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Seeto, J, Nunn, Patrick, Sanjana, S (2012) Human-Mediated Prehistoric Marine Extinction in the Tropical Pacific? Understanding the Presence of *Hippopus hippopus* (Linn. 1758) in Ancient Shell Middens on the Rove Peninsula, Southwest Viti Levu Island, Fiji *Geoarchaeology*, 27:1, pp.2-17.
DOI:10.1002/gea.21385

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Human-mediated prehistoric marine extinction in the tropical Pacific: understanding the presence of *Hippopus hippopus* (Linn. 1758) in ancient shell middens on the Rove Peninsula, southwest Viti Levu Island, Fiji

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Abstract

At the Lapita-era (1100-550 BC) settlements (Bourewa and Qoqo) along the Rove Peninsula in Fiji, valves of the reef-surface-dwelling giant clam *Hippopus hippopus* (long extirpated in Fiji) occur in shell midden. Valve size/weight increase with depth, suggesting that human predation contributed to its disappearance from the Rove Peninsula. The timing of this event is constrained by (a) the confinement of *H. hippopus* remains to the lower part of the midden, (b) their likely association with only the stilt-platform occupation phase at both Bourewa and Qoqo (approximately 1100-900 BC) and (c) radiocarbon ages. All these suggest that *H. hippopus* disappeared from reefs here about 750 BC. Human predation is unlikely to be the sole cause of extirpation of *H. hippopus* in Fiji. More plausible is that humans introduced alien predators or diseases to Fiji that spread independently of humans throughout these islands, although climate and sea-level changes may also have contributed.

Introduction

The earliest people to settle the island groups of the tropical west Pacific (Figure 1) arrived around 3000 years ago and are known today as Lapita, their distinctive cultural traits having been widely commented on (Kirch, 1997a; Green, 2003). Among these was a high dependence on marine foraging, particularly in Remote Oceania where it is likely to have sustained the earliest people almost entirely for the first 50-200 years that they occupied island groups such as Vanuatu (Galipaud & Kelly, 2007), Fiji (Nunn et al., 2004) and Tonga (Burley & Dickinson, 2001). A conspicuous manifestation of the dependence of early Lapita settlers on marine foods is the stilt-houses that they occupied and built out across coastal flats; examples come from the Bismarck Archipelago in Papua New Guinea, the eastern outer Solomon Islands, Vanuatu, and Fiji (Kirch, 2001; Walter & Sheppard, 2006; Galipaud & Kelly, 2007; Nunn, 2007a; Nunn et al., 2006).

There are many unknowns about the degree to which the earliest humans to occupy and routinely interact with these pristine reef-lagoon ecosystems impacted them and altered their ecology. This has sparked a debate about the degree of early human impact in the tropical Pacific Islands, one group of researchers leaning towards the idea of rapid impact shortly after colonization (Kirch & Ellison, 1994; Kirch, 1997b), the opposing group arguing that early-human demands on these environments were likely to have been inherently low-impact (Nunn, 2001; Kennett, Anderson & Winterhalder, 2006). The difficulties of assessing early-human impact on island environments in the western tropical Pacific are compounded by the evidence for climate-driven environmental changes during the Late Holocene (1050 BC to present) that altered environments in much the same way as some infer humans to have done (Nunn, 2007b).

This study focuses on the extinction of a marine species in Fiji and the possibility that this event was a result of human predation. In such cases, whether referring

to terrestrial or marine taxa, the evidence of human involvement in island species extinctions has often been circumstantial owing to the difficulties of precisely dating the remains of the extinct species. This argument applies to the mekosuchine crocodile and the giant iguana that once lived in Fiji (Worthy, Anderson & Molnar, 1999; Pregill & Worthy, 2003) though less so to avifaunal remains, the sharply increased abundance of which shortly after human arrival suggests a direct causal connection (Steadman, 2006).

It has generally been more difficult to detect marine extinctions than terrestrial extinctions because of their relative states of preservation; marine faunal remains are generally more dispersed, extinctions more difficult than localized extirpation to demonstrate conclusively (Dulvy, Sadovy, & Reynolds, 2003). The larger the species, the more confined an individual range, the easier it is to demonstrate extinction. Shell middens are excellent places to detect nearshore (reef-lagoon) ecosystem changes that many include (local) extinctions. This paper describes a giant clam species that was living in Fiji at the time of human arrival but became extirpated in this island group subsequently. Several possible causes of extirpation are discussed.

***Hippopus hippopus* in Fiji and the Pacific**

Hippopus hippopus (Linn. 1758) belongs to the genus *Hippopus* which is a member of the Tridacnidae (giant clams) found throughout the Indo-Pacific (Rosewater, 1965). This family became established in the island groups of the western Pacific during the early Miocene (17-24 Ma: Cloud, Schmidt & Burke, 1956) but is found in fossil deposits from Fiji of only late Cenozoic age (<5 Ma: Ladd, 1934; Schneider and Foighil, 1999). *H. hippopus* was “very common” in Fiji during the Pleistocene (<2 Ma: Adams, Dalzell & Ledua, 1999: 369).

