Using Diversity Indices to Measure Changes in Prey Choice at the Shag River Mouth Site, Southern New Zealand

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ABSTRACT   As in the rest of Polynesia, human colonization of New Zealand marked the beginning of tremendous change for the native flora and fauna resulting in significant habitat destruction and numerous extinctions. The loss of numerous native vertebrates, especially economically impor-tant taxa such as moas and seals, must have greatly affected the foraging economy of southern New Zealand. The effect that declining abundances of native fauna had on subsistence can be understood through the use of foraging theory models. The prey choice model, in particular, can be used to examine how foragers choose the resources they exploit. From this model we can predict changes in the diet that occur with the loss of important resources. In this paper, I explore the use of diversity indices as one means of measuring these dietary changes. Richness and evenness measures of the faunal data from the Shag River Mouth site are used to evaluate predictions made by the prey choice model about changing diet breadth and foraging efficiency. Copyright © 2001 John Wiley & Sons, Ltd.

Key words: diversity measures; New Zealand; foraging theory

Introduction

Environmental change, coupled with the intro-duction of predators following the Polynesian colonization of New Zealand, led to significant habitat reduction and numerous extinctions for native flora and fauna (Anderson & McGlone, 1989; Atkinson & Cameron, 1993). New Zealand fur seals (*Arctocephalus forsteri*), which were found throughout New Zealand prehistori-cally, were reduced to a few rookeries in south-ern New Zealand by the time of Western contact (Smith, 1985, 1989). Over 30 species of birds became extinct and the ranges of many others were greatly reduced (Anderson & Mc-Glone, 1989). Of the bird species that became extinct, over 70% were flightless, while 90% were ground-nesting (Cassels, 1984). The most well-known casualties of the arrival of humans to New Zealand are the moas (Order: Dinor-nithiformes) (Anderson, 1984; Trotter & McCul-

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loch, 1984; Anderson, 1989a,b; Worthy, 1990). As large, flightless, ground-nesting birds, moas epitomize the kind of birds that are most vul-nerable to extinction (Cassels, 1984). Both moas and fur seals are common in archaeological middens from the early prehistoric period (Smith, 1985; Anderson, 1989b). The loss of numerous native vertebrates, especially econom-ically important resources such as moas and seals, must have greatly affected the foraging economy of southern New Zealand.

Research on subsistence change in New Zealand resulting from the loss of native fauna can be traced back to Julius von Haast in the 1870s. Haast argued that the temporal changes he saw in archaeological middens reflected two different groups of people with two separate subsistence patterns (Haast, 1874). Moas were hunted by an earlier Palaeolithic-like peoples with crude tools who were later replaced by or subsumed under the Neolithic Maori. Haast characterized these later peoples as 'shellfish eaters' because of the large surface shell middens found in certain regions of New Zealand.

Although Haast's ideas about population replacement were incorrect, the dichotomizing of prehistory into an early moa-hunting and the later Maori periods has tended to persist (Davidson, 1984; Allen, 1987). Likewise, subsistence change is still largely described in terms of moa and post-moa economies. These interpretations do not address what happened to subsistence as moas went extinct. As Anderson (1982) points out, interpretations of the shift in subsistence are in large part speculative and further work is needed to provide a more complete picture of subsistence change in southern New Zealand.

Evolutionary ecological models provide a means for understanding the effect that declining abundances of native fauna had on subsistence in southern New Zealand. Foraging theory, in particular, is used to model subsistence systems in an evolutionary framework to understand how and why these systems work (Stephens & Krebs, 1986). One model derived from foraging theory, the prey choice model, is used to examine how foragers choose the resources they exploit. Using this model, the kinds of changes to the diet that occur with the loss of important resources can be predicted. Dietary change is typically recognized by changes in the number of taxa present or the relative contribution of each taxon, which can be measured using indices of diversity such as richness and evenness (Grayson & Delpech, 1998; Grayson & Cannon, 1999). To gain a better understanding of subsistence change in southern New Zealand, the predictions made by the prey choice model are tested using richness and evenness measures of the faunal data from the Shag River Mouth site.

