

Shellfishing and the Colonization of Sahul: A multivariate model evaluating the dynamic effects of prey utility, transport considerations and life-history on foraging patterns and midden composition

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Citation: Codding, Brian F., James F. O'Connell and Douglas W. Bird (2014) Shellfishing and the Colonization of Sahul: A multivariate model evaluating the dynamic effects of prey utility, transport considerations and life history on foraging patterns and midden composition. *Journal of Island & Coastal Archaeology* 9(2):238–252.

Abstract. Archaeological evidence of shellfish exploitation along the coast of Sahul (Pleistocene Australia-New Guinea) points to an apparent paradox. While the continental record as a whole suggests that human populations were very low from initial colonization through early Holocene, coastal and peri-coastal sites dating to that time are dominated by small, low-ranked littoral taxa to the near-complete exclusion of large, higher ranked sub-littoral species, precisely the opposite of theory-based expectations, if human populations and predation rates were indeed as low as other data suggest. We present a model of shellfish exploitation combining information on species utility, transport considerations and prey life-history that might account for this apparent mismatch, and then assess it with ethnographic and archaeological data. Findings suggest either that high-ranked taxa were uncommon along the Pleistocene coastlines of Sahul, or that abundant and commonly taken high-ranked prey are under-represented in middens relative to their role in human diets largely as a function of human processing and transport practices. If the latter reading is correct, archaeological evidence of early shellfishing may be mainly the product of subsistence activities by children and their mothers.

Keywords: Shellfish Exploitation | Colonization of Sahul (Australia/New Guinea) | Children's Foraging | Division of Labor | Human Behavioral Ecology

Introduction

Archaeological evidence of early shellfish collecting on Sahul (Pleistocene Australia-New Guinea) points to an apparent paradox. While theoretical predictions from foraging theory lead to the expectation that the earliest foragers on the continent would have encountered abundant large high-ranking shellfish taxa offering relatively high average rates of nutrient return relative to time spent collecting and processing, archaeological data from coastal shell middens indicate that foraging emphasized smaller, much lower ranked shellfish taxa. There are at least three plausible explanations for this pattern:

1. Rapidly changing Pleistocene sea levels kept the abundance of large, high-ranked, slow-growing taxa low, leaving foragers no option but to pursue smaller, lower ranked prey (Beaton 1995).
2. Early human populations were much higher than previously thought, placing sustained

collecting pressure on high ranked prey which rapidly reduced their numbers, leaving only an ephemeral archaeological signature.

3. Transport considerations favored the differential discard of inedible components of relatively high ranked prey at or near the point of acquisition, leaving little or no evidence of their use in base camp middens. The material signature of lower-ranked taxa may then be the result of foraging by children, who experience lower encounter rates with large prey due to their slower walking speed (Bird et al. 2004), and by their mothers, who may be more interested in low-risk than high-energy resources for provisioning young (Codding et al. 2011).

Resolving this issue is crucial to understanding the process through which Sahul was colonized and the early foraging decisions of individuals on a previously unoccupied landscape (O'Connell and Allen 2012). Here we address the problem with a novel model that examines prey utility, transport considerations and life-history. Combined, this approach may better predict both resource exploitation patterns and their archaeological consequences. We assess the model in light of ethnographic and ethnoarchaeological data, then consider its implications for understanding the record of early shellfish exploitation in Sahul.

The Model

Our model is based on well-established ideas about prey choice, central place foraging and life history. These allow us to make predictions about which resources will be more (or less) likely to be targeted, which will be more (or less) likely to be represented in archaeological deposits created by central place foragers, and which will be more (or less) resilient to predation pressure or environmental change.

The prey choice model (PCM) allows the derivation of simple predictions about which

species are more likely to be pursued on encounter (Bettinger 2009, Bird and O'Connell 2006, Charnov and Orians 2006). When searching a patch, a forager will encounter a variety of different resources. If foragers are trying to maximize the rate of nutrient acquisition, then they should preferentially pursue resources with higher post-encounter return rates (e/h), measured as the expected nutrients (e) gained from acquiring a resource (typically measured as energy) over the handling costs (h) associated with pursuing and processing that resource (typically measured in time). If higher ranking resources are sufficiently abundant, then foragers should only take those resources on encounter, passing up all other lower ranking resources; however, as the abundance of the highest ranking resources decline, foragers should begin to take lower ranking resources in rank order. From a forager's perspective, the question is: should I pursue this resource, or pass it up and continue searching for other, higher-ranked resources? The answer depends on whether the post-encounter return rate (e/h) for that resource is expected to increase the overall return rate (E/T) which includes all energy acquired in a patch (E) relative to all in-patch search and handling time (T). These model dynamics allow the derivation of predictions about which taxa a forager should preferentially pursue and a proxy for overall foraging efficiency based on the presence or absence of lower-ranking resources.

Central place foraging models (CPF) allow the evaluation of the costs and benefits of field processing resources or transporting them whole from an acquisition locale to a central place (Bettinger 2009, Charnov and Orians 2006, Metcalfe and Barlow 1992, Orians and Pearson 1979). Once a forager has acquired a resource, they must make decisions about how to best transport that resource to a central place. Assuming that individuals are attempting to maximize the rate at which resources are delivered to a central place, foragers may be better off culling low utility items (i.e., shell or bone) in the field and returning to their central place with only high util-

ity parts (i.e., meat) than making a greater number of trips transporting both high and low utility parts. Assuming constant processing costs across taxa, the net gain in utility as a function of processing (the increase in high utility parts per load) can predict which items are more likely to be field processed at a given distance from a central place. Given that individual shellfish have an edible portion (meat) and a non-edible portion (shell), meat:shell ratios provide a reliable proxy of the potential benefit gained from culling shell in the field, thereby increasing the utility of each load returned home. Those taxa with higher proportions of meat to shell are less likely to be field processed while those with low meat:shell ratios are more likely to be processed in the field. Because larger taxa generally have lower meat:shell ratios and require lower processing costs than smaller taxa (e.g., Bird et al. 2002), these predictions likely hold with the inclusion of processing costs.

Life history models (LFM) provide avenues to investigate variability in the parameters that govern individual growth, maturation, reproduction and mortality, which aggregate to produce population level effects. Because different taxa have different life-history characteristics, they should respond differently to human exploitation, which in turn, will alter a forager's future encounter rates. With invertebrate taxa, life-history parameters such as growth and maturation rates should provide a reliable proxy of the relative susceptibility of a taxon to overexploitation. Likely the result of natural selection (Gadgil and Bossert 1970), the rate of maturation covaries with a number of life-history parameters and can be a predictor of population level parameters (Peters 1983). As such, rates of maturation for individual taxa should provide a relative measure of the likelihood or speed at which a population could recover from exploitation (Whitaker 2008, Whitaker and Byrd 2012). Due to the effects of biological scaling and allometry, body size and post-encounter return rates (at least, for sessile resources, see Bird et al. 2009) should co-vary positively while body size,

meat:shell ratios and maturation rates may covary negatively (Peters 1983). This could be problematic as high ranking resources may be more likely to be processed in the field, but if particular taxa exist as outliers in these relationships (i.e., high ranking, slow-growing but high meat: shell ratios), they should provide key proxies to monitor changes in foraging patterns through time.

