

# Shellfish Resilience to Prehistoric Human consumption in the southern Red Sea: Variability in *Conomurex* *fasciatus* across time and space.

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## Abstract

Intertidal environments have been the main source for mollusc gathering and consumption for at least the last 164,000 years. However, our knowledge of long-term trends is compromised by the fact that the majority of Pleistocene and early Holocene shorelines, and in turn their archaeological sites, are either currently submerged under water or have long been destroyed by sea-level change. Ecological information on the resilience of intertidal resources is crucial in assessing how attractive they were to past humans as a long-term source of food. Of particular interest is the southern Red Sea and its function as the southern gateway out of Africa into Arabia during a period of aridity. The role that marine food sources likely played in this dispersal is underplayed and largely ignored when interpreting periods of terrestrial aridity. Here we analyse the resilience of *Conomurex fasciatus* and report size measurements of over 15,000 specimens from the Holocene shell middens on the Farasan Islands, Saudi Arabia, as an ecological baseline for prehistoric shellfish exploitation to determine the long-term sustainability of shellfish harvesting in an arid environment. Changes in shell-size and relative abundance can indicate whether a species was subjected to changes in the intensity of human harvests and we use this dataset to reconstruct how the species was affected by a known intense exploitation period between 7,360 and 4,780 cal BP. Our results indicate no signs of resource depletion throughout the occupation period and add to the growing body of evidence that marine resources along arid shorelines are an important part of a mixed diet. Further, by measuring size changes occurring during early life stages of *C. fasciatus* we were able to reveal changes in size that were unaffected by

human harvesting pressure and instead suggest patch-selection as the main control. These results have implications for the interpretation of shellfish harvesting during periods of terrestrial aridity and specifically its potential as a reliable food source during the Palaeolithic migration out of Africa.

*Keywords:* Out of Africa, Coastal Archaeology, Farasan, Shell Sizes, Patch Selection, Shell midden

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## 1. Introduction

The southern Red Sea functioned as an important node in the network of human migration through time, most notably during the late Pleistocene (Flemming et al., 2003; Bailey and Flemming, 2008; Nielsen et al., 2017). It was particularly important during the major population movement out of Africa between 65 and 55 ka BP (Nielsen et al., 2017), which dates to a climate period of severe aridity in neighbouring regions (Tierney et al., 2017; Stewart and Fenberg, 2018). This aridity is expressed in a scarcity of vegetation and with it a scarcity of large terrestrial mammals, which would be more readily available during humid periods (Drake et al., 2011; Timmermann and Friedrich, 2016). A growing body of evidence now points towards marine food resources that would have been available during this major migration period despite the aridity on land (Evans et al., 2014; Inglis et al., 2014, 2019; Bailey et al., 2015, 2019; Sinclair et al., 2019). However, little is known about how substantial past marine food resources were and in turn how viable a coastal subsistence was. It is vital to understand their usefulness and their limits for a nuanced interpretation of past human subsistence and in turn long-term mobility of human migration patterns. This lack of information is due to the relatively short research history (Petraglia and Rose, 2009) as well as difficult preservation conditions, skewing chronologies (Durrani, 2001) and removing entire sites (Hausmann et al., 2019b; Bailey et al., 2019). In addition, coastal sites from the Pleistocene period are almost entirely absent due to large scale sea level changes, drowning ancient shorelines and making the necessary datasets virtually inaccessible (Lambeck et al., 2011). To learn more about coastal human ecology of the region, we draw information from well preserved sites of the Red Sea, dating to the mid-Holocene. These sites were occupied during similarly arid period (Arz et al., 2003), as was the case for the main period of human dispersal out of Africa (Tierney et al., 2017). Work on both sides of the Red Sea has documented important archaeological

30 sites that illustrate some of the activities and commonalities that both shores  
31 have shared (Khalidi, 2007, 2010; Mayer and Beyin, 2009; Meredith-Williams  
32 et al., 2014; Hausmann et al., 2019a; Beyin et al., 2019). Archaeological sur-  
33 veys show that marine resources were an important component of coastal  
34 subsistence, evidenced by over 4,000 sites spread along both sides of the Red  
35 Sea (Meredith-Williams et al., 2014). These sites have shell remains as their  
36 main component and are thus referred to as ‘shell middens’ or ‘shell matrix  
37 deposits’. The quantity of sites, the rapid accumulation of some shell de-  
38 posits (Hausmann et al., 2019b), and the increased consumption during the  
39 more arid seasons of the year (Hausmann and Meredith-Williams, 2017b),  
40 indicate the repeated and systematic collection of shellfish with potentially  
41 detrimental impacts on their populations.

42 The resilience (i.e. the ability to sufficiently recover from or respond  
43 to outside damage or disturbance) of shellfish populations to human con-  
44 sumption strongly influences their attractiveness as long term resources.  
45 Their predictability is a main factor explaining why, in many cases, they  
46 came to be relied on as an important part of the diet during the Holocene  
47 (Andersen, 2000; Alvarez et al., 2011; Gutiérrez-Zugasti et al., 2011; Habu  
48 et al., 2011; Bailey et al., 2013; Biagi et al., 2013; Villagran and Giannini,  
49 2014), and also Pleistocene sites frequently exhibit shells within their de-  
50 posits (e.g. (Barker et al., 2012; Gutiérrez-Zugasti, 2011; Jerardino, 2016;  
51 Colonese et al., 2018). In addition to their predictability, shellfish are easily  
52 accessible in the intertidal zone and can be gathered by most members of  
53 a community, providing them with a means of feeding themselves and ac-  
54 quiring tradable resources (Meehan, 1977; Waselkov, 1987; Erlandson, 1988;  
55 Bird, 1997; Thomas, 2015; Hardy et al., 2016; Jerardino, 2016). Despite their  
56 frequent occurrence through time, molluscs can be adversely impacted by hu-  
57 man harvesting activity, and it is unlikely that they remain viable as long  
58 term resources if they are not resilient to such activity (Seeto et al., 2012;  
59 Morrison and Allen, 2017). While coastlines are attractive for many other  
60 reasons (e.g. high terrestrial as well as marine biodiversity, increased connec-  
61 tivity across water, (Bailey, 2004)) a drop in shellfish abundance specifically  
62 could have had some negative impact on the attractiveness of the coastal  
63 near-shore environment as a source for easily gathered food. The resilience  
64 of shellfish species to human harvesting is commonly discussed in coastal ar-  
65 chaeology (Botkin, 1980; Koike, 1986; Claassen, 1998; Mannino and Thomas,  
66 2002; Mason et al., 1998, 2000; De Boer and Prins, 2002) and the general cri-  
67 teria to recognise the potential effects of unsustainable harvesting of a given