The Shag River Mouth or Shag Mouth site is located on the east coast of the South Island of New Zealand (Figure 1). The site covers an area of about 300 × 100 m across a large sand dune near the mouth of the Shag River (Anderson *et al.*, 1996). The site has long history of excavation dating back to the 1870s (Anderson & Smith, 1996). The faunal data for this analysis comes from the 1988 excavation conducted by Atholl Anderson and Brian Allingham (Anderson & Allingham,

Figure 1. Map of New Zealand showing the Shag River Mouth site.

1996). An 8 × 10 m unit was excavated to depths of between 2.5 and 4.0 m. This area of the site contained nine cultural layers, numerous oven pit features, as well as a few postholes. Thirty-one radiocarbon dates on shell, bone, and charcoal produced a sequence that spans from AD 1250 to AD 1450. The vertebrate faunal assemblage used in this analysis consists of 3130 mammal, 11626 bird, and 9842 fish bones (number of identified specimens, NISP). The well-dated sequence and the large faunal sample make the Shag Mouth assemblage ideal for a study of subsistence change.

Prey choice, dietary changes, and diversity measures

The prey choice model predicts which prey or resources a forager will pursue or ignore when encountered while foraging in a relatively homogeneous environment (Stephens & Krebs, 1986). In this model, prey are ranked based on the net energetic return they provide given the costs of capturing and processing them. Resources are added to the diet according to rank. Diet breadth or the range of resources taken will continue to expand, incorporating

the next resource in the ranking until it becomes inefficient to add more lower ranked taxa. This point of diminishing returns occurs when the return rate for the next ranked resource is less than the overall return rate for the set of resources taken into the diet, also known as the mean foraging return rate (Kaplan & Hill, 1992) or overall foraging efficiency (Winterhalder & Goland, 1997). Lower ranked resources are only added to the diet if their return rates are higher than the mean foraging return rate. Incorporating a resource with a lower return rate into the diet would lower the mean foraging return rate, decreasing foraging efficiency. In other words, it would be more efficient to concentrate foraging effort on the higher ranked taxa than to pursue resources with return rates lower than the mean foraging return rate even when those lower ranked resources are encountered.

Diet breadth, or the number of resources taken into the diet, depends on the abundance of higher-ranked prey within the environment (Stephens & Krebs, 1986). In the prey choice model, high ranked taxa are expected to be taken every time they are encountered. Thus, when high ranked prey are abundant, they should comprise a major part of the diet to the near exclusion of lower ranked prey items. Conversely, if high ranked resources are rare, the diet should include a higher proportion of low ranked prey.

Over time, it is predicted that foraging will result in a decline in the encounter rates of prey, a phenomenon termed resource depression (Charnov, 1976). High ranked prey are particularly susceptible to resource depression because they are always taken when encountered. Because the range of resources in the diet will depend on the abundance of high ranked taxa, we can predict from the prey choice model that declining abundances of high ranked taxa in the environment may lead to changes in diet. As encounter rates with high ranked resources decline, these taxa contribute less to the diet. With less focus on higher return prey, foraging efficiency should decline. In addition, the overall foraging return rate may drop to the point where diet breadth expands.

Prey ranks

In ecological or ethnographic studies, prey ranks are determined empirically by measuring return rates and handling costs (costs of capture and processing prey) using a currency such as kilocalories per hour (e.g. O'Connell *et al.*, 1988; Smith, 1991). However, because these kinds of variables cannot be measured in the archaeological record, a proxy measure is needed as an estimate of net return. A number of studies have suggested that body size provides a valid estimate of prey rank (e.g. Hames & Vickers, 1982; Hawkes *et al.*, 1982; Hill *et al.*, 1987; Schmitt & Lupo, 1995). The relationship between body size and prey rank appears to be curvilinear with a point of diminishing returns at very large body sizes (e.g. elephants, whales) due to the significant handling costs of these very large animals relative to their returns (Bayham, 1979; Broughton, 1994, 1999). This relationship generally holds best if prey are taken individually. When prey are taken through the use of mass capture techniques such as nets, then the returns for these prey per capture are expected to be much higher than predicted by size alone (Madsen & Schmitt, 1998; Grayson & Cannon, 1999).

