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Ian Smith

Anthropogenic depletion of New Zealand's avifauna has been widely cited in discussions of the impacts of human colonisation on island environments, but much less attention has been paid to effects upon marine resources. This paper reviews evidence for the nature and consequences of predation upon the most abundant marine mammal, the New Zealand fur seal Arctocephalus forsteri. *Two major phases of exploitation are apparent, involving cropping for food in the early prehistoric period, and a commercial harvest for skins in the early historic period. Changes in fur seal distribution during each exploitative phase are identified, and the extent to which they can be attributed to human predation is evaluated. Some general conclusions are drawn about human impacts on marine resources during island colonisation.*

Keywords: *New Zealand, fur seals, human impact, prehistoric, historic*

Introduction

New Zealand has been an important locus for discussions of interactions between human and animal populations. The 1839 discovery of remains of moas – eleven now extinct species of large flightless birds – stimulated intensive research into their relationship with people that paralleled contemporary debate into human associations with extinct fauna in Europe (Anderson 1989, 97–109). It also placed environmental change and the potential role of people in this at centre stage in New Zealand archaeological research. More than a century and a half of investigation has demonstrated that, along with the moas, at least 23 other species of land birds, three frogs, one bat, several lizards, landsnails and insects had become extinct, and about half of New Zealand's forests disappeared between first human colonisation by Maori about 750 years B.P. and European contact at AD 1769 (McGlone and Wilmshurst 1999, Holdaway 1999, Ramsay 1978, Towns and Daugherty 1994). Determining the causes of processes such as these is generally more difficult than documenting their occurrence, but all appear to be the result of human activities. Anthropogenic fires are seen as the main cause of deforestation (McGlone 1983, 1989). Direct human predation, habitat loss through deforestation, and predation by domestic dogs and Polynesian rats (*Rattus exulans*) introduced by people have been implicated more strongly than climate change or other natural phenomena in recent assessments of faunal extinctions (Anderson 2002, Duncan *et al.* 2001, Nagaoka 2000, Worthy 1999a, 1999b). The magnitude of these environmental changes, the short time period in which they occurred, and the extensive research that has been conducted into them have combined to make New Zealand one of the foremost examples of the impact of human colonisation on island environments (Diamond 2000, Grayson 2001).

Most discussions of the New Zealand case have focussed exclusively or predominantly upon the terrestrial environment. This is not to say that impacts on the marine environment have not been documented. Range reductions and disappearance of larger size classes have been demonstrated for some marine mammals, fish, molluscs and crustaceans (Anderson 1983, Leach and Anderson 1979, Leach *et al.* 1999, Rowland 1976, Smith 1985, 1989, Swadling 1977), but these seldom rate more than passing mention in wider discussions of human impact (*e.g.* Grayson 2001, 8–11). The resulting picture has been unbalanced. Discussion of Maori subsistence practices has focussed upon moa hunting, terrestrial fowling and swidden horticulture, when the archaeo-

logical record shows that, like any island dwellers, they relied strongly upon the resources of the sea (Anderson 1982, Davidson 1984, 131–3, 138–145, Smith 2004). Perhaps more importantly, the lack of attention to human interactions with marine resources has meant that an opportunity to test and refine explanatory models has been missed. In particular, the marine environment is one in which indirect impacts of human settlement such as deforestation and introduced predators are unlikely to have been significant, and thus the effects of direct human predation may be more easily measured.

Examinations of the New Zealand case have also concentrated largely upon the environmental impacts of prehistoric colonisation. While this has been understandable in terms of comparative studies of habitat degradation by small-scale societies, it is again only part of the picture. New Zealand had a second major wave of colonisation following European contact which inaugurated a second major period of environmental change. Few attempts have been made to compare the environmental impacts of these two settlement phases, and to consider how useful analysis of the historic period example might be in furthering understanding of its prehistoric counterpart (*c.f.* Diamond 1984).

This paper is an attempt to address these issues. It is focussed around a review of evidence for human interactions with one of the larger and most abundant members of the marine fauna, the New Zealand fur seal (*Arctocephalus forsteri*). Zoological, archaeological, ethnographic and historical data are used to define the nature and consequences of human engagement with this animal during both prehistoric and historic periods of settlement. Comparisons are drawn between the patterns observed in each of these phases, and with some of these noted for other elements of both marine and terrestrial faunas in order to draw some more general conclusions about human impacts on marine biota during island colonisation.

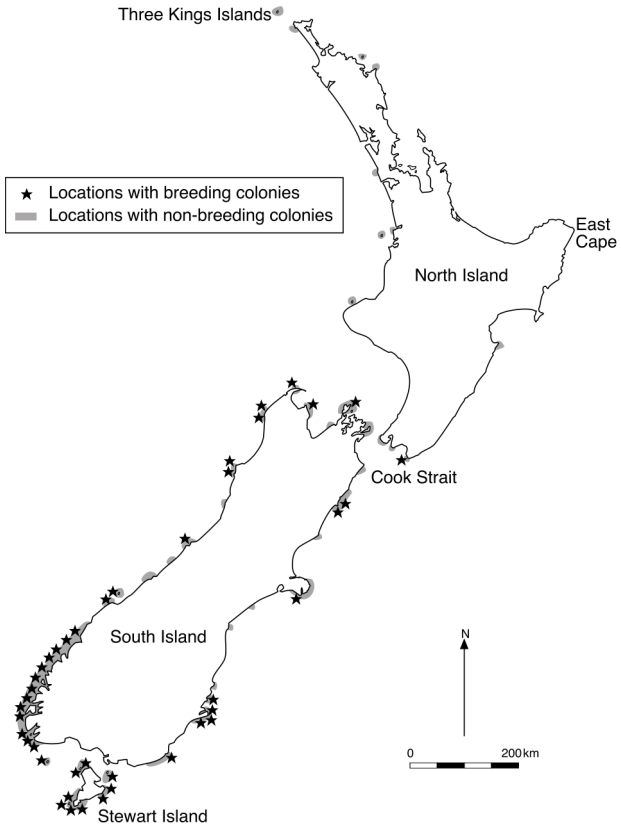

Figure 1. Distribution of fur seal colonies in New Zealand 2002.