Combined, these models allow us to make predictions about which species should be preferentially pursued, which should be more or less likely to end up in archaeological sites and which are more or less likely to be depleted by predation. Following O'Connell (1995), these models can be used to derive specific deductive predictions that can be tested with ethnographic, ethnoarchaeological and archaeological data. Because these predictions are derived from a general theory of behavior, they avoid direct ethnographic analogy.

Predictions

Imagine a parameter space represented by three variables: shellfish utility (e/h , on the Figure 1: y-axis), transport costs (operationalized by meat:shell ratios, Figure 1: x-axis) and susceptibility to overexploitation (measured here through the proxy of maturation rates). How different shellfish taxa fall out within this parameter space should allow us to identify target taxa that will allow us to investigate foraging behavior, midden composition and how they are expected to change over time.

Taxa with very low meat:shell ratios (Figure 1: frame a) should rarely appear in middens due to the low net utility of a load returned to a central place with such a large amount of shell relative to a limited amount of meat. If shellfish rank varies inversely with meat:shell ratios, then evidence for the exploitation of high ranking taxa is unlikely to be recovered from archaeological deposits as their shells should be culled in the field even over short transport distances. This is the case for many molluscan species from this region (Bird and Bliege Bird 2000).

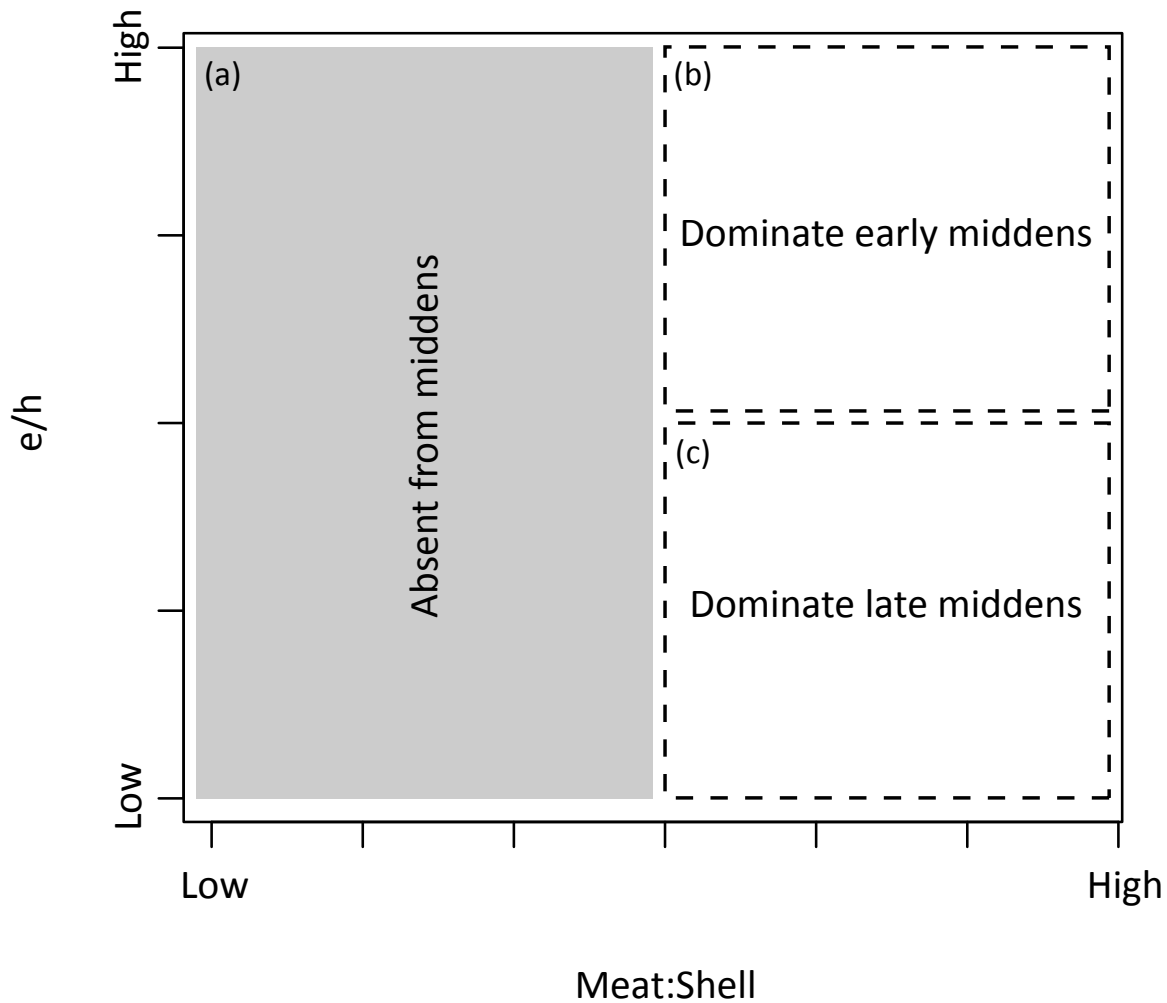


Figure 1: Figure 1. Schematic predictions of midden composition based on the combined effects of each taxon's post-encounter return rate (e/h), and likelihood of field processing (meat:shell ratio). Taxa with low meat:shell ratios (frame a) are less likely to end up in middens as their shells should be frequently culled in the field (unless if the shell itself provides some value). Early middens should be dominated by higher ranking taxa with relatively high meat:shell ratios (frame b). If these become less abundant in the environment due to overexploitation, then foragers should begin to take lower ranking resources which will come to dominate later middens (frame c). The rate of transition in midden dominance from $b \rightarrow c$ depends on the life-history characteristics of the taxa in question: fast growing species should be harder to deplete while slow growing species rapidly decline in abundance. Note: these values are in dimensionless space.

High ranking taxa with high meat:shell ratios (Figure 1: frame b) should always be taken on encounter by foragers and are likely to always be transported whole to the central place. As such, these taxa should dominate early middens. Those with slow maturation rates should be the best source to monitor the effects of resource overexploitation through time. Those that mature early are likely to be fairly resilient to over-exploitation and may dominate middens throughout the prehistoric record.

Lower-ranked taxa with high meat:shell ratios (Figure 1: frame c) should come to dominate later middens if higher ranking resources become less abundant due to overexploitation. Those that take longer to mature will be particularly useful to monitor human foraging and population pressure over time. Those that are relatively resilient to over-exploitation (rapid growth rates and short maturation rates) should dominate later shell middens (and shell mounds) following declines of the highest ranking resources (e.g., Whitaker and Byrd, this issue).

Results

Resource-Specific Attributes

Table 1 provides a summary of available data on shellfish genera post-encounter return rates (e/h), meat:shell ratios and age at maturity for taxa potentially exploited by the earliest inhabitants of Sahul. Mean values are also represented in Figure 2 following the layout of predictions in Figure 1.