H. hippopus has long been known to be extirpated (locally extinct) within the Fiji Islands as well as certain other Pacific Island groups like Guam and, most recently, Tonga (Lewis, Adams & Ledua, 1988; Paulay, 1996). Yet there are extant populations elsewhere in the Pacific Islands region (including in Kiribati, Marshall Islands and Vanuatu) as well as in island groups of the Western Pacific margins such as Papua New Guinea and the Philippines (Wells, 1997).

There are two major differences between *Hippopus* spp. and *Tridacna* spp., the other main genus within the Tridacnidae. *Tridacna* spp. have a well-defined byssal orifice that have no inter-locking teeth whereas *Hippopus* spp. have a very narrow byssal orifice that is bordered by interlocking teeth (Lucas, 1988). The mantle of *Tridacna*, when fully extended, projects laterally beyond the shell margins whereas *Hippopus*' mantle reaches only the margin of the shell when fully extended. Of the two modern species of *Hippopus*, the inhalant aperture of *H. porcellanus* has fringing tentacles which are absent in *H. hippopus* (Rosewater, 1982).

H. hippopus lives in sandy areas of coral reefs down to a depth of 6 metres. Most individuals are found in the shallower part of the range, typically in intensely-lit parts of intertidal reef flats (Griffiths & Klumpp, 1996) and indeed *H. hippopus* has been characterized as a "reef-top" species, which underlines its exposure to marine foragers (Adams, Dalzell & Ledua, 1999: 369). Younger individuals of *H. hippopus* are attached by their byssus to the substrate but adults are unattached (Rosewater, 1962) making the latter easier to collect than other giant clams (Thomas, 2002).

H. hippopus are ciliary filter feeders of plankton that are carried into the mantle cavity by the inhalant feeding current generated by ciliary gill tracts of the clam (Rosewater, 1962). The labial palps sort out the food and undesirable substances are ejected. In common with other tridacnids, *H. hippopus* do not depend entirely on food filtered from the environment but also get nourishment

from symbiotic zooxanthellae which are subject to the same environmental stresses as have been studied more fully in corals (Lesser, 2011). Compared to other clam species, *H. hippopus* has a low weight-specific zooxanthellae population at large size which means that adults have comparatively low absolute photosynthetic rates (Griffiths & Klumpp, 1996), something that may have been a factor in the extinction of *H. hippopus* in Fiji (see below).

Archaeological sites of the Rove Peninsula: interpretation and significance

Several ancient settlement sites dating from the Lapita era (approximately 1100-550 BC), the earliest period of Fiji prehistory, are found along the coasts of the limestone Rove Peninsula in southwest Viti Levu Island (Figure 2A).

The Bourewa archaeological site lies on the windward side of the Peninsula, adjoining a fringing coral reef that is uncommonly broad, almost 3 km in places. Discovered in 2003, Bourewa is regarded as the first place in Fiji to be settled, an event that occurred about 1100 BC when sea level was about 1.5 m higher than today (Figure 2C). The Bourewa settlement endured some 550 years when, in common with all other Lapita-era settlements along the Rove Peninsula, it was abandoned. The three-phase settlement history of the Bourewa site (Nunn, 2007a, 2009) is as follows; dates overlap because of uncertainties of radiocarbon-age calibration.

- Bourewa I, 1260-900 BC – stilt-house occupation, marine foraging dominant; initial occupation at 1100 BC is most probable.
- Bourewa II, 990-750 BC – ground occupation, marine foraging, consumption of brackish-lagoon shellfish, start of horticulture.
- Bourewa III, 830-400 BC – decline of marine foraging, expansion of horticulture; occupation end at 550 BC is most probable.

At the time of its maximum extent, it is estimated that the Bourewa settlement accommodated around 250-300 individuals (Nunn, 2009) and there is no reason to suppose that marine foraging on the Bourewa reef could not have sustained them during the earliest phase of settlement. Today, an estimated 400-500 people living on and around the Rove Peninsula obtain about 30% of their food from this reef as well as surpluses for sale that are equivalent to an additional 30%. Under present climate conditions this relationship appears to be sustainable in the sense that available resources clearly outweigh demand, and no areas are reported to have become unproductive within recent memory.

There is a dense shell midden at the Bourewa site that was excavated on seven occasions (2003-2009) and provides excellent chronological control on the nature, age and duration of the settlement. The earliest houses at Bourewa were stilt-houses, built along a sand barrier extending across the front of a tidal inlet. Following human arrival Bourewa about 1100 BC, the combination of sea-level fall (10 cm/100 years) and the accumulation of shell midden beneath the stilt platforms led to the emergence of this sand barrier about 900 BC in the central part of the site and the probable end of stilt-house occupation.

The Qoqo archaeological site is today on an island (Qoqo Island) located in the middle of an extensive mangrove forest at the mouth of the Tuva River (Figure 2A). About 1000 BC when this site was established on a tombolo connecting the two bedrock islands, the surrounding area was fringing reef (Figure 2B). The earliest settlement also appears to have been a stilt-house settlement (Nunn et al., 2006) although this was discontinued once the tombolo emerged.

Bourewa and Qoqo are the two earliest-known human settlement sites in the Fiji archipelago and the only two to have featured stilt-house occupations, an observation that helps confirm their precedence. In addition, both Bourewa and Qoqo were abandoned at the end of the Lapita era (about 550 BC) and never reoccupied, a fact that makes their Lapita histories easy to isolate. Bourewa and

Qoqo are not the only archaeological sites in these islands to have shell middens containing *H. hippopus* but they are the only ones to be described where shells of this species are present in the lower parts of the sequence but not its upper parts.