New Zealand Fur Seals

The New Zealand fur seal is one of eight species of southern fur seals with more or less discrete geographical ranges spread from antarctic waters through subantarctic and temperate regions to the equator and sub-temperate North Pacific (Rice 1998, 23–27). *A. forsteri* is found on the New Zealand mainland and subantarctic islands (Antipodes, Auckland, Bounty, Campbell, Chatham, Macquarie and Snares Islands), the southern shores of West and South Australia, and on isolated islands off the south coast of Tasmania (Crawley 1990, Shaughnessy *et al.* 1994). The Australian populations are genetically isolated from those on the New Zealand mainland and subantarctic islands (Lento *et al.* 1994, 1997), and it is the latter that are the focus of this paper, and in particular the fur seals on the New Zealand mainland.

The mainland population is today found from the southern tip of Stewart Island to the Three King Islands at the northern end of the country (Figure 1), but occurs discontinuously throughout this range, showing a strong preference for exposed rocky shorelines (Crawley 1990, Bradshaw *et al.* 1999b). Fur seals are most commonly found at either rookeries (breeding colonies) or hauling grounds (non-breeding colonies), but individuals occasionally haul out on almost any suitable coast. For most of the 20th century rookeries were found only around Stewart Island and the south and west of South Island, but they have recently expanded northward as far as the south coast of North Island (Lalas and Bradshaw 2001). Hauling grounds occur both within the breeding range and to the north.

There is a seasonal pattern of aggregation and dispersion in fur seal distribution (Crawley and Wilson 1976, Bradshaw *et al.* 1999a). During the breeding season (November to January) most fur seals are confined to the breeding range. From late October adult males begin to gather at rookeries to establish breeding territories and soon afterwards adult females return from feeding at sea and commence pupping, while non-breeding animals congregate at hauling grounds nearby. Most pups are born in mid to late December, and mating has generally taken place by mid January. From this time on numbers

ashore decline as adult males leave the rookeries and adult females begin to feed at sea, returning at regular intervals to suckle their young.

Outside of the breeding season adult males disperse to hauling grounds beyond the breeding range, accompanied by subadult males and some juveniles. Adult females and pups remain within the breeding range. Because they suckle their young for up to 10 months, females are constrained to foraging relatively near to the rookeries. Satellite tracking of foraging trips show that they never exceed 200 km from the colony of origin and are usually much less than that. These trips are spent almost entirely at sea, with only one recorded instance of a haul out on land (Harcourt *et al.* 2002). Periods of absence average 4.4 days, except in October when about 15 days are spent feeding intensively before the next breeding season (Mattlin *et al.* 1998). Pups are weaned between the end of July and early October. Most remain at the rookeries until late November, although there is some dispersal to adjacent non-breeding areas, probably through temporary forays as the pups become more adept at swimming (Bradshaw *et al.* 1999a). Once adult males begin returning to the rookeries for the next breeding season, the pups relocate to these areas where they are joined by other non-breeding animals.

Although there are some seasonal variations in their activities, New Zealand fur seals always exhibit a strong diurnal rhythm. They are generalist predators that do most of their foraging at night over the outer continental shelf and slope, feeding mainly upon a range of pelagic cephalopod and teleost fish species (Fea *et al.* 1999, Harcourt *et al.* 2002). They spend most of the daylight hours resting or sleeping onshore (Crawley 1990).

New Zealand fur seals exhibit marked sexual dimorphism, with adult males weighing up to 185 kg while adult females seldom exceed 50 kg (Crawley 1990). This dimorphism is reflected osteologically, as are size differences relating to age, and together these provide the key to interpretation of their archaeological remains. Morphological and metrical criteria for identifying fur seal bones as either adult male, adult female, subadult male, juvenile or pup have been developed through analysis of 46 complete or near complete skeletons of fur seals of known age and sex from museum and university collections (Smith 1985, 55–77).

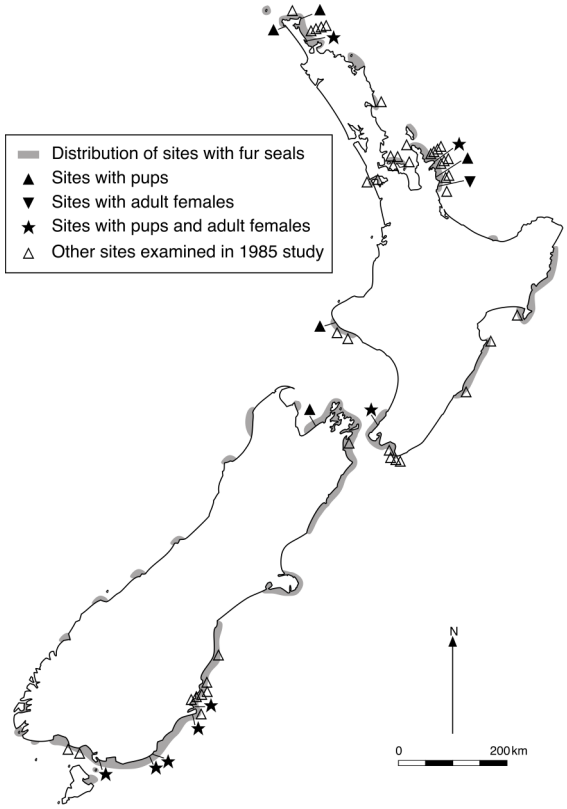

Figure 2. Distribution of prehistoric archaeological sites with fur seal remains.

Prehistoric Exploitation

Marine mammals played a major role in prehistoric subsistence in New Zealand. A recent review of the nutritional composition of diets has shown that they were second only to fish as a source of meat, and were unsurpassed in the supply of fat and caloric energy (Smith 2004). Archaeological evidence for their exploitation was first reviewed in the 1980's (Smith 1985, 1989). Of 180 sites in which marine mammal bones had then been reported, 96% yielded seal remains while only 28.3% contained cetaceans. Species identifications of seals were available for 111 sites, with fur seals represented in 93% of these, New Zealand sea lions (*Phocarctus hookeri*) in 38%, southern elephant seals (*Mirounga leonina*) in 26%, and leopard seals (*Hydrurga leptonyx*) in 6%. Positive identifications of cetaceans were much less common, with pilot whales (*Globicephala* sp.) in 10 and the Common dolphin (*Delphinus delphis*) in one, and it is likely that at least some of the *c.* 30 other species known from the New Zealand region (Baker 1999) were also exploited. These data leave little doubt that fur seals were the main component of the marine mammal fauna exploited by prehistoric Maori.

