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The effects of resource depression on foraging efficiency, diet breadth, and patch use in southern New Zealand

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Abstract

While many studies have examined human impacts on prehistoric environments, few have explicitly examined how foragers adapt to the changing environmental situations that they have created. The goal of this analysis is to study the relationship between human foraging economies and human-related environmental change in southern New Zealand. Foraging theory is used to generate predictions about subsistence change resulting from the declining abundance of important resources such as moas and seals. In particular, these predictions examine changes in (1) the kind of resources exploited (foraging efficiency), (2) the number of resources utilized (diet breadth), and (3) the habitats exploited (patch choice). The predictions are tested using the large assemblage of vertebrate faunal remains from the well-stratified and well-dated Shag River Mouth site. This study shows that using foraging theory models to structure analysis provides a more fine-grained spatial and temporal resolution of subsistence change in southern New Zealand than has been previously achieved.

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Introduction

The impact of humans on the environment has become an important topic particularly today where the effects are often so dramatic. But as many researchers have demonstrated (Dewar, 1984; Kirch et al., 1992; Kohler, 1992; Lamb et al., 1991; MacPhee and Burney, 1991; Redman, 1999; Simmons, 1999; Steadman, 1995), humans have had a long history of modifying their surroundings. Humans have altered the landscape through deforestation and erosion

(McGlone, 1983; Van Andel et al., 1990). They have also introduced competitive species and new predators, among which they can include themselves. The results of these interactions between people and their environment range from relatively benign to the extreme of landscape degradation and extinction.

Plants and animals in island environments are particularly vulnerable to changes brought about by humans. For example, it is estimated that over 50% of the bird species of Polynesia became extinct during the 1000–3000 years between Polynesian colonization and Western contact (Steadman, 1995, 1997). There is a combination of factors that enhance the chances that island species will be severely impacted by human arrival.

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Population size of island fauna is generally smaller than on continents due to the differences in land area. Thus, the loss of individuals within these populations as a result of environmental perturbations is often more severe. In addition, the high occurrence of endemism amongst island species means that there is no replacement population on which to draw. Even for non-endemic species, the distance to source populations is often great, reducing the likelihood of replacement. Finally, many islands have few predators. In the absence of predation pressure, many island species have evolved traits such as flightlessness that become detrimental once predators are added to the environment. These traits have led to significant reductions in population abundances, and even to extinction.

As with other islands, the arrival of people in New Zealand led to significant changes in faunal population abundances and distributions. By the time Western explorers reached New Zealand's shores in the late 1700s, 35 species of birds had become extinct (Cassels, 1984), and the geographic distribution of many other taxa, such as the New Zealand fur seal (*Arctocephalus forsteri*), had been greatly reduced (Smith, 1985, 1989). The best-known example of human impact on New Zealand is provided by the moas (Dinornithiformes), and is often cited as a prime example of overkill extinctions (Anderson, 1984; Diamond, 2000; Martin, 1984). Moas were large, flightless birds whose living relatives are ostriches and emus. The 11 species of moas ranged in size from large turkeys to giants weighing over 250 kg and 2 m in height. Within 500 years of human colonization of New Zealand, moas were extinct (Anderson, 1989a). Although it is likely that habitat destruction played an important role in the extinction of moas, the numerous archaeological middens filled with their remains point to human predation as a significant factor in their demise.

Given that moas appear to have been an important part of the human diet, the decline in moa abundance and their eventual extinction must have had a significant effect on human subsistence practices in New Zealand. Researchers have commented on the resulting changes in subsistence since the beginning of archaeological research in New Zealand. von Haast (1875) noted that the conspicuous remains of moas in early midden deposits were often overlain with deposits that were dominated by fish and shellfish. To explain this pattern, von Haast (1872, 1875) created

a two phase chronology for New Zealand that paralleled chronologies proposed to explain the archaeological record in Europe. He argued that the large middens of moa remains were left by the original inhabitants of New Zealand, the Moa-Hunters. These were thought to be Paleolithic-like peoples with crude tools who hunted the moa to extinction just as prehistoric European ancestors had done with the mammoths and other mega-fauna. The Moa-Hunters were believed to have been replaced later by a migration of the Neolithic Maori to New Zealand. Haast characterized these newcomers as "shellfish eaters" because of the dense shell middens found above the moa remains (von Haast, 1875, p. 98). In essence, moa and shellfish were simply culture historical traits used to distinguish the early Moa Hunters from the later Maori.

New Zealand prehistory continues to be divided into an early moa-hunting peoples and the later Maori, especially in the South Island (Davidson, 1984). Subsistence studies, in particular, have examined subsistence in terms of two periods of time: moa-hunting and post-moa subsistence (Anderson, 1982, 1983). During the early period, "big-game" hunting of moas and seals dominated subsistence practices; after these resources were depleted, the focus shifted to smaller items such as fish, small birds, and shellfish (Anderson, 1982; Anderson and Smith, 1996c,d). Research on this apparently sudden shift from moa hunting to post-moa subsistence patterns has been at a relatively large scale and generally descriptive.

Foraging theory models provide a means for obtaining a more fine-grained understanding of subsistence change resulting from human-related declines in native fauna. The prey choice and patch choice models are ideal for examining the consequences of human alterations to the environment because the models explicitly outline the expected outcomes (Kaplan and Hill, 1992; Smith, 1991). More importantly, resource depression, the reduction of the abundance or availability of high-ranked prey due to human foraging efforts, is often the cause of dietary changes (Charnov et al., 1976).

Although foraging theory models were originally developed to explain observable behavior over relatively short time spans, these models can be and have been used to explain behavioral patterns observable only through the archaeological record (Broughton, 1999; Simms, 1987; Szuter and Bayham, 1989). When the assumptions of the models are closely met, changes to a

resource base have explicit, predictable consequences. Analysis of archaeological faunal remains provides an excellent opportunity to determine the manner in which human populations respond to these long-term changes. In this analysis, the predictions generated by foraging theory models are tested using the vertebrate faunal assemblage from the Shag River Mouth site.

The Shag River Mouth site is one of the best known moa-hunting sites in southern New Zealand. It was originally excavated by von Haast himself, and became one of the type sites for his chronology (Anderson, 1989b; von Haast, 1875). The Shag River Mouth site is located on the east coast of the South Island of New Zealand (Fig. 1). The site is extensive, covering over 30,000 m². Several areas of the site were studied over the last 125 years (Anderson and Smith, 1996b). The faunal assemblage used in the analysis comes from the 8 × 10 m excavation at the Area C (SM/C) or the High Dune excavation. The assemblage from this excavation was analyzed previously as part of a larger study on the site (Anderson et al., 1996). Each vertebrate class was studied and published separately (Anderson et al., 1996f; Anderson and Smith, 1996a; McGovern-Wilson et al., 1996;

Smith, 1996). In this analysis, I reanalyze and synthesize the Shag River Mouth data for all vertebrate classes.

The High Dune excavation (SM/C) assemblage was chosen to test the predictions of the foraging theory models because it meets the data requirements necessary for the analysis. The assemblage consists of a large sample of data from a well-stratified, well-dated, and well-documented site. The High Dune excavation consisted of an 8 × 10 m unit excavated to depths of about 2.5–4.0 m (Anderson and Allingham, 1996). Nine cultural layers, numerous oven pit features, as well as a few postholes were uncovered. Shag River Mouth is one of the best dated excavations in New Zealand with over 30 radiocarbon dates producing a sequence that spans from AD 1250 to 1450 at standard deviations (Anderson et al., 1996e). The excavation also recovered one of the largest faunal assemblages in New Zealand, consisting of over 24,000 identified specimens, and representing over 70 species of fish, bird and mammal (Nagaoka, 2000). The most common taxa in the assemblage are moas, penguins, cormorants, fur seals, dogs, quails, pigeons, barracouta, and cod.

Modeling subsistence change in southern New Zealand

Foraging theory consists of a set of models that make several assumptions. First, it is assumed that foragers make choices that maximize foraging efficiency. Second, a currency used to measure foraging efficiency, such as calories captured per unit foraging time, is assumed to be highly correlated with fitness (Stephens and Krebs, 1986). Thus, in the long run, natural selection is expected to favor foragers that maximize their rate of energy capture. Several foraging theory models can be used to generate predictions about subsistence change in response to declining populations of prey taxa. In particular, I use the prey choice and patch choice models, which predict what resources foragers will choose to exploit and how they use resources across space and time. From these models I generate expectations that are then tested archaeologically using the Shag River Mouth assemblage.