68 species are as follows:

- 69 1. Its abundance relative to other species will decrease.
- 70 2. It will be replaced by another less easily procured/processed species.
- 71 3. The mean shell size will decrease as a result of depletion of the larger  
72 specimens as the target of first preference.
- 73 4. The mean sizes of minimally gathered species will be relatively unaf-  
74 fected.

75 In context with criteria 3 and 4, changes in shell sizes can be deceiving  
76 without knowledge of the age structure of a given species (Claassen, 1998;  
77 Mannino and Thomas, 2002; Bailey et al., 2008), which can help to rule out  
78 environmental effects on the growth rate (e.g. general decline of nutrients  
79 over time). Most importantly, age is an indicator of whether specimens are  
80 old enough to reproduce. Consuming juvenile specimens before they can  
81 spawn a new generation will be more detrimental to the survival of the local  
82 population than consuming specimens that have already successfully repro-  
83 duced. Should harvesting gradually deplete populations until only juvenile  
84 specimens are available, no future generations would be able to grow. A key  
85 question arising from this is whether such intensive shellfish harvesting had  
86 occurred in the arid-period sites in the Red Sea, and whether this could be  
87 used to infer the general attractiveness of coastal environments during peri-  
88 ods of aridity. This has implications not only for Holocene exploitation, but  
89 also for shellfish consumption back into the Palaeolithic and for advancing  
90 the study of Palaeolithic coastal environments.

91 In this study, we aim to provide a diachronic statistical analysis of the  
92 relative abundances and shell sizes of the marine gastropod *Conomurex fas-*  
93 *ciatus* (Born, 1778; the lined conch) across archaeological sites and across  
94 different shorelines on the Farasan Islands to provide insight into coastal  
95 ecologies of the southern Red Sea during arid time periods. We make use  
96 of the Farasan Islands shell midden cluster (Fig. 1) and its large number  
97 of sites, to provide high spatial resolution that takes into account various  
98 geomorphological conditions of the intertidal zone.

### 99 1.1. Background

100 The southern Red Sea seascape consists of hundreds of islands, scattered  
101 along both shorelines together with two major archipelagos, the Farasan



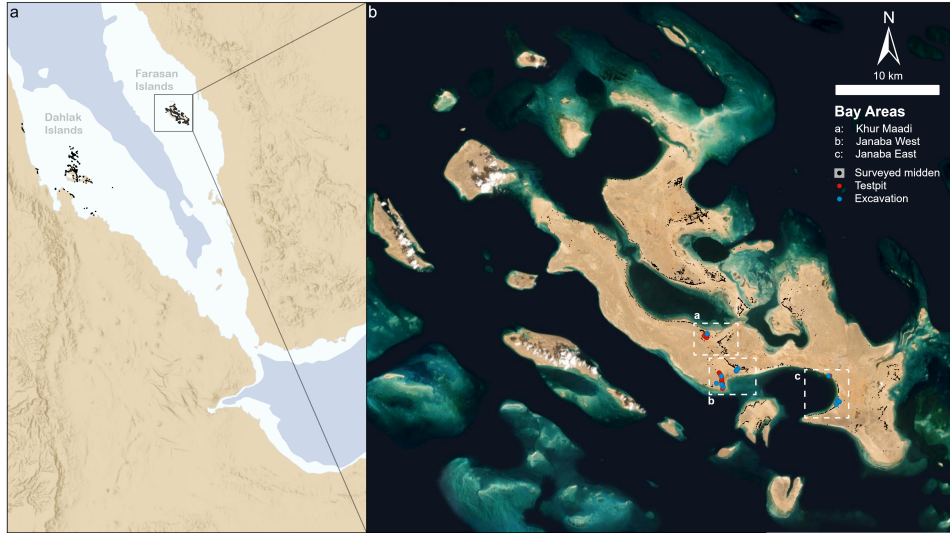


Figure 1: **Overview of the Farasan Island shell midden cluster.** a) Map of southern Red Sea. Black dots indicate shell midden sites in the Red Sea. b) the Farasan Island shell midden cluster. White rectangles indicate the three research areas where sites have been excavate, blue dots: excavations, red dots: test pits, small black dots: surveyed sites.

102 Islands and the Dahlak Islands, situated towards the southern end (Fig. 1).  
 103 The genesis of most islands is linked to the uplift of coral terraces following  
 104 diapirism as a result of this tectonically very active area (Almalki and Bantan,  
 105 2016; Almalki et al., 2015). As such, many islands consist of coral bedrock  
 106 with little or no topsoil’.