Sites with fur seals are widely distributed throughout the country (Figure 2), although they are much less common on west coasts than on the east. The low number of sites in the south-western corner of the country almost certainly reflects very limited and mostly transient human use of this rugged and hazardous high energy coast during prehistory. However the patchy distribution on the rest of the South and North Island west coasts can be attributed mostly to limited availability of suitable rocky shore habitats for fur seals. Absence of suitable habitats accounts for most of the gaps in distribution on the east coast, except perhaps around East Cape and on the south

east coast of the North Island where it seems likely that further sites with fur seals will be found.

Analysis of 100 bone assemblages from 53 sites distributed throughout this range (Figure 2) provided evidence of both the status of these populations and the nature of human exploitation of them (Smith 1985, 1989). As fur seal pups and adult females are found only within the breeding range, the bones of either of these classes in an archaeological site provides strong evidence for the former presence of breeding populations in the vicinity. Pup and/or female bones were identified from 14 sites, half of which occur to the north of the present breeding range (Figure 2). Apart from preliminary suggestions, based upon finds at a single site (Fleming 1962, Smith 1978), this was the first clear evidence that fur seals had once maintained breeding populations in the northern North Island and about Cook Strait. None of the archaeological samples available for study from the central and southern parts of the east coast of the North Island and the central and northern parts of the east coast of the South Island were sufficiently large or well preserved to establish whether breeding populations once existed in these regions, but the frequency with which fur seals occur in sites there makes the existence of such populations seem likely. On the basis of this evidence and subsequent archaeological discoveries (*e.g.* Walter and Smith 1998), it is now widely accepted that fur seals were breeding at suitable localities around both the North and South Islands before the arrival of Maori at about 1,250 AD (Lalas and Bradshaw 2001).

Prehistoric exploitation of fur seals was a land-based pursuit. Although canoes may have been used to gain access to colonies, there is little to suggest hunting from them at sea. Bone harpoon heads occur in some New Zealand sites, but their presence is associated more closely with the distribution of dolphin remains than with seals (Smith 1985, 333–336). Furthermore, the seasonal and diurnal activity patterns of fur seals ensure that they would have been most easily and predictably located at or near to their regularly occupied colonies. It is likely that animals were usually approached by stalking and despatched by a blow to the snout with a heavy club.

Two major exploitative strategies appear to have been utilised (Smith 1985, 337–378). Opportunistic *encounter hunting* is most likely at nearly two thirds of the sites that were examined. These had uniformly low numbers of fur seals (MNI ≤ 2), and together account for less than 25% of all animals identified in the study. Sites at which this strategy was inferred were located at least 10 km from the nearest rocky shore that could have supported a colony. Some were generalised occupation sites that are likely to have been permanent or repeatedly used hamlets, while others were more specialised fishing or shellfishing camps. Fur seal skeletal elements in these sites frequently included both low and high meat utility items, indicating that rather than being from transported carcass parts, these were remains of animals captured nearby, presumably through chance encounters with isolated individuals.

More purposeful *regular cropping* was evidenced at the remaining third of sites. Although fewer in number, these accounted for more than 75% of all the fur seal MNI identified from the sample sites, indicating a more intensive style of predation. In all cases, these sites appear to have been generalised occupations rather than specialised seal hunting sites, with a wide range of other resources also exploited and evidence for a diversity of domestic and industrial activities. Each of these sites is located within a few kilometres of a regularly occupied colony, or a place where one is likely to have existed in the past. Skeletal element representation suggests that the fur seals were generally killed and butchered at or close to the colony, with low meat-yielding or difficult to dismember body parts from animals in the larger size classes often abandoned at the kill site while smaller animals were generally returned as complete or near complete carcasses (Figure 3). It also seems likely that these fur seal were hunted to acquire fresh meat for immediate consumption, as ethnohistorical observations of Maori preparation of seal flesh for preservation indicate that the meat was completely separated from bone at the kill site (Brunner 1848, 284, Stokes n. d., Smith 1985, 12–13). Analysis of growth zones in tooth sections and other seasonal evidence suggests that fur seals were taken at regular intervals throughout the occupation of the sites, which was most commonly, but not exclusively, in the late spring, summer and early autumn. While it is always difficult to evaluate rates of predation from archaeological data, the impression gained from these sites is that it was moderate but persistent, with fur seals being taken only one or a few at a time, but regularly, throughout the time that they were easily available.

The archaeological data also show that the breeding range of fur seals retreated from north to south during the prehistoric period, with estimates of the timing of this withdrawal based upon radiocarbon dates, associations with extinct avifauna and Archaic (early prehistoric) artefact forms (Smith 1989). Subsequent reassessment of New Zealand's prehistoric timescale (Anderson 1991, Higham and Hogg 1997) has required only minimal revision of the chronological ages proposed for these changes. Most importantly, the earliest dates for human settlement throughout the country have shifted from about 1,000 AD to about 1,250 AD, significantly shortening the period during which the fur seal retreat took place. Pup and/or female bones are confined to early prehistoric contexts in the northern North Island, and where reliable radiocarbon dates are available they give calibrated ages in the late 13th or 14th centuries AD. The southern North Island and northern South Island examples are less precisely dated, but are clearly of early or mid-prehistoric ages. In contrast, the southern South Island examples give calibrated radiocarbon ages ranging from the early 13th century to the late 17th century.