The two large bivalves, *Tridacna* and *Hippopus*, would be excellent candidates to monitor foraging pressure given their high rank and slow growth rates. However, given their low meat:shell ratios, they are unlikely to be transported to midden deposits proportionally to the frequency with which they are taken. This expectation is supported by ethnoarchaeological studies indicating that the material record of *Tridacna* and *Hippopus* underrepresent the frequency with which they are actually acquired (see below, Bird and Bliege Bird 2000, Bird et al. 2002).

Table 1: Proxy data for shellfish utility (e/h), transport cost (meat:shell) and susceptibility to overexploitation (age at maturity), ordered by mid-point return rate (e/h).

Taxon	e/h (kcal/hr)	Meat:Shell Ratio	Age at Mat. (yr)
<i>Tridacna</i>	2,622-13,064	0.170	4-5
<i>Hippopus</i>	1,680-9,120	0.115	6-7
<i>Lambis</i>	3,412-5,106	0.092	2
<i>Trochus</i>	977-3,904	0.208	1-2
<i>Cypraea</i>	2,214	0.278	1
Chiton	446-2,228	1.159	1-2+?
<i>Nerita</i>	42-1,106	0.301	1.6
<i>Turbo</i>	520-606	0.248	3-4
<i>Strombus</i>	294-543	0.148	1-2
<i>Asaphis</i>	42-78	0.338	1-2

Data on shellfish returns from Bird and Bliege Bird (2000), Bird et al. (2004), Kennedy (2005) and Thomas (2007); on meat:shell ratios from Bird and Bliege Bird (1997), Erlandson (1988); on age at maturity from Beesley et al. (1998), Munro (1993), Nash (1993) and Yamaguchi (1993).

Unfortunately, within the suite of resources available to the earliest colonists of Sahul (and for which data are currently available), there are no species that can be considered high-ranking with high meat:shell ratios (i.e., falling within parameter space b in Figure 1). Evidence from North America suggests that Abalone (*Haliotis* spp.) likely falls within this region of the parameter space (Kennedy 2005), but conclusive data on Austral species are lacking. The absence of species within this parameter space suggests that efficient tidal foraging in Sahul required field processing. As a result, we are unlikely to acquire an unbiased picture of the prehistoric exploitation of these higher ranking taxa.

With relatively low returns but high meat:shell ratios, small gastropods such as *Nerita* and small bivalves like *Asaphis* also have rapid maturation rates, suggesting they are resilient to overexploitation. As we would predict, these taxa dominate modern middens within permanent villages in the Torres Strait Islands, Australia and Western Kiribati, Micronesia where sustained foraging pressure does not seem to diminish their pop-

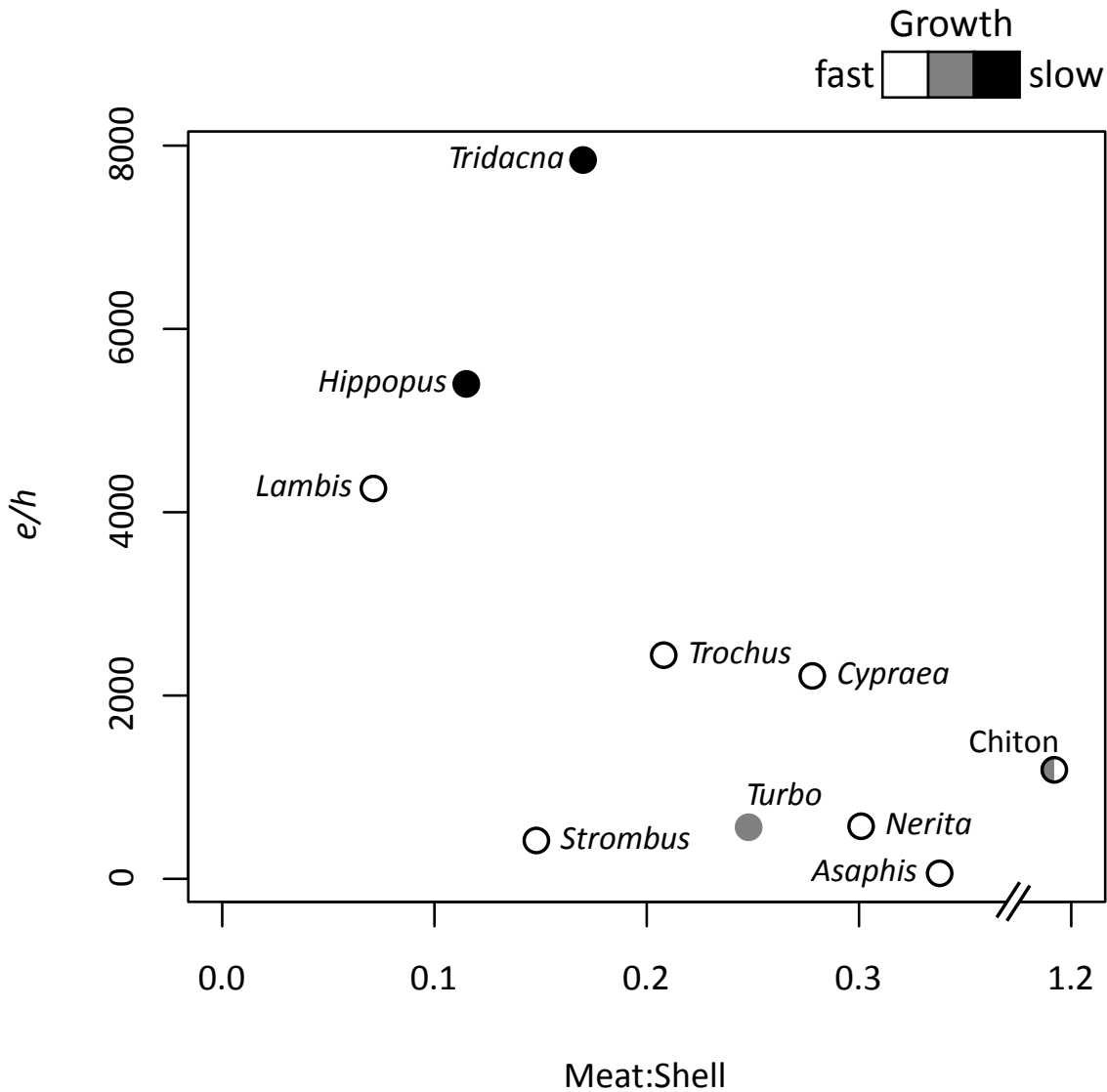


Figure 2: Shellfish genera plotted as a function of post-encounter return rate (e/h) and meat:shell ratios following predictions in Figure 1. Shading indicates growth rates measured by time till maturity from short (white) to long (black). Genera plotted by mid-point values of ranges given in Table 1.

ulations (Bird et al. 2002, Thomas 2007). As these taxa should be resilient to overexploitation, their abundance is unlikely to vary with human foraging and population pressure over time.