107 The sites in this study are all located on the Farasan Islands (Fig. 1b),  
 108 which are on the Arabian side of the Red Sea, about 40 km off-shore but  
 109 inter-connected through smaller islands less than a dozen kilometres apart  
 110 from each other. The landscape is generally arid with an annual precipita-  
 111 tion of only around 100 mm of rain. Holocene climate records indicate that  
 112 this arid period started around 8,000 years ago (cal BP) (Arz et al., 2003)  
 113 and thus covers the timing of shell midden accumulation (Hausmann et al.,  
 114 2019b). Earliest evidence of occupation of the Farasan middens dates to  
 115 7,360 – 7,030 cal BP (OxA-31167, uncalibrated date:  $6870 \pm 38$ ), but the ma-  
 116 jority of contexts dates to between 6,000 and 4,800 cal BP, which is a result  
 117 of the inundation of older shorelines and their sites dating to before 6,000 cal  
 118 BP (Lambeck et al., 2011). The similar aridity of the mid-Holocene to today  
 119 suggests that only a few plants populated the islands, supported by ground-

120 water (Mutairi et al., 2012). However, enough localised vegetation persisted  
 121 to maintain a population of gazelle (*Gazella arabica*). Gazelles likely relied  
 122 on food sources such as foliage, fruits, flowers, and also, to a lesser extent,  
 123 annual and perennial herbs (Wronski and Schulz-Kornas, 2015). Given that  
 124 these food sources are available for gazelle, it is likely that prehistoric humans  
 125 also made use of them, as well as hunting the gazelle itself, bones of which  
 126 are occasionally found in shell middens (Bailey et al., 2013). Seasonality  
 127 data on shellfish has demonstrated that shellfish was eaten year round, but  
 128 that their consumption during arid seasons was more frequent, indicating  
 129 that during these months they were used to compensate for the lack of other  
 130 food sources (presumably plant foods) (Hausmann and Meredith-Williams,  
 131 2017b). The shell midden data thus needs to be interpreted in conjunction  
 132 with an unknown, but significant amount of caloric intake from terrestrial  
 133 flora and fauna as part of a mixed diet. The Farasan Island shell midden  
 134 sites have been excavated in multiple seasons from 2009 to 2013. Getting a  
 135 good understanding of the cluster of over 3,000 sites as a whole meant being  
 136 selective about which sites to excavate and how to use information from one  
 137 site to make inferences about neighbouring sites (Fig. 2).



Figure 2: **Southwards view from JW1807 to neighbouring middens, which continue along the same palaeoshoreline towards the south of Janaba Bay.** Car tire tracks for scale.

138 Sites were selected to cover multiple different bays, representing subtly  
 139 different local environments. These bay areas are called Khur Maadi (KM)

140 and Janaba Bay, which is separated into Janaba West (JW) and Janaba  
141 East (JE). Each site was given a 4-digit number following the bay area code  
142 (e.g. KM1234). The results of the taxonomic analysis from 3 of these 19  
143 sites have already been published: KM1057 and JE0004 (Williams, 2010) as  
144 well as JW1727 (Hausmann and Meredith-Williams, 2017b), with the latter  
145 also including information on changes in size for the marine gastropod *C.*  
146 *fasciatus*.

## 147 2. Materials and Methods

### 148 2.1. *Conomurex fasciatus* (Born, 1778) - the lined conch

149 *C. fasciatus* (previously referred to as *Strombus fasciatus*) (Fig. 3) is a  
150 small, herbivorous true conch (Family Strombidae) that grazes on detritus  
151 and algae in tropical waters. Earlier research on this species is scarce and  
152 its ecology has only been touched on briefly when its use as an environmen-  
153 tal proxy for sea surface temperature was tested (Hausmann et al., 2017,  
154 2019a). The species favors shallow water habitats in and around reefs, in-  
155 cluding clean sand, seagrass beds, sand patches on reef flats, and sandy to  
156 muddy sand bottoms of lagoons and inshore waters (Liverani, 2013; Horton  
157 et al., 2019). *C. fasciatus* possesses a strong foot, allowing it to be very  
158 mobile by jumping short distances of about 30–40cm depending on the pre-  
159 vailing currents. They have been seen to congregate by the hundreds in some  
160 locations of the archipelago (G. Bailey pers. comm.). The shell reaches a  
161 maximum of c. 80 mm in length, with most adult specimens being between  
162 25 and 50 mm. There is a slight degree of sexual dimorphism with adult  
163 females being larger than males. There is no information on the lifespan of  
164 *C. fasciatus* specimens, but it is safe to assume they have a short life span  
165 of only a few years, similar to other smaller Strombid species (Walls, 1980).

166 Different to other mollusc species commonly found in shell middens, *C.*  
167 *fasciatus* grows the majority of its shell during the first year (Hausmann et al.,  
168 2017), a feature among strombids (Radermacher et al., 2009). Maturation  
169 occurs at the end of this growth period, and is visible by the development of  
170 a distinct thickening of the lip. How long and how fast this thickening takes  
171 place is unclear and oxygen isotope sequences indicate that lip growth rates  
172 are anywhere between 3 and 10 mm per year (Hausmann, 2015; Hausmann  
173 et al., 2017). Thus measuring the lip thickness to further determine age  
174 classes, as was done for other species (Ulm et al., 2019), is not possible here.  
175 The proxy for shell size used in this study, which we call the ‘aperture size’,