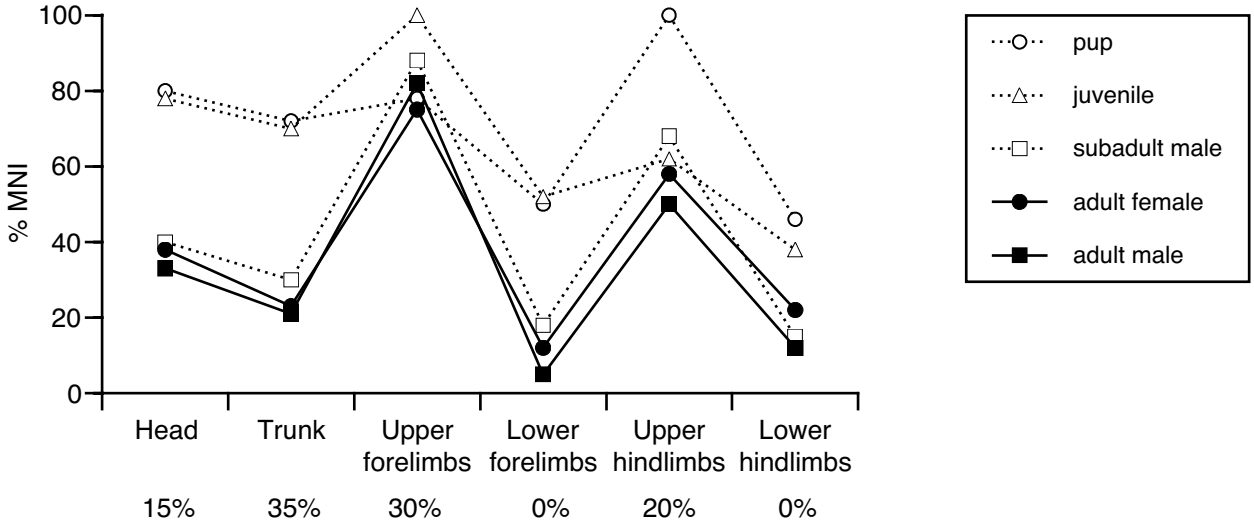

Figure 3. Mean proportions of body parts from each age-sex class of fur seals in six large assemblages (after Smith 1985). Also shown are the percentages of total meat weight from a fur seal represented by each body part.

Approximate ages for the northern limits of breeding in the early, middle and late prehistoric periods are shown in Figure 4.

The regional and temporal occurrence of the two fur seal exploitation strategies varied with changes in fur seal distribution. In the northern North Island, securely dated evidence of regular cropping is confined to the late 13th or 14th centuries, coinciding with the presence of breeding colonies. Opportunistic encounter hunting was also evident at smaller or more specialised sites of the same age and appears to have persisted for about a century after the demise of northern breeding populations, but after *c.* 1,500 AD fur seals completely disappear from the northern archaeological record. In the southern half of the North Island nearly all the well-dated evidence of fur seal exploitation falls in the 13th or 14th centuries. Regular cropping is imprecisely dated but is clearly early prehistoric. Encounter hunting persisted for longer than in the north, with fur seals still appearing as a rare component of late prehistoric faunas. A similar pattern emerges from sites in the northern half of the South Island. Fur seals are common in early sites, and regular cropping was still evident in the 14th and perhaps 15th centuries. However, only encounter hunting is indicated for late prehistoric sites, and in at least some areas, such as the western part of the north coast, fur seals are conspicuously absent after the second half of the 15th century. The southern South Island exhibits the most stable pattern, with both encounter hunting and regular cropping evident at all periods, and with the latter persisting until at least the end of the 17th century at Otago Peninsula on the south east coast.

This stability at a regional scale in the south masks a consistent pattern of change that is evident at a local

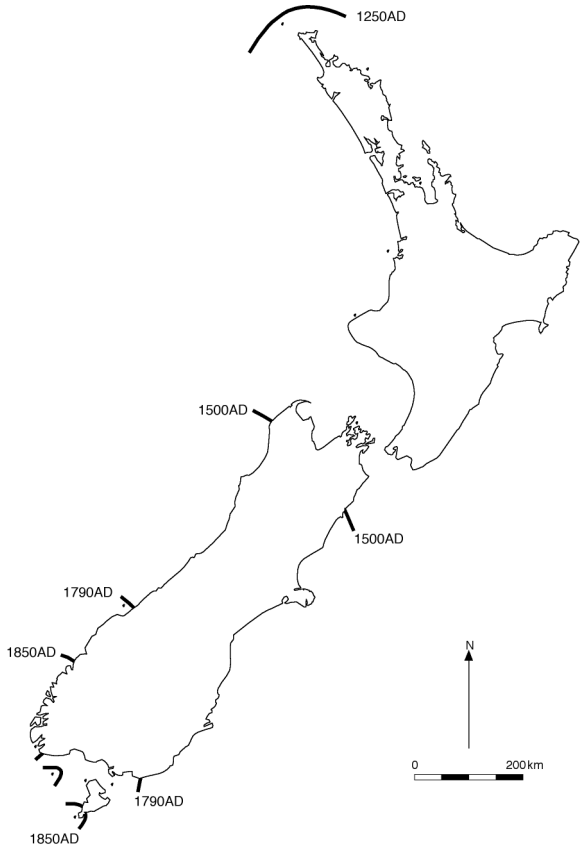

Figure 4. Northern limits of fur seal breeding range estimated for the beginning (1250), middle (1500) and end (1790) of prehistory, and after historic sealing (1850).

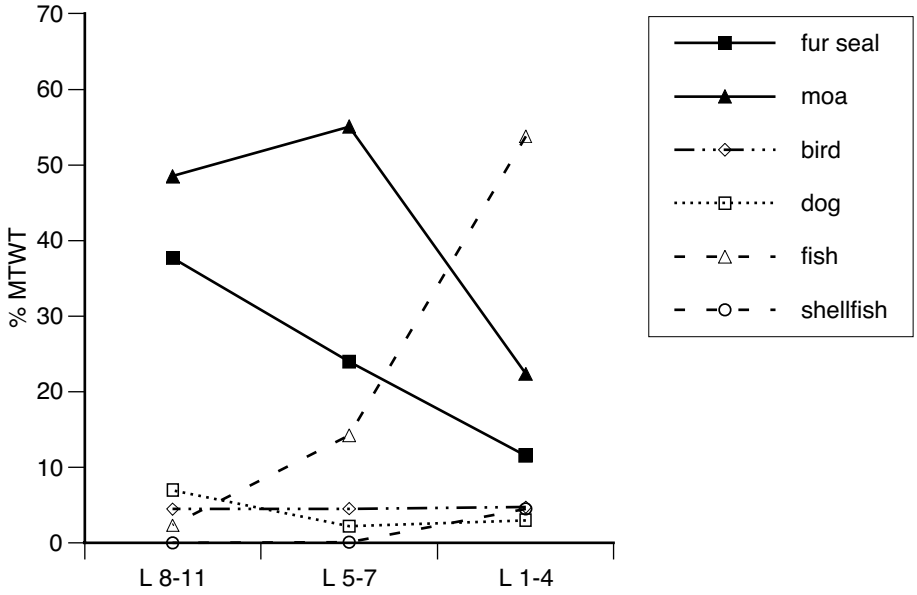

Figure 5. Changes in meat weight from major classes of fauna at Shag River Mouth.

scale. This pattern is illustrated clearly at Shag River Mouth, a small village occupied for about 50 years in the mid to late 14th century on the east coast of the southern South Island (Anderson *et al.* 1996, Anderson and Smith 1996). The site was located less than 2 km from a headland that has been used as a colony by non-breeding fur seals since the 1970's. Presumably, it was used as such in earlier times because fur seal bones in the site were almost all from juveniles and subadult males (Smith 1996). Its inhabitants subsisted by hunting seals, moa, and small birds, fishing, shellfish collecting and foraging for wild plant foods. The relative proportions of animal resources changed dramatically during the course of occupation, with moa and seals giving way to fish as the major source of meat (Figure 5). This change has been attributed to depletion of local stocks of the hunted resources (Smith 1996, Nagaoka 2002), and loss of these easily won, high return resources led to abandonment of the Shag River village less than a century after it was established (Anderson and Smith 1996).