Prey choice model

The foraging decision analyzed by the prey choice model is whether a forager will pursue or

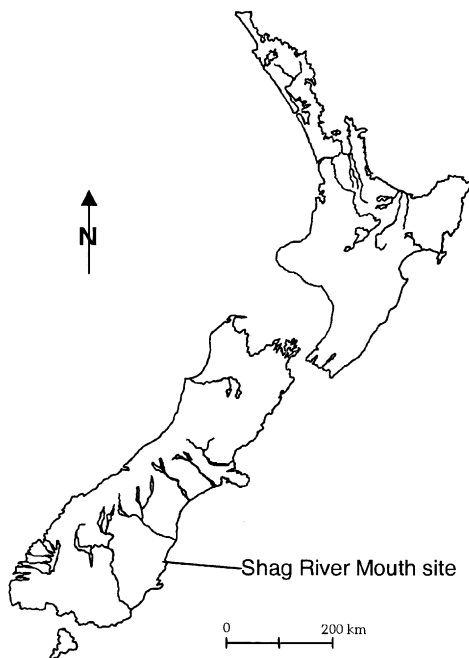


Fig. 1. The Shag River Mouth site, South Island, New Zealand.

ignore a prey item when encountered (Kaplan and Hill, 1992; Smith, 1991; Stephens and Krebs, 1986; Winterhalder, 1981b). Prey types are ranked based on the net energetic return they provide given the costs of capturing and processing them (post-encounter return rate). Foragers will add resources to their diet according to the ranking of the resource. The number of resources pursued, or *diet breadth*, will expand until a point of diminishing returns is reached. In this case, the next ranked resource has a return rate that is less than the mean foraging return rate for the set of resources already being taken into the diet (Kaplan and Hill, 1992; Smith, 1991). It is more efficient for foragers, therefore, to concentrate their effort pursuing the set of higher ranked prey than to add lower ranked resources with lower return rates even when those resources are encountered.

Diet breadth will also depend on the encounter rate with high ranked prey (Stephens and Krebs, 1986). Since high-ranked taxa will be pursued whenever they are encountered, when they are abundant in the environment, foragers will “specialize” on these high-ranked prey, sometimes to the near exclusion of lower ranked prey. When foraging effort is concentrated on high-ranked taxa, *foraging efficiency*, or the net return rate per unit time, will be high (Smith, 1991). Conversely, if high-ranked resources are rare, foragers will use a more generalized strategy, exploiting a wider range of resources that includes more low-ranked prey. If a higher proportion of low-ranked resources is taken, foraging efficiency is lowered. Because the abundance of high-ranked taxa can have a significant effect on dietary choices, the prey choice model can be used to predict how diet will change when abundances of high-ranked taxa in the environment decline.

An important assumption of the model is that prey items are randomly distributed across the landscape so that the probability of encountering a prey type is constant (Smith, 1991; Stephens and Krebs, 1986). However, resources are often not distributed randomly across the environment, but instead tend to clump into spatially discrete areas. When the distribution of resources is patchy, the probability of encountering a prey type increases after an encounter rather than remains constant. In such cases, patches must be defined so that the spatial distribution of resources is relatively homogeneous and prey encounter within patches is random. The expectations of the prey choice model can then be assessed separately for each patch.

Patch choice models

Patch choice models examine how foragers select the patches or environments they exploit and how much time they should spend in each patch. The marginal value theorem (MVT) examines how long a forager should remain in a patch, and was developed to deal with the problem of resource depression (Charnov, 1976; Charnov et al., 1976). *Resource depression* is the decline in the encounter rates of prey resulting from the foraging behavior of predators. Three types of resource depression have been proposed: exploitation, behavioral, and microhabitat depression (Charnov et al., 1976). Exploitation depression is the direct result of harvesting of prey that causes declines in population abundances. The concept of “overexploitation” as presented in the archaeological literature is an example of this type of resource depression (e.g., Anderson, 1997; Kirch and Yen, 1982). Explanations such as the “Pleistocene Overkill” hypothesis assume that this type of predation pressure is the cause for mass population declines and extinctions (Martin, 1973, 1984; Martin and Steadman, 1999; Mosimann and Martin, 1975).

The other two types of resource depression differ from exploitation depression in that declining encounter rates result from a decrease in prey *availability* rather than prey *abundance* (Charnov et al., 1976). Behavioral depression is caused by changes in prey behavior, such as increased alertness, that reduces prey availability and thus encounter rates. With the third type of resource depression, microhabitat depression, prey availability declines because prey relocate to areas that are less likely to be impacted by predators.

Since the MVT assumes that resources are being depleted as a forager moves through a patch, it is useful in understanding how foragers should react to changing prey abundances (Charnov, 1976). As resource depression occurs, the MVT predicts that foragers should leave a patch when the net return rate for the patch drops below the average return rate for all exploited patches, taking into account the costs of moving between those patches (Charnov, 1976). As foragers move from one patch to the next, they should leave behind a trail of patches that have been depleted to similar marginal return rates. Any patch with return rates less than the average return rate will not be exploited. In addition, as the return rate for all patches declines, time allocation within those patches should increase, assuming search times are not changing (Winterhalder, 1981b).

The MVT was designed to address changing encounter rates within a single foraging bout. However, the model can be extended to longer time scales to predict how patches may be added as foraging efficiency declines. If resource depression is lowering encounter rates during a single foraging bout, encounter rates may also be lowered between foraging bouts if sufficient regeneration time has not passed (Cannon, 2000). A decline in encounter rates within a patch will result in a decrease in the gains curve for that patch. This, in turn, will lead to a decrease in the average return rate for the set of patches being exploited. Given this, we can predict that declines in the average return rate may lead to more intensive use of each patch and/or an increase in the number of patches used.

Predictions

From these models several predictions can be generated concerning changes in subsistence resulting from resource depression. First, since high-ranked prey are always taken on encounter, they are particularly susceptible to resource depression. As encounter rates with high-ranked resources decline, these taxa contribute proportionally less to the diet, causing foraging efficiency to decline. In addition, diet breadth, the number of species incorporated in the diet, may increase if the mean foraging return rate drops to the point where adding lower ranked taxa to the diet becomes profitable.

Secondly, if foraging efficiency declines significantly across all patches, then the number of patches exploited may increase or the time allocation across patches may change. As predicted by the MVT, the number of patches exploited will depend on the mean foraging return rate (Charnov, 1976; Orians and Pearson, 1979). Those patches with return rates less than the mean foraging return rate will not be exploited. However, if the mean foraging return rate decreases significantly as postulated in the first prediction, then patches that were previously unprofitable may now be added to the subsistence regime, and the time allocated to each patch should increase.

Measuring predicted changes in the archaeological record

From the predictions presented above we should expect to see changes in foraging effi-

ciency, diet breadth, the number of patches exploited, and the intensity with which patches are exploited. Changes in diet breadth and foraging efficiency should be reflected by a shift in the proportion of high- and low-ranked resources in the diet (Broughton, 1999; Broughton and Grayson, 1993). A diet that is broad and for which foraging efficiency is low will be comprised of more lower ranked taxa than one that is narrow with high foraging efficiency. To test this first prediction, I examine changes in the relative abundance of high- and low-ranked resources. In addition, since it is likely that prey are distributed in a non-random manner, resource patches must be defined and the predictions applied to each patch separately. Finally, if overall foraging efficiency drops significantly, then the pattern of patch exploitation will change. To determine if patches are being added to the subsistence round or if time spent in patches is changing, the relative abundance of high ranked resources from each patch can be measured. If patches are defined in terms of resources exclusively found there, then additions of patches can be detected through the appearance of those defining resources within the diet.

Applying foraging models to archaeological situations

The models and predictions described above were developed for use in ecological time in circumstances where foraging behavior and its outcomes are directly measurable. Because archaeologists do not study human behavior (or prey encounter rates, etc.) directly, but rather the remnants of the physical manifestations of that behavior, applying these models to archaeological situations requires modification (see Grayson and Cannon, 1999 for a discussion of archaeological applications of foraging models). In particular, determining prey ranks and identifying patches entails accepting certain assumptions.

Prey ranks are typically determined by directly measuring return rates and handling costs using a currency such as kilocalories per hour (e.g., O'Connell et al., 1988; Smith, 1991). However, since these variables are not directly observable in the archaeological record, an alternative measure must be used. Research has shown that in many cases body size and prey rank have a predictable relationship suggesting that body size is a suitable proxy for prey rank (e.g., Bayham, 1979; Broughton, 1994, 1999; Hames and Vickers, 1982;

Hawkes et al., 1982; Hill et al., 1987; Schmitt and Lupo, 1995). If this relationship holds, then large-bodied taxa will be high-ranked resources. Each case should be assessed individually since the relationship between body size and prey rank may not hold in situations where the handling costs are significantly greater than expected, thus reducing the net return rate relative to body size.

While body size appears to provide a good estimate of prey rank, other variables may influence such ranks. For example, improvements in procurement technology can affect the ranking of prey by lowering handling costs (Alvard and Kaplan, 1991; Hames and Vickers, 1982; Smith, 1981, 1991; Winterhalder, 1981b). With more efficient pursuit technology, in particular, the handling costs may decline enough so that the net returns, and thus the relative ranking, for a particular prey increases. If the prey's rank increases significantly, then it may be added to the diet. Some examples of such technological improvements include the bow and arrow (Hughes, 1998), nets (Broughton, 1999), and guns (e.g., O'Connell and Marshall, 1989; Smith, 1991; Winterhalder, 1981a). Each of these technologies decreases handling costs by decreasing pursuit time and effort.

An important kind of technological innovation is the use of mass capture techniques. When prey are captured *en masse* instead of individually, the prey item is no longer the individual animal. Rather, the prey item becomes the group of individuals that are captured by the technique. Some examples of mass capture are the use of nets in rabbit drives (Steward, 1938), buffalo jumps (Frison, 1991), or netting of fish (Broughton, 1999). If prey are taken through the use of mass capture techniques, then the returns per capture are expected to be much higher than predicted by the size of the individual animal (Grayson and Cannon, 1999; Madsen and Schmitt, 1998). Thus, the rank of mass captured prey needs to be adjusted accordingly. The role of technological change in determining prey ranks can be examined by studying artifact data and adjusting the ranks accordingly.