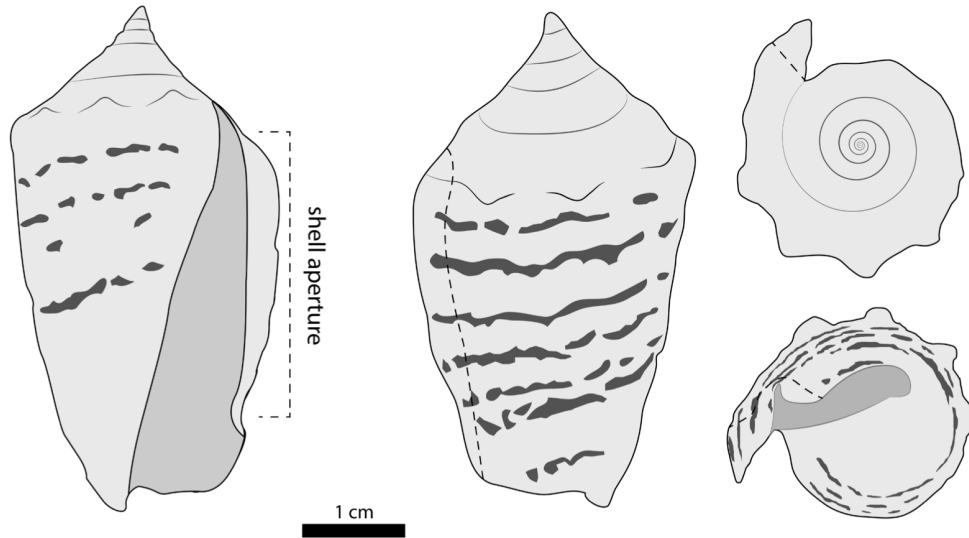


Figure 3: **Drawing of mature *C. fasciatus* shell and the location of the ‘shell aperture’ measurement between the shoulder of the shell and the stromboid notch.** Dashed line on drawings in the centre and on the right indicate the location of the developing lip at the beginning of maturity.

176 is the length measured between the stromboid notch, the location where the  
 177 eye-stalk protrudes and leaves an indentation in the lip, and the upper should-  
 178 er of the shell. This length remains identical throughout maturity and will  
 179 thus resemble the size at maturation. By measuring the shell size at mat-  
 180 uration we thus measure the cumulative result of shell growth-rates during  
 181 youth. These growth rates are dependent on internal as well as external fac-  
 182 tors, including nutrient availability and habitat suitability but also predation  
 183 by other animals or harvesting by humans, provided that gathering extended  
 184 to juvenile specimens (McCarthy, 2007; Giovas et al., 2010). On the one hand  
 185 this limited time-frame prevents the use of size/age-frequency distributions  
 186 to detect human impact on the mature molluscs beyond the point when spec-  
 187 imens mature and thus also means that the impact of harvesting by humans  
 188 remains undetectable, the harvest makes inroads into juvenile specimens at  
 189 the last stage of resource depletion. On the other hand, where human influ-  
 190 ence can be ruled out (i.e. in the absence of juvenile specimens), patterns  
 191 in size-frequency distributions can be linked directly to environmental condi-  
 192 tions (e.g. habitat suitability) controlling the growth rates, providing insight

193 into environmental variation that would otherwise be difficult to achieve.

## 194 2.2. Site sampling

195 The aim of excavations was to access information from stratigraphically  
 196 intact column samples at the centre of selected mounds, which we deemed  
 197 the most likely to provide the longest stratigraphic sequence (Table 1). In  
 198 total, 19 mounds were excavated by digging a cut from the outer rim towards  
 199 the midden centre, where column samples (10 x 25 x 25 cm within layer  
 200 boundaries) were extracted in bulk. In addition, test pitting was carried out  
 201 in 37 sites, to verify internal compositions of sites as they were indicated  
 202 by the surface layers. Because of their limited contextual information, these  
 203 latter datasets will be used in some but not all comparisons presented in this  
 204 study and are highlighted where this is the case.

Area	Site	Start Date [calBP]	End Date [calBP]	Total analysed shell weight [g]	n=apertures
Khur Maadi	KM1057	5250	5030	56,967.00	3,064
	Test Pits	/	/	25,675.89	1,058
Janaba West	JW1705	7360	2820	6,024.82	211
	JW1727	4780	4700	40,647.10	2,013
	JW2298	5710	4810	17,139.75	251
	JW1807	5420	4910	16,106.75	1,203
	JW1864	5940	5480	47,451.25	1,978
	JW3120	6590	5900	21,046.00	515
	JW5697	1790	1400/	1,294.00	/
	Test Pits	/	/	32,897.85	/
Janaba East	JE0003	/	/	1,210.00	10
	JE0004	5580	4830	26,580.75	1,208
	JE0078	5600	4950	28,548.70	1,585
	JE0087	5970	5850	46,493.00	2,156
	JE5642	6160	5730	8,235.00	210

**Table 1:** Overview of sites and material analysed within this study.

206 Each bulk sample was sieved using 1 mm, 2 mm and 4 mm mesh sizes.  
 207 However, any residue smaller than 4 mm was not analysed in great detail  
 208 due to the significant investment in time needed to identify these tiny shell  
 209 fragments. Less than 1 mm size residue was bagged and labelled as 'Un-  
 210 sorted Residue'. Residue that was larger than 1 mm but less than 2 mm was

211 briefly sorted to extract small shells or fish bone; the remainder was added  
212 to the 'Unsorted Residue' for potential later re-examination. Residue that  
213 was larger than 2 mm but less than 4 mm was sorted to extract all small  
214 shells, fish bone, or anything that appeared noteworthy. However, this was  
215 not an exhaustive process and this residue (2–4 mm) was therefore bagged  
216 separately and labelled 'Rough Sorted Residue', indicating that some mate-  
217 rial may have been missed and require further investigation at a later date in  
218 order to extract more detailed information. Lastly, residues over 4 mm in size  
219 were fully sorted and the only remaining materials that were not identified to  
220 species were small pieces of shell, stone and breccia which were bagged and  
221 labelled as 'Sorted Residue'. Whole and partial shells were sorted into species  
222 using a range of references (Bosch et al., 1995; Abbott et al., 1983; Coleman,  
223 2002; Debelius, 2000; Lieske et al., 2004; Mordan, 1980, 1986; Neubert, 1998;  
224 Oliver, 1992; Oliver et al., 2004; Sharabati, 1984; Vine, 1986; Zuschin and  
225 Oliver, 2003). If a partial shell could not be individually identified but could  
226 be identified to its genus it was labelled as that (e.g. 'Arca species' or 'Chama  
227 species'). Burnt shell as either whole or fragments was separated out and  
228 recorded as 'Burnt Shell'. This amounted to only a small total of 3,362 g,  
229 with an average of 1% of relative abundance per site.