Similarly brief periods of sedentary occupation sustained by exploitation, and consequent rapid depletion, of local fur seal colonies and moa populations, are now envisaged for early period settlements that have been re-examined not only in southern New Zealand (Anderson and Smith 1992, 1996, Smith 1999) but also in central (Higham *et al.* 1999) and northern regions (Anderson and Wallace 1993). The extent to which direct human predation was responsible for this repeated pattern of localised depletion of fur seal stocks, and the wider distributional changes that have been observed, will be examined further below.

Historical Exploitation

On the face of it, fur seal exploitation during the historic era presents a very different picture. It was a commercial industry, rather than a subsistence pursuit, and was focussed almost exclusively upon the recovery of skins from hunted animals. This harvest was prosecuted largely from outside the country by hunters who spent only brief periods on New Zealand's shores then departed along with the skins, which were onsold to markets in China and London. It was also very short-lived, with virtually all the recorded activity taking place between 1792 and 1839 (Smith 2002).

However, there are also similarities with its prehistoric counterpart. Historic period sealers pursued a range of strategies (see below), all of which focused upon regularly occupied colonies. This tied the location of their activities to the breeding distribution of fur seals just as closely as seasonal cropping had influenced settlement location in earlier times. Methods of procurement were almost identical, with colonies usually approached by boat and animals stalked and dispatched with clubs. The outcomes were also similar, with depletion of fur seal numbers, contraction of the distribution of colonies, abandonment of settlements based upon their exploitation, and the demise of their pursuit as a mainstay of economic activity.

A recent review of evidence for this industry (Smith 2002) shows that it is as yet better known through historical documents than the archaeological record, although 30 definite or probable historic sites have been identified (Figure 6). These are concentrated on the south-western coast of the South Island and exhibit very little overlap with the distribution of prehistoric sites with fur

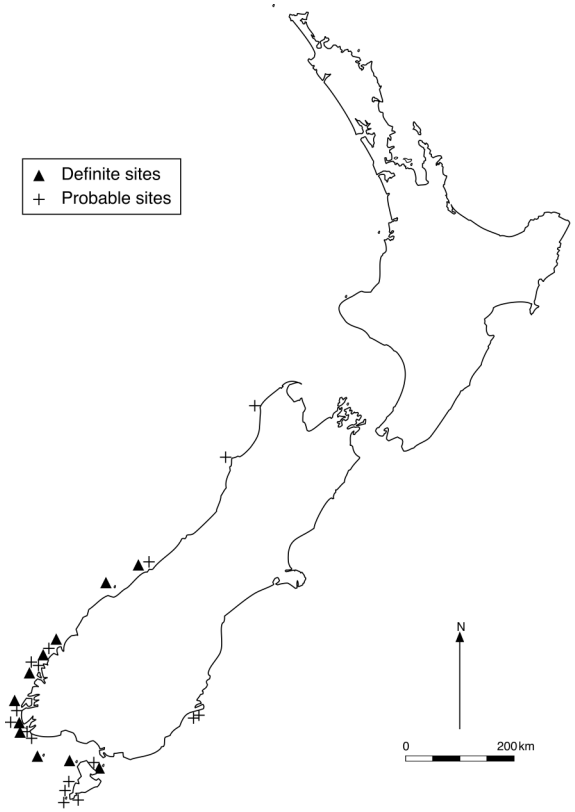

Figure 6. Sites of the historic sealing industry.

seal remains (*c.f.* Figure 2), providing further confirmation of the restricted area to which fur seals were confined by the end of prehistory. As already noted, the south-western South Island was little used during prehistory, and modern fur seal colonies there are remote and generally difficult to access (Wilson 1974). The historical evidence of this industry is comprised mainly of records concerning the movements and cargoes of ships plying the trade, mostly out of Sydney, Australia, along with a small number of eyewitness accounts and other primary descriptions. At least 113 sealing voyages are known to have operated on the New Zealand mainland between 1791 and 1839, with another 35 possibly calling there during voyages elsewhere in the New Zealand sealing region. Quantified data on cargoes are lacking for about 18% of these, and there is sometimes uncertainty about precisely which island group they had come from; however, the available information indicates that the minimum number of fur seals taken from the New Zealand mainland during this period falls somewhere between 167,000 and 372,000 (Figure 7).

The historic period sealers utilised three exploitative strategies. *Intensive localised harvesting* was conducted by shore-based gangs. These groups were set down by ship at specific locations near to one or more colonies for the express purpose of harvesting and preparing fur seal skins before being collected again. They typically comprised 6 to 12 men who were usually stationed for periods of 6, 12 or 18 months. Of the 15 locations at which it is certain this type of activity took place, repeat visits by shore-based gangs are confirmed for only four and may have occurred at another three, suggesting that predation was often at a level sufficient to seriously deplete accessible local populations. It is also noteworthy that sealing voyages known to have serviced such gangs are confined to three brief periods: the first prospecting of New Zealand colonies in 1792–93, a 'rush' to newly discovered colonies around Stewart Island in 1808–10; and in 1821–22 at the beginning of a brief 'revival' of the New Zealand trade (Figure 7).

Intensive mobile harvesting by ship-based gangs was probably the most common and longest lasting strategy in the New Zealand industry. Ships would bring sealers to the coast and anchor in a safe harbour near to one or more colonies, which would be worked by gangs operating from whale boats, but using to the mother ship for their living quarters. Once seal numbers at those colonies diminished, gangs could easily be moved elsewhere. This mobility appears to have been a particularly important strategic consideration during two phases of the industry: the first 'rush' to the New Zealand mainland between 1803 and 1807, when it would have aided the discovery of new colonies; and during the decade after 1812, when declining returns suggest that it was much more difficult to locate productive colonies (Figure 7).

