Sustainable harvesting of *Conomurex luhuanus* and *Rochia nilotica* by Indigenous Australians on the Great Barrier Reef over the past 2000 years

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Abstract

Offshore island colonisation and use around the northern Australian coastline in the mid-to-late Holocene is associated with expanding Aboriginal and Torres Strait Islander populations and intensifying land-use activities. However, few explicit tests of the long-term effects of shellfish forager decision-making and associated impacts on intertidal ecosystems in these newly colonised island environments have been undertaken. We report morphometric analyses on two key reef flat Great Barrier Reef shellfish species, strawberry conch *Conomurex luhuanus* (n=360) and top shell *Rochia nilotica* (n=45), from two late Holocene archaeological shell midden assemblages on Lizard Island, northeast Queensland. Human foraging pressure was assessed through reconstructions of population age structure across time, highlighting the importance of determining size-at-age habitat preferences and species behaviour patterns when assessing long-term anthropogenic impacts on shellfish populations. Results show no evidence for resource depression across the late Holocene which is broadly in keeping with previous findings at other locales on the Great Barrier Reef, but contrary to expectations of resource intensification models. We conclude that the rich and abundant resources of reef flat environments were resilient to relatively low intensity and likely episodic Indigenous foraging. This sustainability contrasts with the scale and impacts of intensive industrialised harvesting in the historic period.

Keywords: archaeomalacology; *Conomurex luhuanus*; *Rochia nilotica*; Great Barrier Reef; morphometrics; resource depression; ecosystem resilience

Highlights

• Reef flat shellfish were harvested in large numbers on the northern Great Barrier Reef

• Size-at-age criteria were applied to *Conomurex luhuanus* and *Rochia nilotica*

• Morphometric data show no resource depression of *C. luhuanus* or *R. nilotica*

• Key reef flat shellfish were resilient to relatively low intensity foraging

1. Introduction

Aboriginal and Torres Strait Islander contemporary lifeways and oral histories along with ethnographic and archaeological studies demonstrate the centrality of the sea and marine resources to people living along the length of the Great Barrier Reef (e.g. Haddon 1935; McNiven 2015; Rowland 1982; Thomson 1934; Ulm 2011). Although archaeological evidence demonstrates Aboriginal occupation of the Great Barrier Reef extending to 9000 years ago (Barker 2004), a significant increase in shellfish exploitation only occurred around 3000 years ago coincident with a suite of changes in the archaeological record (Barker 2004; Beaton 1985; Lourandos 1997; McNiven et al. 2014; Rowland et al. 2015; Ulm 2011, 2013; Ulm et al. 1995; Williams et al. 2015). Coastal archaeological trajectories in the region are often cited as exemplars of complex hunter-gatherer-fishers intensifying economic and social production across the late Holocene (Barker 2004; Lourandos 1997), although patterns are complicated by differential preservation of sites (Bird 1992; Rowland 1989), environmental change (Beaton 1985), uneven and inadequate sampling (Langley et al. 2011) and a lack of comparability in data recovery, analysis and reporting (Ulm 2002). Arguments for and against resource intensification in northeast Australia have focussed on changing numbers of sites and rates of site establishment and use, rather than detailed study of individual taxa to investigate long-term effects of shellfish forager decision-making and associated influences on intertidal ecosystems.

Human foraging can produce a range of alterations to shellfish populations including modifications to the configuration of population structure and the range of species exploited, the body size of exploited species, declining abundances of preferred species available for exploitation, local extirpation and extinction (e.g. Morrison and Allen 2017; Seeto et al. 2012; Spennemann 1987; Swadling 1976; Walter

1998); but in some cases shellfish populations are also resilient to human harvesting practices (e.g. de Boer and Longamane 1996; Giovas 2016; Harris and Weisler 2017; Poteate et al. 2015).

Within island and coastal archaeology discourse, there is increasing evidence that small islands are not as marginal and fragile to human impacts as often framed within earlier literature (e.g. Anderson 2002). In fact, these land- and seascapes provided critical terrestrial and marine resources that were often not readily available elsewhere, and played an important role in structuring social, political, and economic change across space and time (e.g. Giovas 2018; Keegan et al. 2008; McNiven 2015; Napolitano 2013; Pavia et al. 2013). Reported long-term resource sustainability on small islands has been attributed to an interplay between complex marine habitat structure (climate, environment, substrate etc), a focus on a diverse range of taxa, and the use of flexible foraging strategies that broadly targeted a wide range of habitat types, which has the potential to support marine ecosystem resilience and mitigate against human foraging effects (e.g. Campbell and Butler 2010; Carder and Crock 2012; Giovas 2016; Rick 2011; Szabó and Amesbury 2011).

Reef flat shellfish are uniquely suited to test human foraging effects on exploited population structure and the associated resilience of these intertidal ecosystems. Unlike mobile finfish, sea mammals and reptiles, shellfish are relatively sessile making them both highly attractive to and theoretically highly vulnerable to human foraging. *Conomurex luhuanus* and *Rochia nilotica* are both highly visible and gregarious. Both have similar meat:shell ratios (Codding et al. 2014:Table 1) and, as gastropods, generally require heating to assist meat extraction (Meehan 1982). Therefore, both species are unlikely to be field processed on the reef flat of the lagoon (cf. Bird and Bliege Bird 1997), but rather returned to terrestrial locations for processing, consumption and discard. Excavation of two archaeological sites on Lizard Island yielded shellfish assemblages extending to 4000 years ago. Morphometric analyses on *C. luhuanus* and *R. nilotica* from these assemblages provide an opportunity to test alterations in the size-at-age of these exploited shellfish populations as a proxy for human foraging intensities on key Great Barrier Reef flat species during the late Holocene.

2. Background

Human-derived resource depression or declines in rates of prey capture are frequently tested using models derived from optimal foraging theory, which broadly posit that foragers will implement fitness maximising behaviours to increase resource return relative to effort expended by initially targeting high return resources and habitats (Allen 2012; Bird and O'Connell 2006; Charnov 1976; Gremillion 2002; Smith 1983; Winterhalder 1986; Zeder 2012). According to these models, resource depression

will be represented by a decline in foraging efficiency, such as alterations in prey age structure (e.g. Broughton 2002; Nagaoka 2002). Archaeological records documenting human exploitation of shellfish resources from a variety of geographic and environmental contexts have reported diverse effects on exploited populations through time including, positive, negative, and negligible alterations (e.g. Braje et al. 2007; Faulkner 2009; Giovas et al. 2013; Poteate et al. 2015).

Table 1 provides a summary of the key archaeological criteria used by researchers to test human foraging effects on shellfish populations (after Botkin 1980; Claassen 1998; de Boer and Prins 2002; Faulkner 2009, 2013; Jerardino 1997; Mannino and Thomas 2002; Mason et al. 1998; Spennemann 1987; Swadling 1976, 1986).

Table 1: Summary of criteria to assess human foraging pressure in archaeomalacological assemblages.

Criteria No.	Description
1	Relative abundance of preferred shellfish species will decrease through time;
2	Mean shellfish length will decline through time;
3	Sexually mature shellfish will decline through time expressed as a decline in the size-at-age of a species population;
4	The mean size of exploited shellfish populations will be smaller than unexploited shellfish populations;
5	Shellfish species that are not easy to collect will increase through time;
6	Shellfish species that are not easy to process will increase through time.