If body size is an appropriate proxy for prey rank, then seals and moas, the largest vertebrates in New Zealand, are expected to have been high-ranked resources. Of the three species of seals taken, by far the most common in archaeological middens is the New Zealand fur seal (*A. forsteri*). Male fur seals can weigh up to 185 kg while females average about 50 kg (Crawley, 1990). Moas ranged in size from 1.0 to 2.5 m, the largest species of which, *Dinornis giganteus*, is estimated to have weighed up to 220 kg (Anderson, 1989a,b; Worthy, 1990). The taxa common in archaeological middens, such as *Euryapteryx gravis* and *Emeus crassus*, were much smaller, weighing about 60 kg. Thus, as the largest taxa in New Zealand, it is likely that moas and seals were also the highest ranked taxa. Given that moa and seal populations decreased dramatically throughout New Zealand following human colonization, the prey choice model predicts that the decline of these high ranked taxa will cause foraging efficiency to decline and may cause diet breadth to increase.

Diversity measures

Diversity measures can be used to measure the expected changes in foraging efficiency and diet breadth resulting from declining populations of moas and seals. In ecological studies, diversity indices are used to understand the structure of a population by measuring species numbers, species abundances, and proportional abundances across species (Magurran, 1988). The number of species present in a population is called richness. A rich environment is one with many species. Species abundance is measured using evenness indices. A population where all species are found in the same abundance is highly even. An unevenly distributed population is where the abundance of species is unequal. The proportional abundance of species incorporates both species numbers and abundance into one measure, and is sometimes referred to as heterogeneity (Magurran, 1988). In this analysis I will be examining changes in evenness and richness to measure foraging efficiency and diet breadth, respectively.

The decline in foraging efficiency expected with a decrease in the encounter rates of high ranked taxa may be measured using evenness. Because evenness tracks the abundance of taxa, differences in the measure can reflect the changing importance in the diet of high ranked taxa relative to lower ranked ones (Grayson & Delpech, 1998), particularly in situations where the high ranked taxa were once abundant. The situation at Shat Mouth fits this scenario quite well. Since high ranked prey are expected to be taken every time they are encountered, the initial distribution of prey taken should be very uneven. As these abundant high ranked prey decline in number, lower ranked taxa may comprise an increasingly larger proportion of the diet, i.e. the utilized taxa will be more evenly distributed. The evenness index used in this analysis (Shannon index/ln(NTAXA)) varies between 0 and 1. A measure of 0 indicates that only one class is represented. When the index equals 1, each class is represented in equal numbers (Magurran, 1988). If foraging efficiency de-

creases, this should be reflected by an increase in the evenness index.

One problem with evenness is that it does not take into account the position of prey in a rank-ordered set: it can remain unchanged even though resource exploitation is changing. For example, 80% of the assemblage may be comprised of Prey 1, while Prey 2 comprises the remaining 20%. Later, Prey 2 may increase to 80%, while Prey 1 declines in abundance to 20%. The evenness values would be the same in both situations, but the diet has changed markedly. Thus, as with NTAXA, an increase in evenness may be meaningful, but the lack of change may be unequivocal. To determine if diet is changing when evenness is unchanging, the proportion of individual prey types must also be examined.

Richness is used to examine changes in diet breadth because it can be used to count the number of prey types used. As large bodied, high ranked prey populations are declining, the mean foraging return rate may decline to the point where it is profitable to add lower ranked taxa to the diet. If diet breadth expands, this should be reflected by an increase in richness.

Archaeological analyses of diet breadth have focused on the number of taxa (NTAXA) present in a faunal sample (Broughton & Grayson, 1993; Grayson & Delpech, 1998). If diet breadth is increasing over time, then NTAXA is expected to increase. The use of NTAXA for determining diet breadth has been criticized as being an inappropriate measure because it represents the average diet breadth taken (Madsen, 1993). If NTAXA measures average diet breadth, it is not likely to be sensitive enough to track minor changes in diet over time (Broughton & Grayson, 1993; Grayson & Delpech, 1998). Others, however, argue that NTAXA measures the maximum rather than the average diet breadth. As such, NTAXA provides an appropriate estimate of diet breadth, but it may be better at distinguishing differences rather than similarities between samples. Both evenness and richness measures can be influenced by sample size (Grayson, 1984). As such, the role of sample size in structuring the data must be assessed.