The moderately sized gastropod *Turbo* provides a welcome exception: with relatively long times to maturity and high meat:shell ratios, we should expect that *Turbo* will be exploited when the abundance of higher ranking resources are low, and should be one of the first taxa within this lower-ranked set to exhibit overexploitation. As such, diachronic trends in the exploitation of *Turbo* should provide a key proxy to understand foraging pressure on shellfish species, and as such, a proxy for human population densities. With by far the most extreme meat:shell ratio, chiton (class Polyplacophora) may also fall within this category. Larger species of chiton are likely to have higher return rates and slower maturation rates, while still maintaining relatively high meat:shell ratios; unfortunately, precise data are not available for Austral species. Based on observations of Meriam shellfishers by one of the authors (DWB), limited data on chiton exploitation by contemporary foragers may result from low encounter rates with larger chiton coupled with consistent decisions to pass over smaller chiton in search of more profitable taxa.

An Ethnographic Test

Previous ethnoarchaeological investigation with Meriam Islanders in the Torres Strait explored the archaeological consequences of trade-offs that shellfishers face in acquiring, handling, and transporting a number of the taxa that Pleistocene foragers would have likely encountered on colonizing Sahul (Bird 1996, Bird and Bliege Bird 1997, 2000; Bird et al. 2002, 2004). Consistent with expectations framed by the prey choice model (PCM), Meriam restrict the suite of taxa they handle on encounter to those shellfish that will increase overall foraging efficiency (E/T) while collecting on the reef flat or harvesting within the rocky shore. For example, while reef flat collecting, foragers routinely select exposed tridacnid clams (*Tridacna* spp. and *Hip-*

popus hippopus), *Lambis lambis* conch, and large *Trochus niloticus* specimens, all of which significantly increase overall foraging return rates if handled on-encounter. Conversely adult shellfishers almost always pass over specimens that offer returns for time handling that will reduce foraging efficiency: small *Strombus (Conomurex) luhuanus* conch, small *Trochus*, and small bivalves embedded in the reef. Meriam also pay close attention to changes in patch return rates while intertidal foraging, and switch from reef flat collecting to rocky shore harvesting (for *Asaphis violascens* clams and *Nerita* spp. snails) when an incoming tide depresses the overall return rate from collecting in the mid-littoral below that expected from harvesting in the near shore.

While observed time allocation and selectivity are consistent with predictions generated by the PCM and patch residence models, they are in sharp contrast to the frequency of different taxa of shellfish found in either contemporary or prehistoric shellmiddens on the Meriam Islands. The most important resources for contemporary collectors (especially large tridacnids and *Lambis lambis*) are very rare in the archaeological deposits, which are dominated by small gastropod shells (especially nerites, small strombids, and small *Trochus niloticus*; Bird et al. 2002). We can account for these differences by considering the effects of differential field processing and age-linked differences in foraging returns. While reef flat collecting, children walk slower and encounter high ranked resources at a lower rate than adults, resulting in lower overall return rates and a predictably broader range of selectivity that includes the smaller gastropods. So while both adults and children collect the higher ranked shellfish on-encounter, only children regularly collect the abundant small strombids and small specimens of *Trochus niloticus* that are common in the shell middens. But why are tridacnid and *Lambis* shell, which make up the bulk of shellfish harvested, so rare in the deposits? If we consider how time spent field processing can increase the ratio of high to low util-

ity parts (meat:shell), the central place foraging model discussed above generates precise predictions about which types of molluscs should be field processed if a forager's goal is to increase the rate at which shellfish meat can be transported home. The model well anticipates the fact that Meriam foragers almost always cull the shells of large tridacnid clams and *Lambis* conch while on the reef. These shellfish offer high post-encounter return rates and have low meat:shell ratios, and thus field processing quickly frees up more space for more meat, and more time for more foraging and transport. As such, Meriam adults and children commonly forage well beyond the predicted thresholds at which in-bulk transportation (without culling the valves) of these large shellfish will increase the home delivery rate of meat. Conversely, the smaller reef flat shellfish that children often collect, along with rocky shore taxa such as *Asaphis* and *Nerita* that both adults and children harvest, are always transported in-bulk, and foragers very rarely cross the predicted field processing thresholds while collecting these prey. We suspect that Pleistocene foragers would have faced similar trade-offs when shellfishing in intertidal zones.

Early Middens in Sahul

Data are available for at least six Pleistocene middens (coastal and peri-coastal sites yielding marine shell) with dates older than 30kya. Buang Merabak (Leavesley and Allen 1998, Rosenfeld 1997) and Matenkupkum (Gosden and Robertson 1991) are located on New Ireland, Kilu (Wickler 2001) on the northern end of the Solomon Islands and Noala Cave (Veth et al. 2007), Mandu Mandu Creek (Morse 1988), and Devil's Lair (Dortch 2004) are located along the coast of modern day Western Australia.¹ For more detailed summaries on the dating of each site, see Allen and O'Connell (2003, 2008), O'Connell and Allen (2004, 2007, 2012) and

¹Early middens (pre-30kya) for which data were unobtainable include other sites along the Cape Range of northwestern Australia (Przywolnik 2008, Morse 1988, Morse 1993).

O'Connell et al (2010). Evidence for shellfish exploitation at many of these sites is extremely sparse; nonetheless, the available data allow us to run an initial test of these predictions.

Higher ranking species with low meat:shell ratios are rare in these early middens. At Buang Merabak, chiton, *Turbo* and *Nerita* dominate the Pleistocene assemblage (Leavesley and Allen 1998). At Kilu, *Nerita* dominates assemblages dating before the Late Holocene (Wickler 2001). At Matenkupkum, Gosden and Robertson (1991) report extremely large *Turbo* shells, indicating the exploitation of lower ranked taxa, but assuming that human predation will drive down shellfish size (e.g., Klein and Steele 2013) only limited predation pressure on these taxa. While *Tridacna* is absent from the faunal assemblages recovered from these early levels, Leavesley and Allen (1998) report that large *Tridacna* shells and *Turbo* opercula, originally recorded as white chert, were used to manufacture tools at Buang Merabak. This suggest that these taxa were taken on encounter, likely for their food and shell, but only transported and deposited within midden contexts for purposes relating to the latter. This also suggests that such high-value shell might be secondarily transported away from middens for subsequent use, a pattern that may further bias such a taxon's representation in the archaeological record.