Claassen (1998) emphasises that the mean age of shellfish and the ratio of adults to juveniles, are the most important factors for identifying foraging pressure by people. Identifying the age of shells at particular maturity intervals is crucial for detecting changes in population structure that may relate to foraging pressure, with many shellfish species exhibiting a diverse range of growth patterns during different life-cycle stages (e.g. Faulkner 2009; Giovas et al. 2010; Mannino and Thomas 2002). While the importance of determining age profiles of exploited shellfish populations through time has been widely acknowledged, in reality, determining size-at-age of zooarchaeological samples is challenging owing to complications of local ecological factors that influence growth rates, sexual dimorphism effects, fragmentation and taphonomic processes and a frequent lack of available modern ecological literature for comparison to archaeological populations (e.g. de Boer et al. 2000; Harris and Weisler 2018). Shell growth analysis has been employed by some researchers to determine size-at-age-at-death of exploited shellfish species (e.g. Cannon and Burchell 2009; Mannino and Thomas 2001;

Quitmyer and Jones 2000). In lieu of sufficient data to reconstruct age structures of exploited archaeological shellfish populations, two approaches are frequently employed.One utilises maximum shell length as a proxy for size-at-age, and the other more commonly utilises shell length as a means of assigning individuals to binary juvenile/non-juvenile categories to track changes in this ratio through time (e.g. Faulkner 2013; Giovas 2016; Hockey and Bosman 1986). However, not all shellfish lengthen as they mature (e.g. Strombidae), so use of the maximum length can produce inaccurate reconstructions of age profiles (e.g. Campbell 2008, 2015; Poiner and Catterall 1988). Furthermore, these approaches are only useful for determining size-at-sexual maturity rather than individual age, which is necessary for understanding variability in human foraging practices and habitat preferences of shellfish species.

This study emphasises the importance of quantifying the presence and absence of size-at-age characteristics to supplement determinations of harvesting pressure by people based solely on measurements of shell length. While it is rare that a single stressor will drive declines in size-at-age profiles and that these assessments can unequivocally be attributed to human foraging pressures (e.g. Braje et al. 2012; Giovas el at. 2010; Faulkner 2010; Jerardino 1997; McClanahan et al. 2014; Whitaker 2008), the incorporation of size-at-age determinations can enhance our ability to investigate the complex anthropogenic and environmental processes that mediate shellfish population structure over millennia, and the archaeological signature of these processes. Critically, while all criteria outlined in Table 1 must be evaluated in combination when testing the effects of human foraging on shellfish populations, this study highlights the particular importance of determining size-at-age habitat preferences and species behaviour patterns (e.g. age or sex division congregation) for directly testing forager impacts on intertidal ecosystems.

3. Materials and methods

### 3.1 Archaeological case study sites

Lizard Island is a high (359 m) granite continental island within the Great Barrier Reef of Queensland, northeast Australia, approximately 30 km northeast of Cape Flattery on the mainland (Figure 1). Lizard Island and the adjacent Palfrey Island, South Island, Osprey Island, and Seabird Islets enclose a large lagoon, with extensive fringing reefs and hosting high biodiversity. The Dingaal Aboriginal cultural landscape is dominated by numerous stone arrangements (Fitzpatrick et al. 2018) and shell middens (Lentfer et al. 2013).

Site 3 Mangrove Beach Headland Midden (MBHM) is located on a small headland on the southern coast of Lizard Island (Mills 1992; Specht 1978). In 2013, a 1 m x 1 m square was excavated by trowel in 59 x c.2.5 cm-thick excavation units (XUs) within stratigraphic units (SUs) to a maximum depth of 151.74 cm. Excavated materials were passed through a 2.36 mm mesh sieve. The cultural deposit was dominated by shellfish remains of *C. luhuanus*, *R. nilotica*, *Tridacna* spp. and *Lambis lambis*, with occasional stone artefacts, fish bone, turtle bone and charcoal. Fourteen conventional radiocarbon dates were obtained from surface *Anadara antiquata*, and in situ charcoal samples collected during excavation (Table 2). The surface dates to 533 cal BP and the base to 4036 cal BP (median dates).

Site 17 Freshwater Bay Midden (FBM) is situated on the southwestern side of Lizard Island. In 1992, Mills (1992) excavated a 1 m x 0.5 m trench (Trench 1 divided into Squares A and B) by trowel in 20 x c.5 cm-thick XUs and sieved through nested 5 mm and 2.5 mm mesh. Cultural materials ceased at c.120 cm. The shell assemblages from Squares A and B were used in this study. The cultural deposit was dominated by shellfish remains of *C. luhuanus*, *R. nilotica*, *Tridacna* spp. and *Lambis lambis*, with occasional stone artefacts, fish bone, turtle bone, dugong bone and charcoal. In 2009, Lentfer et al. (2013) undertook a further excavation (Trench 2); however, these materials were not available for analysis. Six radiocarbon determinations on *R. nilotica* and charcoal samples are reported from Trench 1 (Mills 1992) and Trench 2 (Lentfer et al. 2009) (Table 2). The surface dates to 74 cal BP and the base to 3656 cal BP (median dates).

At both Site 3 MBHM and Site 17 FBM shellfish foraging was the dominant component of the subsistence regime, particularly the focused exploitation of *C. luhuanus and R. nilotica*. Specifically, the Site 3 MBHM shellfish assemblage is characterised by low taxonomic richness (NTAXA=6) and is dominated by *C. luhuanus* (NISP=1770; MNI=1256; Weight=8066.9 g) and *R. nilotica* (NISP=4290; MNI=47; Weight=6751.1 g), which together account for ~92% of total site NISP and 97% of total site MNI. The other species identified include clams (*Tridacna* spp.), spider conch (*Lambis lambis*), nerite (*Nerita* spp.), and oyster (Ostreidae), but these species are represented by a total MNI of 44 and NISP of 544, and were identified in low abundances throughout the sequence. Similar taxonomic composition was reported by Mills (1992) for Site 17 FBM, however, only weights of identified specimens was determined. We reanalysed all *C. luhuanus* (MNI=1108; Weight=10,615.3 g) and *R. nilotica* (MNI=13; Weight=2283.5 g) remains from the site, which are currently housed at the Queensland Museum, and determined these two species are also the most abundant by MNI and weight for Site 17 FBM. Other species recorded by Mills (1992) include yellow cone (*Conus quercinus*), *Lambis lambis*, green turban (*Turbo marmoratus*), blood cockle (*Tegillarca granosa*), *Tridacna* spp., giant triton (*Charonia tritonis*), and hooded oyster (*Saccostrea cuccullata*). Similar to trends noted for