As discussed above, the fine-grained prey choice model assumes that prey distribution is homogeneous across space so that the encounter of a prey type does not affect the probability of encountering that prey type again (Stephens and Krebs, 1986). Prey distribution, however, is often clumped so that certain prey types are more likely to be encountered in particular areas across space.

In such cases, dietary studies that rely on foraging theory must first define patches that create more homogeneous groupings of prey types.

Since human foragers tend to forage widely, it is likely that multiple patches are being exploited. Ethnographically, patches have been defined using a number of different variables such as habitat types, procurement methods, and seasonality of use (Smith, 1991). Because most of these variables require a significant amount of reconstruction to identify, defining patches to meet the fine-grained assumption has been problematic in archaeological dietary studies. Usually patches are broadly defined according to environments or habitats. Since patches, such as "terrestrial" or "marine", are still fairly coarse, encounter rates within these patches still may not be random. For example, Broughton (1999, pp. 52–53) places deer and elk in the same patch, but acknowledges that while there is some overlap, elk tend to favor grasslands while deer are more likely to be found in woodland areas.

The alternative is to create patches that define more specific environments, such as woodland, grassland, or estuarine. Again, this can be problematic because prey may crosscut a range of environments. For example, in Polynesia, marine fish are often categorized as inshore, offshore, or pelagic. However, a number of taxa such as jacks (Carangidae) and barracuda (Sphyraenidae) can be found and procured in all of these patches (Allen, 1992).

The New Zealand situation also requires that other factors be taken into consideration. Patch definition is constrained by the paleoenvironmental reconstructions currently available, which in New Zealand tend to be at a gross scale (Anderson and McGlone, 1992). In addition, our knowledge about the life histories of extinct species is often incomplete. Given these two constraints, the patches defined are necessarily broad. Three patch types are defined for this analysis: offshore, coastal and inland. For the purpose of this analysis, offshore resources, such as barracouta and albatrosses, are defined as those that require canoes to access. The coastal patch includes resources encountered along the shore and coastline. They include seals, sea birds, and fish that can be taken from shore. Inland resources are all other terrestrial resources that can be obtained inland of the coast. The taxonomic data from the Shag Mouth assemblage have been divided into patches based on life histories and ethnographic data on procurement techniques (Tables 1–3). The

Table 1
Numbers of identified specimens for the inland patch by layer

Taxon	Layers									Total
	2	4	5	6	7	8	9	10	11	
Moa	540	1394	1398	1781	1537	559	771	89	60	8129
NZ quail	161	470	199	13	50	5	2		1	901
NZ pigeon	30	127	29	4	10	2		1		203
Fairy Prion	1	153	1		1					156
Red/Yellow Crowned Parakeet	12	42	36	1	9	1				101
Fluttering Shearwater	2	42		1						45
Tui	6	24	3	3		1	1			38
NZ pipit		8	5	13	2	2			2	32
Diving Petrel	1	19	1	2						23
Grey Duck	6	12	4		1	2				25
Black-fronted Tern		17	5	2	1					25
NZ Dotterel		15	1		2					18
Weka	2	5	2							9
Saddleback	1	2	1		1					5
Grey Teal	2	2	1							5
Brown Teal		5								5
NZ snipe	1	3								4
SI Pied Oysteratcher	1	3								4
NZ Robin		4								4
Laughing Owl			1	1	1					3
Paradise Shelduck	1							2		3
Bellbird		1		1						2
Piopio		1	1							2
Freshwater Eel		2								2
Black-billed Gull			1	1						2
SI Kokako		1								1
Banded Rail		1								1
NZ Scaup		1								1
NZ Swan		1								1
Wrybill		1								1
NZ falcon			1							1
Kaka			1							1
Auckland Island Merganser sp.			1							1
Inland total	767	2356	1692	1823	1615	572	774	92	63	9754

predictions of the models will be tested for each of the three patches separately.

I was able to divide up almost all of the taxa into one of the three patches. One notable exclusion from the dataset is the Polynesian rat (*Rattus exulans*), which comprised about 2.8% of the identified faunal remains. Ethnographically, rats were described as being procured by traps set in the forest and among the grass (Best, 1942; Buck, 1950), and would fall in the inland patch. However, the presence of gnawing on bones recovered from the site indicates that rats also occurred in and around the site, which is located in the coastal

patch. Thus, rats could be pursued in either the inland or the coastal patch. Since I could not determine from which patch the rats were being exploited, they were excluded from this analysis.

These analytical patches tend to minimize the overlap of prey across other patches. However, because these units are broadly defined, prey distribution may not be completely homogeneous within each patch. The inland patch, in particular, is diverse in terms of the habitats represented, and thus may create a situation where sequential encounters with prey within this patch would not have been random. Thus, in the analyses to

Table 2
Numbers of identified specimens for the coastal patch by layer

Taxon	Layers									Total
	2	4	5	6	7	8	9	10	11	
NZ Fur Seal	136	144	305	301	504	95	92	24	25	1626
Dog	87	291	39	35	25	5	5	4	10	501
Blue Penguin	17	36	56	70	121	30	5	2	5	342
Blue Cod	39	70	2	55	31	4	2			203
Wrasses	26	94	30	19	13	4				186
Black Cods	3	51	9		15		1			79
Stewart Island Shag	5	10	7	5	4	7	8	1	10	57
Spotted Shag	6	7	4	13	6			1	2	39
Hooker's Sea Lion		2	2	3		3	6	8	4	28
Yellow-eyed Penguin		1	4	8	2	6	2		1	24
Black-backed Gull		5	1	9	3					18
Shore Plover	4	14								18
Scorpionfish	3	13	2							18
Elephant Seal	1	1	2	5	2	3	3			17
Sea Perch		4	8							12
Red-billed Gull		2	3							10
Blue Moki	1			3	3					7
Fiordland-crested Penguin		4			2					6
NZ Dotterel		3	1							4
Little Pied Shag	1	1			1					3
Erect-crested Penguin			2			1				3
Rock Cod	2									2
Mullet			1							1
Coastal total	331	753	478	531	732	158	124	40	57	3204

Table 3
Numbers of identified specimens for the offshore patch by layer

Taxon	Layers									Total
	2	4	5	6	7	8	9	10	11	
Barracouta	1305	5751	757	90	67	8	5			7983
Red cod	103	990	41	7	5	1			1	1148
Albatross	125	413	18	11	8	1				576
Ling	27	92	19	2						140
Trumpeter	2	10	6	5	11					34
Hapuku	4	13	1							18
Gemfish		5								5
Tarakihi		2								2
Warehou	2									2
Offshore total	1568	7276	842	115	91	10	5	0	1	9908

follow, I will assess how well the fine-grained assumption of the prey choice model is being met.

Measuring changes in foraging efficiency

The prey choice model predicts that as high-ranked prey abundances decline, more effort will

be spent foraging for prey with lower return rates, thus resulting in a decline in foraging efficiency. Foraging efficiency can be measured by examining the relative proportion of high and low-ranked prey. Two different means of measuring foraging efficiency can be used: evenness and indices of the abundance of large-bodied taxa relative to small-

bodied taxa. The analysis of changes in evenness is presented elsewhere (Nagaoka, 2001). This analysis will focus on the use of index measures of foraging efficiency.

Comparative indices that measure changing proportions of high- to low-ranked taxa have been used more extensively than evenness for measuring foraging efficiency because they lack the ambiguity that plagues evenness measures (Bayham, 1979; Broughton, 1994, 1997, 1999; Szuter and Bayham, 1989). If body size is assumed to be an appropriate proxy for prey rank, then it follows that the relative abundance of large to small-bodied taxa will measure foraging efficiency. Indices are created that compare a large-bodied or high-ranked taxon to a smaller one within each patch:

$$\Sigma \text{ large taxon} / \Sigma [\text{large taxon} + \text{small taxon}].$$

For example, in western North America, the artiodactyl index compares the proportion of artiodactyls to that of the smaller leporids (e.g., Broughton, 1999; Cannon, 2000; Szuter and Bayham, 1989). Larger index values indicate higher proportions of the high-ranked taxon and thus, greater foraging efficiency. If foraging efficiency is declining, then there should be a decline in the index values over time.

Just as these types of indices are used to track changes in foraging efficiency by comparing the shift from high to lower ranked taxa, they can also be used to study changes in patch use by comparing the proportion of taxa from one patch to that from another patch.

$$\Sigma \text{ taxon from Patch A} / \Sigma [\text{taxon from Patch A} + \text{taxon from Patch B}].$$

A decline in the index indicates a shift from the Patch A taxon to Patch B taxon. If the Patch B taxon is smaller in size than the Patch A taxon, then the index would reflect an overall decline in foraging efficiency, as well as a shift in time allocation across patches.

Measuring changes in diet breadth

If high-ranked resources decline sufficiently to significantly lower the mean foraging return rate, then lower ranked resources will be added to the diet (Stephens and Krebs, 1986). As with foraging efficiency, there are two ways to measure diet breadth. In this analysis, the relationship between

taxonomic richness (number of taxa or NTAXA) and sample size (NISP) is used. The other method of studying diet breadth using taxonomic richness is presented in Nagaoka (2001).