Occurrence of *H. hippopus* at Bourewa and Qoqo

There is some mystery about why *H. hippopus* became locally extinct (extirpated) in Fiji but not in other island groups, the most common explanation being to do with both excessive predation and low resilience in Fiji compared to elsewhere (Braley, 1989). Until now, there has been no evidence with which to test such ideas, but during the 2007-2008 summer's field research (Phase 6) at Bourewa, 47 valves of *H. hippopus* were recovered from deep within the early layers of the site and a further 15 from the ground surface along the eroding beach front (Table 1). Basic morphometric analysis was carried out on these shells (Figure 3).

The histogram of (reconstructed) valve weights (Figure 3A) shows a distribution that could be interpreted in a number of ways. Assuming it is meaningful (rather than sampling bias), it is possible that the larger weight group (1600-3200 g) represents most of the individuals gathered by the earliest people at a time when the reef was in a comparatively pristine condition. The corollary to this is that the smaller weight group (0-1200 g) includes most of the individuals collected later in the settlement history of the area when larger individuals could no longer be found. Some confirmation of these inferences comes from the plots of weight and height against depth (Figure 3B and 3C) which show how larger individuals occur generally lower down the midden sequence. Neither of these relationships is particularly strong, perhaps because of factors associated with clam-gathering strategies (a range of sizes collected at one time) and differing times of clam-shell incorporation into the midden relative to collection times.

A likely interpretation of these data is that when the first settlers at Bourewa arrived, *H. hippopus* was living on the fringing reef and became attractive as a food source to the earliest settlers because of its great size and accessibility. As demand grew and/or environmental conditions deteriorated, so the mean size of available *H. hippopus* decreased.

The issue of accessibility is important, given that in comparable situations, because the shells of *H. hippopus* are considered too heavy to carry far, the meat is removed from the clams where they are found (Bird, 1997). The fact of large *H. hippopus* valves being found in the shell middens at Bourewa and Qoqo (see Table 1) suggests *either* that these clams had other uses that made it necessary to bring them to the (over-water) stilt-house village *and/or* that they lived so close to it that the effort involved in transporting them was considered unimportant.

The former option might be favoured if clam shells were used to transport freshwater from springs coming out of the surrounding reef flats. Such springs exist off Bourewa and Qoqo today and may have provided cleaner, less saline water than their earliest inhabitants were able to find on the limestone Rove Peninsula, which today is notoriously dry. Also, while the people of the Bourewa and Qoqo settlements worked shell to produce valuables, tridacnids were not their favoured raw material (Szabó, 2010).

The latter of the two options is favoured because the reef at Bourewa (and probably that beneath the mangrove forest that now exists at Qoqo) is a true fringing reef, extending unbroken outwards from the shore. Even though no clams are found living within 150 m of the shore today, this is attributed to disproportionate human predation pressure because the habitats in which *Tridacna* spp. are observed to be living are identical to those of the inner reef. It therefore seems plausible to suppose that *H. hippopus* was abundant within a

few tens of metres of the Lapita stilt village and that whole valves were carried there on account of this proximity.

At the Bourewa site, the form of the stilt village can be reconstructed from the distribution of postholes found in the excavations (Figure 4). This reconstruction is possible if it is assumed, not unreasonably, that Lapita-era postholes found at the site supported raised structures and that those parts of the site where no (or few) postholes are found did not support such structures. The relationship between the reconstructed form of the stilt platforms and the occurrence of *H. hippopus* is instructive.

All samples of *H. hippopus* come from beneath or on the edges of the stilt platforms, an observation that suggests that most consumption of *H. hippopus* occurred at the time when people at Bourewa occupied stilt platforms and these clams were to be found comparatively close by. To test this hypothesis, radiocarbon age determinations were obtained for nine *in-situ* specimens of *H. hippopus* (Table 2). Other than the anomalously old shell (from Pit C9R), all others probably lived during the two earliest phases of site history, most perhaps during the earliest phase that was coincident with the existence of the stilt-house occupation. This confirms the inferences from stratigraphy and distribution (relative to stilt platforms) that *H. hippopus* collection and consumption occurred only during the earlier history of the Lapita settlement at Bourewa.

One radiocarbon age is clearly anomalous, predating known human arrival at Bourewa by as much as 900 years. Although other explanations are possible, it is likely that this specimen is that of a long-dead individual whose shell was brought onshore to bolster a large post holding up this part of the platform, something also suggested by the depth at which it was found (-125 cm). Fortuitously, this anomalously old date does demonstrate that *H. hippopus* was living on the reef off Bourewa before human arrival, something inferred for Fiji by

Adams, Dalzell & Ledua (1999), and was probably one of its earliest large-size invertebrate colonizers.

There is a moderately strong correlation between median age and depth, as well as between various size parameters and age (Figure 5) . These relationships confirm the earlier inference that larger older individuals of *H. hippopus* are found in the lower parts of the Bourewa midden and were therefore collected exclusively by earlier human occupants of the site.