Site 3 MBHM, *C. luhuanus* and *R. nilotica* were dominant throughout the sequence, and other species were present in low abundances. As *C. luhuanus* and *R. nilotica* were the most abundant taxa by MNI and weight reported from the Sites 3 and 17 assemblages, morphometric analyses was conducted on these species to explore human harvesting pressure effects and intertidal forager decision-making.
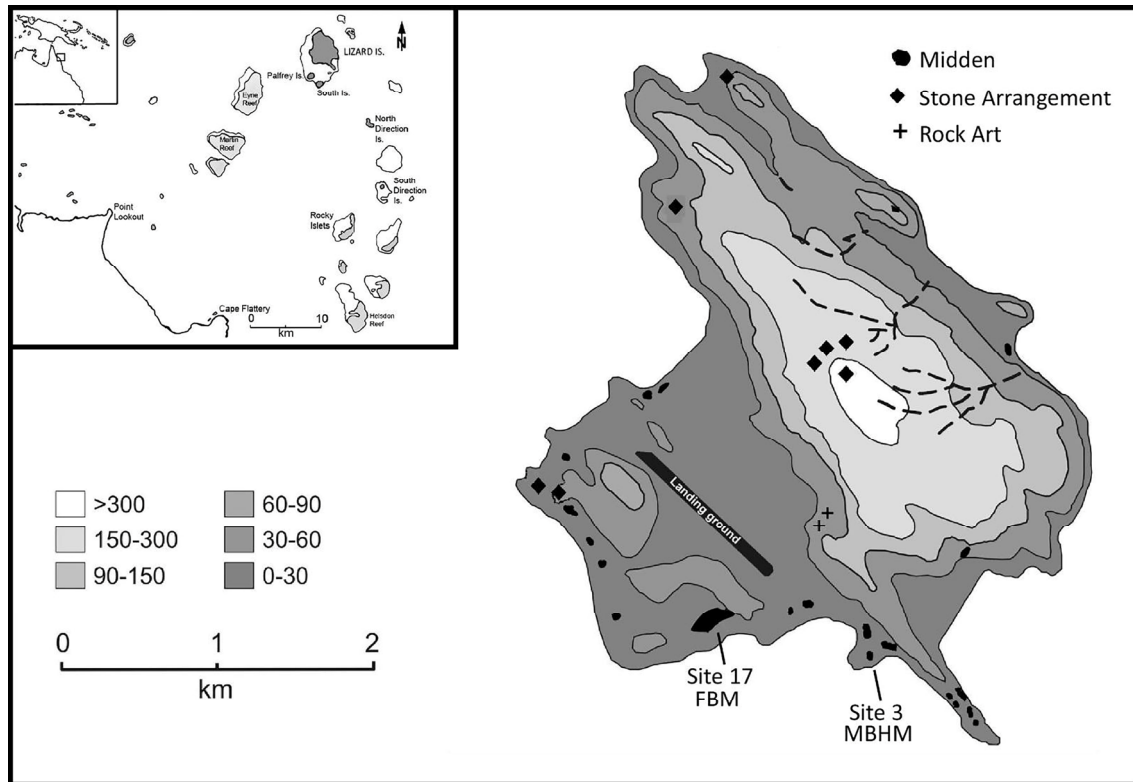
Fig. 1: Lizard Island location map showing Site 3 MBHM and Site 17 FBM (after Lentfer et al. 2013:Figure 2). Dashed lines indicate drainage lines. Shading indicates elevation in metres.

Table 2: Summary of radiocarbon ages for Site 3 MBHM, Square A, and Site 17 FBM, Trench 1 and Trench 2, Lizard Island. Radiocarbon ages for were calibrated using OxCal 4.1.3 (Bronk Ramsey 2009) and the IntCal13 and Marine13 datasets (Reimer et al. 2013), with a ΔR of 12±10 for marine samples (Ulm 2006). * = date may extend out of range (i.e. modern)

Site	Lab. No.	XU	Depth (cm)	Sample	Method	δ¹³C‰	Conventional ¹⁴C Age (years BP)	Calibrated Age BP (95.4%)	Calibrated Age BP Median
Site 3 MBHM	Wk-37131	-	0	*A. antiquata*	AMS	1.7±0.1	948±25	491-610	533
	Wk-37132	-	0	*A. antiquata*	14C	1.7±0.1	965±27	500-619	548
	Wk-37129	-	0	*A. antiquata*	AMS	1.7±0.1	981±25	510-624	562
	Wk-37133	-	0	*A. antiquata*	14C	1.8±0.1	985±30	509-629	567
	Wk-37128	-	0	*A. antiquata*	14C	0.6±0.1	1002±31	518-639	578
	Wk-37130	-	0	*A. antiquata*	AMS	1.8±0.1	1008±25	525-638	582
	Wk-38696	3	5.12-7.54	charcoal	AMS	-	747±21	665-723	681
	Wk-38697	10	23.32	charcoal	AMS	-	1836±21	1711-1824	1772
	Wk-38698	16	39.92	charcoal	AMS	-	3144±22	3268-3444	3372
	Wk-38699	20	50.02	charcoal	AMS	-	3151±21	3275-3445	3377
	Wk-38700	24	60.62	charcoal	AMS	-	3149±21	3273-3445	3376
	Wk-38701	27	66.42	charcoal	AMS	-	3148±21	3272-3445	3375
	Wk-38702	30	72.42	charcoal	AMS	-	3136±22	3258-3441	3365
	Wk-38703	44	108.82	charcoal	AMS	-	3689±21	3932-4090	4036
Site 17 FBM	Wk-2689	1	0-5	*R. nilotica*	14C	3.5±0.2	450±55	0*-227	74
	Wk-2690	7	28.5-34.2	*R. nilotica*	14C	3.9±0.2	2150±60	1564-1869	1725
	Wk-2691	20	99.8-116.2	charcoal	14C	-25.7±0.2	2970±80	2928-3360	3136
	Wk-30014	7	60-70	charcoal	AMS	-25.4±0.2	1059±29	926-1052	962
	Wk-30012	12	110-120	charcoal	AMS	-25.5±0.2	2919±34	2961-3165	3062
	Wk-30013	14	130-140	charcoal	AMS	-25.6±0.2	3408±31	3575-3812	3656

3.2 *Conomurex luhuanus*

Conomurex luhuanus (Linnaeus, 1758) (syn. *Strombus luhuanus*), commonly known as the strawberry conch, are medium-sized marine gastropods (~80 mm max. length) distributed across the western Pacific (Carpenter and Niem 1998:475; Wada et al. 1983:17). Found to a maximum water depth of 20 m, they are herbivores or detritus feeders commonly associated with sand habitats, but are also found on rubble and rock substrates, and areas of live coral cover (Carpenter and Niem 1998:475; Catterall and Poiner 1983:171).

C. luhuanus commonly occur in mixed age/sex colonies or aggregations of up to 100-200 individuals with a reported spatial density of between ~0.5 and 30 individuals per m² (Poiner and Catterall 1988:191-194). Within colonies, frequent spatial segregation occurs between age-classes, often due to variations in habitat preference, however, individuals can move on average between 10 and 30 m every 6-30 months (Catterall and Poiner 1983:171). Younger individuals spend more time buried 1-2 cm beneath the surface of subtidal sandy substrates (Catterall et al. 2001:605) prior to maturation and associated migration to rock and rubble substrates of the intertidal reef flat (see Poiner and Catterall 1988:194). In tropical areas such as the Great Barrier Reef, individuals are expected to have a lifespan of seven years (Catterall et al. 2001:606). On average adolescent *C. luhuanus* range in length between 50 and 80 mm (Carpenter and Niem 1998:475). Following sexual maturity at 2-3 years of age, shell lip thickness, rather than total shell length, becomes a more robust indicator of age (Poiner and Catterall 1988:193). Individuals are sexually trimorphic, which includes a male, female, and masculinised female category. Masculinised females tend to be larger than both females and males, and the shell width/length ratio is largest for males given that the shell is squatter than for female or masculinised females. However, sex distinctions are more robustly determined using soft tissue anatomy than shell size alone (Reed 1995).