One problem that afflicts the use of taxonomic richness is that it often covaries with sample size (Grayson, 1984). When this is the case, it is unclear if the changes in NTAXA over time are due to changing diet or simply sample size differences. Fortunately, the relationship between richness (NTAXA) and sample size (NISP) can be used as another means of measuring changes in diet breadth (Grayson and Delpech, 1998). The slope and intercept of the regression line describing the relationship between NTAXA and NISP reflect the rate at which taxa are being added as sample size increases. A sample that produces a steep slope and/or a high intercept value has more taxa represented at any given sample size than a sample with a gradual slope and a low intercept value. Thus, if diet breadth is increasing as predicted, we should expect the regression coefficients describing the relationships between NTAXA and NISP to increase significantly. By examining the changes in the rate at which taxa are added, we can thus determine when diet breadth changes significantly.

Changes within the inland patch

The changes predicted by foraging theory models that are discussed above are contingent upon the declining encounter rates of high-ranked taxa within patches. Since body size is likely to be a good indicator of prey rank, it is assumed that moas, as one of the largest taxa in New Zealand, are high-ranked taxa within the inland patch. As high-ranked prey, encounter rates for moas is expected to decline over time due to human foraging efforts.

The expected decline of moa abundances is well-documented in the New Zealand archaeological record. Anderson's (1989b) analysis of dated moa hunting sites in southern New Zealand documents the timing of the decline of moas regionally. Between 1000 and 400 BP, there are numerous sites with an abundance of moa remains. The peak of moa hunting occurred between 600 and 700 BP. After 400 BP, very few archaeological sites contain moa remains, suggesting a dramatic decline in moa abundance. By the time of European discovery of New Zealand in the late 1700s, moas were extinct.

The Shag Mouth site was occupied during the period when the number of moa hunting sites across New Zealand was declining. As a high-ranked taxon, moas should have been taken every time they were encountered. Thus, their relative abundance within the Shag Mouth faunal assemblage should reflect population abundances. The proportion of moas in the inland sample decreases significantly over time (Fig. 2; $r_s = -0.93$, $p = 0.003$). Moa accounts for about 95% of the inland sample from the lowest layer (Layer 11), but decreases to 65% in the uppermost layer (Layer 2). Given the decline in the abundance of the large-bodied, high-ranked moas at the Shag Mouth site, it follows that foraging efficiency declined and diet breadth may have increased with the decrease in moa populations.

Foraging efficiency within the inland patch

As discussed above, the prey choice model predicts that with the decline of high-ranked prey, foraging efficiency will decrease. If foraging efficiency is decreasing due to the decline in high-ranked prey abundances, then the ratio of large- to small-bodied taxa, as representatives of high- and low-ranked taxa respectively, is expected to decrease. In constructing an index comparing high- and low-ranked resources, moa are used as the large-bodied, high-ranked prey type. For comparison, the index requires a small-bodied taxon found in the same habitat as moas. The Zealand quail (*Coturnix novaezelandiae*) meets both of these criteria. In contrast to moas, the quail was very small in size, weighing only 2–5 kg. Thus, a shift away from moas and toward a reliance on quail would indicate a significant decline in foraging efficiency, given the presumed differences in net returns. Most importantly, quail inhabited open

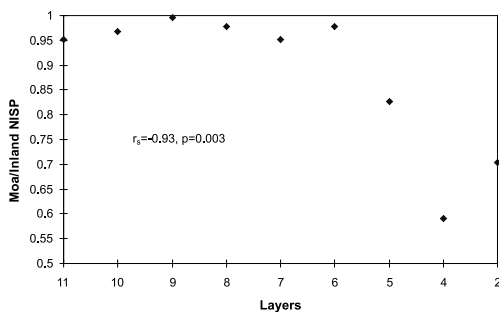


Fig. 2. The relative abundance of moa in the inland sample across layers.

country like many moa species, particularly *Euryapteryx geranoides* and *Emeus crassus*, which are the most common moa taxa identified in the assemblage (Anderson et al., 1996f). As such, quail and moa are likely to have been encountered simultaneously. In addition, early historic accounts describe how Maori took quail individually by placing snares along well-traveled paths in the grass (Anderson, 1994; Best, 1942). Thus, any shifts in the index are not likely to be due to changes in procurement techniques from individual to mass capture. And as the second most abundant taxon in the inland assemblage after moas, quail comprises about 9% of the total inland sample. Thus, their abundances are less likely to be affected by sample size than would a rarer taxon.

A decrease in the moa–quail index ($\Sigma \text{ moa} / \Sigma (\text{moa} + \text{quail})$) would represent increasing exploitation of the diminutive quail and thus, decreasing foraging efficiency within the inland patch. The statistic used to test the significance of this relationship is Cochran's test of linear trends (Cannon, 2001; Zar, 1996). This is a chi-square analysis that takes into account the natural ordering of a sequence, such as a temporal trend across stratigraphic layers. In the case of the moa–quail index, the statistic tracks changes in the proportion of moas relative to quail across layers or time. Cochran's statistic is comprised of three types of chi-square analyses. The first is the traditional chi-square, called the total chi-square, which tests the relationship between the two variables. The total chi-square is subdivided into two components: one tests the variation that is due to the linear trend; the other examines the departure from the linear trend. It is the chi square for the linear trend (χ^2_{trend}) that is used to test whether the proportion of moa to quail changes significantly over time.

Fig. 3 shows that the moa–quail index decreases significantly over time ($\chi^2_{\text{trend}} = 734.7$, $p < 0.001$), and the index is not correlated with sample size ($r_s = -0.48$, $p = 0.194$). In the lower layers, the very low index values indicate that moa dominates to the near exclusion of quail. Between layers 2 and 6, the index drops significantly. The pattern shows that within the inland patch, moas comprise less of the diet through time, suggesting that foraging efficiency is declining.

The assumption behind the comparisons between high- and low-ranked taxa like the moa–quail index is that changes are due to resource depression. That is, the decline in the index is assumed to be caused by the depression of the

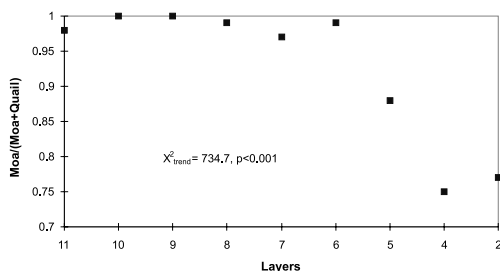


Fig. 3. The moa–quail index of the inland patch by layer.

high-ranked taxa rather than an increase in the lower ranked one, and that the decline in prey abundances is due to human foraging rather than natural environmental change (Broughton, 1999; Grayson and Cannon, 1999). There is little question that moa decline and extinction was due not to exogenous causes, such as climate change, but to human action through habitat alteration and predation (Anderson, 1989a). However, there is evidence for environmental change that could have affected the quail population positively in such a way that resource depression may not be the cause of the declining foraging efficiency.

During the prehistoric era, widespread deforestation led to the creation of more open habitat across New Zealand (McGlone, 1983). At the Shag Mouth site, pollen data document a similar pattern of local vegetational change. The vegetation in the area shifts from closed forest to more of an open forest with a shrubby understory, and finally to an open habitat dominated by grass and bracken ferns (Boyd et al., 1996). The creation of more open country may have favored quail populations, which would have increased the encounter rates of quail. Quail appear to have been a part of the diet throughout the occupation of the Shag Mouth site (Table 1), thus it is likely that they were always taken on encounter. Consequently, if quail encounter rates increased, then the proportion of quail in the diet should also increase. Thus, the changes in the moa–quail index may be due in part to increasing quail populations rather than just decreasing moa populations.

To determine if quail abundances increased due to the creation of new habitat, the proportion of quail in the Shag Mouth assemblage is compared to that of a forest bird, the New Zealand Pigeon (*Hemiphaga novaeseelandiae*). The pigeon was chosen because it a large, and thus high-

ranked, forest bird that, like the quail, is present throughout the assemblage. It is expected that the open habitat required by quail would be created through the clearing of forested areas. This, in turn, would be detrimental to pigeon populations. To test this prediction, I compare quail and pigeon abundances with the following index:

$$\Sigma \text{quail} / \Sigma (\text{quail} + \text{pigeon}).$$

It is expected that if deforestation led to an increase in quail populations and a decline in pigeon populations, then the quail–pigeon index should increase over time. The quail–pigeon index does increase slightly, but the change is not significant (Fig. 4; $\chi^2_{\text{trend}} = 0.12$, $p = 0.74$). Thus, it appears that while vegetation patterns changed in and around the Shag Mouth site as demonstrated by the pollen data, these local changes did not have a significant impact on the proportion of pigeons and quails within the entire inland patch. This supports the conclusion that the changes in foraging efficiency tracked by moa–quail index are caused by declining abundances of moa and not by a significant increase in the quail population.