Results and discussion

The predictions I have developed from the prey choice model are contingent upon the decline of the encounter rates for high ranked taxa. Since body size is likely to be an appropriate proxy for prey rank, moa and seals are expected to be high ranked taxa represented in the Shag Mouth assemblage. It is well documented that moa and seals populations declined in abundance over time around New Zealand (Smith, 1985; Anderson, 1989b), but it is important to determine if they were declining during the occupation of the Shag Mouth site.

Anderson's (1989a) analysis dating the moa hunting period in southern New Zealand provides a chronology for moa decline. There are numerous sites with an abundance of moa remains that date between 1000 and 400 BP, with a peak between 600 and 700 BP. After 400 BP, however, there are very few sites that contain moa remains. By the time of European colonization of New Zealand in the early 1800s, moas were extinct. So between 600 and 400 BP, about the time that the Shag Mouth site was occupied, the number of moa hunting sites decreased, suggesting that moa populations also declined. Indeed, the Shag Mouth data support this interpretation. Since high ranked taxa are expected to be taken every time they are encountered, the relative abundance of moas in the faunal assemblage should reflect encounter rates or population abundances. In the Shag Mouth assemblage, moas decrease significantly from 95% to 65% ($r_s = 0.93$, $p = 0.003$) during the occupation of the site. Thus, it appears that moa populations were declining during the time the site was occupied.

Fur seal populations also appear to have declined significantly during the occupation of the Shag Mouth site. By examining sex and age specific categories of fur seal remains from archaeological sites around New Zealand, Smith (1985) found that fur seal distributions across New Zealand changed significantly following the arrival of humans. Fur seal breeding colonies were once widely distributed throughout coastal New Zealand. By about AD 1500, fur seals disappeared from the North Island. On the east

coast of the South Island, breeding colonies were replaced by non-breeding colonies in the late prehistoric, about AD 1500–1700 (Smith, 1985, 1989). When European sealers arrived in the late 1700s, breeding colonies were confined to the South Island's remote south and west coasts. Like the moa, the relative abundance of fur seals at the Shag Mouth site declines significantly over time ($r_s = 0.82$, $p = 0.023$) indicating the seal populations were dwindling. The cause of this change in the distribution of fur seals is attributed to human predation. Not only are seal remains abundant in archaeological sites throughout New Zealand, it seems that juveniles and subadults were targeted. Smith (1989) argues that culling these young animals greatly reduced breeding populations to the point where not only did the number of rookeries declined, the successful breeding rookeries were found only in areas away from human occupation.

Thus, the available evidence indicates that in southern New Zealand, moas and seals were high ranked taxa that declined in abundance over time. The prey choice model predicts that as the encounter rates for these taxa decrease, foraging efficiency will decline. This will be marked by an increasing proportion of low ranked taxa in the diet. Likewise, as low ranked taxa increase in dietary importance, diet breadth may expand to include previously ignored taxa.

An important component of the prey choice model is the assumption that the spatial distribution of prey is random, not clumped, so that the probability of encountering any prey type is equal across space (Stephens & Krebs 1986). In the real world, however, prey distribution typically is not random, but patchy. When this is the case, the prey choice model and the expectations generated from the model are applied to each patch separately.

Patches are defined so that they are homogeneous spatial entities that better meet the assumption of random encounter rates. The patch types created for the Shag Mouth analysis divide resources up based on the location of where they were most likely taken: offshore, coastal and inland. While these patches could be sub-divided into more fine-grained patches (e.g. inland divided up into riverine, alpine,

grasslands, etc.), the number of assumptions or reconstructions made had to be balanced with the need to create homogeneous patches.

To test the prey choice model predictions across patches, taxa were divided among the three patches based on their specific life history characteristics. For the purpose of this paper, only the data from the inland and coastal patches are presented. Within the inland patch, there are 33 taxa represented in the Shag Mouth faunas, with moas as the highest ranked taxon. For the coastal patch, seals are the highest ranked prey of the 20 taxa in the assemblage. Although the assumptions of the prey choice model require each patch to be examined separately, I believe it will also be useful to compare the predictions of dietary change for the overall assemblage changes with the same predictions within each patch.