Experimental harvesting and intertidal monitoring of modern Great Barrier Reef *C. luhuanus* populations suggests that due to their life-history characteristics this species would be resilient to human harvesting pressures (e.g. Catterall et al. 2001; Catterall and Poiner 1987). Pertinent life-history characteristics include: younger individuals tend to be buried, which offers a degree of protection; recruitment of individuals from less easily accessed subtidal aggregations/colonies can occur when intertidal populations are depleted; the benthic stages of development are mobile, which facilitates movement from the subtidal to intertidal for reproduction; and finally the pelagic larvae stage occurs over 3-4 weeks and disperses over many hundreds of kilometres, which allows continued recruitment for populations with a reduction in the number of sexually mature individuals available for reproduction. These life-history traits ultimately provide populations with a degree of reproductive

resilience (Catterall et al. 2001; Catterall and Poiner 1983, 1987). However, if populations are intensively exploited, Poiner and Catterall (1988) suggest that a shift in the distribution of ages represented in a colony/aggregation will occur and on average the proportion of juveniles and subadults available for continued exploitation will be higher than adults.

Furthermore, Catterall et al. (2001) demonstrated that siltation from dredging and cyclone activity directly and indirectly had a greater impact on population density than human harvesting. This case particularly highlights the importance of considering a multiple versus single stressor approach when evaluating long-term change in archaeological shellfish populations (Giovas et al. 2010; Harris and Weisler 2018), given that some of the effects of dredging were ameliorated by cyclone activity, due to removal of accumulated silt, but aggregations/colonies situated closer to the reef edge were impacted by strong winds and waves. A multitude of external pressures (e.g. anthropogenic and environmental) have the potential to produce indirect and direct effects on *C. luhuanus* populations, which can theoretically result in positive and/or negative outcomes for species density and recruitment (Catterall et al. 2001; Catterall and Poiner 1983, 1987). Here the incorporation of size-at-age when considering these potential effects facilitates a consideration of changes in the population structure of exploited *C. luhuanus* through time.

Table 3 categorises *C. luhuanus* size-at-age using shell lip thickness and shell length measurement attributes combined with morphological observations. Sexual variability could not directly be measured, but is incorporated in the general morphological observations of size-at-age (Table 3). Following Poiner and Catterall (1988:192), lip thickness 'was measured (to the nearest tenth of a mm) at the shoulder of the body whorl, with calipers inserted to a point level with the notch adjacent to the posterior canal … in adults, or to a point level with the junction of the lip and the shell apex in juveniles'. Shell length is the posterior to anterior measurement. See Poiner and Catterall (1988:Figure 2) for illustration of landmarks.

Table 3: Approximate size-at-age and morphological attributes of *C. luhuanus* based on individuals from the Great Barrier Reef, Australia, and southern Papua New Guinea (after Asigau 1988; Carpenter and Niem 1998; Catterall et al. 2001; Poiner and Catterall 1988; Swadling 1977).

Age Description	Age (years)	Measurement Attributes	Morphological Observations
Adult	3+	Lip thickness 4 mm+ Length to 60 mm	Siphonal notch depth is twice the width; posterior notch fully developed; lip is thickened
Adolescent	2-3	Lip thickness 2.0-3.9 mm Length to 60 mm	Siphonal notch as wide as it is deep; posterior notch developing; lip thickening starting
Yearling	1-2	Lip thickness 2 mm Length to 40 mm	Siphonal notch twice as wide as it is deep; posterior notch starting to develop; no lip thickening
Juvenile	0-1	Lip thickness 2 mm Length to 40 mm	No siphonal notch; posterior notch not developed; no lip thickening

3.3 *Rochia nilotica*

Rochia nilotica (Linnaeus, 1767) (syn. *Trochus niloticus*, *Tectus niloticus*), commonly known as top shell, are large (165 mm max. length) marine gastropods. Their natural distribution extends from the Andaman Islands, the Philippines and throughout Indonesia, New Guinea, Australia, the Solomon Islands, and as far east as New Caledonia (Lemouellic and Chauvet 2008). The diet of *R. nilotica* includes green algae and red seaweeds, foraminifera, and benthic diatoms (Gimin and Lee 1997a; Lemouellic and Chauvet 2008).

Generally, *R. nilotica* prefer habitats situated along the windward margin of coral reefs, with large populations often associated with reefs that have an outer reef exposed at low tide and a boulder strewn windward zone (Lemouellic and Chauvet 2008; Nash 1993). Specifically, this species occupies two microhabitats: (1) shallow reef flat intertidal zones and (2) deeper subtidal coral reef flat lagoons and fringes to a depth of ~10 - 15 m (Carpenter and Niem 1998; Castell 1997; Lemouellic and Chauvet 2008; Magro 1997). Castell (1997:216) notes that juveniles (2-50 mm max. diameter) live in shallow reef flat intertidal zones for around 2 years until they reach sexual maturity as adolescents (Purcell et al. 2004:329) and before migrating to deeper subtidal reef slopes. Denser congregations in subtidal

habitats also occur among adult populations and are particularly susceptible to foraging pressure (Amos 1997; Dolorosa et al. 2010; Magro 1997).

R. nilotica growth rates and size-at-age are influenced by geography and local ecological factors (Lemouellic and Chauvet 2008; Nash 1985; Purcell 2004; Rao 1936). As *R. nilotica* of the Great Barrier Reef mature, growth is continual throughout their life, but at around 6 years of age growth rate decreases and plateaus through to 15 years of age (Lemouellic and Chauvet 2008:Figure 5). Compared to contemporary populations from Japan, New Caledonia, Vanuatu and Wallis Island, size-at-age for Great Barrier Reef *R. nilotica* populations tends to be larger throughout their life, specifically, base diameter measurements at any given age tend to be greater than other Pacific Ocean populations (Lemouellic and Chauvet 2008). No external sexual dimorphism is exhibited by the species, and instead sex determinations relate to gonad colour (Dobson and Lee 1996; Lemouellic and Chauvet 2008).