Diet breadth within the inland patch

As I have discussed, a decline in the abundance of high-ranked taxa may lower the mean foraging return rate to the point where diet breadth increases. To determine if diet breadth is expanding as moa populations are declining, the relationship between NTAXA and NISP is examined. Since changes in diet breadth should be linked to the decline in the abundance of the high-ranked taxa, which for the inland patch are moas, we can examine the relative abundance of moa in the sample to determine when diet breadth may be expected to increase. A drastic decline in the relative abundance of moas occurs during that

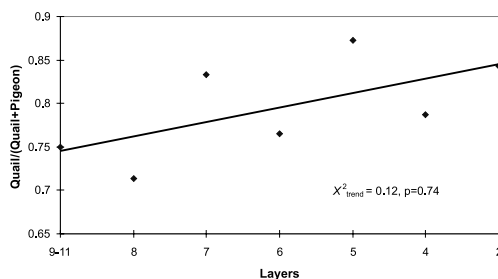


Fig. 4. The quail–pigeon index for the inland patch by layer.

period between Layers 5 and 6 (see Fig. 2). Therefore, Layers 2–5 and 6–11 should produce significantly different regression coefficients if diet breadth is increasing due to declining moa abundances. Specifically, the sample from Layers 2–5 should have a steeper slope and/or large intercept value than Layers 6–11 if diet breadth is increasing over time.

As can be seen in Fig. 5, two significantly different populations are indeed represented in the inland patch data ($t = 4.84$, $0.05 > p > 0.02$). The sample from the younger layers (Layers 2, 4, 5) is described by a regression line with a much larger intercept and a slightly steeper slope than that from the older layers (Layers 6–11). While the correlation between the variables in the upper layers is extremely high, there are so few points that the relationship is not statistically significant. The presence of two statistically different relationships between NISP and NTAXA indicates that for any give sample size, there are more taxa found in the upper layers than in the lower layers and the rate at which taxa are added is higher. In other words, more taxa are being utilized during the later occupation of the site. In addition, the increase in diet breadth is directly linked to the decline of moas in the diet. Moas comprise a higher percentage of the inland sample in the lower layers than in the upper layers (Fig. 5).

While NISP–NTAXA relationships can reflect diet breadth, they can also be influenced by other factors. In particular, differential fragmentation and skeletal element representation can lead to an overrepresentation of NISP or an underrepresentation of NTAXA that can cause the differences seen in the NISP–NTAXA relationship (Grayson and Delpech, 1998). As a result, the influence of these factors on the NISP–NTAXA relationship must be examined.

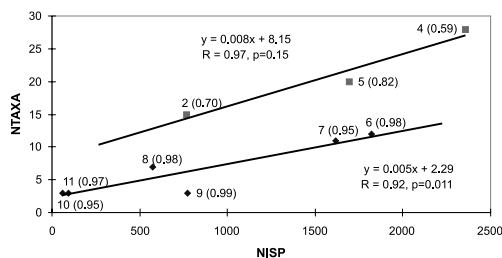


Fig. 5. The relationship between NISP and NTAXA for the upper and lower layers of the inland patch sample with the proportion of moas in parentheses for each layer.

The degree of skeletal element fragmentation can affect the number of identifiable specimens represented. A higher fragmentation rate will increase the NISP per NTAXA, resulting in a regression line with a lower slope. Thus, if the NISP–NTAXA analysis above is affected by differential fragmentation, then we should expect that the sample with the lower slope, in this case the sample from the lower layers, will have a higher fragmentation rate than the upper layers sample. To determine if the rate of fragmentation is changing, I compare bone fragmentation patterns for the sample from the upper to the one from the lower layers. Bone fragmentation is measured by the ratio of the number of identified specimens identified for each element (NISP) to the minimum number of elements (MNE). An increase in the ratio would indicate that there are more fragments per skeletal element represented, i.e., fragmentation is increasing. If differential fragmentation is causing the differences between the NISP–NTAXA relationships, the sample from the lower layers should have a significantly higher NISP relative to MNE than the upper layer. Chi-square analysis shows that the proportions of NISP to MNE from the upper and lower layers, however, are not significantly different (Table 4: $\chi^2 = 0.05$, $p = 0.82$). Since fragmentation between both samples is similar, differential fragmentation is unlikely to have affected the NISP–NTAXA relationship.

Differential representation of skeletal elements has also been identified as a factor that can affect the NISP–NTAXA relationship (Grayson and Delpech, 1998). The proportion of elements may change over time due to changes in field processing (Bartram, 1993; O'Connell et al., 1988, 1990) or preservation factors (Lyman, 1984, Lyman and Fox, 1989). If the number of elements being

Table 4
Numbers of identified specimens (NISP) and minimum number of elements (MNE) for moa leg elements

Layer	NISP	MNE
2	50	21
4	199	68
5	81	49
6	165	82
7	74	42
8	15	13
9	26	13
10	7	4
11	3	3

returned to the site or preserved decreases over time, it will appear that the NISP has decreased relative to the NTAXA, or more specifically that NTAXA has increased, which will result in a higher slope between NISP and NTAXA. Thus, if skeletal element representation is affecting the NISP–NTAXA analysis, we should expect that the high slope sample should have significantly fewer elements represented.

To test for the effects of differential elemental representation, the frequency of moa elements from the upper and lower layers sample was compared using chi-square analysis (Grayson and Delpech, 1998). The proportion of elements represented in the two samples is significantly different (Table 5; $\chi^2 = 300.8$, $p < 0.001$). Examination of the adjusted residuals shows that several elements are significantly over- or underrepresented in each assemblage. Those elements that are significantly ($p < 0.05$) underrepresented in the sample with the higher slope, or in this case, the upper layers sample, are most likely to affect the analysis.

The underrepresented elements in the high slope sample are the phalanges and the tarsometatarsi. If they significantly affect the NISP–NTAXA analysis, then their removal from the data should produce plots between the upper and lower layers that are not significantly different. Fig. 6 shows the replotted NISP–NTAXA data. Both samples are still statistically different ($t = 4.65$, $p < 0.05$). Thus, although there may be differences in the elements being transported back to the site, they do not appear to be significantly affecting the NISP–NTAXA relationships.

In sum, the NISP–NTAXA relationship data demonstrate that a major shift in diet seems to

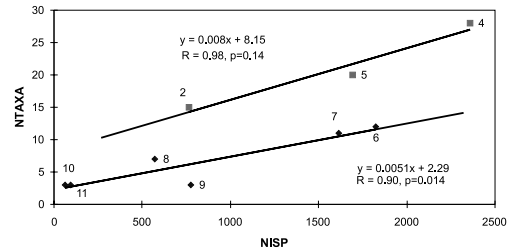


Fig. 6. The NISP–NTAXA relationships with moa phalanges and tarsometatarsi removed.

occur between Layers 5 and 6. At this time, there is a substantial decline in moa abundances that appears to have lowered foraging efficiency to the point where the number of taxa represented in the inland assemblage increases significantly. Thus, in addition to a decline in foraging efficiency, diet breadth for the inland patch is increasing with the declining abundances of the high-ranked resource, moas.

Changes within the coastal patch

As with the inland patch, the predicted dietary changes within the coastal patch are contingent upon the declining encounter rates of high-ranked taxa within patches. Based on body size, the high-ranked resources within the coastal assemblage are the pinnipeds. The distribution of pinnipeds, particularly the New Zealand fur seal (*Arctocephalus forsteri*), changed significantly after the colonization of humans. The range of breeding colonies and their populations declined dramatically during the prehistoric period. Smith (1985, 1989) argues that this restriction in the range of pinnipeds is due to human foraging and not environmental factors. By the time of European contact, successful rookeries were found only in areas of New Zealand far removed from human occupation. At the Shag Mouth site, pinniped abundances also declined. Fig. 7 shows the relative abundance of New Zealand fur seals (*Arctocephalus forsteri*), Hooker's sea lions (*Phocarctos hookeri*), and elephant seals (*Mirounga leonina*). Over 97% of the pinniped sample is comprised of New Zealand fur seal (see Table 2). The decline in relative abundance of these three pinniped species is significant ($r_s = -0.73$, $p = 0.036$). Since these large-bodied, and thus high-ranked, taxa show a pattern of declining abundances, it follows that within the coastal

Table 5
Number of moa skeletal elements (NISP) from the upper and lower layers

Element	Upper layers	Lower layers
Skull/Mandible	23	25
Vertebra	280	357
Sternum	26	18 ^a
Rib	188	251
Innominate	48	32 ^a
Femur	16	26
Tibiotarsus	204	163 ^a
Tarsometatarsus	22 ^a	45
Fibula	40	24 ^a
Phalanx	203 ^a	396

^a Significantly underrepresented ($p < 0.05$).

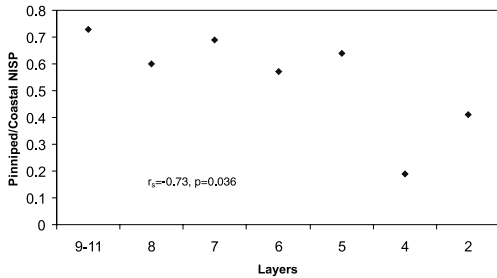


Fig. 7. The relative abundance of pinnipeds in the coastal sample.

patch foraging efficiency should have declined and diet breadth may have increased.

Foraging efficiency within the coastal patch

As in the inland patch, foraging efficiency is expected to decline as the abundance of the high-ranked prey, in this case, pinnipeds, declines. Since foraging efficiency is expected to decline as populations of high-ranked taxa decline, the large- to small-bodied taxon index is used to track these changes in foraging efficiency. As the largest taxa in the coastal assemblage, the three pinniped species (New Zealand fur seal, Hooker's sea lion, elephant seal) are the large-bodied prey used in this analysis. Two taxa are used as small-bodied prey to compare against the pinnipeds: dog (*Canis familiaris*) and wrasses (Labridae).

