

# Changing Fish Use on Mangaia, Southern Cook Islands: Resource Depression and the Prey Choice Model

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**ABSTRACT** This study applies the prey choice model from foraging theory to explain changing human use of fish during the 700-year occupation of Tangatatau Rockshelter, Mangaia, southern Cook Islands. The prey choice model suggests that predators will focus initially on high ranked prey, turning to lower ranked prey if abundance of higher ranked prey declines. It is suggested that increasing human population size would have resulted in increases in harvesting pressure and ultimately prey resource depression. To apply the prey choice model to archaeological faunal records and based on previous research, prey ranks are estimated using overall attributes of taxon body size; the larger the taxon, the higher the rank. Two indices, the Marine and Freshwater Fish Index, are developed to estimate the ratio of high to low ranked prey and are calculated for each zone of the rockshelter. Over time, the indices show a decreasing abundance of high ranked prey and increasing abundance of low ranked prey, which supports the view of resource depression. Skeletal elements from two of the high ranked prey, Serranidae and *Anguilla* sp., are measured to examine taxon-specific changes in fish body size/age that would indicate direct human exploitation pressure. Evidence for a decline in Serranidae body size over time suggests that some of the decline in prey abundance and encounter rates results from direct harvesting pressure along with behavioural adjustments in the prey. Sample sizes for *Anguilla* were insufficient for statistical treatment. Environmental and technological factors that might also affect prey abundance and taxonomic representation do not satisfactorily account for the patterns. Overall, the increasing use of lower ranked prey suggests a decline in foraging efficiency, given higher energetic costs associated with their use. The study adds to a growing body of evidence that Polynesians profoundly affected the indigenous biota on islands they colonized. Copyright © 2001 John Wiley & Sons, Ltd.

*Key words:* prehistoric fish; prey choice model; Polynesian fishing; Oceania archaeology

## Introduction

Across Polynesia, recent study of archaeofaunal sequences, plant macrofossils, and sediment and pollen cores has shown that colonizing human populations profoundly affected island biota—either through direct human predation, predation by human-introduced domesticated animals, or landscape modification (Anderson, 1983; McGlone, 1983; Flenley & King, 1984; Kirch *et al.*, 1991; Kirch & Ellison, 1994; Steadman, 1995). A number of researchers working in tropical Polynesia have suggested as well that

human subsistence systems changed over the centuries after initial colonization, from an initial focus on marine resources to a focus on terrestrial resources (domesticated plants and animals) (Kirch, 1973; Allen, 1992a). Such changes are thought to have occurred because human harvesting would have depleted indigenous fauna or because growing human populations would have required the higher caloric outputs supplied with agriculture or both factors.

It may be profitable to place questions of human-caused resource depletion and subsistence change in Polynesia into a theoretical framework such as that provided by foraging models, especially the prey choice model.

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Researchers working with archaeofaunas in western North America (Broughton, 1994, 1995, 1997; Janetski, 1997; Grayson & Cannon, 1999) and numerous ethnographic settings around the world (Smith & Winterhalder, 1992) have demonstrated the explanatory power of such models in accounting for subsistence change. Most of these studies have been concerned with understanding the process of resource intensification, which in general terms suggests that people made increasing use of marginal, lower-ranked resources as human populations grew and as higher-ranked resource abundance declined. It is suggested often that the shift in resource use occurred because human predation depressed the abundance of higher ranked resource or results from the per capita reduction in densities of higher ranked resources (Broughton, 1994). For example, in reviewing the late Holocene vertebrate archaeofauna from the Sacramento Valley of California, Broughton found a decline in abundance of large terrestrial vertebrates and an increase in abundance of small resident freshwater fishes over time (Broughton, 1994). Informed by the prey choice model from foraging theory, Broughton suggests that these subsistence shifts reflect resource intensification or a decline in foraging efficiency (wherein more energy is harnessed, but individuals must spend more energy, per unit time in the process).

The prey choice model holds that a predator's most efficient strategy is to take the highest rank prey when it is encountered. Whether lower ranked prey are taken depends on the encounter rate with the higher ranked resources. Encounter rates are based primarily on prey densities—low-ranked prey will enter the diet more frequently as the abundance of higher ranked prey declines. If mobility is limited or if the predator population increases, then resource depression of the high-ranked prey is likely to occur.

Basically, the prey choice model suggests that human foragers will pursue high ranked resources first, because such resources provide the highest energetic returns (and ultimately, natural selection will favour predators that operate like this). Predators will shift to lower ranked resources as higher ranked ones become less common.

Using this model requires that we rank food resources according to their profitability, that is, their post-encounter return rates. Broughton offers several theoretical and empirical reasons for using body size as a proxy measure for prey rank (Broughton, 1994, 1995). Up to a certain size, the larger the animal, the higher the rank. Madsen and Schmitt have pointed out that this relationship probably holds when single individuals are the target (Madsen & Schmitt, 1998). However, if multiple individuals are pursued at one time such as with mass harvesting (netting, poisoning, etc.) then the biomass of the entire group would be a more appropriate unit of comparison. The relevance of technology to questions of capture efficiency is addressed below.