Overall assemblage changes

Evenness values for the assemblage as a whole were plotted across layers with the oldest layers to the left (Figure 2). Layers 9 through 11 were combined because their sample sizes were significantly smaller than for the other layers. Rank order correlation was used to test the relationship of evenness across time. The least squares line is only used to emphasize the direction of the trend. Over time, evenness increases significantly and it is not correlated with sample size ($r_s = 0.357$, $p = 0.43$). The increase in evenness indicates that an increasingly larger portion of the diet is being comprised of lower ranked taxa. Thus, as the importance of low ranked resources increases, foraging efficiency declines significantly during the occupation of the site.
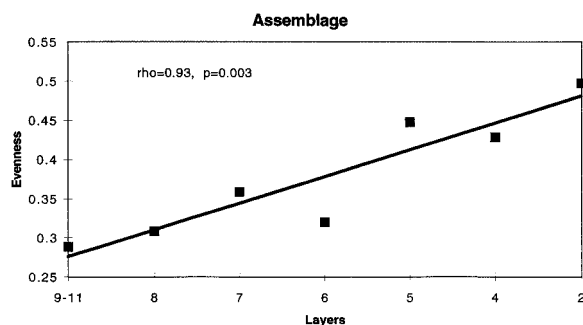

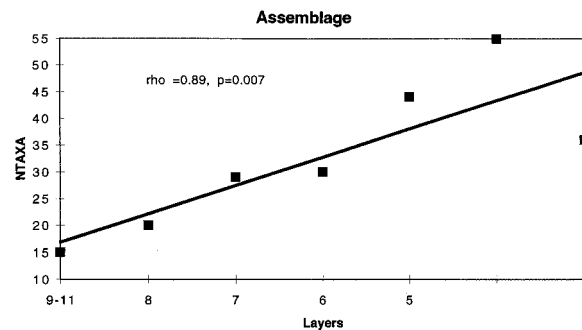Figure 2. Plot of assemblage evenness across layers.

Figure 3. Plot of NTAXA for the assemblage across layers.

If the abundance of high ranked taxa declines significantly, it may lower foraging efficiency and the mean foraging return rate enough so that the diet breadth increases over time. NTAXA also increases over time (Figure 3), but it is significantly correlated with sample size ($r_s = 0.93$, $p < 0.001$). Because either variable, an increasing sample size or increasing number of taxa, could be driving the relationship (Grayson, 1984; Grayson & Delpech, 1998), the results of this analysis are ambiguous. Nevertheless, for the assemblage as a whole, it appears that as high ranked resources such as moas and seals decline in abundance, lower ranked taxa comprise an increasingly larger portion of the diet with a possibility of more taxa being added over time.

Patch changes

As required by the prey choice model, the data is divided up amongst the defined patches. The predictions of the model will be applied to the inland and coastal patches separately. Figure 4 shows the evenness values for the inland patch plotted across all layers. Layers 9 through 11 are again combined because of the very small samples for those layers. Evenness increases significantly over time, varying from very low evenness values of 0.006 up to 0.36. Evenness corresponds with the dominance of moa exploitation in the inland patch. Moa decline from 98% to 65% of the sample over time. Thus, as moa populations decline, foraging efficiency decreases as lower ranked taxa become increasingly important.
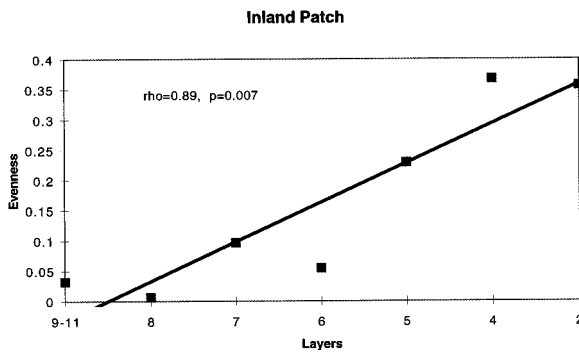
Inland Patch

rho=0.89, p=0.007

Figure 4. Plot of evenness for the inland patch across layers.