At peri-coastal sites along the shore of modern day Western Australia, shellfish taxa are dominated by different genera specific to the local environment; but even so, the taxa exploited at these sites share characteristics with those exploited in the Bismarks. At Noala Cave on the Monte Bello Islands, foragers were exploiting a variety of whelks (*Terebralia*, Veth et al. 2007), which are expected to be low ranked. Perhaps at odds with findings elsewhere, the earliest layers at Mandu Mandu Creek reveal chiton and baler (*Melo*) (Morse 1988). While precise data on these taxa are not yet available, what we know suggests that they may be relatively high ranked with high meat:shell ratios (Figure 1, frame b). If these were large chiton and *Melo*, this evi-

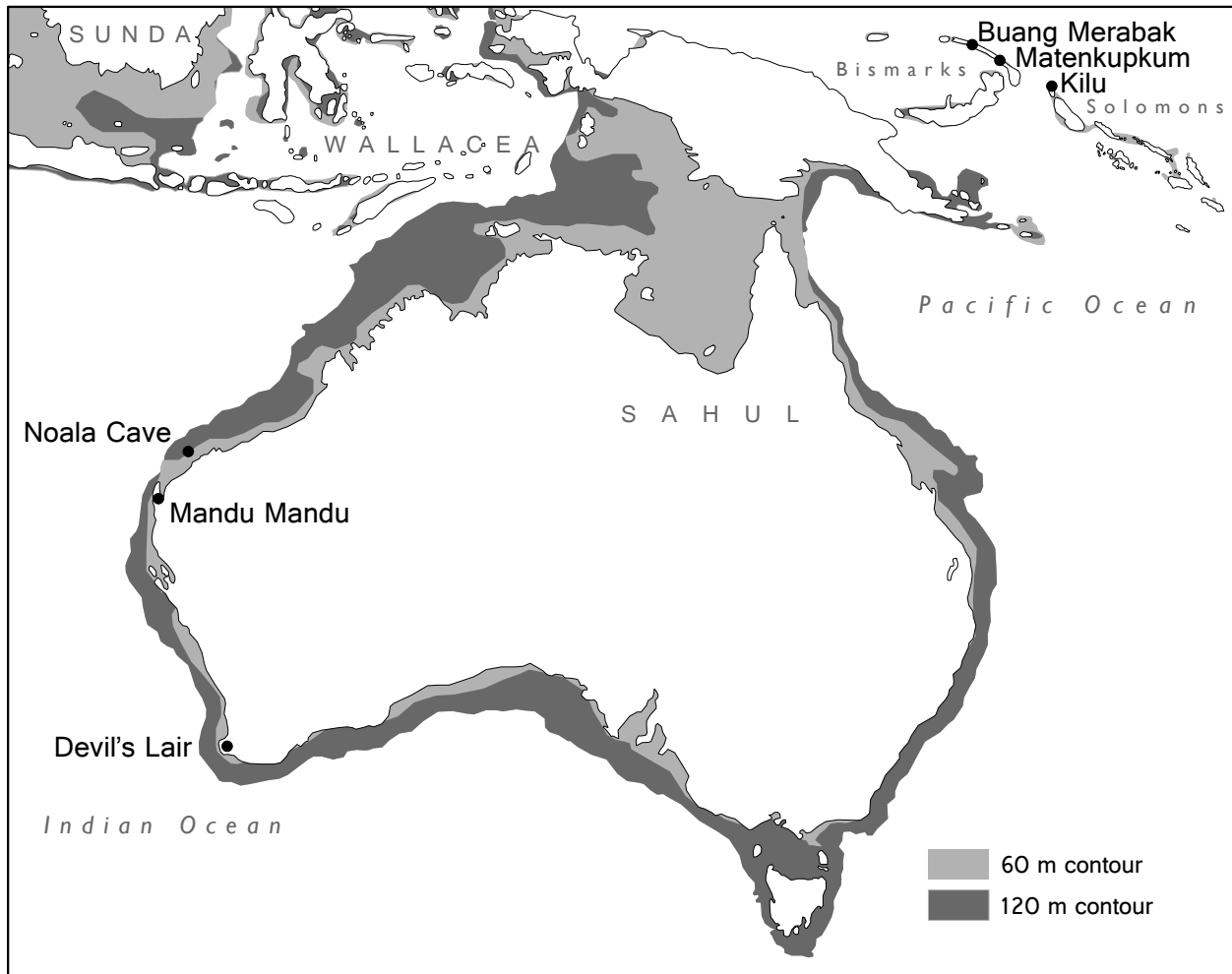


Figure 3: Map of coastal and peri-coastal archaeological sites with evidence of marine shell exploitation prior to 30kya.

dence for the exploitation of high-ranking taxa during this interval supports the idea that large, high-ranking taxa were present, pursued on encounter, but only transported to central places when meat:shell ratios were high or when the shells has some added value. This might also be true in the southwestern corner of the continent, where small fragments of abalone (*Haliotis*) are some of the only taxa represented in the early levels at Devil's Lair (and at Tunnel Cave; Dortch 2004; J. Dortch, personal communication 2013). Abalone too likely falls within the parameter space shown in Figure 1, frame b representing high-rank and high meat:shell ratios, leading us to expect that it will often be transported whole. The additional value of abalone shell for ritual, ornamental or other purposes beyond subsistence likely increase the probability that it will often be transported whole. This is consistent with finds at Carpenter's Gap, where early levels contain pearl shell (O'Connor 1999).

Diachronic Trends at Buang Merabak

Temporal trends from the well reported finds at Buang Merabak can further our understanding of these patterns. As predicted from our model, while we should not expect high-ranking, low meat:shell taxa to be deposited at central places, we should be able to monitor the abundance of *Turbo* and chiton through time as an indicator of foraging pressure.

As evident in Figure 4, the temporal trends at Buang Merabak show a significant decline in the proportion of *Turbo* ($\tau = 17.6, p = 0.0361$) and a marginally significant decline in the proportion of chiton ($\tau = 4.2, p = 0.1498$) through the Pleistocene. These are mirrored by a marginally significant increase in *Nerita* ($\tau = 7.0, p = 0.0905$).² Such patterning has also been reported at Kilu (Wickler 2001). While significant, declines in the relative abundance of *Turbo* and chiton occur over a long span of time, suggesting that it

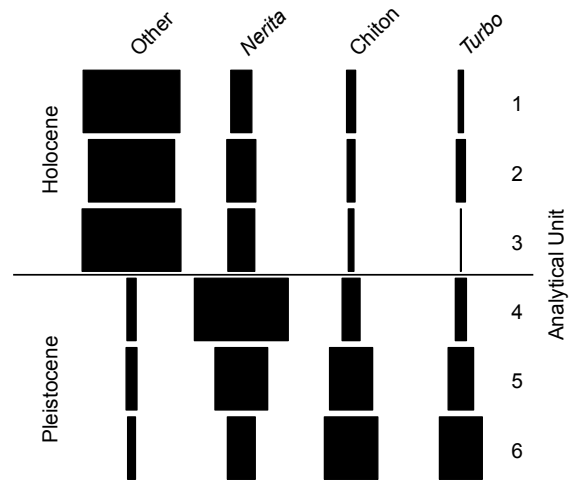


Figure 4: Battleship plot showing the proportion of total weight per analytical unit for important Pleistocene shellfish taxa at Buang Merabak. Data from Leavesley and Allen (1998), shown here in Table 2. Based on radiocarbon dates from Rosenfeld (1997), analytical unit 6 (2-sigma range 38,090-34,523 cal BP), 5 (24,141-22,505 cal BP) and 4 (24,782-23,356 cal BP) date to the Pleistocene, while analytical units 3, 2 and 1 all date to the Holocene (2-sigma ranges calibrated in OxCal 4.2.2, Bronk Ramsey 2009, using a marine curve from Reimer et al. 2009 and local correction by Petchey et al. 2004). The two most abundant taxa in the earliest Pleistocene deposits (*Turbo* and chiton) are also relatively slow growing. Their overexploitation through the Pleistocene is mirrored in the rising dominance of faster-growing *Nerita*. Discontinuity between the Pleistocene-Holocene record is likely due to sea level stabilization at distances closer to the site (see Lambeck and Chappell 2001).