A transition to *small-scale mobile harvesting* conducted by boat-based gangs took place during the 1820's when rapidly declining returns, despite an increased frequency of voyaging (Figure 7), led most sealing operators to diversify into a mixed trade. Gangs were now deposited with their whale boats on a stretch of coast along which they would search for fur seals, staying in huts, caves or camping on shore, and collecting provisions from supply depots. The ship, meanwhile, plied other trade before collecting gangs and their cargo at a prearranged rendezvous point. From about 1825, boat-based gangs were also operated by residents of three or four small settlements on the New Zealand coast who sold their harvest of skins to passing ships.

The sealing industry had come to a virtual standstill by 1840, but it is clear that fur seals were still present on parts of the New Zealand coast, albeit in much reduced numbers. Sporadic small-scale hunting ventures are reported throughout the remainder of the 19th century, even after the introduction of legislation to protect fur seals in 1873 (Smith 2002). Information about the location of these activities, along with observations recorded during the first scientific survey of the south-western South Island in 1863 (Hector n. d.), allow a reasonable estimate to be made of the areas to which fur seal breeding was restricted at the end of the commercial sealing era (see Figure 4).

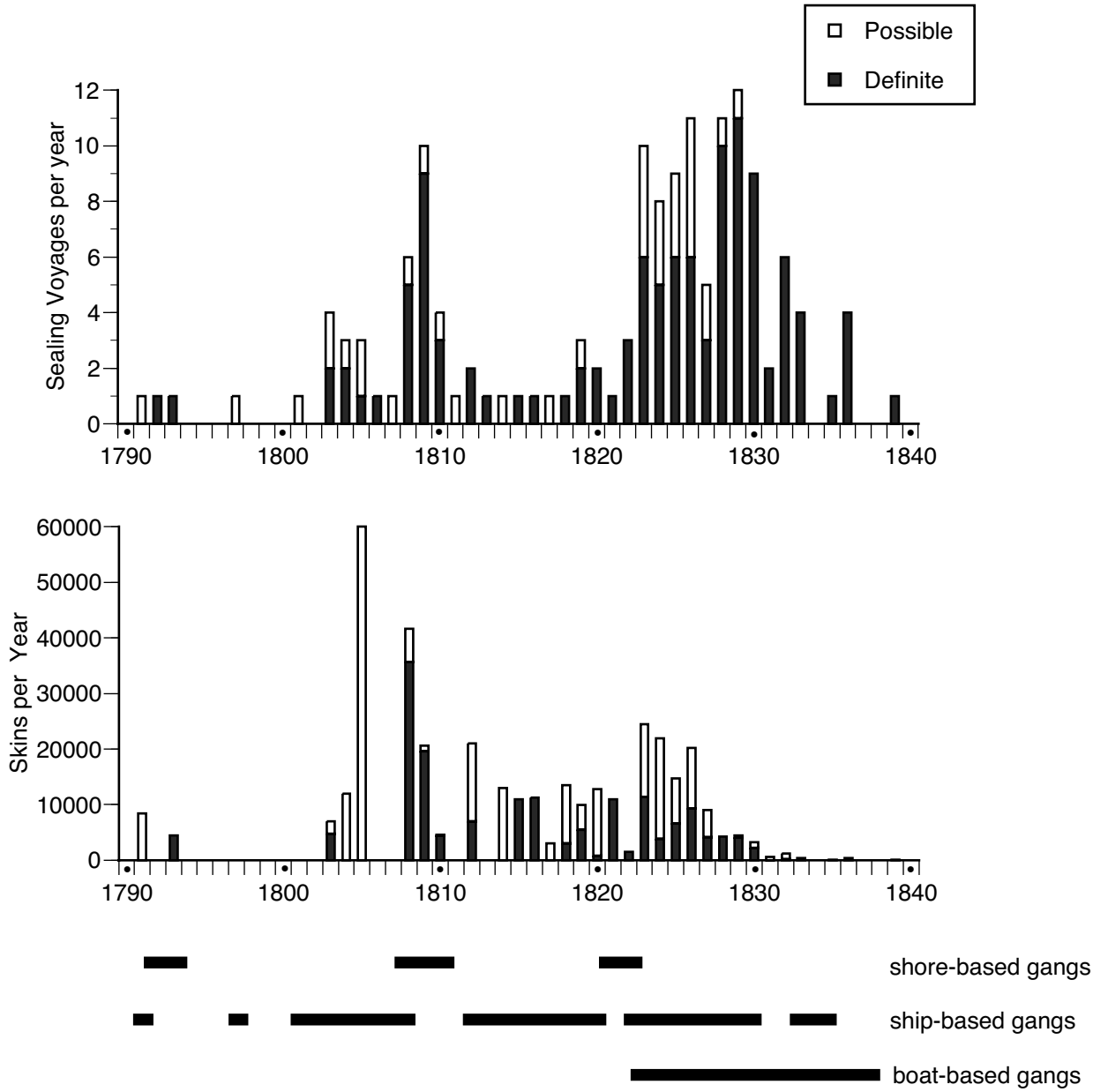

Figure 7. Characteristics of historic sealing on the New Zealand mainland: (top) voyages by sealing ships; (middle) returns of fur seal skins; (bottom) periods of operation of three types of sealing gangs.

Causes of Distribution Change

The large number of skins taken within the short time span of the historic sealing industry has left no doubt that the reduction in fur seal numbers and distribution during the early 19th century were due solely to direct human predation. This observation was self evident to participants in the industry by the 1820's (McNab 1907, 256) and to early scientific writers with either first or second hand knowledge of the industry (Heaphy 1863, Hector 1892, Chapman 1893). More recent examination suggests that there is no reason to dispute this. Lalas and Bradshaw (1998) have argued that, with the high intensity of predation throughout this period, it is reasonable to model population decline using a constant arithmetic rate of change. On this basis, a population would be reduced to less than 2% of its original size in just 25 years by the loss of 15% of its members each year, while this process would take 37 years with a 10% annual rate of decrease. The historical record of seal skin returns (Figure 7) suggests that the actual rate of population decline was of this order, with almost half of the documented harvest accrued in just nine seasons between 1803 and 1812, and 98% taken by 1829.