230 During the shell sorting we encountered some problems that related pri-  
231 marily to shell degradation and a lack of reference material. These were  
232 sorted out in the following manner: The *Chama* species were frequently  
233 colourless with heavy erosion particularly of the exterior surface and many  
234 were been identified as *Chama pacifica* (Broderip 1835); this may in some  
235 cases have been a wrong identification. Some of the smaller shells were also  
236 identified as *Chama pacifica* but may be different species such as *Chama as-*  
237 *perella* (Lamarck 1819) and *Chama aspersa* (Reeve 1846). Consequently in  
238 the later identifications all *Chama* were often identified generically as '*Chama*  
239 *Species*'. It was decided that it would not be necessary to retrace and re-  
240 classify for this particular analysis but it may be necessary in the future if a  
241 different kind of analysis is required.

242 The *Pinctada* species were classified as '*Pinctada Species*', although it is  
243 likely that three different species are present: *Pinctada margaritifera* (Lin-  
244 naeus 1758), *Pinctada radiata* (Leach 1814) and *Pinctada nigra* (Gould  
245 1850). The shell of *Pinctada* was generally too worn and broken for any  
246 certainty in separation of species.

247 The third possible misidentification relates to the *Chicoreus* species where  
248 some shells identified as *Chicoreus ramosus* (Linnaeus 1758) may in fact be

249 *Chicoreus virgineus* (Röding 1798). Again it was not necessary to re-examine  
250 this distinction for this type of analysis as these two species occupy very  
251 similar ecological niches. For a similar discussion regarding the difficulties in  
252 analysing mollusc remains and the potential for over-identification see Szabo  
253 (2009).

254 The primary unit used in the following analysis is weight. This unit is not  
255 unproblematic, as it is not directly related to either shell size or meat weight,  
256 and can change dramatically pre and post deposition depending on the pro-  
257 cessing technique (i.e. roasting), subsequent hearths on top of shell deposits,  
258 or the effects of leaching (Faulkner, 2011; Oertle, 2019). However, the Farasan  
259 Islands have had very little precipitation since the mid-Holocene, reducing  
260 the influence of leaching. Additionally, while we saw evidence of hearths and  
261 roasting in the deposits, these were of very limited extent, pointing towards  
262 very short episodes of heating and no intense use of fires, as would be required  
263 to induce significant weight changes (Oertle, 2019). In addition, shell weight  
264 is not influenced by fragmentation, which plays a substantial role in our de-  
265 posits. This influence is especially true for the main component, *C. fasciatus*,  
266 which has thin shell walls and fragments easily and into many parts, which  
267 is why we did not use NISP (Number of Identified Specimens) for our study.  
268 Lastly, we chose not to use MNI (Minimum Number of Individuals), as it  
269 excludes species where the NRE (Non-Repetitive Element) is not present,  
270 which we wanted to avoid, due to many species being present in only minor  
271 quantities (for a more detailed discussion on the subject see also Claassen  
272 (2000), Glassow (2000) and Mason (2000).

273 A proxy for shell size was found for *C. fasciatus* shells by measuring the  
274 size of the aperture (Fig. 3) using digital calipers to the nearest hundredth  
275 of a millimeter. This method increased sample sizes, because it allowed the  
276 inclusion of specimens that were partially fragmented and where the total size  
277 or width were not preserved. The aperture itself preserves comparatively well  
278 as it is a robust part of the shell. While measures of other species dimensions  
279 were also taken, a focus on *C. fasciatus* was undertaken because it is the  
280 dominant species in most layers and sites (Bailey et al., 2013).

281 All records were made on paper and subsequently transferred to digital  
282 media. All analyses were carried out in R (Team R, 2013) and site spe-  
283 cific data can be accessed in the Supplementary Materials as well as online  
284 (Hausmann et al., 2020). For the comparison of mean aperture sizes through  
285 time we were restricted by the number of radiocarbon-dated layers and sites,  
286 meaning that some sites were not considered (see Table 1) and that layers

287 were assigned dates based on the interpolation of minimum and maximum  
288 ranges of the individual sites at a high degree of chronological resolution.  
289 This method is not sufficient to reveal synchronicities between sites, but was  
290 deemed sufficient to structure the mean aperture size data for an overview  
291 of intra-site changes and a general comparison between bay-areas.

### 292 3. Results

#### 293 3.1. Species composition

294 As shown previously (Bailey et al., 2013; Hausmann and Meredith-Williams,  
295 2017b), the majority of shell weight derives from *C. fasciatus* shells. This is  
296 true for almost all analysed sites (Table 2, Fig. 4) as well as for bay areas  
297 (KM:91% of *C. fasciatus*, JW:84%, JE:85%) as a whole (Fig.5). Other com-  
298 mon species are *Chama* sp. (KM: 4%, JE: 3%), *Spondylus spinosus* (KM:  
299 2%, JE: 1%), *Chicoreus* sp. (JW: 2% and JE: 7%), *Pinctada* sp. (JW: 3%,  
300 JE: 2%) Also, *Arca avellana* features commonly in JW (3%).