Polynesia is an appropriate place to apply the prey choice model to study resource intensification and subsistence change. As noted above, much research throughout the region documents the many ways that colonizing human populations affected biota and landscapes. Moreover, since fish would have been a key caloric and protein source for people living on islands, it is reasonable to consider whether human predation on fishes in particular, resulted in the depression of certain high-ranked prey populations and whether that depression resulted in the taking of more marginal, lower ranked resources.

In this paper, I draw on the prey choice model in interpreting the 700-year record of human use of fish on Mangaia, southern Cook Islands.

## Environmental context

Mangaia is located in the southern Cook Islands of south-central Polynesia, over 150 km from the nearest island. Mangaia is small, having a land area of only 52 km<sup>2</sup>. Geologically, the island can be subdivided into several concentric zones (Figure 1) (Kirch *et al.*, 1995). The innermost zone consists of a highly weathered volcanic core. The exterior portion of the island is ringed by uplifted limestone reef (*makatea*) which is 1–2 km wide and 10–70 m high. A narrow fringing reef, 100–150 m wide, rings the

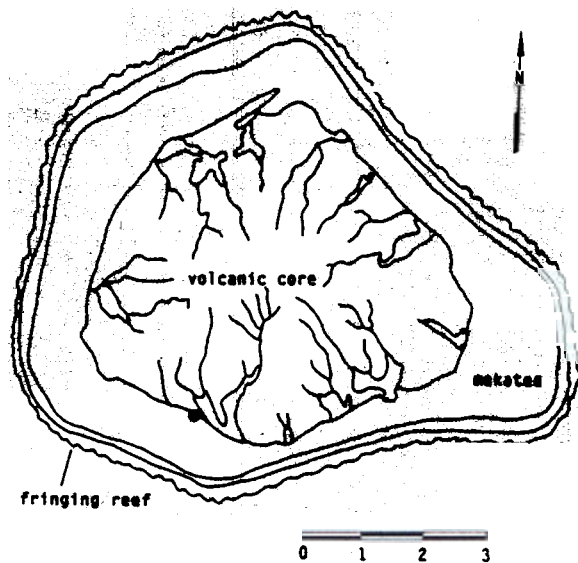


Figure 1. Map of Mangaia showing location of Tangatatau Rockshelter.

island. The volcanic core has a radial drainage system; streams flow from the interior core down to the *makatea*, forming, in some locations, ponds against the *makatea*. Subterranean conduits through the limestone connect the interior freshwater system to the sea. Study of pollen and sediments from cores taken across the island (Kirch & Ellison, 1994) suggests that during the mid-Holocene, five large lakes occupied the basins; most of these are now reed or taro swamps. Infilling of lakes occurred in three phases of erosion of the volcanic core hillsides, beginning about 2500 BP; Kirch & Ellison (1994) suggest that hillside erosion resulted from deforestation by humans (but see Spriggs & Anderson, 1993, for an alternative view).

Aquatic habitats on Mangaia include fresh and brackish water interior streams and lakes. Marine habitats include the narrow and shallow fringing reef; tidal pools and surge channels that cut through the fringing reef; the steeply sloping reef edge that can be accessed at low tide; and the offshore zone that small boats can access through several narrow channels or passes around the island that cut through the fringing reef.

## Tangatatau Rockshelter (MAN-44)

The archaeological assemblage discussed here is from Tangatatau Rockshelter, located in the *makatea* escarpment on the southern side of the island (Figure 1). The site was excavated during 1989 and 1991 under the direction of Patrick Kirch and David Steadman as part of a large interdisciplinary study tracking anthropogenic environmental change and its effects on the evolution of social/cultural systems (Kirch *et al.*, 1995). The site is large (ca. 225 m<sup>2</sup> under the drip-line) and has depths to 1.5 m of cultural deposit. The stratigraphy was divided into 19 analytic zones. The faunal remains in the deepest layer, zone 1, are probably noncultural, based on the near absence of modified objects and features. Here I focus study on faunal remains from clear cultural contexts, which were recovered from zones overlying this basal layer. Because the temporal relationship of zones 18 and 19 to the other zones is unclear, this review also excluded remains from these zones. Thirty C-14 dates place human occupation of the rockshelter between 1000 and 1700 cal AD. Matrix was screened through 1/8" (3.2 mm) mesh. Over 35000 bones and teeth were recovered from the rockshelter and 90% of these are fish (Kirch *et al.*, 1995). This study focused on materials from a large 25 m<sup>2</sup> block whose sediments could be assigned to analytic zones.

I focused taxonomic analysis on seven paired elements (dentary, articular, premaxilla, maxilla, quadrate, hyomandibula, cleithrum), quantified taxonomic abundance using Number of Identified Specimens (NISP) (Grayson, 1984), and identified 1475 specimens that represent 52 taxa and 29 families (Butler VL. Fish remains from Tangatatau Rockshelter, in preparation) (Table 1). A wide range of fish taxa are present; six taxa, *Eleotris* sp., *Anguilla* sp., Serranidae, cf. *Cirrhitis* sp., Labridae, and Acanthuridae, comprise most (about 80%) of the identified fish fauna.