²Pearson's correlation analyses run in R (R Development Core Team, 2013). Figure 4 produced using the battleship.plot function in the plotrix library.

Table 2: Shell weight (g) by taxa across chronological analytical units at Buang Merabak.

Taxa	1	2	3	4	5	6
<i>Cypraea</i>	90.6	223.0	16.6	0.0	0.0	13.6
<i>Strombus</i>	34.2	62.8	1.2	0.6	0.0	0.0
<i>Isognomon</i>	15.3	66.1	4.7	0.0	0.0	0.0
<i>Trochus</i>	41.4	153.0	83.8	23.9	12.5	9.3
Barnacle	50.0	136.9	797.9	8.9	0.9	2.0
Limpet	7.8	26.5	33.3	24.2	0.5	0.0
<i>Nerita</i>	52.7	226.0	258.0	1398.4	122.0	265.8
<i>Tectarius</i>	2.5	3.1	11.3	79.2	11.3	49.9
Chiton	22.6	61.0	53.9	267.3	99.7	509.4
<i>Turbo</i>	13.1	71.1	7.9	165.5	58.9	408.9

From Balean (1989) reported in Leavesley and Allen (1998), see also Rosenfeld (1997). Given their high meat:shell ratio, chiton likely contributed more to the early diets than is represented by shell weight alone (Leavesley 2004).

took most of the Pleistocene record before human populations were high enough to place consistent pressure on these taxa. This interpretation is supported by the radiocarbon probabilities from Buang Merabak which suggest intermittent occupations (Figure 5a) and occupational estimates from neighboring Australia, which suggest very low populations levels during this time (Figure 5b; Williams 2013). These findings suggest that Pleistocene occupations at Buang Merabak were intermittent, perhaps covarying negatively with the distance to the coast (cf., Figure 5a and 5c), and were always at a low densities.

Discussion

This paper began with a conundrum: the archaeological record suggests that the earliest colonizing populations of Sahul disproportionately exploited low-ranked littoral shellfish species, despite theoretical predictions to the contrary. While a number of hypotheses could be proposed to explain this conundrum, we suggest that these can be assessed by incorporating models of prey efficiency, transport utility and life-history to predict the targets of foraging, the resulting midden composition and the potential impact of human foraging on shellfish species. In light of our model, the conundrum actually makes sense:

high-ranking shellfish taxa available to the early foragers of Sahul had low meat:shell ratios (Figure 1: frame b). As it would not make economic sense to transport shell from these taxa (unless if the shell itself had some added value; e.g., Leavesley and Allen 1998), we should not expect middens to contain shell from these taxa. But what then accounts for the deposition of lower ranking littoral shellfish species?

Given the extremely low estimated population levels and intermittent occupation of sites like Buang Merabak, it seems unlikely that the acquisition and deposition of low-ranked taxa was due to overexploitation of higher ranking taxa. If the abundance of these larger high-ranked species declined rapidly, then we might have evidence for a larger colonizing population placing more pressure on resources than traditionally assumed. However, given the long period of time that passed before human populations reached densities required to overexploit fairly slow growing taxa like *Turbo*, we suggest that human population densities were quite low, their mobility quite high, and as such, they placed minimal predation pressure on the littoral environment. Combined with evidence for the rapid dispersal of peoples along the coastlines of Sahul, this implies that it takes very little impact to make adjacent, unoccupied patches more appealing to foraging populations (O'Connell and Allen 2012).

It still could be that these taxa occurred in low

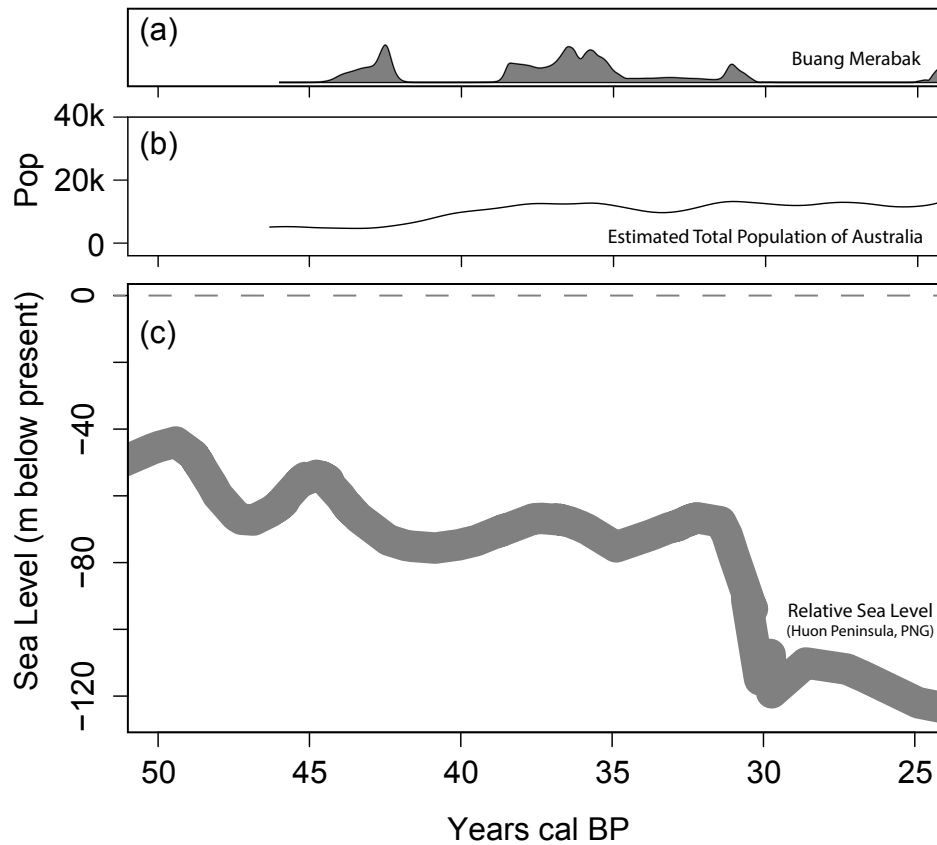


Figure 5: Occupational history of Buang Merabak (a, Leavesley 2004, Leavesley and Allen 1998, summed calibrated radiocarbon probabilities from OxCal 4.2.2, Bronk Ramsey 2009, using a marine curve from Reimer et al. 2009 and a local correction by Petchey et al. 2004) relative to the estimated total population of Australia (b, assuming a founding population of 5,000 people, Williams 2013) and estimated fluctuations in sea level (c, Lambeck and Chappell 2001).

abundance due to the natural effects of a fluctuating coastline (Beaton 1995). While alternative lines of evidence (such as paleontological finds) will be required to test this further, we suspect that habitats (e.g. broad fringing reefs) supporting healthy populations of some of the highest ranked shellfish (such as *Tridacna*) would have been commonly encountered when Sahul was first colonized (Pope and Terrell 2008). But again, that such taxa are high-ranked and often associated with low meat:shell ratios leads us to suspect that they would have been important prey options whose archaeological presence was heavily filtered by field processing. This agrees with ethnographic observations on tropical reef flat foraging, where highly ranked *Tridacna* are always exploited on-encounter, but the valves are rarely transported back to a central place (Bird et al. 1997, 2002, 2004; Thomas 2007).