Area	Site	<i>Conomurex fasciatus</i>	<i>Pinctada</i> sp.	<i>Chicoreus ramosus/virgineus</i>	<i>Chama pacifica</i>	<i>Spondylus spinosus</i>	<i>Tricornis (Strombus) tricornis</i>	<i>Plicatula Plicata</i>	<i>Arca</i> sp.	<i>Pleuroploca trapezium</i>	<i>Ostrea</i> sp.
Khur Maadi Test pits	KM1057	93			4	2					
	KM1048	4		11	27	27		28	1		
	KM1050	93	5	1	2	3			1		
	KM1051	65	1	2	17	6	1	3	2		
	KM1052	89		1	6				2		
	KM1053	95		1	1	3					
	KM1054	49		18	14	5		2	6		
	KM1056	22			4	30	21		3		
	KM1304	100									
	KM1307	100									
	KM1313	99					1				
	KM1317	86			2		3	6	2		
	KM1328	95		1	1				1		
	KM1330	67			19			3	3	1	1
	KM1335	99					1				
	KM1336	100									
Janaba West	JW0001	68		3			13		4		1
	JW0002	39	1	36	4		9		3	5	
	JW0003	25	2	23	25		17	3			
	JW0004	94	1	1	2		1		1		
	JW0005	84			8		2				

Area	Site	<i>Conomurex fasciatus</i>	<i>Pinctada</i> sp.	<i>Chicoreus ramosus/virgineus</i>	<i>Chama pacifica</i>	<i>Spondylus spinosus</i>	<i>Tricornis (Strombus) tricornis</i>	<i>Plicatula Plicata</i>	<i>Arca</i> sp.	<i>Pleuroploca trapezium</i>	<i>Ostrea</i> sp.
	JW0006	92	1		2		1				
	JW0007	98						1	5		
	JW0008	79	3	2	1		1				
	JW0009	85	4	1	4				1		1
	JW0010	96			2				3		
	JW0011	52	8	28					2		1
	JW0012	86	3	1	2		1	1			1
	JW0013	84	5	6	1						
	JW0014	86	5	1	1				5		1
	JW0015	54	15	9	5			2			2
	JW0016	91	4		1		1		2		
	JW0017	5	69	1	1			8	1		9
	JW0018	63	25		2			6	1		1
	JW0019	10	55	4	14	6		5			4
	JW0021	93									
	JW1705	75					1		1		
	JW1727	67			1		1		11		1
	JW1807	92	1		1		1				
	JW1864	99									
	JW2298	73	9					1	1	5	1
	JW3120	95					4				
	JW5697		60							25	13
Janaba East	JE0003	18	9	46	1	1		1		23	

Area	Site	<i>Conomurex fasciatus</i>	<i>Pinctada sp.</i>	<i>Chicoreus ramosus/ virgineus</i>	<i>Chama pacifica</i>	<i>Spondylus spinosus</i>	<i>Tricornis (Strombus) tricornis</i>	<i>Plicatula Plicata</i>	<i>Arca sp.</i>	<i>Pleuroploca trapezium</i>	<i>Ostrea sp.</i>
	JE0004	64	8	15	5	4		2			
	JE0078	86		9	4						
	JE0087	98		1							
	JE5642	92	1	2	3	1					

301

302

Table 2: Site composition in shell weight percentage. Note that numbers were rounded to the

closest percent, except for values between 0 and 1, which were rounded up to 1

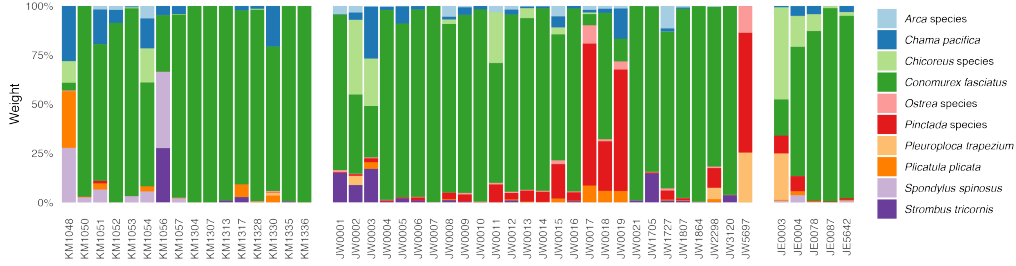


Figure 4: **Species composition by site.** Note that the graph only represents the main identified species as listed in Table 2

While these are not the main edible species and the relative abundance is low, they indicate the range of harvested areas as well as the nature of processing shellfish at the individual sites. Simpson indices and Shannon's Evenness have been calculated to assess changes in species diversity (Supplementary material), however with *C. fasciatus* being a dominant component of the overall composition, Simpson's Index is strongly controlled by the relative abundance of *C. fasciatus* in each layer, with little to no long-term trends through the individual site stratigraphies.

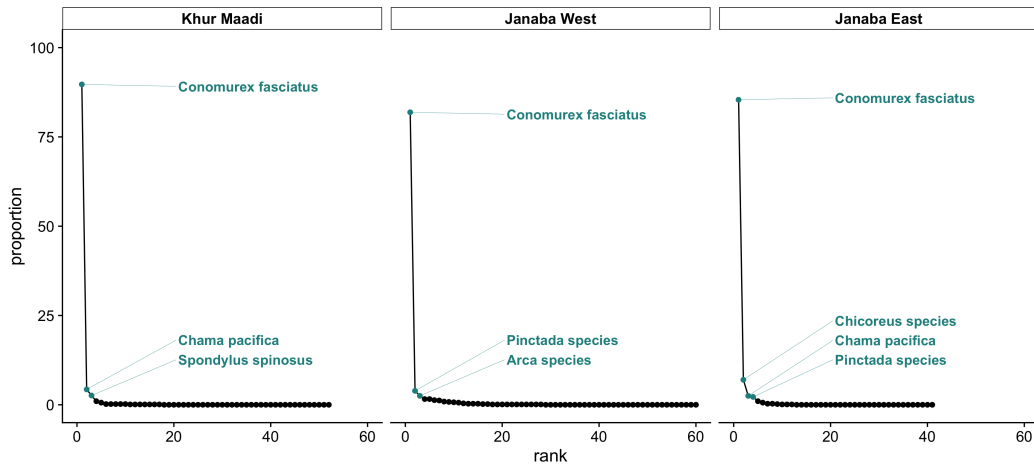


Figure 5: **Dominant species in each bay area shown as weight percentage.** Named species represent more than 2% of the overall weight