The *kuri* or Maori dog was chosen to compare with seals because of its size and relative abundance in the assemblage. Like most Polynesian dogs, the *kuri* is a small breed that is estimated to weigh about 13–15 kg (Clark, 1997). Dogs, pigs and chickens were the three domesticated animals transported by Polynesians as part of the colonization process (Kirch, 1984). In New Zealand, dogs were the only domesticated found archaeologically and were a part of the diet until the historic introduction of other meat sources such as cattle and pigs (Buck, 1950). After the New Zealand fur seal, dog is the most abundant taxon in the coastal assemblage.

The pinniped–dog index,

$$\Sigma \text{ pinniped} / \Sigma (\text{pinniped} + \text{dog}),$$

tracks changes in the abundance of the large-bodied seals relative to the smaller Maori dog. Lower pinniped–dog index values represent declining foraging efficiency as more dog is taken relative to the much larger pinnipeds. The pinni-

ped–dog index shows a pattern of declining foraging efficiency similar to that of the inland patch (Fig. 8). Pinnipeds decline significantly relative to dog ($\chi^2_{\text{trend}} = 383.2$; $p < 0.001$), although the decline seems to occur a little later than in the inland patch. The pinniped–dog index declines between Layers 4 and 5 while a dramatic decline in the moa–quail index occurs between Layers 5 and 6 (see Fig. 2). The pinniped–dog index is not correlated with sample size ($r_s = -0.41$, $p = 0.355$). Thus, as seals comprise a smaller portion of the diet, foraging efficiency in the coastal patch declines.

There are a couple of potential problems with using dog in this comparison. As domesticated animals, dogs may have been found mostly around human habitation areas, and thus they may not have overlapped significantly with seals, which inhabited the nearby rocky or sandy coastline. Since the site is located along the shoreline, the likelihood of encountering both prey in the same patch may have been highest during the initial occupation of the site when nearby seal habitats were being exploited. In addition, because dogs were likely to have been in close proximity to human habitation, pursuit costs may have been much lower for dogs and are less likely to have changed than pursuit costs for seals. If the exploited seal habitat shifted further from the site, then the pinniped–dog index may be measuring changing distance costs rather than foraging efficiency. However, the analysis of relative skeletal abundance and utility suggests that the distance to seals may not have changed significantly over time (Nagaoka, 2000).

A more severe problem is that domesticated animals such as dogs may not fit the assumptions of the prey choice model. The issue of incorporating domesticated animals into foraging theory models is complex, and has not been adequately

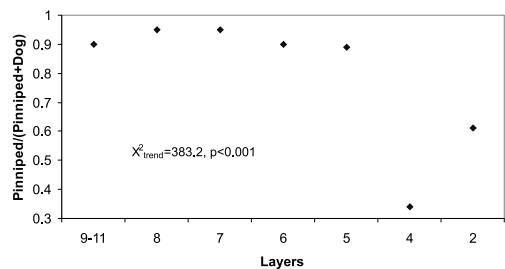


Fig. 8. The pinniped–dog index of the coastal patch by layers.

addressed in the literature. In particular, domesticated animals are not always taken upon encounter and essentially have pursuit costs that are zero. Because dogs need not always be taken upon encounter, their harvest does not compete with the foraging effort for pinnipeds. Dogs, then, should constitute a distinct patch. If this is the case, then the pinniped–dog index may not be measuring changes in foraging efficiency within the coastal patch, but changes in patch use resulting from changes in foraging efficiency across patches.

Given the possible problems of using dogs, another index was created using wrasses to examine changing foraging efficiency. These inshore fish are small, weighing under a kilogram. If foraging efficiency is declining in the coastal patch, then the pinniped–wrasse index (Σ pinniped/ Σ (pinniped + wrasse)) should decrease. Like the pinniped–dog index, the pinniped–wrasse index declines significantly over time (Fig. 9; $\chi^2_{\text{trend}} = 151.4$; $p < 0.001$). The decline is relatively steady with the exception of Layer 4, for which the proportion of wrasse to pinnipeds is much greater than expected. The index represents a shift from the larger pinnipeds to the smaller wrasses, indicating a decline in foraging efficiency over time within the coastal patch.

While predation undoubtedly affected prehistoric seal distributions (Smith, 1985, 1989), the possibility that climatic change could have influenced seal abundances, and thus the pinniped indices, must be explored to determine if resource depression is the cause of the decline in foraging efficiency. Environmental or climatic change could affect breeding patterns or the availability of food. For example, breeding success can be linked to thermoregulation: males with territories that have access to tidepools or are close to the water

are able to cool themselves more readily and have higher reproductive success than males that do not (Reidman, 1990).

If climatic changes caused the prehistoric decline in fur seal abundance and distribution, this change would have to be unidirectional. That is, if temperatures rose continually over the course of the last 1000 years, the pinniped breeding success of seals would have decreased, causing a decline in population abundances across New Zealand, and/or a shift in the distribution of fur seal populations to cooler regions. The climatic data, however, does not show a steady directional trend in temperatures that may have led to a decline in seal populations during the prehistoric occupation of New Zealand (Grant, 1994). Instead, temperature fluctuated between warmer and colder periods during the prehistoric period. Oxygen isotope data on a speleothem from the north end of the South Island produced a pattern where the mean average temperature has fluctuated significantly since Polynesian colonization (Wilson et al., 1979).

Dendrochronological and $\delta^{13}\text{C}$ data from a 1000 year old kauri tree (*Agathis australis*) produced a pattern of troughs and peaks similar to the speleothem data. However, the two differ on the timing of those warmer and cooler periods. Grinsted and Wilson (1979) argue that the kauri dates are more accurate than those for the speleothem data, are thus more appropriate for describing the timing of temperature fluctuations. In either case, there is no unidirectional change in temperature during the prehistoric period to explain the decline in seals across New Zealand.

While climate does not explain the decrease in seal abundance across the country, it may be that temperatures changed unidirectionally during the period represented by the occupation of the Shag Mouth site. The Shag Mouth site was occupied for 50–200 years, probably from some time between the AD 1200 and AD 1400 depending on interpretations of the radiocarbon dates. Whether using the speleothem or kauri tree data, the temperature fluctuated during this period, rather than steadily declined or increased. As a result, the data do not suggest that changing seal abundances during the occupation of the site were the result of changing climate. Human foraging remains the best explanation for the decline of seal populations.

In sum, the analyses indicate that large prey comprise an increasingly smaller proportion of the diet over time. Thus it appears that foraging

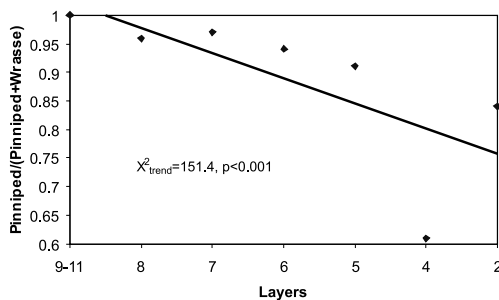


Fig. 9. The pinniped–wrasse index of the coastal patch by layers.

efficiency is declining in the coastal patch. In addition, the evidence suggests that human foraging efforts are likely to have been the cause of this shift in foraging efficiency.

Diet breadth within the coastal patch

With a decrease in the encounter rates of high-ranked taxa and the corresponding decline in foraging efficiency, diet in the coastal patch may broaden. To test if the number of resources utilized increases over time, I once again examine changes in the relationship between richness and sample size. Changes in diet breadth are expected to be linked to the decline of the high-ranked prey, which for the inland patch are seals. Thus, the relative abundance of pinnipeds can be examined to determine where the change in the rate at which NISP and NTAXA is expected, and where the samples should be divided. The decline in pinniped abundances appears to be less marked and occurs later than for moas in the inland patch (see Figs. 2, 3, and 5). The relative abundance in pinnipeds seems to decrease between Layers 4 and 5 (Fig. 7). Based on this, the sample is subdivided into two, with Layers 6–11 comprising the lower layer sample and Layers 2–5 in the upper layer sample. As the apparent inflection point in the pinniped relative abundance plot, Layer 5 could be included in either the lower or upper layer sample. However, it is included with Layers 2 and 4 as the upper layer sample as a matter of convenience so that the decrease can be described statistically. If diet breadth is increasing in the coastal patch, then it is expected that the regression line for the upper layer sample should have a steeper slope and/or larger intercept value than the lower layer sample.

As with the inland sample, the NISP–NTAXA relationship for the upper layers (Layers 2, 4, 5) is significantly different from that of the lower layers (Layers 6–11) (Fig. 10; $t = 115.4$, $p > 0.001$). The regression line for sample from the upper layers has a slightly higher slope and a larger intercept than that from the lower layers. The correlation between NISP and NTAXA for both the upper and lower layers is very high, but while the NISP–NTAXA relationship for the lower layers sample is significant, there are so few points in the upper layer sample that the relationship is not statistically significant. The significant differences between regression coefficients of the two samples indicate that the NTAXA found in the upper sample is greater than that found in the lower

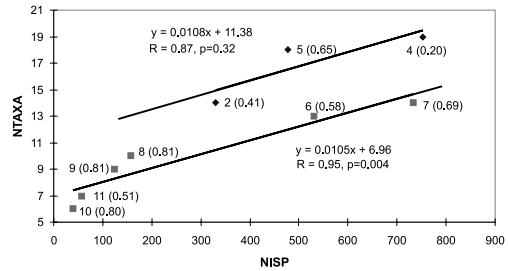


Fig. 10. The relationship between NISP and NTAXA for the upper and lower layers of the coastal patch sample with the proportion of pinnipeds for each layer.

layers, i.e., diet breadth is expanding significantly over time.