The important conclusion from the age determinations is that no *H. hippopus* was incorporated into the midden during its later stages of accumulation, perhaps 750-550 BC. Given the predilection of earlier settlers for *H. hippopus*, this observation is best explained by the contemporary absence of *H. hippopus* from the reefs close to Bourewa and Qoqo. Since comparable information is not available from elsewhere in the Fiji archipelago, it cannot be said whether this was part of a widespread disappearance of *H. hippopus* or merely localized.

Interpretation

H. hippopus is the only tridacnid species to have become extinct within Fiji (and other island groups) so it is worth summarizing the principal reasons for its heightened vulnerability to extinction compared to other giant clam species. *H. hippopus* –

- filter feeds, which renders it vulnerable to increased sea-surface turbidity.
- receives food produced by photosynthetic symbionts(zooxanthellae) which are liable to become bleached when stressed, particularly as a result of sea-surface temperature warming.
- has comparatively small numbers of symbiotic zooxanthellae (relative to size) and thus photosynthesizes slowly compared to other tridacnids,

which means that *H. hippopus* is disproportionately affected by factors (like increased sea-surface turbidity) that reduce light penetration in shallow water.

- has a very low tolerance to heat compared to other tridacnids, as demonstrated by the sharp decrease in production/respiration exhibited in warming water (Blidberg et al., 2000).
- lives almost exclusively in nearshore reef-top locations, making it generally easier for humans to locate than other tridacnids that occur in deeper water and/or farther offshore¹.
- grows to large sizes, making it attractive to coastal peoples as a food source.
- is unattached to the substrate in adulthood, making it comparatively easy to remove, especially for foragers who lack a knife that is essential for removing other giant-clam species from the substrate (Thomas, 2002).
- may be a less successful colonizer than other giant-clam species, perhaps even liable to be crowded out of suitable habitats by more aggressive species (Govan, Nichols & Tafea, 1988).

Acknowledging these aspects of vulnerability and building on the interpretation of the data from Lapita-era settlements along the Rove Peninsula, five explanations, not mutually exclusive but discussed separately below, are envisaged for the extirpation of *H. hippopus* during the Lapita era in Fiji. Given that *H. hippopus* lived for perhaps several hundred thousand years in island groups of the tropical western Pacific Ocean (like Fiji), it is likely that humans contributed significantly to its extirpation.

¹ A study of Nukakau Island in New Britain Province (Papua New Guinea), where contemporary ethnographic studies have long informed the understanding of Lapita marine foragers, it was found that *H. hippopus* was commonly collected by women and young children who paddled and poled to adjacent reef areas (Swadling and Chowning, 1981).

1. ***Overexploitation by humans***

There is no doubt that humans are capable of having major impacts on clam populations; in many parts of the world, “there is compelling evidence that foragers have had a significant impact on mollusc populations” (Mannino & Thomas, 2002: 463). A much older yet possibly analogous situation to that involving *H. hippopus* described from the Rove Peninsula comes from the Red Sea where the recently-discovered *Tridacna costata* sp. nov. may have been targeted by out-of-Africa migrants of *Homo sapiens* 125,000 years ago resulting in it being brought to the brink of extinction (Richter et al., 2008). The question remains as to whether such impacts could extirpate a clam species in a diverse archipelago like Fiji, where there are more than 300 habitable reef-fringed islands as well as hundreds of large offshore reefs where giant-clam species are living. The key may lie in understanding the probable nature of these impacts.

The inferred disappearance of *H. hippopus* from the Bourewa reef around the middle of the Lapita era is consistent with the notion that the people living there consumed all that lived there, at least beyond a threshold where the population could become re-established. Such a threshold could refer to stock density, something that plays a major role in giant-clam reproductive success (Adams, 1988). This threshold could also refer to recovery potential: a comparable situation with giant clams in Solomon Islands, where *H. hippopus* is extant, concluded that “recovery of over exploited populations is slow indicating low recruitment rates” (Govan, Nichols & Tafea, 1988: 8).

There are no age data on the time of disappearance of *H. hippopus* from other reefs in Fiji, although the fact that it evidently disappeared from these earlier than recorded in ethnographic history hints at a great age for its Fiji-wide extirpation².

² This situation contrasts with that in the neighbouring Tonga island group where *H. hippopus* is also now extinct but where elderly fishermen questioned a decade ago recalled where this species once lived and even how it tasted (www.tellusconsultants.com/tongan.html [accessed in May 2011]).

It is possible that, as along the Rove Peninsula, humans occupying Fiji coasts during the first millennium BC did in fact consume most individuals of *H. hippopus*, leaving the remainder unable to recover and condemned to extirpation. Yet while continuing to allow for a role for human impact, this explanation cannot satisfactorily account for the extirpation of *H. hippopus* throughout Fiji at this time. For although Lapita settlements were established in most parts of the archipelago (Clark & Anderson, 2001, 2009), population densities are likely to have been comparatively low and direct human impact uneven. Whole areas of reef with populations of *H. hippopus* are unlikely to have been visited by people.

Echoing earlier doubts about whether human foraging can result in extinction of particular shellfish species (Hockey, 1994), later work concluded that, owing to the mobility of foragers and their preference for acquiring food from well-endowed nearshore ecosystems, it is highly unlikely that extinction could result from foraging alone (Mannino & Thomas, 2002). Much of the present and recent endangerment of giant-clam species has been due to their exploitation for non-subsistence purposes, particularly for their shells.

