meals distributed over multiple scats has been reported and can amount to an

overestimate in the number of fish of more than 30% when all structure techniques are used (Tollit et al. 2003).

The SSFO method, like FBR, is based on an equal weighting of each scat (Olesiuk et al. 1990, Laake et al. 2002). The SSFO model estimates diet composition by presence only, while FBR determines composition by enumerating bones and estimating prey size. We used diet scenarios with four prey species consumed in very different amounts and collected all scats. Such a scenario is likely to be the greatest challenge to the accuracy of any index that uses frequency of occurrence data. As shown in our simulations (Figs. 3 and 4), the fish species that numerically dominated the diet was always underestimated, with species fed in smaller quantities typically overestimated, unless recovery rates were low. Use of multiple structures increases the chance of counting the first fish (and hence presence), and therefore the likelihood of counting those prey species fed in small numbers. Thus the FO indices perform less well when more elements or structures are used and performance of these indices is likely to be optimal when scats have low species diversity and approximately equal prevalence. Typically FO methods tend to predict prey species proportions close to 1 divided by the number of species consumed; thus perhaps the worst-case scenario is when structures from many large fish are found in a scat with a single structure from one small fish of a different species.

In addition, if the time taken for bones of different species to pass through the gut varies (as seen in Steller sea lions, see Tollit et al. 2003), then this may affect the probability of detecting prey species in scats deposited on shore following a trip to sea. Some alternate kind of transit rate correction factor may be needed to account for the error introduced by some species whose remains pass through in many scats, and others whose remains pass through quickly in few scats.

These simulations have highlighted some of the major differences between frequency of occurrence and biomass reconstruction indices. In the first simulation where large fish were unimportant in the diet (<8% of diet) and passage probabilities were the same for all species/structures, the four indices had similar inclinations in over- and underestimating large and small species. Here, few large fish (pollock and salmon) were eaten but remains were still present in scats; thus both occurrence and MNI methods overestimate the proportion of these species in the diet. In the second simulation, a relatively large species (pollock) made up a large part of the diet and had a relatively high passage probability. When a species' remains dominate in scats but other species' remains are also present, FO methods underestimate the importance of this dominant species. In this second simulation, the overestimation of pollock using BR methods and the high degree of variability is not attributable to MNI, but instead primarily is a result of different passage probabilities by species. VBR and FBR both overestimate pollock's importance in the diet due to

the higher passage rate of pollock structures, and the lack of appropriate correction factors.

Correction factors correct for some of these differences in the volumetric indices, and thus both biomass reconstructions showed improvements with their application (lower panels in Figs. 3 and 4). However, correction factors do not completely overcome problems caused by MNI methods. From our small-scale study, it is clear that unless new methods are devised to count the number of individuals represented by multiple structures, then a paired bone with a correction factor applied represents the best method when using biomass reconstruction indices to describe diet. Better counting methods should be explored, for example one that doesn't rely on rounding up to the nearest integer, but uses observed proportions and/or a synthesis of multiple structures. However, this method would undoubtedly lead to additional time to analyze scat samples, as well as increasing the necessary species identification skills. Ideally, if a paired bone is chosen, then it would be the most robust available (i.e., has the highest passage probability), not simply the easiest to identify.

The approach described here (combining computer simulations with data from captive feeding studies) can provide a valuable framework for additional studies. It also appears that differences in estimators occur particularly because of the interaction between prey size and passage probability and their inherent assumptions, as well as from enumeration errors that then translate to errors in biomass reconstruction indices. Increasing the range of diet scenarios tested and selecting the best choice between these indices should be a priority in any future simulation work.

Acknowledgments

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