Frequently described as one of the most commercially important gastropod species in the Pacific, historically, *R. nilotica* is an important food resource, but the nacreous shell also provides critical economic benefits as it is useful for handicrafts and jewellery (Amos 1997; Heslinga and Hillmann 1981; Purcell 2004). *R. nilotica* population declined across the region during the mid-to-late twentieth century, and researchers were concerned with managing and restocking these depleted reefs using hatchery grown juveniles (e.g. Castell 1997; Gimin and Lee 1997a, 1997b; Long et al. 1993). Modern fisheries research indicates that *R. nilotica* life-history and species behaviour characteristics strongly contribute to the high susceptibility of this species to human foraging effects (e.g. Castell 1997; Heslinga 1981; Nash 1993). *R. nilotica* have a larval phase of only a few days, which limits dispersal potential and increases the likelihood of populations on a single reef being self-seeding and lowering the chance of recruitment from other geographically disperse populations if numbers of sexually mature individuals are low (Heslinga 1981; Nash 1985, 1993). Recently, Berry et al. (2017) characterised genetic diversity between sites situated ~300-500 km apart on the coastal Kimberley reefs and oceanic atolls—on the edge of the Australian continental shelf—and noted clear genetic sub-division, which suggests genetic and demographic separation between populations. However, local currents and environmental conditions will influence genetic divergence between populations (e.g. Borsa and Benzie 1996). Other factors that may influence *R. nilotica* susceptibility to overharvesting include being long-lived (10+ years), their large size, relatively late sexual maturation at 2 years of age, and living in well-defined and easily accessed habitats (Heslinga 1981; Long et al. 1993; Nash 1985, 1993). Size-at-age determinations support reconstructions of the exploited population structure through time to better understand the potential impact of human foraging and/or other external pressures.

Lemouellic and Chauvet (2008:4) note that the strongest metric to indicate age is the diameter of the base of the shell at the widest point (see Table 4). See Lemouellic and Chauvet (2008:Figure 2) for illustration of landmarks. Sexual variability could not directly be measured, but is incorporated in the general morphological observations of size-at-age (Table 4).

3.4 Analytical Procedures

Morphometric analysis was applied to *C. luhuanus* and *R. nilotica* specimens as outlined in Tables 3 and 4 (see Aird 2014 for details). All specimens retained in the sieves were evaluated for analysis, however, owing to fragmentation, only those *C. luhuanus* (n=359) and *R. nilotica* (n=45) specimens with intact landmarks were used in this study. Landmarks were measured to the nearest 1 mm using Mitutoyo CD-6˝CX Absolute Digimatic Calipers. Foraging pressure criteria outlined and reviewed in Table 1 were then compared to the Site 3 MBHM and Site 17 FBM morphometric datasets. The data were periodised into 250 year analytical units from each site using available radiocarbon dates to examine whether significant differences in the age of *C. luhuanus* and *R. nilotica* are present in the Site 3 MBHM and Site 17 FBM assemblages. Data from the two sites are considered separately and together to show broad-scale harvesting trends of *C. luhuanus* and *R. nilotica* during the late Holocene. The observed patterns are further investigated using one-way ANOVA and one-way independent t-tests.

Table 4: Approximate size-at-age and morphological attributes of *R. nilotica* based on individuals from the Great Barrier Reef (after Castell 1997:216; Lemouellic and Chauvet 2008:6; Purcell et al. 2004:329; Rao 1936:477; Swadling 1986:143).

Age Description	Age (years)	Measurement Attributes	Morphological Observations
Adult	10+	Base diameter 137-147 mm	Base whorl of the shell expands across the width in adult individuals; upper body whorls remain straight-sided
	9	Base diameter 133-137 mm	Fluting on outer whorl sutures decrease with age; younger individuals have distinct fluting on all sutures
	8	Base diameter 128-133 mm	
	7	Base diameter 121-128 mm	
	6	Base diameter 112-121 mm	
	5	Base diameter 100-112 mm	
	4	Base diameter 84-100 mm	
	3	Base diameter 63-84 mm	
Adolescent	2	Base diameter 36-63 mm	Shell is straight-sided in adolescent and juvenile individuals
Juvenile	0-1	Base diameter 0-36 mm	

4. Results

4.1 *Conomurex luhuanus*

The Site 3 MBHM assemblage of *C. luhuanus* with measurable lip thicknesses (n=224) occurs between 500 and 2000 cal BP (Fig. 2-3). The majority (64.7%) of *C. luhuanus* lip thicknesses measure between 2.5 and 3.75 mm. Few individuals at the lower end of the scale measure 1.0-2.5 mm (23.6%); however, a pulse of individuals measuring between 2.0 and 2.25 mm is present (8.5%). A single outlier in the Site 3 MBHM assemblage measures 5.1 mm.

The Site 17 FBM *C. luhuanus* assemblage is distributed between 0 and 2000 cal BP, with an absence between 250 and 500 BP. The lip thickness size distribution mirrors Site 3 MBHM, even though there are fewer individuals (n=136). The dominant size range occurs between 2.75 and 4.0 mm (61.0%), with a pulse occurring between 2.0 and 2.25 mm (8.8%). Unlike Site 3 MBHM, more individuals occur in the 4-5.25 mm size range (10.3%), with a single outlier at 5.8 mm. Like the Site 3 MBHM outlier (5.1 mm), the Site 17 FBM outlier (5.8 mm) may be representative of masculinised female individuals (Reed 1995).

Figure 3 illustrates *C. luhuanus* pooled age groups and the high representation of adolescent relative to adult individuals at both Site 3 MBHM and Site 17 FBM based on lip thickness measurements (juvenile/yearling 0-2 mm, adolescent 2.0-3.9 mm, adult 4 mm+). In each 250-year time interval, adolescent *C. luhuanus* comprise the majority of the assemblages at Site 3 MBHM and Site 17 FBM, with the highest abundance of individuals at both sites occurring between 500 and 750 cal BP (Fig. 3). Adult individuals are poorly represented in the combined assemblage across all time periods. Full descriptive statistics are presented in Table SI1.
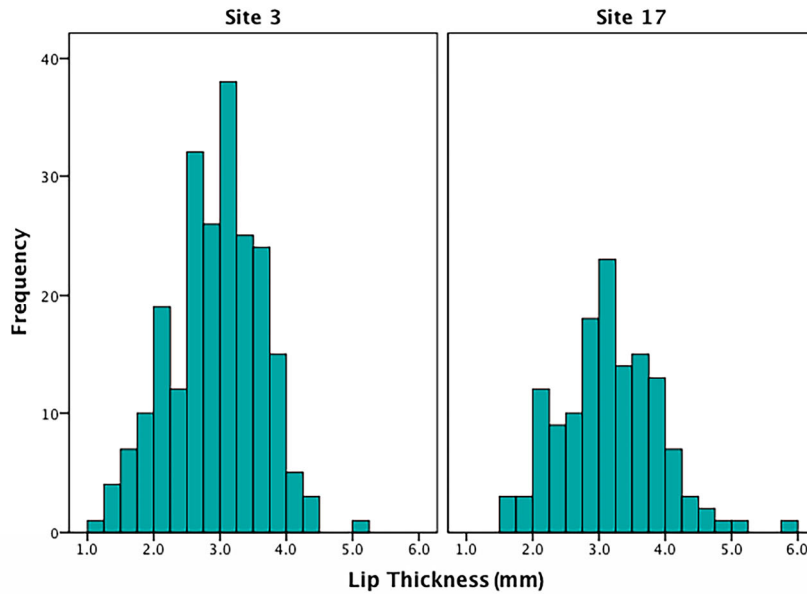
Fig. 2: Frequency of lip thicknesses of *C. luhuanus* individuals at Site 3 MBHM (n=224) between 500 and 2000 cal BP and Site 17 FBM (n=136) between 0 and 2000 cal BP. Each bar represents a 0.25 mm size range.
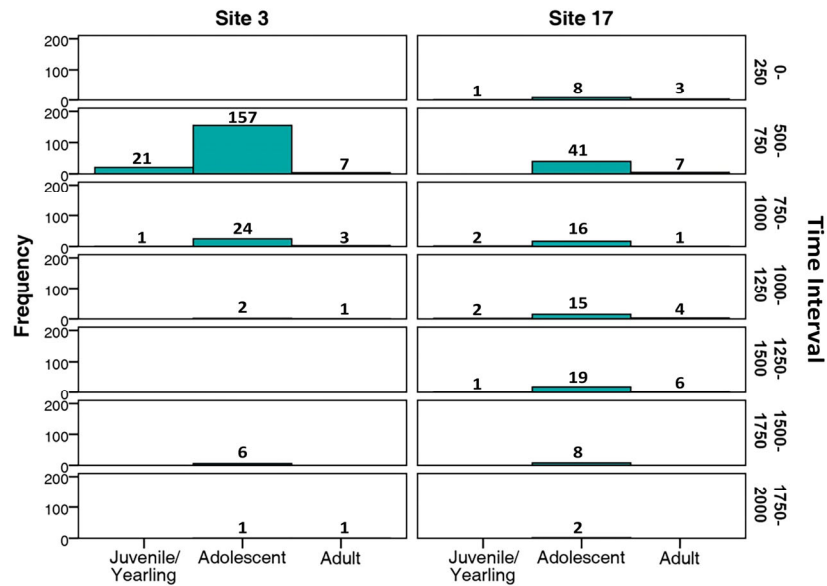