Both *Eleotris* sp., a small, goby-like fish, and *Anguilla* sp., freshwater eel, are catadromous, which means that phases of their life histories are spent in fresh and marine habitats. *Eleotris* spawns in freshwater; its larvae float to sea where they mature and return to freshwater as

Table 1. Frequency (NISP) of fish taxa by zone, Tangatatau Rockshelter

Taxon	2	3	4	5	6	7	8	9	10	11	13	14	15	17	Total
Eleombranch		1	1											1	3
<i>Anguilla</i> sp.	26	5	14	1	2	3	4		2				11	2	70
Muraenidae		4		16	5	4	18	1		2	3		1		54
Congridae		2	7	5	1		8	3					1		29
Synodontidae			1												1
Belontiidae		1													1
Holocentridae		1	6				5								14
Myristinae	1	1	1				3		1						8
Holocentrinae	2	4	7	4		5	10	3	4						42
<i>Fistularia</i> sp.					4										4
Scorpaenidae		1	1				2								5
Serranidae	16	18	28	15	6		21	3	2				4		115
<i>Kuhlia</i> sp.		1	2												3
Carangidae		4	3		1										11
cf. <i>Decapterus</i> sp.		1	2		2										7
cf. <i>Caranx</i> sp.			1												1
cf. <i>Aphareus</i> sp. (Lutjanidae)															1
cf. <i>Monotaxis grandoculis</i>															1
Mullidae				2			2								8
cf. <i>Mulloides</i> sp.							1								1
cf. <i>Parupeneus</i> sp.	2														5
cf. <i>Pempheris oualensis</i>						2									2
Kyphosidae		3	3				3								10
Pomacanthidae															1
Pomacentridae	1	1	1		2	2	3								11
cf. <i>Abudefduf</i> sp.	1	1	1				1								4
cf. <i>Cirrhites</i> sp.	19	34	36	23	9	12	62		2				24	3	225
Mugilidae							3								3
cf. <i>Mugil</i> sp.													1		1
cf. <i>Polydactylus saxifilis</i>				1			2						5		8
Labridae	4	9	13	15	3	4	38	2	2	3	3		6		104
cf. <i>Gomphosus</i> sp.		3					3								6
cf. <i>Thalassoma</i> sp.	1	8	13	10	3	4	30	2		2					74
cf. <i>Anampses</i> sp.	3	3	2				1								10
cf. <i>Hemigymnus</i> sp.			2				2								4
cf. <i>Halichoeres</i> sp.			2				1								3
cf. <i>Cheilinus</i> sp.		6	2												8
cf. <i>Thalassoma/Halichoeres</i> sp.			4				6								13
Scaridae	2	7	1												11
Scarinae		9	2												13
Sparisomatinae		2	2				5								10
<i>Eleotris</i> sp.	70	20	53	11		21	62	4	4		1		69	2	322
Acanthuridae	12	27	21	21		9	47	2	4		3		8	2	162
cf. <i>Acanthurus</i> sp.	5	9	3	4		1	14								36
cf. <i>Ctenochaetus</i> sp.															1
cf. <i>Naso</i> sp.															
cf. <i>Bothus</i> sp.			1												
Ballistidae		2	6	5		5	8								30
cf. <i>Rhinecanthus</i> sp.		1		2		1	8								13
cf. <i>Xanichthys</i> sp.															
cf. <i>Cantherhines</i> sp.															
<i>Diodon</i> sp.															
Total	167	192	244	139	56	79	375	22	26	11	12		135	16	1475
Number of taxa	17	33	34	19	21	19	31	10	13	7	6		15	11	52

juveniles. *Anguilla* spends its adult life in freshwater and leaves the interior through subterranean conduits in the limestone to spawn at sea; juveniles return to freshwater where they mature. The other taxa are found strictly in marine, primarily nearshore habitats. During my field visit in 1991, I observed them either on the fringing reef, the surge channels and tide pools, or on the sloping reef edge adjacent to the fringing reef.

### Temporal change in fish use

As noted above, if resource intensification of the fishery occurred, we would expect to see a progressive decline in abundance of high ranked fish resources and an increase in lower ranked resources over time. Given the relationship between body size and rank, we can track the contribution of different ranked prey to the diet, using general attributes of fish body size.

There are obviously a number of ways to measure changes in fish resource use. Recognizing a key assumption of the prey choice model, namely the fine-grained search assumption, helps to define some of the conditions that need to be considered. The fine-grained search assumption requires that predators seek all prey types simultaneously and that prey are randomly encountered in a relatively homogenous environment. To best meet the requirements of this assumption, Broughton (see also Smith, 1991) recommends distinguishing prey types that occupy different habitats and that would have been captured using different technologies, insofar as this can be estimated. For this study, I examined changing fish resource use in two distinct habitats or resource patches, freshwater and marine, and consider ways of controlling for technology.