### 3.2. *C. fasciatus* size distributions by area

Aperture size frequency distribution diagrams (Fig. 6a) show an area-specific grouping of shell sizes (in mm) at Khur Maadi (mean: 22.9, SD: 1.8), Janaba West (mean: 21.4; SD: 1.7), and Janaba East (mean: 19.7; SD: 1.5). A one-way ANOVA test indicates that these are significantly different ( $p < 0.001$ ) and a post-hoc Tukey-Kramer test shows that this is the case for all pairings (adj.  $p < 0.001$ ). Grouping the mean apertures sizes by site reveals some overlap between sites of different bay areas (note the clear overlaps in Fig. 6b JW1807 to KM1052 as well as KM1048 and KM1056), with the largest mean aperture size in KM1054 (23.5 mm) and the smallest mean aperture size in JE0004 (18.9 mm). Figure 6b also reveals that the biases in different quantities of measured shell specimens per site have little influence on mean aperture size per bay-area (i.e. sites with many measurements do not dramatically skew the average value per area). Not surprisingly, the largest shell specimen (31.84 mm) was found in KM1057, which is part of Khur Maadi Bay. The smallest specimen (10.60 mm) was found in JE0087, which is part of Janaba East. It belonged to the small quantity of juvenile specimens that are reflected in the rare outliers, which occur well beyond the size range of the majority of *C. fasciatus* specimens. Juvenile specimens are exceptionally rare ( $< 0.8\%$ ), pointing towards some degree of pre-selection that preferentially targets specimens which had already developed the characteristic lip. While site-level distributions of aperture sizes indicate bi-modality for some sites (e.g. JW1705, JE0078), this bi-modality is not consistent and insufficiently clear to be interpreted with confidence in terms of sexual dimorphism.

### 3.3. *C. fasciatus* size distributions through time

Comparing mean aperture sizes through time was only possible for the sites that have been radiocarbon dated (Table 1; KM1057, JW1727, JW1807, JW1864, JW2298, JW3120, JE0004, JE0078, JE0087, JE5642).

The trend through time estimated for all sites as a group (blue line in Fig. 7a) demonstrates some short-term variability, but with no indication of a clear long-term trend. However, when sites are subdivided into groups by bay area, a two-sample t-test indicates significant differences between earlier (6,250–5,800 cal BP) and later (5,000–4,800 cal BP) periods in Janaba West and Janaba East (Janaba West:  $t = 3.9$ ,  $df = 1218$ ,  $p < 0.001$  and Janaba East:  $t = 13.4$ ,  $df = 579$ ,  $p < 0.001$ ). The purple line for Janaba East in Figure 7 clearly describes a trend towards smaller sizes, while in Janaba West

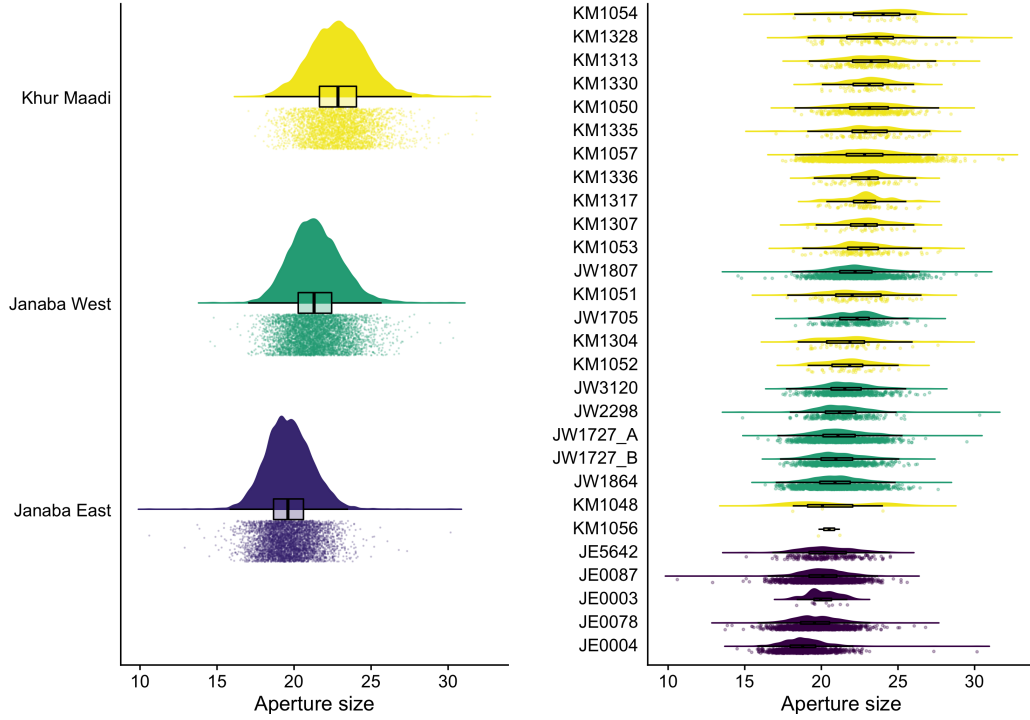


Figure 6: **Raincloud plots of the aperture sizes by area (left) and by site (right)** Each raincloud plot consists of a distribution curve on the top, a boxplot indicating the individual quantiles, and each individual measurement as a point within the point cloud at the base. For more information see Allen et al. (2018).