If diet breadth is increasing in the coastal patch due to declining pinniped abundances, then the lower layer sample should have higher proportions of pinnipeds than the upper layers sample. Fig. 10 shows the NISP–NTAXA regression plots with the seal proportions in parentheses for each of the layers. Although the pattern is not as dramatic as in the inland sample, in general, the proportion of pinnipeds is greater in the lower than in the upper layers. The low relative abundance of pinnipeds in Layer 11 (0.51) is likely due to the small sample size for the layer. Thus, it appears that the increase in diet breadth is related to the decline in seal abundances.

As discussed in the analysis of the inland patch, differential fragmentation and skeletal element representation can affect the NISP–NTAXA relationship in a manner similar to diet breadth changes (Grayson and Delpech, 1998). Thus, the effect of these two factors must be determined before interpretations about diet change can be made. Differential fragmentation can inflate NISP and lower the slope of the regression line. The relevant fragmentation values are presented in Table 6. Once again, chi-square analysis shows that the NISP and MNE values from the upper and lower layers are not significantly different (Table 6: $\chi^2 = 0.195$, $p = 0.67$). Thus, it is unlikely that fragmentation has led to the patterns seen in the NISP–NTAXA analysis.

Because differential skeletal element representation can affect the NISP–NTAXA relationship by underestimating NISP, elemental data for otariid seals and dogs are examined. These two taxa were chosen because they comprise about two-thirds of the coastal assemblage. Elemental counts from the upper and lower layers (Table 7) are compared using chi-square analysis. Because the

Table 6
Number of identified specimens (NISP) and minimum number of elements (MNE) for otariid skeletal elements

Layer	NISP	MNE
2	96	67
4	128	68
5	242	163
6	209	138
7	347	239
8	63	44
9	81	44
10	16	13
11	25	16

Table 7
Number of otariid and dog skeletal elements (NISP) from the upper and lower layers

Element	Upper layers	Lower layers
Skull/Mandible	62	140
Vertebra	76 ^a	185
Rib	66	153
Scapula	21	33
Humerus	21	14 ^a
Radius	27	31
Ulna	19	4 ^a
Innominate	15	27
Femur	17	28
Tibia	11	20
Fibula	12	13
Metapodials	92	142
Podials	25 ^a	84
Phalanx	148	260

^aSignificantly underrepresented ($p < 0.05$).

skeletal element representation from the two layers differs significantly ($\chi^2 = 55.2$, $p > 0.001$), it is possible that differential skeletal element representation is affecting the NISP–NTAXA relationships.

Since elements that are significantly underrepresented in the high slope sample are likely to create differences between the two samples, these elements need to be removed from the NISP–NTAXA datasets and the data reanalyzed in order to test for their effect on the analysis. The vertebrae and podials were the two elements underrepresented in the high slope sample (Table 7). These were removed from the NISP counts and the relationship between NISP and NTAXA recalculated (Fig. 11). The two samples remain significantly different ($t = 93.7$, $p < 0.001$). Thus, it appears that the NISP–NTAXA relationships are not being affected by differential fragmentation or differential elemental representation.

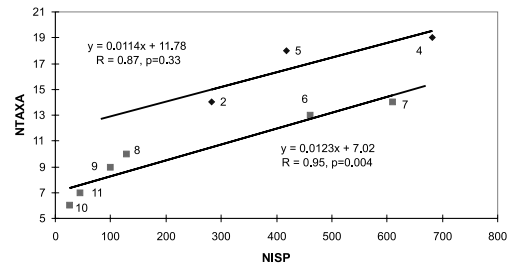


Fig. 11. The NISP–NTAXA relationships with otariid and dog vertebrae and podials removed.

In sum, resource exploitation appears to be more generalized in the coastal patch than it is in the inland patch. However, the outcome of declining abundances of high-ranked prey remain the same. Foraging efficiency appears to have declined as the larger taxa comprised a smaller proportion of the diet. In addition, a wider range of taxa were likely to have been taken as pinniped abundances decline. That is to say, diet breadth in the coastal patch increased over time.

Changes within the offshore patch

The pattern for the offshore patch is expected to be different from that of either the coastal or inland patches because it contains no large-bodied resources such as moas and seals. As such, the offshore patch may have been the lowest ranked of the three patches, and would have been the last patch to be added to the subsistence regime. If offshore resources were not exploited initially, then the patch choice models predict that this patch should have been added when the mean foraging return rate for all utilized patches declined below the expected return rate of the offshore patch. Alternatively, if the offshore patch was being utilized throughout the occupation of the site, but only minimally, foraging theory predicts that patch residence time will increase as the mean foraging return rate declines.

Indeed, it appears that the offshore patch was not regularly used until late in the Shag Mouth sequence. The offshore component makes up less than 10% of the Shag Mouth faunal assemblage until the uppermost layers where it comprises up to nearly 60% of the total assemblage (Fig. 12), a trend that is not significantly correlated with sample size ($r_s = 0.71$, $p = 0.11$). During the early period of the site occupation, the offshore patch appears to have been used only occasionally.

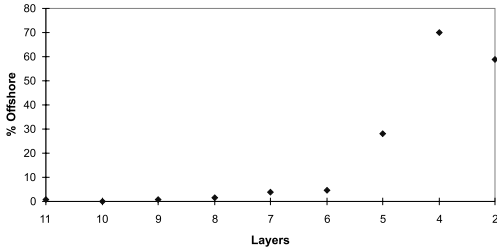


Fig. 12. The relative abundance of resources from the offshore patch by layer.

The marginal value theorem predicts that patches will be added if foraging efficiency and the mean foraging return rate for all utilized patches declines significantly (Charnov, 1976). To demonstrate that this late use of the offshore patch is due to declining foraging efficiency within the two other patches, and thus over all patches, I compare the relative abundance of an offshore resource to high-ranked resources from the other two patches. In particular, barracouta, the primary resource exploited in the offshore patch, is compared with the high-ranked resources, pinnipeds and moas, from the coastal and inland patches:

$$\Sigma \text{ moa} / \Sigma (\text{moa} + \text{barracouta}),$$

$$\Sigma \text{ pinnipeds} / \Sigma (\text{pinnipeds} + \text{barracouta}).$$

Barracouta are much smaller than either moas or pinnipeds, weighing about 1–3 kilograms (Armitage et al., 1981). Thus, a decrease in the indices would indicate a shift in resource exploitation from the coastal and/or inland patches to the offshore patch, as well as a decrease in foraging efficiency across all patches.

Both the moa–barracouta and the pinniped–barracouta indices show the increasing importance of barracouta. The moa–barracouta index decreases significantly over time (Fig. 13; $\chi^2_{\text{trend}} =$

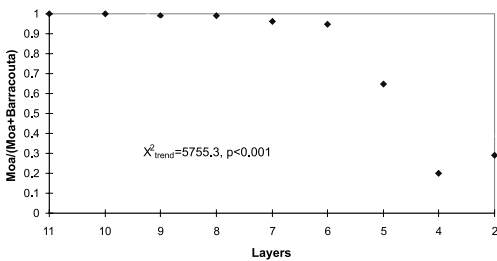


Fig. 13. The moa–barracouta index by layer.

5755.3, $p < 0.001$). Moa dominates until Layer 5 when barracouta becomes important. A similar pattern can be seen for the pinniped–barracouta index (Fig. 14; $\chi^2_{\text{trend}} = 4167.2$, $p < 0.001$). Pinnipeds decline significantly relative to barracouta. This shift begins earlier in the sequence and is slightly more gradual than for moas. Currently, there is no evidence to suggest that barracouta populations were increasing relative to either moas or seals over time. Thus, it appears that resource exploitation expanded to include significant use of the offshore patch as the foraging efficiency for the other patches declined.

Over time, the pattern of exploitation within the offshore patch also appears to change. Evenness measures can characterize whether exploitation patterns are more generalized or specialized (Nagaoka, 2001). High evenness values indicate that the pattern of exploitation is generalized, whereas low evenness values indicate a specialized pattern of exploitation. Within the offshore patch, evenness values for the lower layers are relatively high, suggesting that initial use of the offshore patch was generalized. Over time, evenness declines indicating increasingly specialized use of the patch (Fig. 15; $r_s = -0.77$, $p = 0.07$).

One possible interpretation of the barracouta indices and evenness results is that initial exploitation of the offshore patch may have been

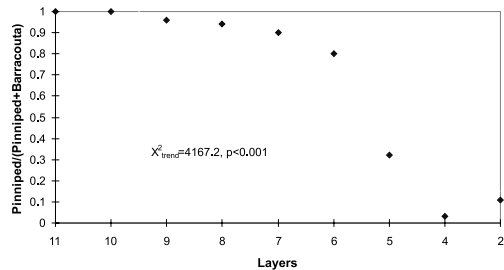


Fig. 14. The pinniped–barracouta index by layer.