Regarding the freshwater resource patch, there are two taxa to consider and rank: *Anguilla* sp. and *Eleotris* sp. Species level identifications, unfortunately, could not be made for these taxa. While there is clearly inter-specific variation in body size among species of these genera, all of the extant *Anguilla* species reach considerably larger sizes than species of *Eleotris*. Two *Anguilla* species (*A. obscura*, *A. megastoma*) are recorded for

the Cook Islands; two additional species, *A. australis* and *A. marmorata* may be present (Jellyman, 1991). The maximum size of these species range from about 850 mm for *A. obscura* (Jellyman, 1991) to over 1500 mm for *A. marmorata* (Castle, 1986). Research on the species of *Eleotris* present in the South Pacific is extremely limited. Only *E. fusca* has been reported for the Cook Islands (Jellyman, 1991); this species reaches only 260 mm in length (Hoese, 1986). Insofar as body size is an appropriate index of prey profitability, *Anguilla* should rank higher than *Eleotris*. Where ethnographic accounts are available, such as with the Maori in New Zealand, freshwater eel was a highly valued food source, probably for its high protein and oil content as well as caloric value (Marshall, 1987). Finally, ethnographic records show that species in the two genera were captured using both mass capture and solitary methods (traps, angling, spearing) (Buck, 1945).

I developed indices for the Tangatatau fish fauna that provide a ratio of large to small-bodied prey types; the larger the ratio, the greater the contribution of larger prey. For the prey types in the freshwater patch, I created the Freshwater Index, or:

$$\frac{\Sigma \text{NISP } Anguilla}{\Sigma \text{NISP } Anguilla + \Sigma \text{NISP } Eleotris}$$

which was calculated for each zone in the rockshelter, containing at least 30 identified specimens.

Similarly, I calculated an index to track changing frequencies of large and small fish from the broadly defined marine resource patch. I included nine taxa (Table 2) in the index that could be separated into relative body size classes based on known lengths attained (Myers

Table 2. Fish taxa included in the Marine Index and dominant feeding strategy

Large taxa	Small taxa
	<i>Cirrhitus</i> sp., C
	<i>Thalassoma</i> sp., C
	Acanthuridae, O/H

C, carnivore; O/H, omnivore/herbivore.

1989) by members of the taxa. The 'large' taxa include forms that typically reach lengths much greater than 300 mm, while the 'small' taxa are generally much smaller than 300 mm. For example, the 'large' taxon Kyphosidae, includes species that reach lengths from 370 to 700 mm. The 'small' taxon *Tbalassoma* primarily includes species that rarely reach 200 mm in length, and only one whose maximum size is slightly greater than 300 mm in length. All members of the Cirrhitidae are quite small; *Cirrhitus*, another 'small' taxon included in the index can reach about 230 mm in length. The nine taxa included in the comparison together represent about 70% of the marine fish fauna, which suggests that temporal changes in the frequency of these large and small-bodied marine fishes should reflect general changes in marine fish resource use as a whole. The Marine Fish Index:

$$\frac{\Sigma \text{NISP Large Marine Taxa}}{\Sigma \text{NISP Large Marine Taxa} + \Sigma \text{NISP Small Marine Taxa}}$$

was calculated for each zone in the rockshelter where NISP was 30 or more.

To reiterate, researchers that use the prey choice model to explore questions of resource intensification, suggest that prey body size is a proxy measure of prey rank or profitability. In the Mangaian case, if we see a decline in frequency of large-bodied taxa over time, from the lower zones to the upper zones in the rockshelter, this could be taken as a measure of resource intensification or a decline in foraging efficiency—that is, over time, human predators increasingly pursued resources that produce lower energetic returns.

Figures 2 and 3 show that there is an inverse relationship between relative zone age and index. Over time, from the lower to the upper zones of the rockshelter there is a decreasing abundance of large-bodied fishes and increasing abundance of small-bodied fishes, which would suggest that people were making use of increasingly lower ranked fish resources over time. Spearman's rank order correlation coefficients, comparing relative zone age with the Freshwater and Marine Indices are both negative and significant (Freshwater Index:  $r_s = -0.65$ ,  $0.05 > p > 0.025$ ; Marine Index:  $r_s = -0.52$ ,

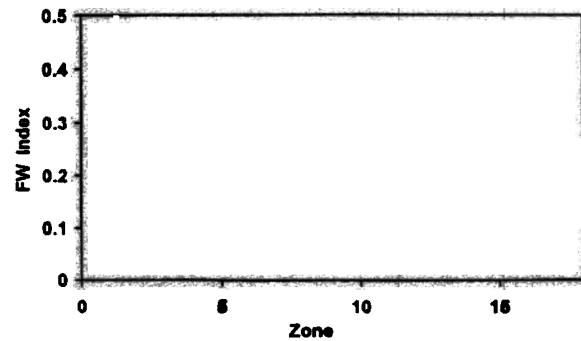


Figure 2. Plot of the Freshwater Index by zone.