2. *Effects of alien predators and diseases*

The principal cause of the extirpation of *H. hippopus* may therefore not have been direct predation but may still have been moderated by humans. By analogy with recent thinking about terrestrial human impact in the Pacific Islands (Athens et al., 2002), when humans arrived in the Fiji Islands, they may have inadvertently introduced alien predators and diseases to shallow-water marine ecosystems perhaps bringing about massive, unanticipated and undesired changes in their ecology within a few hundred years.

A similar explanation was proposed for the existence of temporal hiatuses in coral-reef surface growth revealed by radiocarbon dating of fossil mid- and late-

Holocene corals in various parts of Fiji (Nunn, 2001). These hiatuses, some lasting up to 1000 years, mark times when no corals apparently grew on reef surfaces where previously and subsequently some grew. The hiatuses were at different times in different island groups within the Fiji Islands, which militated against the cause being associated with a single group-wide event such as a tsunami or an earthquake or a temporary dip in sea level. Rather it seemed more plausible to suppose that the hiatuses represented coral dieback resulting from predators or diseases introduced by itinerant human groups in the process of colonizing the archipelago. This may have been a contributory cause of the decline of *H. hippopus* within the Fiji Islands.

It is difficult to speculate about the exact nature of the alien predator or disease that may have been carried unknowingly by Lapita voyagers from reef to reef across the Pacific. Yet a scenario in which predators or disease-vectoring agents found themselves introduced from the more biodiverse and complex ecosystems of Near Oceania to the less biodiverse and simpler ones of Remote Oceania (see Figure 1) does seem plausible. There is certainly a well-known potential for coral diseases to radically modify reef ecology within short periods of time but very little information about the causes of these diseases (Richardson, 1998; Jackson et al., 2001). Infections of *H. hippopus* populations in Micronesia and the Philippines by rickettsiales-like organisms were reported by Norton et al. (1993) as having been responsible for the deaths of up to 60% of juveniles (< 11 months).

3. *Increased sea-surface turbidity*

All giant clams are filter feeders but get most of their food from photosynthetic zooxanthellae that live symbiotically within them. This dual mode of feeding is a useful adaptation in shallow-water marine habitats where water may be only rarely turbid. But when turbidity increases, particularly for prolonged time periods,

both forms of feeding may suffer in consequence. Inhalant siphons used for filter feeding may become choked with the excess sediment, something to which *H. hippopus* is particularly liable because it lacks the tentacles around the inhalant mouth that all *Tridacna* species (except *T. gigas*) have. And, especially for clams living more than one metre below low-tide level, there may be insufficient light penetration to allow the zooxanthellae to photosynthesize. The net result is that the clam may die.

Turbidity can increase in inshore reef-lagoon waters for various reasons, natural or human-associated. Prolonged turbidity increases would result from increased terrestrial sediment inputs, such as would result from increased precipitation or forest clearance. Many nearshore shellfish species have decreased in number today as a result of increased sediment inputs, typically from the conversion of forest to cropland (van der Meij, Moolenbeek & Hoeksema, 2009).

The available evidence suggests that the Lapita inhabitants of Bourewa subsisted largely by marine foraging from the time of their arrival about 1100 BC to the time when they were joined by a new group of migrants about 850 BC who introduced cultivars of taro (*Colocasia esculenta*) and yam (*Dioscorea esculenta*) (Horrocks & Nunn, 2007; Nunn, 2009). This led to the start of horticulture in the area which, combined with the changes to the nearshore environment associated with sea-level fall, may have led to increased sediment inputs to this area. More than any other giant-clam species, it was *H. hippopus* that lived closest to the shore and, as a filter feeder, would have been particularly vulnerable to the increased sedimentation.

4. Sea-level fall

During the 550-year occupation of the Rove Peninsula settlements by the Lapita people, sea level fell by some 55 cm (Nunn & Peltier, 2001). The environmental

effects of this have been documented for the Bourewa site, where the tidal inlet that existed at the start of Lapita occupation was transformed into a brackish-water coastal lagoon and eventually dried up (Nunn, 2005). It has been argued that these changes and those on the adjoining reef flat impacted the nearshore marine resource base to such an extent that the Lapita people abandoned the area (Nunn, 2009).

If it is assumed that the reef flat which fringed the Rove Peninsula was in an optimal condition for diversity of marine habitats at the start of Lapita occupation 1100 BC, then the progressive sea-level fall would have seen this diversity progressively decline as occupation continued. The reasons would have been because of

- the emergence of the shallow reef surface, especially around high tide, perhaps killing the subtidal biota (perhaps including some *H. hippopus*) after prolonged exposure;
- the consequent creation of barriers to water circulation within the lagoon, which caused stagnation in the shallow pools where giant clams are likely to have been living; reduced water circulation is implicated in the spread of rickettsiales-like diseases affecting *H. hippopus* (Norton et al., 1993).