If our interpretations of these results are correct, it seems that the most reasonable explanation for the high abundance of low-ranking taxa at early sites may result from the differential foraging constraints faced by children and their mothers. Because children generally walk more slowly than adults and because they may have less strength and skill in processing, they are likely to have lower encounter rates with high ranked prey and are less able to field process taxa even when it might be desirable to do so (Bird and Bliege Bird 2000, Bird et al. 2004, Meehan 1982). Further, given the limited availability of alternative caregivers expected with smaller populations (Codding et al. 2011), mothers with young children will generally experience greater trade-offs between childcare and foraging. Intertidal shellfish foraging provides an activity with lower costs of childcare than other alternatives (e.g., sub-tidal foraging, pelagic fishing, etc.) and despite being low return, shellfish (especially small taxa) are characterized by low acquisition variance, making them ideal resources for provisioning dependents (Codding et al. 2011). Indeed, cooperative parent-juvenile units may do better overall by working together in lower-return activities than by working apart (Hawkes

et al. 1995, Kramer 2011).

While this seems like the most plausible explanation for the Pleistocene record of shellfishing on Sahul given the available evidence, more work is required to truly understand these patterns. Continued archaeological and paleoenvironmental work is necessary, but research might benefit most from continued ethnoarchaeological and simple actualistic experiments. This includes simple measures of utility, processing costs and meat:shell ratios for key species (e.g., *Halitois*, *Melo* and chiton) and additional studies of well-known taxa (e.g., *Turbo*, *Nerita* and *Asaphis*) to further our understanding of variability within species. Additional work along these lines should greatly improve our interpretations of the archaeological record and allow us to solve such conundrums as the record of early shellfishing by the colonists of Sahul.

Acknowledgments. Thanks to Richard Klein for suggesting the idea for this symposium and collection of papers. We remain indebted to the Meriam Community for hosting DWB's ethnographic work over many years, which was supported by the National Science Foundation and the LSB Leakey Foundation. This paper has benefited from comments, suggestions and work by Jim Allen, Rebecca Bliege Bird, Shannon Arnold-Boomgarden, Joe Dortch, James Holland Jones, Peter Veth, Adie Whitaker, and David Zeanah. Three anonymous reviewers provided detailed comments that greatly improved the final result.

References

- Allen, J. and J.F. O'Connell. 2003. The long and the short of it: Archaeological approaches to determining when humans first colonised Australia and New Guinea. *Australian Archaeology* 57:5–19.
- Allen, J. and J. F. O'Connell. 2008. Getting from Sunda to Sahul. In *Islands of Inquiry: colonization, seafaring and the archaeology*

- of maritime landscapes (G. Clark, F. Leach and S. O'Connor, eds): 31–46. ANU E Press, Canberra: Australian National University.
- Balean, C. E. 1989. Caves as refuge sites: an analysis of shell material from Buang Merabak. BA Honours Thesis, Department of Prehistory and Anthropology, Canberra: Australian National University.
- Beaton, J. M. 1995. The transition on the coastal fringe of greater Australia. *Antiquity* 69:798–806.
- Beesley, P. L., G. J. B. Ross and A. Wells (eds). 1998. *Mollusca: The Southern Synthesis*. Australian Biological Resources Study. CSIRO Publishing. Parts 1 & 2.
- Bettinger, R. L. 2009. *Hunter-Gatherer Foraging: Five Simple Models*. New York: Eliot Werner Publications.
- Bird, D. W. 1996. *Intertidal Foraging Strategies Among the Meriam of the Torres Strait Islands, Australia: An Evolutionary Ecological Approach to the Ethnoarchaeology of Tropical Marine Subsistence*. Ph.D. dissertation, University of California, Davis.
- Bird, D. W. and R. Bliege Bird. 1997. Contemporary shellfish gathering strategies among the Meriam of the Torres Strait Islands, Australia: Testing predictions of a central place foraging model. *Journal of Archaeological Science* 24(1):39–63.
- Bird, D. W. and R. Bliege Bird. 2000. The ethnoarchaeology of juvenile foragers: Shellfishing strategies among Meriam children. *Journal of Anthropological Archaeology* 19(4):461–476.
- Bird, D. W. and J.F. O'Connell. 2006. Behavioral ecology and archaeology. *Journal of Archaeological Research* 14:143–188.
- Bird, D. W., R. Bliege Bird, and B.F. Coddling. 2009. In pursuit of mobile prey: Martu hunting strategies and archaeofaunal interpretation. *American Antiquity* 74(1):3–29.
- Bird, D. W., R. Bliege Bird and Richardson, J. L. 2004. Meriam ethnoarchaeology: Shellfishing and shellmiddens. *Memoirs of the Queensland Museum, Cultural Heritage Series* 3(1):183–197.
- Bird, D. W., J.L. Richardson, P.M. Veth, and A.J. Barham. 2002. Explaining shellfish variability in middens on the Meriam Islands, Torres Strait, Australia. *Journal of Archaeological Science* 29(5):457–469.
- Blurton Jones, N. 1986. Bushman Birth Spacing: A Test for Optimal Interbirth Intervals. *Ethnology and Sociobiology* 7:91–105.
- Bronk Ramsey, C. 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51: 337–360.
- Charnov, E. L. and G.H. Orians. 2006. *Optimal foraging: Some theoretical explorations*. Mimeo: Department of Biology, University of Utah, Salt Lake City, UT. Digital version of 1973 edition. Available online at <http://repository.unm.edu/handle/1928/1649>.
- Coddling, B.F., R. Bliege Bird and D.W. Bird. 2011. Provisioning offspring and others: risk-energy trade-offs and gender differences in hunter-gatherer foraging strategies. *Proceedings of the Royal Society, B*. 278: 2502–2509.
- Dortch, J. 2004. *Palaeo-environmental change and the persistence of human occupation in south-western Australian forests*. British Archaeological Reports. Oxford: Archaeopress.
- Erlandson, J. 1988. *Of Millingstones and Mollusks: Cultural Ecology of Early Holocene Hunter-Gatherers on the California Coast*. PhD Dissertation. Santa Barbara: University of California.