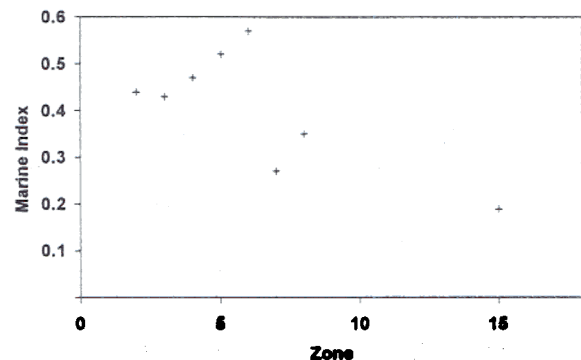


Figure 3. Plot of the Marine Index by zone.

$p = 0.05$ ;  $df = 8$ ). I note as well that the indices are not correlated with the sample size of the zone (Freshwater Index:  $r_s = -0.32$ ,  $0.25 > p > 0.10$ ; Marine Index:  $r_s = -0.09$ ,  $p > 0.25$ ;  $df = 8$ ).

In short, the fish faunal data show an empirical trend towards increasing abundance of small-bodied fish over time. Such a result is expected if resource intensification occurred, where human exploitation practices effectively lowered the encounter rates with high ranked prey through excessive predation, forcing the use of low ranked prey. However, encounter rates with high ranked prey could also decline because of environmental change, independent of human predation, which adversely affected large-bodied organisms. As well, a shift in use towards smaller-bodied prey may be completely independent of the abundance of the high ranked prey (and encounter rates), if technological change took place that increased the return rates of low ranked prey items (Madsen & Schmitt, 1998). Before presuming human-caused



resource depression caused the pattern in the faunal data, it is important to consider factors such as these (Broughton, 1997; Grayson & Cannon, 1999).

## Search for causes

### *Technological change*

It is possible that shifts in fish representation are linked to technological change. When Broughton and others use declines in abundance of large-bodied prey and increases in abundance of small-bodied prey to argue for declines in foraging efficiency, they are assuming that prey capture technology did not change so as to elevate the rank of small prey above that of large prey. If there are changes in technology, however, from individual fish capture to mass harvesting of multiple individuals at one time, for example, then the decline in prey body size may not reflect a decline in foraging efficiency (or resource intensification) (Madsen & Schmitt, 1998). Drawing on ethnographic and fishery data from the Truckee River of eastern California, USA, Lindstrom (1996) has estimated return rates on fishes of various sizes, taking into account capture methods. When fishes are consumed fresh, smaller fishes caught in mass provide higher energetic returns than large fish caught individually. Importantly, Lindstrom also found that when large *and* small fish are captured through mass harvesting, return rates are much higher for large individuals than small ones.

Given the significance of technology to questions of foraging efficiency and intensification, clearly it would be useful to link specific prey to the technology used to capture them. Unfortunately, as others have pointed out (Broughton, 1994, 1995), such reconstructions are probably impossible to render in detail. On the other hand, depending on the context, evidence of large-scale change or stability in capture technology might be estimated using the artifact record or behavioural ecology of prey.

In Oceania, fish hooks, notched stones ('net weights'), and intertidal stone traps have been

used to identify certain fishing strategies (Kirch, 1980, 1985; Allen, 1992a,b). The decline in frequency of fish hooks from late Holocene-aged archaeological sites on Aitutaki, Cook Islands, led Allen (1992a) to argue for a decline in angling, and increased use of nets. At Tangatatau, the frequency of fish hooks declines dramatically above zone 8 (Figure 4), which also would seem to argue for a decline in angling on Mangaia. Close inspection of changing frequency of other artifact classes at the rockshelter suggests another explanation, however. As shown in Figure 5, hook frequency across zones closely mirrors that of adzes/adze fragments and 'other' artifacts (e.g. modified basalt, coral, bone). Indeed, the rank order frequencies of the three artifact groups are significantly and highly correlated (hook versus adzes:  $r_s = 0.8440$ ,  $p < 0.001$ ; hooks versus 'other' artifacts:  $r_s = 0.8374$ ,  $p < 0.001$ ). The frequency of *all* artifact classes declines above zone 8, not just the fish hooks. These data suggest that the changing frequency of fishhooks is probably telling us more about intensity of cultural use and disposal patterns than about changing fishing technology. Thus, at least for the rockshelter site, the culturally modified objects do not help us sort out the extent of technological stability or change.

Others working with Oceanic fish faunas have used fish feeding behaviour to help identify capture methods (Leach & Intoh, 1984; Leach *et al.*, 1984; Allen, 1992b; Butler, 1994). Briefly, this work takes the position that knowing what fish eat and how they acquire food can tell us something about how they were captured by humans (Butler, 1994). Herbivores/omnivores that graze directly on the reef or sessile

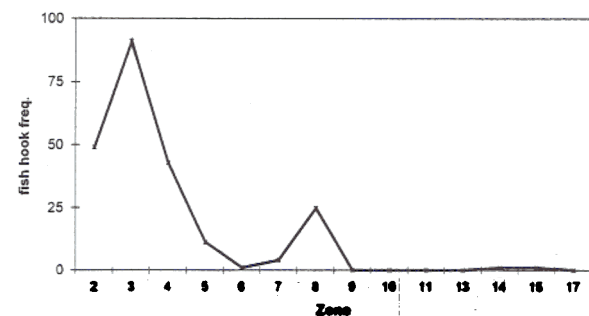


Figure 4. Frequency of fish hooks by zone.