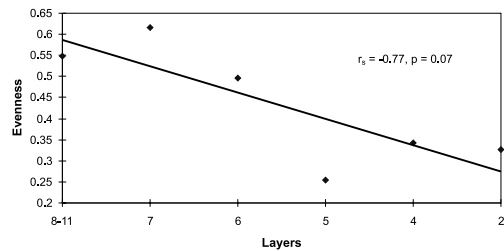


Fig. 15. Evenness values for the offshore patch by layer.

opportunistic, possibly in conjunction with travel to other areas via canoes. In other words, the entry into the patch may not have initially been for foraging purposes. Instead, initial use of the patch may have been as part of “embedded” hunting where resources were procured opportunistically while traveling through the patch for other non-hunting related purposes (O’Connell and Hawkes, 1981, 1984). Later, around Layer 5, the offshore patch became a regular part of the subsistence regime as foraging efficiency declined in the other patches. The significant decrease in evenness suggests that after the offshore patch was added, exploitation focused primarily on barracouta. Indeed, barracouta eventually comprise a large portion of the overall diet.

An alternative interpretation is that the offshore patch was always included in the foraging regime, but time allocation was initially very low. As foraging efficiency declined in the other two patches, time allocation within the offshore patch increased and/or technological improvements occurred. If initially, the offshore patch was a low-ranked patch in which foragers spent little time, then the resources exploited should be the higher ranked resources. Over time as overall foraging efficiency declined, time allocation increased and exploitation within the offshore patch broadened as in the other patches. However, the evenness data suggests that exploitation became more specialized. The decline in evenness may instead represent a change in hunting types or pursuit technology used to capture offshore resources. While barracouta is the dominant resource exploited in the offshore patch, red cod and albatross are also exploited throughout the sequence. Initially, a hook-and-line technology may have been used with hand lines that were deployed vertically via jigging for pursuing resources that can be found around offshore reefs. This type of technology is quite generalized in the type of prey that it can capture, providing access to predatory fish, such as red cod and barracouta, within the entire water column. Later on, in addition to the jigging technique, the more specialized technique of trolling may have been added to pursue schooling barracouta feeding on the surface, as well as albatross that may have been associated with these schools.

In essence, the offshore patch may actually consist of two hunt types: one characterized by trolling, the other by jigging. Hunt types have been used elsewhere to define patches (see Smith, 1991), thus the offshore patch may consist of two

separate patches based on the different hunt types represented. If this is the case, then the jigging hunt type/patch may have been used throughout the sequence, while the trolling hunt type/patch may have been added late during the occupation of the site. At Shag Mouth, jigging fishhooks are found throughout the sequence, while barracouta lures were only recovered from Layers 2 and 4, suggesting that trolling is a late phenomenon (Anderson and Gumbley, 1996).

Although barracouta lures enter the record late, it is likely that the trolling technology was brought by the Polynesian colonists. The exact origins of the form of trolling lures used for barracouta is uncertain, but they may have been derived from minnow lures, and ultimately developed from the East Polynesian bonito lures, a trolling technology that would have arrived with the colonists (Anderson and Gumbley, 1996). It is likely then, that since trolling technology was always available, the apparent increase in barracouta exploitation during the later occupation of the Shag Mouth site is driven not by innovations in procurement technology, but to resource depression of seals and moas within the coastal and inland patches.

In sum, the differences in the two interpretations arise from an inability to identify the nature of the earliest exploitation of the offshore patch. The patch may have been included in the foraging radius throughout the sequence and the amount of time allocated to the patch simply increased after a significant decline in the overall foraging efficiency. Alternatively, the offshore patch may not have been used initially, but was added to the foraging radius later. While the nature of changing offshore resource use is unclear, it appears to be linked to declining overall foraging efficiency. Only after moas and seals decline do offshore resources play a significant role in overall subsistence patterns at Shag Mouth.

Discussion and conclusions

Evolutionary ecological models have been used before to study subsistence change in New Zealand. Anderson (1981) used foraging theory models to examine the impact of human predation on shellfish populations. This study, however, is the first analysis to use these models to study changes in diet due to declines in vertebrate resource abundance. As discussed earlier, subsistence change in New Zealand has been broadly

described as a shift from moa exploitation, which dominated the early period, the exploitation of smaller taxa such as fish and small birds in the later period. While this general pattern still holds, this analysis provided a more detailed picture of subsistence change as the abundance of important resources declines.

Early in the Shag River Mouth sequence, the inland and coastal patches appear to be the main focus of resource exploitation. Within the inland patch, foraging initially specialized on moas. As moa populations declined, foraging efficiency declined as lower ranked, smaller taxa, such as quails came to comprise a larger percentage of the diet. Foraging efficiency within the inland patch appears to have declined to the point where lower ranked resources that were previously ignored were added to the diet.

The pattern for the coastal patch is similar, although not as dramatic. As in the inland patch, as the populations of large-bodied, high-ranked pinnipeds declined, more foraging effort was invested in obtaining lower ranked resources and foraging efficiency decreased. However, evenness analysis suggests that resource exploitation in the coastal patch was broader than for the inland patch throughout the occupation of the Shag Mouth site (Nagaoka, 2001). While seals were the most important taxon in the patch for most of the sequence, a number of other resources such as shags, penguins, dogs, and fish were taken in significant numbers throughout the occupation. In addition to declining foraging efficiency, the diet also expanded to include lower ranked taxa.

As the foraging efficiency for the inland and coastal patches, and thus overall foraging efficiency decreased, use of the offshore patch increased. The patch may not have been used early on because of associated travel costs (i.e., exploitation via canoes), as well as the relatively low returns for offshore resources. Or the patch may have been used throughout the occupation, but time spent foraging in it only increased later. In either case, only after moa and seal populations start to decline do offshore resources with a focus on the exploitation of barracouta contribute significantly to the overall diet.

This picture of subsistence change at Shag Mouth is more fine-grained than previous research in the region because the methodology focused on documenting variability across time and space. For example, because the data were divided up by patch as required by the models, I

was able to document differences in the exploitation of resources across and within different areas around the site. In addition, by analyzing change across stratigraphic layers rather than aggregating data by groups of layers or by site, I was able to document temporal trends in subsistence change. Contributing to the detail of this analysis is the unusually large size of the sample.

As is often the case, changes in subsistence are likely to have repercussions in other aspects of the culture, such as settlement patterns. Anderson and Smith (1996c,d) discuss how settlement change in southern New Zealand is likely linked to resource availability. Sedentary, permanent settlements such as Shag Mouth are possible because the resources needed to support these settlements are abundant, aggregated, and predictable across time and space. During the initial occupation of the region, foragers had access to rich habitats with abundant resources. Seals, seabirds, and fish could be harvested along the coast, while moas and other birds were taken from the forest, grasslands, or estuaries. The eventual abandonment of Shag Mouth and other village sites around 400 BP is believed to be due to declines in regional resource availability. As local depletion occurs, foragers can no longer sustain themselves in this one area and move their settlements to new unexploited areas as is predicted by the patch choice model. During this post-village period, settlement becomes more mobile, dispersed, and probably seasonal. To better understand settlement changes resulting from declining resource availability, more research on the timing of abandonment as well as analyses such as this one are required. As a database of regional patterns in subsistence change resulting from resource depression is developed, we can better understand regional subsistence and settlement change (e.g., Cannon, 2000).

Finally, while moas are promoted as a prime example for the overkill model (Diamond, 2000; Martin, 1984), the data from the Shag Mouth site do not fit the patterns described by the model. According to the overkill model, hunters specialize on megafauna until the prey become extinct. However, one of predictions of the prey and patch choice models is that if the availability of a high-ranked prey type declines over time, then the number of prey pursued will increase if overall foraging efficiency declines significantly. If foragers specialize on a prey type until it becomes extinct, then the net returns during the period before extinction would be so low that very few foragers

could be supported. Indeed, at Shag Mouth, even though exploitation in the inland patch focused on moa hunting, the overall exploitation pattern was broad, and expanded over time to over include 70 vertebrate taxa by the end of the site occupation.

The overkill model also predicts that hunters exploit megafauna until they become locally extinct before moving on to another area. As others have pointed out (e.g., Smith, 1991; Winterhalder, 1981b), the marginal value theorem predicts that, in areas of an abundance of high-ranked prey, foragers will remain in a patch only a short time before moving on to another area that has not been depleted. So foragers can affect prey abundances locally, but before local extinction occurs, they move on to other unexploited higher return areas. Again, the data from the Shag Mouth site supports this prediction. Although moas comprise a smaller proportion of the diet over time, their remains still make up over 20% of the total assemblage at the end of the occupation of the site. It appears that moas were still present in the region and that the site was abandoned before they became extinct.

Even if local extinction of moas occurred during the occupation of the Shag Mouth site, the role of habitat destruction in the extinction cannot be ruled out. Habitat loss and fragmentation are known to play an important role in extinction, so much so that a major aspect of conservation biology focuses on understanding their effects on species survival (e.g., Gilpin and Soulé, 1986; Young and Clarke, 2000). Significant vegetational changes occurred during the prehistoric period in New Zealand (McGlone, 1983; McGlone and Wilmhurst, 1999), and around the Shag Mouth site (Boyd et al., 1996). Yet no one has demonstrated that these environmental changes did not have a major effect on the availability of moa habitat, and thus moa populations. So even for moas, there is little evidence to suggest that extinction resulted simply from human hunting.

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