Predictions that inner-reef shellfish species in the Pacific Islands would undergo local extinctions during sea-level falls (regressions) are borne out by fossil data (Paulay, 1996). An analogous situation is inferred to have arisen from sea-level fall during the AD 1300 Event (approximately AD 1250-1350) in the tropical Pacific (Nunn, 2007c). For example, the long-distance inter-island trade in shells of the pearl-oyster (*Pinctada margaritifera*) from Aitutaki Island (Cook Islands: Walter, 1996) ceased abruptly 550-450 ¹⁴C yr BP (~AD 1400-1500) as a result of increased sediment in their lagoonal habitat (Allen, 1992). It is envisaged that the inputs of sediment did not increase significantly in volume but that its mobility

within the lagoon decreased sharply as a result of sea-level fall. Specifically many pearl-oyster habitats were smothered by sandy sediment on which they were unable to grow. There are also abundant empirical data from the islands of Micronesia (northwest Pacific Ocean) which show that the fall of sea level which occurred during the AD 1300 Event led to a decline of mangrove-dwelling *Anadara* and an increase of sand-burrowing *Strombus* (Amesbury, 1999, 2007). Similar situations have been described for this period elsewhere in the tropical Pacific (Szabó, 2001; Nunn, 2007c; Morrison, 2010).

5. Changed sea-surface temperatures

There are examples of seawater temperature changes contributing to molluscan extinctions, although the contribution of sea-level change to these is unacknowledged (Taviani, 1998). Experimental research on the sensitivity of giant clams to elevated seawater temperatures show that *H. hippopus* is more sensitive than other common tridacnids on account of the sharp decreases in production/respiration that occur when the surrounding water warms, a conclusion that receives support from observations during the 1998 El Niño in the Philippines during which bleaching and mass mortality of *H. hippopus* was observed (Blidberg et al. , 2000).

More recent work found a strong positive correlation between sea-surface temperature and shell growth in *H. hippopus* (Aubert et al., 2009). Of particular interest is that abrupt, short-lived drops in sea-surface temperature led to significant and sustained reductions in shell growth. It is therefore possible that the cooling which accompanied the sea-level fall around the Rove Peninsula during the period of its Lapita settlement contributed to the extirpation of *H. hippopus* here and perhaps elsewhere in the Fiji archipelago.

Implications for understanding early human impact on marine resources

It is possible that all five explanations discussed in the preceding section contributed to the extirpation of *H. hippopus* in Fiji. As noted earlier, the fact that this clam had lived in Fiji for probably several hundred thousand years, surviving many changes in climate, sea level and environment, implies that it was the presence of humans in the ecosystem that tipped the scale towards extirpation. On the other hand, it is doubtful whether humans can by themselves cause the extinction or extirpation of marine mollusc species (Mannino & Thomas, 2002). This conclusion seems applicable to the issue of the pre-modern extirpation of *H. hippopus* within Fiji for, had this been a result solely of unsustainable levels of human predation, it is unlikely that *H. hippopus* would have disappeared so completely from the archipelago, given that some reefs were so far from centres of human occupation. So while the process of extirpation may have been moderated by the presence of humans, even impossible in its absence, there is a requirement for an archipelago-wide cause (such as a newly-introduced disease or a climate-driven environmental change) of extirpation.

One key question that needs to be answered before a complete understanding of the cause(s) of extirpation of *H. hippopus* in Fiji can be reached is what relation the apparent disappearance of *H. hippopus* about 750 BC from the reefs around the Rove Peninsula has to the extirpation of this species throughout the Fiji archipelago. It seems unlikely that the two observations are unrelated. Further, it seems plausible to suppose that the former presaged the latter, although the time frame from local (around the Rove Peninsula) to archipelago-wide extirpation is unknown.

It is clear that both climate and sea level were changing during the period of occupation (1100-550 BC) of the Lapita settlements along the coasts of the Rove Peninsula. Temperatures are estimated to have fallen by perhaps 1-2°C while sea level fell by 55 cm (Nunn, 1999; Nunn & Peltier, 2001). Such changes

certainly have the potential to change reefal ecology but, given that they are far from being unprecedented, they must have been only a contributory cause of the extirpation of *H. hippopus* in Fiji.

More compelling is the idea that humans inadvertently introduced diseases and/or predators that attacked *H. hippopus*, perhaps killing individuals only in particular age groups (Dulvy, Sadovy & Reynolds, 2003). While such introductions may have needed humans to transport them across the 1100-km wide ocean gap that separates Fiji from Vanuatu (to the west), they might have been able to spread by themselves throughout the Fiji archipelago where inter-reef ocean gaps rarely exceed 10 km.

Conclusions

It is concluded that the extirpation of *H. hippopus* in the Fiji Islands occurred because humans arrived and commenced interacting with nearshore reef environments. In addition there was an archipelago-wide cause of extirpation; while other conclusions are possible, that favoured here involves an introduced disease and/or predator. Other, largely localized, contributory causes resulted from direct human impact and included the unsustainable harvesting of *H. hippopus* and the effects of increased terrestrial sediment loads (from land clearance) entering shallow nearshore areas.

More research on the timing of the disappearance of *H. hippopus* from Fiji reefs, as could be determined from studies of other Lapita-age shell middens in these islands, might help resolve the issues of whether that described from the Rove Peninsula was part of a widespread or a localized such event. This in turn would improve insights into the dominant mechanism(s) behind the extirpation of *H. hippopus* in Fiji.