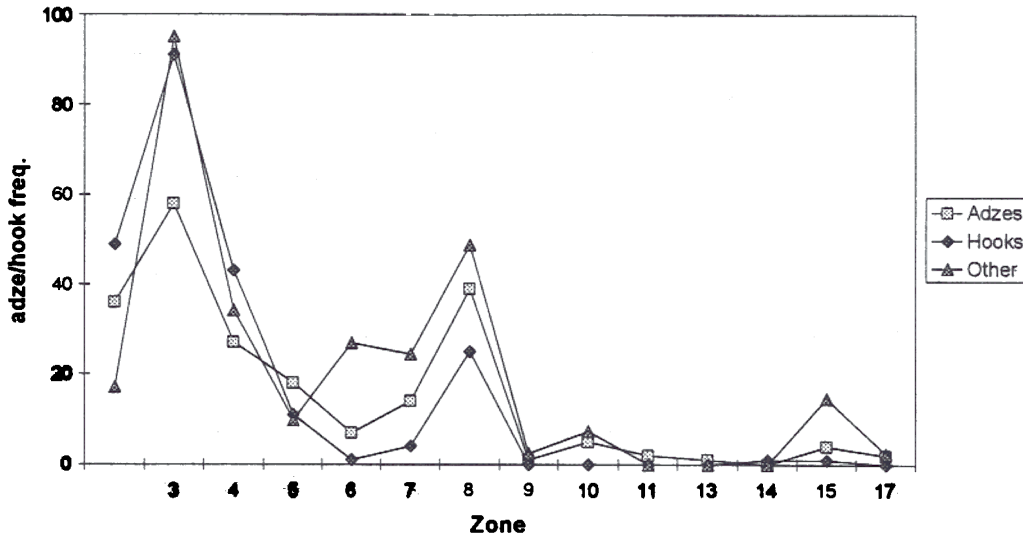


Figure 5. Frequency of fish hooks and other artifact classes by zone.

plants, or slow-moving invertebrates, typically have small, terminal mouths, with reduced, modified or absent teeth. Such fish are not attracted to active prey and unlikely to bite at a baited hook. In contrast, carnivorous fishes that consume active prey (other fishes or mobile invertebrates) have relatively large jaws with teeth designed to procure and handle prey and such fish are attracted to baited hooks. That there is some link between fish feeding strategy and capture method is supported by ethnographic records of capture methods and modern subsistence fishery data from Oceania (Butler, 1994). These data indicate that carnivores are more likely to be caught using hook and line (than other types of feeders), while herbivores/omnivores are more likely to be caught using mass capture methods (than other types of feeders). To obtain some crude measure of change or stability in capture methods, then, one can examine a fish faunal sequence for the kinds of feeding strategies represented.

In the case of Tangatatau, if capture technology shifted towards greater use of mass harvesting, one would predict an increase in the frequency of herbivores/omnivores over time. The faunal data do not indicate this. All but two of the 11 taxa included in the Freshwater and Marine Index are carnivores (Table 2) (Hiatt & Strasburg, 1960; Myers, 1989; Randall *et al.*,

1990). The relative frequency of the herbivores/omnivores, Kyphosidae and Acanthuridae, varies across zones but does not increase over time. Such fishes are most prevalent in zone 5 and are least abundant in the uppermost zone 15 (Figure 6). Overall consistency in feeding types represented across zones supports the notion that capture methods were generally stable throughout occupation of the rockshelter.

*Environmental change*

Detailed study of pollen and sediments from multiple basins on the island indicate significant landscape changes occurred about 2500 years ago. While the role of humans in causing the

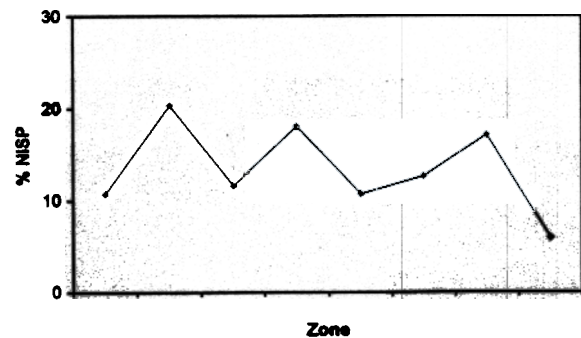


Figure 6. Frequency (%NISP of all fish taxa) of herbivores/omnivores by zone.