Coastal Patch

rho=0.57, p=0.18

Figure 6. Plot of evenness for the coastal patch across layers.

Conversely, richness is increasing significantly over time within the inland patch (Figure 5). Neither NTAXA nor evenness is significantly correlated with sample size. Thus, for the inland patch, resource exploitation appears to have focused mainly on moa procurement for much of the occupation of the site. As moas declined in abundance over time, subsistence became less specialized with lower ranked resources becoming increasingly important. In addition, the decline in moas was significant enough to lower the mean foraging return rate so that diet breadth expanded to include more lower ranked resources.

The pattern of resource exploitation for the coastal patch is quite different from that of the inland patch. Evenness does not change significantly over time, but remains moderately stable (Figure 6). The evenness values indicate that resource exploitation in the coastal patch is more generalized than in the inland patch. Fur seal is the most abundant resource in the sample throughout most of the sequence, but foraging in the coastal patch does not focus on seals alone. Other taxa, such as dog, shags, and
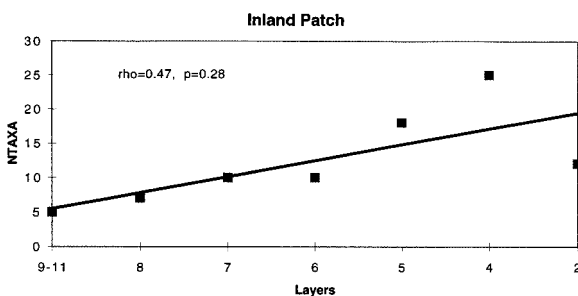
penguins are also being taken in significant numbers throughout the sequence. It is also important to recognize that similar evenness values do not mean that resource utilization is unchanging. As discussed above, sample proportions can remain the same, but the taxa that correspond to those proportions may change. Analysis of changes in the proportions of individual taxa are required to determine if resource exploitation in the coastal patch is changing.

The changes in rank and proportion for coastal taxa are presented in Table 1. There is a shift from the larger, higher ranked taxa such as Hooker's sea lion, Stewart Island Shag, and Yellow-eyed Penguin to smaller ones such as Blue Penguin, blue cod, and wrasses. Since high ranked taxa are expected to be taken every time they are encountered, the decline in the rank of larger taxa should reflect declining foraging efficiency. Because evenness measures do not take into account the rank of taxa, other researchers have used indices that compare large taxa to smaller ones to measure changes in foraging efficiency (Bayham, 1979; Broughton, 1999). The results of this analysis, which is presented in detail elsewhere (Nagaoka L. *Extinction, Resource Depletion, and Subsistence Change in Southern New Zealand*. PhD dissertation, Department of Anthropology, University of Washington, Seattle, 2000), indicates that a shift from larger to smaller taxa does occur over time, suggesting that foraging efficiency is declining.

With a decline in foraging efficiency, the diet may broaden. NTAXA increases significantly for the coastal patch (Figures 7 and 8), however, this measure is significantly correlated with sample size ($r_s = 0.76$, $p = 0.046$). Another means of examining diet breadth in cases where sample

Inland Patch

rho=0.47, p=0.28

Figure 5. Plot of NTAXA for the inland patch across layers.

Table 1. The five most abundant taxa for each layer in the coastal patch

| Rank	Layers						
	9–11	8	7	6	5	4	2
1	Fur Seal (63.8)	Fur Seal (60.1)	Fur Seal (68.9)	Fur Seal (56.7)	Fur Seal (63.8)	Dog (38.6)	Fur Seal (41.1)
2	Stewart Island Shag (8.6)	Blue Penguin (19.0)	Blue Penguin (16.5)	Blue Penguin (13.2)	Blue Penguin (13.2)	Fur Seal (19.1)	Dog (26.3)
3	Dog (8.6)	Stewart Island Shag (4.4)	Blue Cod (4.2)	Blue Cod (10.4)	Dog (8.2)	Wrasses (12.5)	Blue Cod (11.8)
4	Hooker's Sea Lion (8.1)	Yellow-eyed Penguin (3.8)	Dog (3.4)	Dog (6.6)	Wrasses (6.3)	Blue Cod (9.3)	Wrasses (7.9)
5	Blue Penguin (5.4)	Dog (3.2)	Black Cods (2.0)	Wrasses (3.6)	Black Cods (1.9)	Black Cod/Blue Penguin (6.8)	Blue Penguin (5.1)
Total %	94.5	90.5	95.0	90.5	91.9	97.9	92.2

Percentages are presented in parentheses.