Fig. 3: Pooled age groups of *C. luhuanus* at Site 3 MBHM (n=224) and Site 17 FBM (n=136) per 250-year time interval. Each bar represents one of three age categories: yearling/juvenile 0-2 years, adolescent 2-3 years and adult 3+ years (see Table 3 for categories and attributes). No shell size data available for the >250-500-year time interval.

Lip thickness was used to document changes in the age of archaeological *C. luhuanus* individuals through time. As determined by one-way ANOVA a significant difference was found in the age of individuals from Site 3 MBHM ($F_{(4, 217)}=3.8$, $p=.005$) between 500 and 750 cal BP and 1000 and 1250 cal BP, and 500 and 750 cal BP and 1750 and 2000 cal BP. One-way independent t-test results showed that the most significant difference exists between the 500 and 750 cal BP ($M=2.86$, $SD=.66$) and 1000 and 1250 cal BP ($M=3.78$, $SD=.51$) time intervals, $t(184)=-2.37$, $p=0.19$,. However, these time intervals are still consistently represented by a high proportion of adolescent individuals. No significant difference in the age was found in the Site 17 MBHM assemblage of *C. luhuanus* ($F_{(6, 127)}=1.4$, $p=.195$) between 0 and 2000 cal BP.

4.2 *Rochia nilotica*

The Site 3 MBHM assemblage of *R. nilotica* with measurable maximum base diameters (n=38) occurs between 500 and 2000 BP. The dominant group of *R. nilotica* measure between 70 and 110 mm in length (73.7%); however, a spike of *R. nilotica* individuals exhibiting length values of between 90 and 100 mm (31.6%) occur (Fig. 4). A few smaller specimens occur between 20 and 40 mm (Fig. 4). Fig. 5 identifies the pooled age groups of *R. nilotica* at Site 3 MBHM (juveniles 0-36 mm, adolescents >36-63 mm, adults >63-147 mm). Adult *R. nilotica* dominate every 250-year time interval between 500 and 2000 cal BP. The highest frequency of *R. nilotica* occurs between 500 and 750 cal BP. The Site 17 FBM assemblages was not included in the assessment of abundance and distribution due to a small sample size (n=7).However, it is important to note that these individuals appear in 250-year time intervals: 500 and 750 cal BP (n=4) and 1750 and 2000 cal BP (n=3). Full descriptive statistics are presented in Table SI2.

No significant difference in age or size was identified in *R. nilotica* from Site 3 MBHM ($F_{(4, 31)}=2.0$, $p=.107$) between 500 and 2000 cal BP. Similarly, no statistically significant difference was found in the age or size of *R. nilotica* between 500 and 2000 cal BP using combined datasets from Site 3 MBHM and Site 17 FBM ($F_{(4, 39)}=1.1$, $p=.344$).
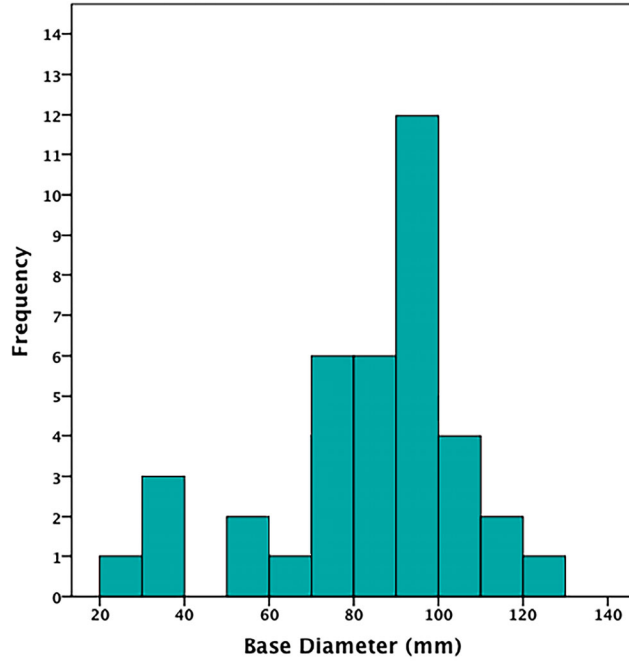
Fig. 4: Frequency of base diameters of *R. nilotica* individuals at Site 3 MBHM (n=38) between 500 and 2000 cal BP. Each bar represents a 10 mm size range.
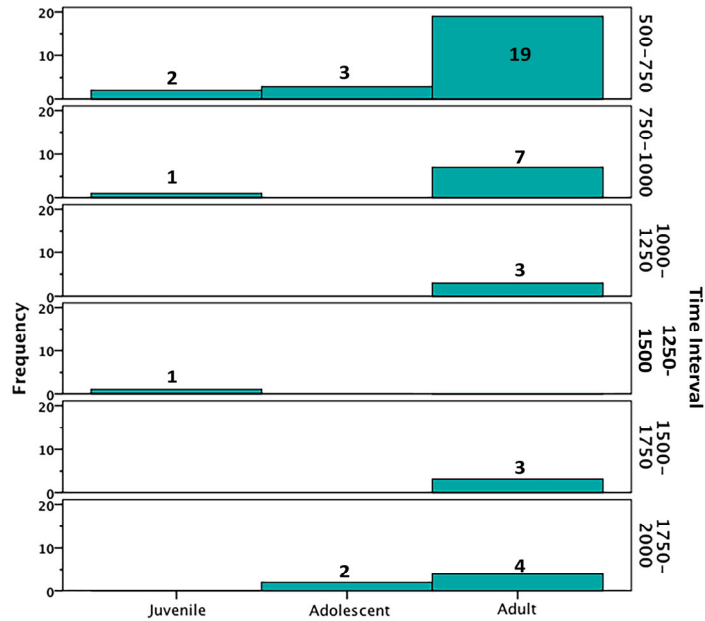

Fig. 5: Pooled age groups of *R. nilotica* at Site 3 MBHM (n=38) and Site 17 FBM (n=7) per 250-year time interval. Each bar represents an arbitrary age category.