changes is debated (Spriggs & Anderson, 1993; Kirch & Ellison, 1994), researchers agree that interior volcanic hillsides were cleared of most forest vegetation, which led to slope erosion and infilling of valley bottoms. Could such environmental changes have differentially affected fishes of different sizes, causing the decrease in abundance of large-bodied fishes (*Anguilla* and the large marine fish)? It will be difficult to fully address the relevance of environmental change because of our limited knowledge of the biology and life history of the tropical freshwater and marine fishes involved. Undoubtedly, hillside erosion and basin infilling affected the size and configuration of the freshwater system, as well as water conditions (turbidity, temperature), but whether *Anguilla* would have been more vulnerable than *Eleotris* to such changes is unknown. On the other hand, landscape change probably had little effect on the marine system and the fishes inhabiting that system. As a *makatea* island, Mangaia lacks surface drainage. Most of the sediment eroded from the volcanic slopes was likely trapped in the interior basins, against the inner rim of the *makatea*, rather than deposited on the fringing reef. There is currently no evidence that marine habitats were affected by late Holocene erosion of the internal basins. Thus, even if one wanted to assert that the documented environmental changes were responsible for the reduction in abundance of *Anguilla*, it would be difficult to use environmental change to explain the reduction in abundance of large marine fishes.

#### *Human-caused resource depression*

The above discussion suggests that environmental and technological change do not satisfactorily explain the shifts in fish representation. Is there better evidence that human predation is directly responsible? To address this question, it is useful to consider several ways predators can depress prey resources, effectively lowering encounter rate (Charnov *et al.*, 1976). *Exploitation depression* occurs when encounter or capture rate declines because of direct predator harvesting. *Behavioural depression* occurs when prey alter their behaviour (flocking, schooling, increased alert-

ness) to avoid being eaten. *Microhabitat depression* refers to the situation where prey move to a new location making it more difficult for the predator to find the prey than was the case originally.

Exploitation depression can be measured directly through study of the demographic structure of prey populations. Numerous studies demonstrate that predators, including humans, can alter prey population dynamics—and the fisheries literature is filled with examples where human harvesting has resulted in declines in maximum and average age/size of exploited fishes (Beverton & Holt, 1957). At least for fishes, given the relationship between age and body size, and fish bone size and body size (Casteel, 1976), we can use archaeological fish bone measurement to track changes in the demographic structure of exploited fish. Behavioural and microhabitat depression, while potentially important in setting encounter rates, are much more difficult to measure archaeologically (Broughton, 1995). I will return to this issue below.

To estimate exploitation depression of the fish populations represented at Tangatatau, I measured dentaries from *Serranidae* and *Anguilla* sp, the dominant, large, high ranked taxa in the Marine and Freshwater Fish Indices (see Butler in preparation, for description of measurement landmarks). Dentaries were selected because they are the most abundant and well-preserved element in the assemblage. If declines in the frequency of high ranked fishes in the faunal collection result from human exploitation pressure, fish body size, as reflected in the bone size of these taxa, should decline over time. (I recognize the problem with tracking body size changes for specimens identified only to the family or genus level. Decline in body size documented may reflect an actual decline in size/age attained by a species, due to exploitation pressure, or it might reflect the capture of smaller-bodied species. In both cases, a decline would support the view that people were making use of smaller-bodied resources, if not that human exploitation pressure caused a shift in population dynamics.) For this comparison, I included remains from zone 1, where the taphonomic origins are unclear. Whether the zone 1

remains reflect human predation or that by birds, the fish remains provide an estimate of fish body size prior to extensive human use of the rockshelter.

The results are mixed. On the one hand, the mean and maximum sizes of serranid dentaries show a decline over time (Table 3; Figure 7). Granting the small sample sizes (note several zones have a single measured specimen), the decline in size certainly supports the case for human-caused resource depression, at least for the marine taxon. The *Anguilla* data, however, show no clear temporal trend in size (Table 4; Figure 8). Unfortunately, very few specimens were recovered above zone 4, indicating that it is impossible to make a strong case for changes in fish body size, including a decline, even if it actually occurred, using dentaries for this taxon.

It is possible as well, that high ranked prey abundance (and encounter rates) may have declined because of behavioural responses or habi-

Table 3. Serranidae dentary measures (mm) by zone

Zone	Mean	N	S.D.	Range
1	10.07	1		
2	5.38	2	1.78	6.63-4.12
3	4.14	4	1.30	6.03-3.05
4	8.06	2	3.53	10.56-5.56
5	5.02	1		
6	5.92	1		
8	2.78	1		--
9	2.31	1		--

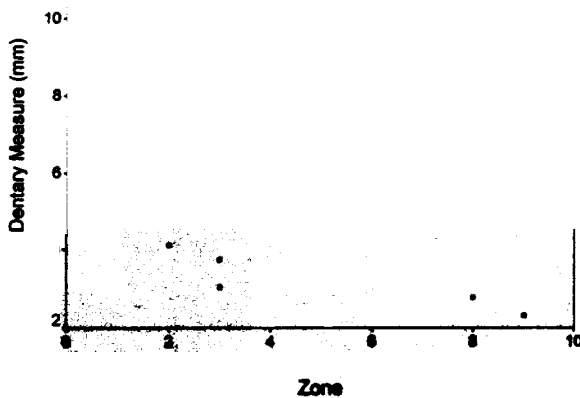


Figure 7. Plot of dentary size by zone, Serranidae.