With its longer timescale and less certainty about the

intensity of harvest, the prehistoric case is more open to alternative explanations. As climate change, habitat degradation and the impacts of introduced predators have been implicated in the population histories of some other classes of fauna in New Zealand, it is important to assess their significance in relation to the fur seal.

The influence of climate on marine mammal distributions is poorly understood (Wursig *et al.* 2002). In the case of the New Zealand fur seal, initial zoological research suggested that the then observed limits of breeding were influenced by meteorological factors that would induce heat stress in animals attempting to maintain breeding territories or bear and suckle young further to the north (Wilson 1974, Mattlin 1978). If these had been limiting factors, then distributional changes might be explained by cooler climatic conditions during the early prehistoric period promoting a wider breeding range, and a mid-prehistoric warming phase causing its retreat. Exactly the opposite is proposed under the broad two phase model of climate change once favoured by many archaeologists, which postulated a warmer and more settled phase between the 10th and 16th centuries and deterioration between the 17th and 19th centuries (Leach and Leach 1979, Davidson 1984). Nor are the required conditions met under more recent climatic reconstructions which indicate that from *c.* 850 to 1,850 AD there were relatively short periods of slightly cooler and slightly warmer temperatures at frequent intervals both before and after the observed retreat of fur seals (Salinger 1988).

The climatic hypothesis is further undermined by recent examinations of fur seal terrestrial habitat use. These studies have demonstrated that the sites preferred for breeding have broken, rocky terrain, and are frequently located at the foot of steep cliffs, and that both these attributes provide shelter that enhances low-cost thermoregulation, ameliorating the effect of high summer air temperatures (Bradshaw *et al.* 1999b). Perhaps most significantly, northward expansion of the breeding range since the 1970's, during a period of climatic warming (Salinger and Mullan 1999), provides strong evidence that distribution is not constrained by climate.

Habitat degradation can also be ruled out as a causative factor. Although human settlement brought about extensive modifications to the landscape (Anderson 2002), there was no significant loss of the rocky shores favoured by fur seals. The turbidity of inshore waters may have increased as a result of increased erosion following forest clearance, but this would not have impacted on fur seal food stocks, because their main foraging grounds are offshore over bottom depths of 100–300 m (Harcourt *et al.* 2002). Nor is it likely that their food supply was depleted by human fishing, because the latter was generally confined to shallow inshore waters (Anderson 1997). Although fur seal diet includes species commonly taken by people, their major prey are arrow squid (*Nototodarus sloanii*), benthic octopus (*Octopus* spp.), lanternfish (Myctophidae), ahuru (*Auchenoceros punctatus*) and hoki (*Macrorunus novaezelandiae*) (Bradshaw 1999, 8.6, Fea *et al.* 1999) that were not part of the prehistoric human fishery (Anderson 1997).

Fur seal populations are not likely to have been seriously disturbed by the predators that arrived in New Zealand with the first human settlers. Rats can be safely dismissed as a threat, but dogs would have been capable of harassing and harming smaller members of the population. Fatal attacks on young fur seals are occasionally reported today (*e.g.* Massey News 1999), although these appear to be on isolated individuals rather than regular predation upon colonies. A greater threat may have existed if there was a substantial feral dog population during prehistory, but the extent to which this was the case is not known. Even if this were so, the frequent use by fur seals of offshore islets and stacks as breeding sites (Dix 1993, Taylor *et al.* 1995, Ryan *et al.* 1997, Bradshaw 1999) would have ensured protection of pups during their most vulnerable early months.

With alternative explanations rejected, it remains only to consider whether direct human predation could feasibly have brought about the observed changes in distribution. In the absence of clear data on either fur seal population size or human population dynamics during prehistory, it is difficult to model predation pressure. Lalas and Bradshaw (1998) point out that, averaged over the 800 year prehistoric period, reduction of the population to 2% of its original size represents a mean annual rate of decrease of just 0.5%, or, if accomplished in 200 years, the decline averages 2% per year. Actual predation rates would have to be much higher than this to make a significant impact. Most populations easily sustain low levels of harvesting (Caughley and Gunn 1996), and, as polygynous breeders, fur seals offer the potential for selective cropping of young males without necessarily impacting on survival of the species. Indeed, the Northern fur seal (*Callorhinus ursinus*) population increased dramatically during the first half of the 20th century with a managed off-take of about 35% of two to five year old males (Kenyon and Scheffer 1954), and the sustainable yield calculated for the South African fur seal (*Arctocephalus pusillus*) in the late 1970's was 35% of pups of both sexes (Bonner 1981). Detailed investigation of *C. ursinus* exploitation at the Ozette site has shown that persistent offtake, predominantly of young males, was sustained over several hundred years without depletion of the population (Etnier 2002). However, prehistoric exploitation appears to have extirpated this species from other parts of the mainland North American west coast (Burton *et al.* 2001, Hildebrandt and Jones 1992, Lyman 1995). Modern attempts at managed culling have not always been sustainable either – the Namibian take of *A. pusillus* is the only fur seal harvest still in operation (Seal Conservation Society 2003) – indicating that there are both successes and failures in the prehistoric and historical records.