5. Discussion

This study provides the first comprehensive investigation of shellfish foraging practices in the Lizard Island Group on the northern Great Barrier Reef. While habitat complexity and associated faunal biodiversity is high across the lagoon and fringing reefs of Lizard Island and its adjacent islands, shellfish, specifically *C. luhuanus* and *R. nilotica* dominate the assemblages at both Site 3 MBHM and Site 17 FBM throughout the entire occupational sequences. There is no evidence of prey switching or a shift to less easily procured or processed species, nor is there significant alterations in the range of species exploited through time. The majority of *C. luhuanus* harvested from the reef during the late Holocene were adolescents and adult *R. nilotica* dominated assemblages across the 1500 year period. There is no major change in the exploited *C. luhuanus* and *R. nilotica* population structure represented at each site. However, it should be emphasised that while no major change through time in the exploited *C. luhuanus* and *R. nilotica* population structure was observed, we are not arguing that active management of shellfish resources occurred. Instead, considering the limited dataset available, we suggest that the available data do not support any of the indicators of human foraging pressure outlined in Table 1, though future work and increased sample size will be required to examine these trends more comprehensively.

The targeted exploitation of *C. luhuanus* and *R. nilotica*, in addition to the other minor component shellfish species at both sites, suggests foraging efforts predominately targeted intertidal benches, shallow subtidal reef flats, subtidal sandy substrates and reef slopes. The dominance of adolescent *C. luhuanus* at both sites indicates more focused foraging efforts on subtidal sandy substrates, a trend potentially driven by the high aggregation rates of this species. For instance, a stock assessment of benthic fauna conducted across Milne Bay Province, Papua New Guinea found *C. luhuanus* numbers to be as high as 50+ per 3.2 m² transect (Skewes et al. 2002). Furthermore, historic observations on Utian Island, Papua New Guinea recorded the collection of 1753 individual *C. luhuanus* in 1 hr and 15 min by three woman foraging on the expansive sandy reef flats (Kinch 2003). Poiner and Catterall (1988) suggest a *C. luhuanus* colony with a higher proportion of juveniles and adolescents relative to adults may indicate intensive human foraging. Available evidence from Site 3 MBHM and Site 17 FBM suggests people were generally exploiting adolescent individuals from subtidal habitats, as such this archaeological trend is potentially representative of sustained targeted foraging behaviour rather than resource depression, particularly given the population age structure remained stable through time. However, we currently have limited understanding of shellfish foraging prior to 2000 cal BP on Lizard Island, particularly the condition of shellfish populations when these particular sites were first occupied. Future work will be required to examine whether cultural and/or environmental factors may have altered shellfish populations prior to the occupation and discard of shellfish remains at Site 3

MBHM and Site 17 FBM. Nonetheless, it is important to note that all size-classes (juvenile, adolescent, and adult) for both *C. luhuanus* and *R. nilotica* were generally represented in varying abundances through time. Given the correlation between size-class and preferred habitat for both *C. luhuanus* and *R. nilotica*, this may also indicate the implementation of foraging strategies that broadly targeted a wide range of habitat types. Based on life-history traits *R. nilotica* could be considered the most susceptible to human foraging pressure. However, based on available data there is no indication of external pressures altering the shellfish community structure available for exploitation of either reef flat species tested in this study.

These findings are generally in keeping with other studies conducted on Indigenous marine faunal foraging and hunting in northeast Australia, but with some interesting exceptions, such as the exploitation of nerites from eastern Torres Strait and the Whitsunday Islands. Urwin et al.'s (2016) study of dugong hunting in Torres Strait over the past 1000 years showed no evidence for over-exploitation, despite the susceptibility of dugong to over-hunting owing to slow maturation and reproductive rates. Carter's (2004) study in the Meriam Islands in the eastern Torres Strait found minimal change in *Lambis lambis*, *Tridacna* spp. and *R. nilotica*, but discernible change in *N. undata* and *C. luhuanus*. At Sokoli, *N. undata* slightly decrease in size after 1400 years ago, while *C. luhuanus* increase in size between 2600 and 1800 years ago and then are stable. At Ormi, both *N. undata* and *C. luhuanus* increase in size between site initiation at 2600 years ago and termination at 1600 years ago. Ulm's (2006b) study in the southern Great Barrier Reef showed no significant change in the mean size of *Anadara trapezia* (as measured by five attributes: length, height, width, weight and hinge length) throughout five deposits dating to the past 3900 years. Barker (2004:70, 127) found a consistent decline in the size of *N. undata* at Nara Inlet 1 over the past c.1500 years. Over the same time interval, Barker (2004:127) found a decrease in the average size of *Saccostrea cuccullata* at Hill Inlet Rock Shelter 1, but no significant change in the size of *N. undata* in the assemblage. The decline in *N. undata* size at both Sokoli and Nara Inlet 1 over the past 1500 years is an interesting commonality across the broader Great Barrier Reef region that requires further investigation, particularly the influence of local and/or regional drivers of change at these sites.

Based on available evidence, albeit from a limited sample size, Lizard Island intertidal and subtidal foraging of *C. luhuanus* and *R. nilotica* appears to be sustainable across the late Holocene, that is, there is no evidence for population collapse, or major alterations in the exploited population structure of either species over the past 2000 years. Notions of resource persistence were characterised by Jones et al. (2016:106) in their metadata analysis of the central Californian coastal fishery where the 'combination of a relatively low human population and highly productive fishery resulted in a clear

case of epiphenomenal sustainability'. Hence, sustainability is attributable to the combination of a massive resource versus the relatively low intensity Indigenous fishery (see also Codding et al. 2014). In other regions, such as the West Indies and Pacific Islands, millennial scale resource sustainability on islands has been attributed to resource resilience (e.g. Carder et al. 2007; Giovas 2016; Harris and Weisler 2017), whereby the implementation of flexible foraging strategies that target a range of marine environments and functionally diverse taxa, with life-history traits and behaviours that promoted stability under human foraging (e.g. strawberry conch), together supported long-term resource sustainability. However, future investigations will be necessary to provide additional datasets to more comprehensively test long-term exploitation of a range of marine resources in the region, including resource resilience, examinations of resource intensification models in this geographic context, and trajectories of small island colonisation for the northern Great Barrier Reef.