Table 4. *Anguilla* dentary measures (mm) by zone

Zone	Mean	N	S.D.	Range
1	1.35	8	0.31	1.74-0.99
2	1.29	6	0.37	1.74-0.74
3	1.76	1		--
4	1.34	4	0.43	1.88-0.88
8	2.01	1		
15	1.58	1		--
17	1.13	2	0.21	1.28-0.99

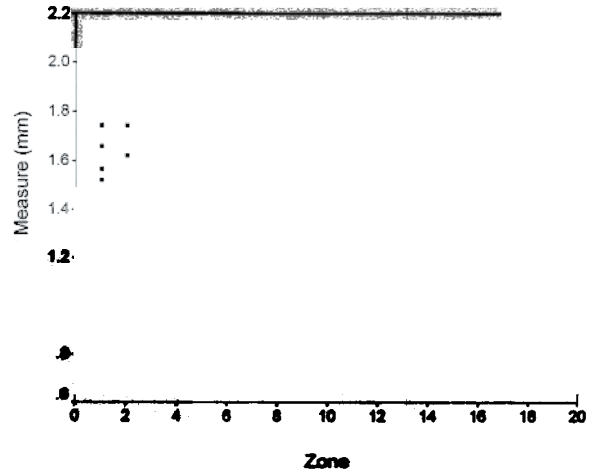


Figure 8. Plot of dentary size by zone, *Anguilla* sp.

tat shifts made by the prey, in the face of human predation pressure. Such avoidance behaviours can persist for extended periods (Charnov *et al.*, 1976), without, unfortunately, leaving an archaeological signature.

In short, while evidence suggests human caused exploitation depression of the primary high ranked marine taxon, Serranidae, the case for human depletion of *Anguilla* cannot be evaluated with available data.

## Conclusions

For over 20 years, prehistorians working in remote Oceania have been concerned with understanding subsistence change (Groube, 1971; Kirch, 1973; Dye, 1990; Allen, 1992b; Sweeney *et al.*, 1993). Issues of particular interest include documenting the changing importance of introduced, agricultural foodstuffs versus indigenous faunal and floral resources, the role of humans

in depleting indigenous biota and modifying landscapes, and determining the extent to which human population growth was a dependent or independent factor in the process of subsistence change. As discussed above, foraging models, like the prey choice model discussed here, have much to offer studies of subsistence change because they provide testable predictions against which the archaeological record can be evaluated.

This study applied the prey choice model to evaluate changes in fish use from Tangatatau Rockshelter on Mangaia in the southern Cook Islands. The prey choice model predicts that human foragers will initially procure high ranked prey, turning to low ranked prey if the abundance of high ranked prey declines. Key factors that would cause declines in prey abundance are predator population growth and reduced mobility. There is support for both of these conditions on Mangaia. In the early 1800s, after decades of European contact and likely reduction in population size due to introduced disease, population size was estimated at about 3000 people; population density on Mangaia was one of the highest in central Polynesia, at 150 persons/km<sup>2</sup> of arable land (Kirch, 1994). While direct archaeological evidence for human population growth (e.g. number of houses/unit time) is not available for Mangaia (in fact, significant infilling of valley bottoms make it unlikely that a detailed settlement history can be documented), it is reasonable to suggest that the high population density at historic contact reflects centuries of population growth. Regarding mobility, a number of studies suggest a constriction in inter-island travel and interaction in the several centuries before European contact (Irwin, 1992; Weisler, 1997). Moreover, Mangaia's great distance from other islands suggests that local, near shore and freshwater fish stocks would be the target of the fishery, not those on distant islands, due to high transport costs.

Trends in the fish faunal data from Tangatatau Rockshelter follow the predicted response: over time, high ranked fish resources decline in frequency and lower ranked resources increase in abundance. Resource depression caused by human predation is the best

explanation for these trends, although small sample sizes for *Anguilla* were insufficient to identify a trend in declining body size. The study suggests that the prehistoric fishery depleted near shore marine and freshwater fish populations and that the fishers in turn, adjusted to the changes, by taking resources of lower rank. The changes do not correspond to technological change, insofar as fish feeding strategies and modified objects are valid markers of technological change. Thus, the increase in use of lower ranked fishes suggests an overall decline in foraging efficiency. Finally, this study joins a growing body of evidence that shows how profoundly Polynesians affected the indigenous biota on islands they colonized (Kirch & Hunt, 1997).

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### Notes

In calculating the Spearman's rho ( $r_s$ ) correlation coefficient for the relationship between zone relative age and resource use index, the eight zones were arbitrarily assigned values from 8 to 1, with 8 representing the deepest/oldest zone and 1 representing the uppermost/youngest zone.

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