Acknowledgments

Both the Faculty of Islands and Oceans and the Faculty of Science, Technology and Environment at the University of the South Pacific provided funds to enable this study and the radiocarbon dating it involved. Discussions with Dr Frank Thomas, Dr Susanne Pohler, Roselyn Kumar and Ledua Kuilanisautabu were helpful.

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Captions for figures

Figure 1. Map of the western tropical Pacific showing the main island groups. Archaeologists commonly divide the region into Near Oceania and Remote Oceania, the former characterized by larger higher islands closer together with greater terrestrial biodiversity than the latter. The Lapita culture began in the Bismarck Archipelago of Papua New Guinea and spread eastwards beginning about 1330 BC reaching its maximum extent with outposts in Tonga and Samoa about 900 BC. Blue arrows show likely migration routes.

Figure 2. The earliest (Lapita-era) human settlements in Fiji are on the Rove Peninsula, southwest Viti Levu Island (after Nunn, 2009; Nunn et al., 2006). The founder settlement is believed to have been established at Bourewa about 1100 BC; that at Qoqo within the following century. Bourewa and Qoqo are the only two stilt-house settlements known from Fiji and these appear to have been positioned to allow optimal access to nearshore marine resources.

A. The modern geography of the Rove Peninsula showing the uncommonly broad fringing coral reef along its southwest side. At the time of its human colonization about 1100 BC, the Rove Peninsula was an island 1-2 km off the shore of larger Viti Levu Island.

B. Environmental reconstruction of the Qoqo area 1000 BC (after Nunn et al., 2006). Even though the area around Qoqo is now covered with mangrove forest, midden evidence suggests that at the time the Lapita people established their stilt-house settlement on a tombolo, the

area was fringing reef. Note that since the time of this reconstruction, sea level has fallen a net 1.5 m resulting in the emergence of the tombolo.

- C. Environmental reconstruction of the Bourewa area 1100 BC (after Nunn, 2009). An undersea sand ridge is occupied by people living in stilt houses, a location that allowed access to both reef foods and those of a tidal (non-reefal) inlet. The earliest stilt-house occupation is shown (see also Figure 4) as is the maximum extent of the settlement (about 550 BC). Note that since the time of this reconstruction, sea level has fallen a net 1.5 m resulting in the drying up of the inlet and emergence of the sand ridge.

Figure 3. Weight and morphometric analysis of *H. hippopus* valves found at the Bourewa and Qoqo sites; raw data in Table 1.

- A. Valve-weight distribution.
- B. Plot of weight against depth.
- C. Plot of height against depth.

Figure 4. Distribution of *H. hippopus* in the central part of the Bourewa site. Pits in which specimens were found are outlined in bold. All other pits excavated are shown. The distribution of postholes found in excavations is also shown. The greatest density of postholes is equated with the reconstructed form of stilt-house platforms, shaded in this map, which represent the earliest phase of settlement. Note how the finds of *H. hippopus* are associated with these platforms, suggesting (independently of the

radiocarbon dates) that this species was associated exclusively with the earliest period of settlement here.

Figure 5. Analysis of radiocarbon ages of the nine specimens of *H. hippopus* from Bourewa (details in Table 2).

- A. Plot of median age against depth.
- B. Plot of valve width against median age.
- C. Plot of valve weight against median age.
- D. Plot of valve height against median age.

Captions for tables

Table 1. Morphological characteristics of individual *H. hippopus* valves from shell middens at Bourewa and Qoqo (Rove Peninsula).

Table 2. Radiocarbon dates for specimens of *H. hippopus* from Bourewa. All dates from the University of Waikato Radiocarbon Dating Laboratory corrected using marine correction factor (δR) of 43 ± 12 years (Hughen et al., 2004) and calibrated using OxCal v3.10 (Bronk-Ramsey, 2005).

Figure 1



Figure 2



Figure 3

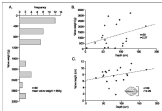


Figure 4

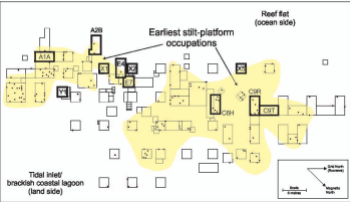


Figure 3

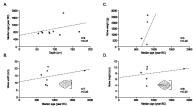


Table 1. Morphological characteristics of individual *H. hippopus* from Bourewa and Qoqo.