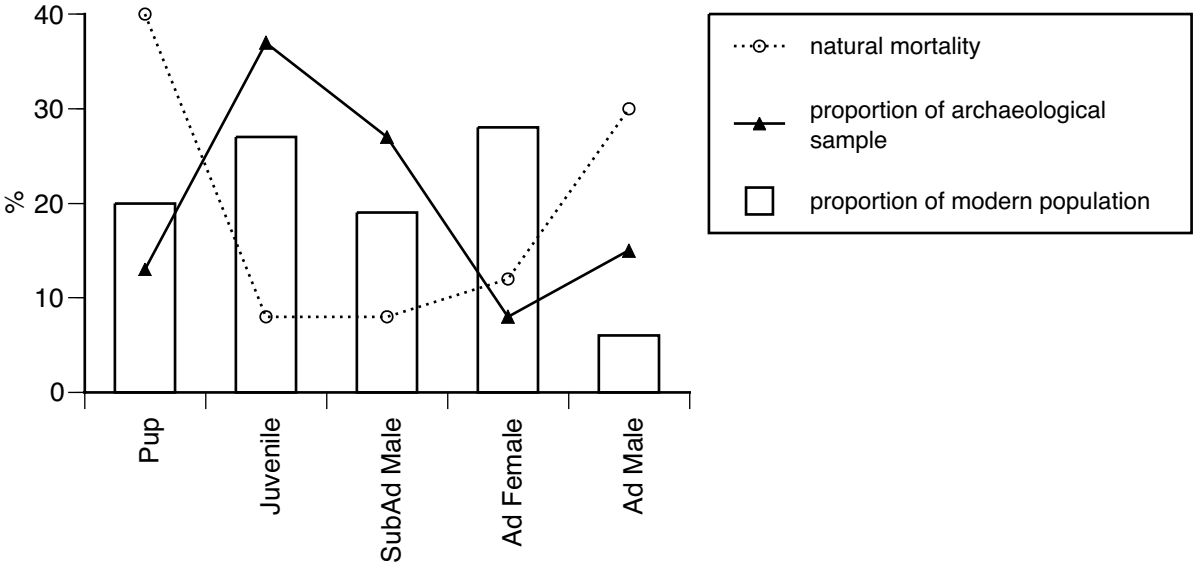

Figure 8. Population composition and natural mortality rates of fur seals.

The archaeological data from New Zealand show that juvenile (37%) and subadult male (27%) fur seals make up greater proportions of the total archaeological sample than would be expected from their representation in the modern population (Figure 8), although whether this was due to deliberate selection is less clear. Adult males are also over-represented, and as these are the three age-sex groups that disperse most widely, it may be the higher chance of encounter that produced the observed pattern. Whether deliberate or not, the age-sex distribution of the prehistoric kill is unlikely to have threatened overall population viability.

The archaeological record, wherever it is sufficiently detailed, shows that fur seals were initially a major focus of subsistence effort, but they diminished in abundance within a matter of decades rather than centuries, suggesting that prehistoric exploitation was locally intensive. On this basis, it can be argued that effective rates of predation were high at the local level and that they impacted on fur seal distribution through serial depletion of local colonies rather than through even reduction of numbers throughout its range.

Three factors combine to make New Zealand fur seal colonies particularly vulnerable to sustained local hunting. The species is not migratory (Bradshaw *et al.* 1999). While some age-sex classes disperse during the non-breeding season, others are resident throughout the year within the breeding range. Secondly, they exhibit strong fidelity to both their place of birth and to non-breeding localities they have used before (Bradshaw *et al.* 2000). Finally, their colonies are small compared to those of most other fur seals, with none on the New Zealand mainland and near shore islands today exceeding about 8,000 and with most significantly smaller (Baird 1994, Watson pers. comm). The current recolonisation of former breeding territory is fuelled in part by density-dependent movement out from some of the long established colonies (Bradshaw *et al.* 2000), suggesting that they are approaching carrying capacity. Prehistoric colonies are unlikely to have been much larger because potential colony sites in regions further north are generally constrained in size (Smith 1985). In these circumstances it is not unreasonable to propose that locally intensive predation could threaten the viability of local fur seal populations.

If this were the case, we would expect to see the impact of hunting on fur seal distribution at a regional level in more or less direct proportion to the density of human settlement. While initial human populations appear to have been widely dispersed throughout New Zealand, sustained growth in numbers was possible only in those areas where prehistoric horticulture could be practiced (Anderson 2002). The most favourable regions for this were around the coast of the northern North Island, which supported the highest prehistoric populations, while the lowest numbers were in the southern South Island where climatic conditions made horticulture impossible (Davidson 1984, 58). Thus it is no surprise that the archaeological record shows fur seals retreated first from the northern North Island, and persisted for longest in the far south.

Conclusions

Fur seals were a significant resource for both prehistoric and historic period settlers in New Zealand. For the former, they were the pre-eminent source of hunted meat, while their skins became the first target of commercial exploitation by the latter. In each case, the distribution and availability of fur seals influenced the location and duration of human settlements. In turn, both phases of exploitation depleted the fur seal population, leading to a retreat in its distribution to confined *refugia* on the most inaccessible stretches of coast. Together these examples provide the clearest demonstration in New Zealand's history of human impacts on marine biota.

They also show that depletion of the fur seal population can be attributed directly to human predation. This was the case not only during the brief, cataclysmic historic industry, but also during the longer, lower intensity prehistoric phase of exploitation. The latter observation is of particular importance because, in complementary examples from the terrestrial environment, it has been difficult to disentangle the relative importance of hunting by people from the effects of habitat modification and the depredations of introduced predators.

While the case of the fur seal demonstrates that on its own prehistoric hunting could have significant effects on a population, it would be inappropriate to infer from this that all of the observed impacts on terrestrial fauna were the result such activities. Indeed, comparison between fur seals and their largest terrestrial counterparts suggests otherwise. The eleven species of moa appear to have been hunted in a manner broadly comparable to the prehistoric exploitation of fur seals, yet they were all extinct within about 250 years of first human settlement (Anderson 2002), while fur seals suffered only depletion of population and reduction of range. Although variations in vulnerability to hunting probably also played a part, the major difference between these two cases is that the terrestrial environments occupied by moas were changed dramatically by the arrival of people in ways that the marine environment was not.

Both cases of fur seal exploitation examined here also illustrate an important factor that operated to limit the impact of hunting. While the locally intensive predation practiced in early prehistoric New Zealand extirpated fur seals from northern New Zealand, there is no evidence for a shift of human populations to the south where fur seals were still available, nor did their disappearance from the east coast of the South Island in late prehistory lead to a shift to the southwest. Instead, attention was focussed upon alternative resources, principally fish, small birds, shellfish and dogs (Smith 2004). Likewise, once the returns to commercial sealers fell below an economic level they turned their attention to other trade goods such as whale oil, flax and timber (Smith 2002). In each case, hunters switched their focus to other resources before fur seals were completely wiped out because the alternatives offered easier ways of ensuring desired cultural and economic outcomes.

On a more general level, this case study suggests that there were at least two ways in which marine fauna were buffered from impacts of human settlement of island environments. Firstly, it has shown that human-induced changes to marine ecosystems were minimal compared to those seen on land, limiting the impact upon marine fauna to those brought about by direct predation. Secondly, the marine environment provided *refugia* from human predation. In the present case, it was remote coastlines which were difficult for people to access, but for many marine species it is the vast oceans themselves that are beyond the direct reach of all except the most recent harvesting technologies. Together these factors have given marine fauna a greater resilience than terrestrial fauna in the face human exploitation.

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