- Gadgil, M. and W. H. Bossert. 1970. Life historical consequences of natural selection. *The American Naturalist*, 104(935): 1–24.
- Gosden, C. and N. Robertson. 1991. Models for Matenkupkum: interpreting a late Pleistocene site from southern New Ireland, paupa new guinea. In Report of the Lapita Homeland Project, number 20 in Occasional Papers, pages 20–45. Department of Prehistory, Research School of Pacific Studies, Canberra: Australian National University.
- Hawkes, K. J. F. O'Connell and N. G. Blurton Jones. 1995. Hadza Children's Foraging: Juvenile Dependency, Social Arrangements, and Mobility among Hunter-Gatherers. *Current Anthropology* 36(4):688–700.
- Kennedy, M. 2005. An Investigation of Hunter-Gatherer Shellfish Foraging Practices: Archaeological and Geochemical Evidence from Bodega Bay, California. PhD Dissertation. Davis: University of California.
- Klein, R.G. and T. E. Steele. 2013. Archaeological shellfish size and later human evolution in Africa. *Proceedings of the National Academy of Sciences*, published ahead of print June 17, 2013, doi:10.1073/pnas.1304750110.
- Kramer, K. 2011. The evolution of human parental care and recruitment of juvenile help. *Trends in Ecology and Evolution* 26(10):533–540.
- Leavesley, M. G. 2004. Trees to the Sky: Prehistoric Hunting in New Ireland, Paupa New Guinea. PhD Dissertation. Canberra: Australian National University.
- Leavesley, M. G. and J. Allen. 1998. Dates, disturbance and artefact distributions: Another analysis of Buang Merabak, a pleistocene site on New Ireland, Papua New Guinea. *Archaeology in Oceania* 33:63–82.
- Meehan, B. 1982. Shell Bed to Shell Midden. Canberra: Australian Institute of Aboriginal Studies.
- Metcalf, D. and K. R. Barlow. 1992. A Model for Exploring the Optimal Trade-off between Field Processing and Transport. *American Anthropologist* 94:340–356.
- Morse, K. 1988. Mandu mandu creek rockshelter: Pleistocene human coastal occupation of north west cape, Western Australia. *Archaeology in Oceania* 23(3):81–88.
- Morse, K. 1993. New radiocarbon dates from the north west cape, Western Australia: A preliminary report. In *Sahul in Review: Pleistocene Archaeology in Australia, New Guinea and Island Melanesia*, (M.A. Smith, M. Spriggs, and B. Fankhauser, eds): 155–163. The Australian National University, Canberra.
- Munro, J. L. 1993. Giant clams. In *Nearshore Marine Resources of the South Pacific* (A. Wright and L. Hill, eds): 431–449. Institute for Pacific Studies.
- Nash, W. J. 1993. Trochus. In *Nearshore Marine Resources of the South Pacific* (A. Wright and L. Hill, eds): 451–495. Institute for Pacific Studies.
- O'Connell, J. F. 1995. Ethnoarchaeology Needs a General Theory of Behavior. *Journal of Archaeological Research* 3(3):205–255.
- O'Connell, J. F. and J. Allen. 2004. Dating the colonization of Sahul (Pleistocene Australia-New Guinea): A review of recent research. *Journal of Archaeological Science* 31(8):835–853.
- O'Connell, J. F. and J. Allen. 2007. Pre-LGM Sahul (Pleistocene Australia-New Guinea) and the archaeology of early modern humans. In *Rethinking the Human Revolution* (P. Mellars, K. Boyle, O. Bar-Yosef, and C. Stringer, eds):

- 395–410. McDonald Institute for Archaeological Research, Cambridge University, Cambridge.
- O'Connell, J. F. and J. Allen. 2012. The restaurant at the end of the universe: modeling the colonization of Sahul. *Australian Archaeology* 74:5–17.
- O'Connell, J. F., J. Allen, and K. Hawkes. 2010. Pleistocene Sahul and the origins of seafaring. In *The Global Origins and Development of Seafaring* (A. Anderson, J. Barrett, and K. Boyle, eds): 57–68. The McDonald Institute for Archaeological Research, Cambridge University, Cambridge.
- O'Connor, S. 1999. 30,000 Years of Aboriginal occupation: Kimberley, North West Australia. Number 14 in *Terra Australis*. ANH Publications and The Centre for Archaeological Research, Canberra: The Australian National University.
- Orians, G. H. and N.E. Pearson. 1979. On the theory of central place foraging. In *Analysis of Ecological Systems* (D.J. Horn, G. R. Stairs and R.T. Mitchell, editors): 155–177. Ohio State University Press.
- Petchey, F., M. Phelan and J.P.White. 2004. New ΔR values for the southwest Pacific Ocean. *Radiocarbon* 46: 1005–1014.
- Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge University Press.
- Pope, K.O. and J.E. Terrell. 2008. Environmental setting of human migrations in the circum-Pacific region. *Journal of Biogeography* 35:1–21.
- Przywolniak, K. 2008. Long-term transitions in hunter-gatherers of coastal northwestern Australia. In *Desert Peoples: Archaeological Perspectives* (P. Veth, M. Smith and P. Hiscock, eds): 117–205. Oxford: Blackwell.
- R Development Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reimer, P. J., M. G. L. Baillie, E. Bard, A. Bayliss, J.W. Beck, P.G. Blackwell, C. Bronk Ramsey, C.E. Buck, G.S. Burr, R.L. Edwards, M. Friedrich, P.M. Grootes, T.P. Guilderson, I. Hajdas, T.J. Heaton, A.G. Hogg, K.A. Hughen, K.F. Kaiser, B. Kromer, F.G. McCormac, S.W. Manning, R.W. Reimer, D.A. Richards, J.R. Southon, S. Talamo, C.S.M. Turney, J. van der Plicht, and C.E. Weyhenmeyer. 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon*, 51: 1111–1150.
- Rosenfeld, A. 1997. Excavation at Buang Merabak, Central New Ireland. *The Indo-Pacific Prehistory Association Bulletin (The Chang Mai Papers, Vol. 3)* 16:213–224.
- Thomas, F. R. 2007. The behavioral ecology of shellfish gathering in Western Kiribati, Micronesia 1: Prey choice. *Human Ecology* 35:179–194.
- Veth, P., K. Alpin, L. Wallis, T. Manne, T. Pulsford, E. White, and A. Chappell. 2007. *The Archaeology of Montebello Islands, North-West Australia*. BAR International Series 1668. British Archaeological Reports.
- Whitaker, A. 2008. *The role of human predation in structuring prey populations in Northwestern California*. PhD Dissertation. Davis: University of California.
- Whitaker, A. and B.F. Byrd. 2012. Boat-based foraging and discontinuous prehistoric red abalone exploitation. *Journal of Anthropological Archaeology* 31:196–214.
- Wickler, S. 2001. *The Prehistory of Buka: Stepping Stone Island in the Northern Solomons*. Terra Australis. Department of Archaeology

and Natural History, and Centre for Archaeological Research, Australian National University.

Williams, A. N. 2013. A new population curve for prehistoric Australia. Proceedings of the Royal Society, B.doi: 10.1098/rspb.2013.0486.

Yamaguchi, M. 1993. Green snail. In Nearshore Marine Resources of the South Pacific (Wright, A. and L. Hill, eds): 488–511. Institute for Pacific Studies.