A. Midden samples (n=47)

Site	Pit	Depth (cm)	Length (cm)	Width (cm)	Height (cm)	Estimated weight of one valve (g)
Bourewa	X5	5	6.2	5.6	nr	70
Bourewa	E2	17	nr	nr	nr	nr
Bourewa	E2	18	nr	nr	nr	nr
Bourewa	E2	21	nr	nr	nr	nr
Bourewa	E2	22	nr	nr	nr	nr
Bourewa	E2	25	nr	nr	nr	nr
Bourewa	E2	26	nr	nr	nr	nr
Bourewa	E2	27	nr	nr	nr	nr
Bourewa	E4	28	18.7	14.5	6.9	530
Bourewa	E2	30	nr	nr	nr	nr
Bourewa	E2	46	nr	nr	nr	nr
Bourewa	E6	47	17.6	18.2	8.8	1000
Bourewa	E10	47	nr	nr	nr	nr
Bourewa	E6	48	18.7	9.4	7.4	1000
Bourewa	E6	50	23.7	15.4	7.8	1200
Bourewa	C22A	54	nr	nr	nr	nr
Bourewa	E5	54	nr	nr	nr	nr
Bourewa	C6H	55	nr	nr	nr	nr
Bourewa	E10	55	26.3	19.3	8.9	2100
Bourewa	X1	55	5.6	6.4	nr	95
Bourewa	A2A	56	nr	nr	nr	nr
Bourewa	E10	56	24.5	16.2	8.8	800
Bourewa	E5	59	17.6	11.6	5.8	500
Bourewa	A1A	65	10.5	8.1	nr	nr
Bourewa	C9T	65	31.9	21.1	9.3	2928
Bourewa	E7	65	10.5	7.8	3.6	110
Bourewa	E2	66	nr	nr	nr	nr
Bourewa	BS2	78	17.9	15.3	7.5	nr
Bourewa	E4	83	nr	nr	nr	nr
Bourewa	E6	84	5.6	3.6	1.7	51
Bourewa	E4	85	nr	nr	nr	nr
Bourewa	Y1	85	16.4	11.5	6.1	nr
Bourewa	E1	88	24.5	14.4	9.3	2200
Bourewa	E7	97	31	20.6	10.1	2600
Bourewa	X2	105	7.9	12.3	nr	250
Bourewa	E6	106	14.6	11	6.3	498
Bourewa	E6	113	nr	nr	nr	nr
Bourewa	E7	115	22.8	14.9	8.1	680
Bourewa	E6	116	17.8	8.8	7.8	910
Bourewa	E2	117	nr	nr	nr	nr
Bourewa	E6	117	nr	nr	nr	nr
Bourewa	E6	119	nr	nr	nr	nr
Bourewa	C9R	125	23	18	9.4	nr
Bourewa	E6	127	21.5	13.4	11.3	3200
Bourewa	E2	133	nr	nr	nr	nr
Qoqo	F1A	135	5.6	9.2	nr	nr
Qoqo	F1B	165	3.6	5.4	nr	nr
Bourewa	A2B	170	23.7	17.9	9.4	2050

B. Samples from surface collection (n=16)

Site	Pit	Depth (cm)	Length (cm)	Width (cm)	Height (cm)	Estimated weight of one valve (g)
Bourewa	sc	na	12.1	8.3	3	142.2
Bourewa	sc	na	12.5	8.7	3.2	144.8
Bourewa	sc	na	12.3	8.5	3.7	151.2
Bourewa	sc	na	12.4	8.7	3.6	159.8
Bourewa	sc	na	12.5	8.8	4	217.8
Bourewa	sc	na	12.5	8.8	4.1	232.4
Bourewa	sc	na	12.7	9	4.5	378.7
Bourewa	sc	na	14.1	9.2	4.4	409.6
Bourewa	sc	na	15.3	11.6	5.3	439.4
Bourewa	sc	na	19.1	13.4	6.4	742
Bourewa	sc	na	21	12.9	6.4	911
Bourewa	sc	na	19.1	13.7	6.5	1092.9
Bourewa	sc	na	19.2	14.9	6.7	1129.6
Bourewa	sc	na	23.2	16.9	7.6	1714
Bourewa	sc	na	24.1	17.5	7.5	1882.2
Bourewa	sc	na	26.7	18.6	7.6	2100

nr = not reconstructable

sc = surface collection

na = not applicable

Table 2. Radiocarbon dates for specimens of *H. hippopus* from Bourewa. All dates from the University of Waikato Radiocarbon Dating Laboratory corrected using marine correction factor (δR) of 43 ± 12 years (Hughen et al., 2004) and calibrated using OxCal v3.10 (Bronk-Ramsey, 2005).

<i>Pit</i>	<i>Sample</i>	<i>Laboratory number</i>	<i>Depth (cm)</i>	$\delta^{13}C$	<i>Conventional radiocarbon age (BP)</i>	<i>Calibrated radiocarbon age (cal BP)</i>	<i>Calendar age</i>
C9R	Bourewa C9R/125	Wk-23225	125	2.7 \pm 0.2	3899 \pm 40	3950-3680	2000-1730 BC
E7	Bourewa E7/97	Wk-28029	97	2.9 \pm 0.2	3027 \pm 40	2860-2680	910-730 BC
A2B	Bourewa A2B/170	Wk-23226	170	2.9 \pm 0.2	3016 \pm 39	2850-2670	900-720 BC
E4	Bourewa E4/85	Wk-28027	85	3.1 \pm 0.2	3005 \pm 39	2840-2660	890-710 BC
E7	Bourewa E7/65	Wk-28030	65	2.9 \pm 0.2	2994 \pm 40	2840-2650	890-700 BC
Y1	Bourewa Y1/85	Wk-23222	85	3.0 \pm 0.2	2997 \pm 38	2840-2650	890-700 BC
A1A	Bourewa A1A/65	Wk-23223	65	3.0 \pm 0.2	2985 \pm 36	2830-2610	880-660 BC
C6H	Bourewa C6H/55	Wk-23224	55	2.8 \pm 0.2	2963 \pm 39	2790-2540	840-590 BC
E7	Bourewa E7/115	Wk-28028	115	2.7 \pm 0.2	2884 \pm 39	2720-2450	770-500 BC