Coastal Patch

rho=0.78, p=0.038
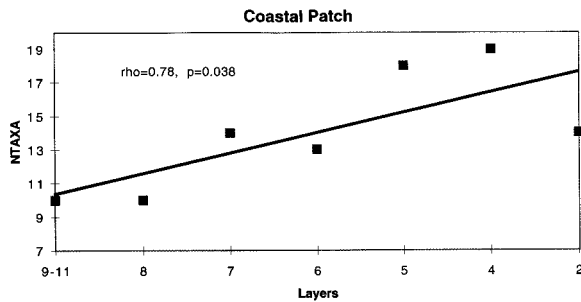
Figure 7. Plot of NTAXA for the coastal patch across layers.
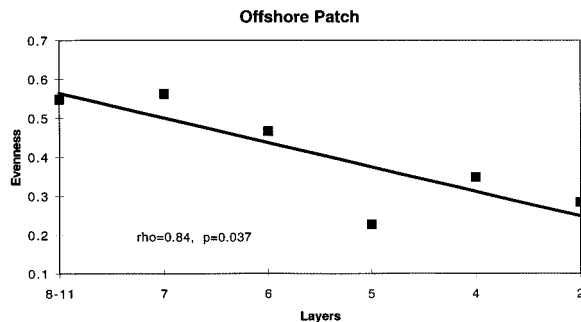
Offshore Patch

rho=0.84, p=0.037

Figure 8. Offshore patch evenness plotted across layers.

size and NTAXA are correlated is to compare the rate at which taxa are added as sample size increases (Grayson & Delpech, 1998). An increase in this rate may indicate that diet breadth is expanding. As with the indices described above, the details of an analysis of sample size and NTAXA will be presented elsewhere (Nagaoka, 2000). However, the initial results suggest that the rate at which taxa are being added with increases in sample size is increasing over time. In other words, more taxa are being utilized during the later occupation period than prior.

Examining each patch separately shows that there are significant differences in the pattern of exploitation across habitats. In the inland patch, moa exploitation was predominant early on. As moa populations declined, the number of resources used increased greatly and a larger proportion of the diet was comprised of lower ranked resources. In contrast, foraging in the coastal patch was more evenly distributed among fewer resources throughout the occupation of the Shag Mouth site. Thus, the

changes are not as dramatic as those seen in the inland patch. At the beginning of the occupation of the site, seal exploitation dominated, with shags and larger penguins also an important component. As the abundances of seals, as well as probably the shags and large penguins, declined, the smaller species of penguin and several fish species end up comprising a larger percentage of the diet. While the general patterns of dietary change were evident at the scale of the whole assemblage, detailed examination of the patch-specific changes provides valuable information about spatial variability in changing resource use.

Summary

As exemplified through the analysis of the Shag Mouth assemblage, richness and evenness measures can be important tools for examining the predictions about dietary change generated from foraging theory models. However, a full understanding of the trends in evenness requires detailed examination of the proportions of individual taxa being utilized. This analysis shows that studying changes in the assemblage as a whole is informative, but more detailed results are produced by analysing individual patches as required by the fine-grained assumptions of the prey choice model. By examining trends in patches, we can better understand how different habitats are being exploited and how this changes over time. In the Shag Mouth case, different patterns of change emerge for each patch. In the inland patch, as moas dwindle, diet shifts to become less specialized on moas with more taxa being utilized. The pattern for the coastal patch requires further analysis to determine the meaning of the unchanging evenness values, but it may be that as seals are declining, other taxa are increasing in importance. While these are just the initial results of my study, it is clear from this analysis that foraging theory models can provide a means for better understanding of subsistence change in southern New Zealand.

Acknowledgements

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