In contrast to the majority of archaeological evidence for shellfish foraging on the Great Barrier Reef, intensive exploitation of live top shell took place during the first half of the twentieth century after the collapse of the pearl shell fishery. Taylor (1925:218 cited in Daley 2014:68) reports that by 1916 500 tons of top shell were harvested annually, primarily for export to the Japanese market. Although size limits (>51 mm in diameter) were placed on top shell harvesting in the early 1950s to conserve stock, the use of shell for button-making was declining in favour of plastics, signalling the end of large-scale extraction. In any case, top shell stocks appear to have survived with reports of shells up to 203 mm in diameter (Rees 1962:102 cited in Daley 2014:70), and in the Lizard Island Group records note the taking of 15 tons of top shell in a 3 month period in early 1964. Daley (2014:70) concludes that thousands of tons of top shell were harvested from the Great Barrier Reef between 1912 and the 1950s. The industrialised scale of the historical fishery contrasts sharply with the likely low foraging pressure of Aboriginal people in the Lizard Island Group. Similar contrasts between pre-European resource stability and historical instability have been reported for the Pacific herring fishery across the Pacific Northwest (McKechnie et al. 2014).

Modern fisheries management throughout the Pacific to reduce human impacts on inshore, midshelf and outershelf environments has led to intensified conservation efforts. Archaeological records of marine resource exploitation across the globe are key repositories of information on past human-environment interactions. Erlandson and Rick (2008:1, 10) explain that 'humans have the heaviest impact on near-shore and coastal areas' and that the significance of zooarchaeological studies that address (1) optimal foraging strategies and/or patterns and, (2) make use of morphometric datasets, 'is that they can be readily compared to paleontological, historical, and recent ecological data sets to construct relatively long and continuous records of change in marine ecosystems'. As such, pre-

European baseline data for fisheries including shellfish and finfish has the potential to contribute to existing Great Barrier Reef fishing management strategies.

6. Conclusion

This study highlights the importance of determining size-at-age species behaviour patterns (e.g. age or sex division congregation) to directly assess the potential for forager impacts on intertidal ecosystems. Using size-at-age determinations derived from *C. luhuanus* and *R. nilotica* shell morphometric data for two Lizard Island sites suggests that shellfish community structure available for exploitation remained stable over the past 2000 years. However, there is currently no detailed evidence available regarding shellfish foraging before 2000 years ago on Lizard Island. Hence, future work will need to address this temporal gap in the data, particularly to consider the availability of shellfish resources and the factors that influenced conditions throughout the mid-to-late Holocene. Available evidence, albeit a small sample size, indicates the potential resilience of these shellfish resources to human foraging effects. These outcomes contribute to the growing discourse on small island archaeology, which suggests that these environments were perhaps not inherently fragile and the occurrence of human-induced resource overexploitation and extinction was not assured. Long-term marine resource use datasets are valuable for understanding past and present human lifeways and their impacts to island and coastal marine resources. Efforts to restore and sustain reefs including critical resources such as shellfish are necessary for the livelihood of human populations that access these resources across the Great Barrier Reef, but also to support health and resilience of the reef into the future.

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Supplementary Information

Table SI1

Descriptive statistics for *C. luhuanus* lip thickness per-250 year time interval from Site 3 MBHM and Site 17 FBM.

Site	Cal BP	Depth (cm)	Mean (mm)	Median (mm)	Std. Dev. (mm)	Min (mm)	Max (mm)	n=	Juve n(%)	Adol n(%)	Adul n(%)
Site 3 MBHM	500-750	0-3.8	2.88	2.97	0.66	1.42	5.12	185	21 (11.35%)	157 (84.86%)	7 (3.78%)
	750-1000	3.8-8.6	3.12	3.2	0.64	1.75	4.17	28	1 (3.57%)	24 (85.71%)	3 (10.71%)
	1000-1250	13.4-18.2	3.78	3.64	0.51	3.36	4.36	3	0 (0.00%)	2 (66.67%)	1 (33.33%)
	1500-1750	18.2-23.1	3.22	3.48	0.57	2.24	3.74	6	0 (0.00%)	6 (100.0%)	0 (0.00%)
	1750-2000	23.1-25.7	3.97	3.97	0.53	3.59	4.35	2	0 (0.00%)	1 (50.00%)	1 (50.00%)
Total								**224**	**22 (9.82%)**	**190 (84.82%)**	**12 (5.36%)**
Site 17 FBM	0-250	0-5.7	3.15	3.17	0.7	1.83	4.07	12	1 (8.33%)	8 (66.67%)	3 (25.00%)
	500-750	10.3-14.8	3.29	3.22	0.59	2.15	4.79	48	0 (0.00%)	41 (87.23%)	7 (14.89%)
	750-1000	14.8-19.4	2.82	2.62	0.79	1.94	5.01	19	2 (10.53%)	16 (84.21%)	1 (5.26%)
	1000-1250	19.4-23.9	3.1	3.01	0.96	1.51	5.92	21	2 (9.52%)	15 (71.43%)	4 (19.05%)
	1250-1500	23.9-28.5	3.26	3.36	0.69	1.6	4.38	26	1 (3.85%)	19 (73.08%)	6 (23.08%)
	1500-1750	28.5-34.2	2.85	2.72	0.68	2.16	3.9	8	0 (0.00%)	8 (100.0%)	0 (0.00%)
	1750-2000	34.2-50.6	2.86	2.86	0.15	2.75	2.97	2	0 (0.00%)	2 (100.0%)	0 (0.00%)
Total								**136**	**6 (4.44%)**	**109 (80.74%)**	**21 (15.56%)**

Table SI2
Descriptive statistics for *R. nilotica* maximum base diameter per-250 year time interval from Site 3 MBHM and Site 17 FBM.

Site	Cal BP	Depth (mm)	Mean (mm)	Median (mm)	Std. Dev. (mm)	Min (mm)	Max (mm)	n=	Juve n(%)	Adol n(%)	Adul n(%)
Site 3 MBHM	500-750	3.8	86.45	92.6	19.97	21.38	109.14	20	1 (5.00%)	2 (10.00%)	17 (85.00%)
	750-1000	3.8-8.6	82.54	88	21.77	34.34	102.05	8	1 (12.50%)	0 (0.00%)	7 (87.50%)
	1000-1250	8.6-13.4	104.68	98.15	14.45	94.64	121.25	3	0 (0.00%)	0 (0.00%)	3 (100.0%)
	1250-1500	13.4-18.2	21.58	21.58	0	21.58	21.58	1	1 (100.0%)	0 (0.00%)	0 (0.00%)
	1500-1750	18.2-23.1	84.23	70.71	24.47	69.5	112.49	3	0 (0.00%)	0 (0.00%)	3 (100.0%)
	1750-2000	23.1-25.7	64.67	65.45	26.19	38.09	90.47	3	0 (0.00%)	1 (33.33%)	2 (66.67%)
Total								38	**3 (7.89%)**	**3 (7.89%)**	**32 (84.21%)**
Site 17 FBM	500-750	10.3-14.8	69.59	65.95	32.81	34.16	112.31	4	1 (25.00%)	1 (25.00%)	2 (50.00%)
	1750-2000	34.2-50.6	77.49	87.72	20.63	53.74	91.02	3	0 (0.00%)	1 (33.33%)	2 (66.67%)
Total								7	**1 (14.29%)**	**2 (28.57%)**	**4 (57.14%)**