348 this trend is not quite as visible due to a short-lived increase between 5,500  
 349 and 5,000 cal BP. Khur Maadi Bay only features one dated site (KM1057;  
 350 5,250–5,030 cal BP), and exhibits no consistent tendency to size reduction  
 351 over time. However, when the data are further subdivided into individual  
 352 site sequences, the consistent time trends disappear (Fig. 7c). Moreover,  
 353 the intra-site variation is relatively small compared to the range of variation  
 354 when sites are grouped by bay area. In other words, the long-term time  
 355 trends apparent in Fig. 7b are largely illusory, resulting from the conflation  
 356 of short-term individual site sequences, each with its own range of aperture  
 357 sizes.

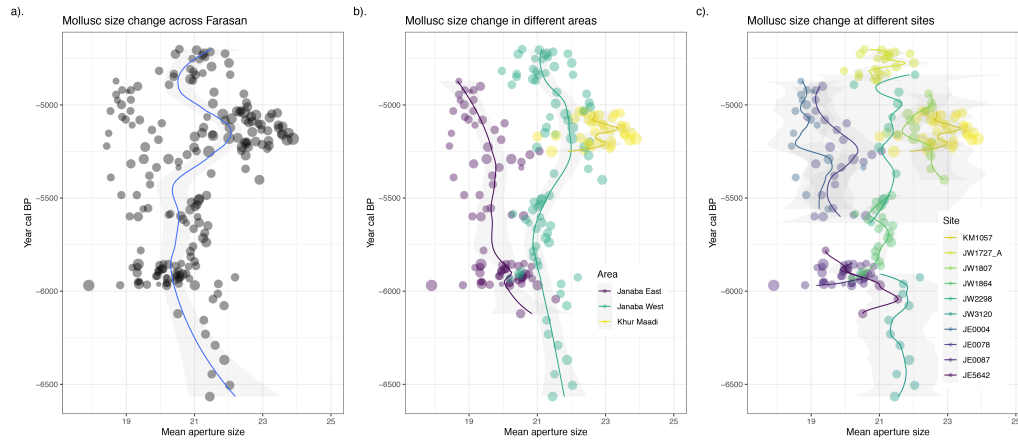


Figure 7: **Mean aperture sizes through time.** **a**, all mean aperture sizes through time without spatial grouping; **b**, mean aperture sizes by bay area; **c**, mean aperture sizes by site. The size of the each circle indicates the standard error of the measurements in that sample. Lines describe mean aperture size calculated through LOESS (locally estimated scatterplot smoothing) with a grey confidence interval of 95%.

## 4. Discussion

### 4.1. Species composition

Taxonomic analyses showed that *C. fasciatus* was consistently the main site component by weight (and due to its small size likely also by MNI). While other species were also exploited (especially at JW5697 and JE0003), the main gathering activities focused on *C. fasciatus*. This could be a product of this species being easily gathered (they congregate in large quantities in shallow water (0.5–1.5 m) and are not attached to rocks or corals). A potential bias towards *C. fasciatus* in our sites could be a result of how *C. fasciatus* was being processed in prehistory: in bulk and at the immediate shore. There are other species that were also accessible, but their shells are less likely to find their way into midden deposits. For instance, this may be the case with *Tridacna* sp. (the giant clam) (sparsely found in JE0004). Due to its size, and the fact that it cements itself to a hard substrate, it is easier to cut the shellfish meat out of the shell at the time of collection and while still in the water (Bird, 1997). The shell itself thus gets discarded in the subtidal rather than being brought back to the shore for processing, as is the case for other shell species, many of which require heating to extract the meat (Waselkov, 1987). While the above biases need to be taken into

377 consideration, we are confident that they are not substantial enough to affect  
378 our conclusions about the dominance of *C. fasciatus* as the principal target  
379 species.

#### 380 4.2. Shell sizes

381 The morphology of the dominant species *C. fasciatus* restricted our win-  
382 dow of opportunity for analysing size frequency distributions juvenile and  
383 young adult specimens. Thus any indications of reduced frequencies of older  
384 and larger specimens, indicating over-harvesting, are not detectable. Nev-  
385 ertheless, with less than 0.8% of juveniles in our assemblage, we can rule out  
386 that juvenile specimens were targeted and that over-harvesting to a degree  
387 where specimens were eaten prior to being reproductively active has taken  
388 place. One caveat to this is the fragility of juvenile lips in comparison to ma-  
389 ture, thicker lips, which provide more protection. It is therefore possible that  
390 juvenile specimens are under-represented because of differential preservation.  
391 While this bias is difficult to quantify, we do not expect it to significantly  
392 shift the proportion of juvenile specimens above a few percent. With the re-  
393 production of specimens being unaffected (not counting the positive effect on  
394 fecundity (Harding et al., 2008) of older specimens) and *C. fasciatus* retain-  
395 ing its role as dominant species throughout the midden accumulation period,  
396 the resilience of *C. fasciatus* to prehistoric human harvesting can be argued  
397 to be substantial. This aspect is especially noteworthy given the large quan-  
398 tities of shellfish represented by the over 3,000 midden sites on the Farasan  
399 Islands (Meredith-Williams et al., 2014), the year-round collection of shells  
400 (Hausmann and Meredith-Williams, 2017b), and shell accumulation rates  
401 of up to 1.7 m per century per site (Hausmann et al., 2019b). This puts  
402 the Farasan middens apart from other sites, where studies have indicated  
403 significant impacts on mollusc populations by prehistoric or pre-contact har-  
404 vests (Mannino and Thomas, 2002; Morrison and Hunt, 2007; Klein, 2008;  
405 Faulkner, 2009; Erlandson et al., 2011; Hunt et al., 2011). That being said,  
406 evidence of small to no changes (Rick et al., 2016) or even increase in shell  
407 size following human harvesting is becoming more common (Giovas et al.,  
408 2010; Thakar, 2011). It should be noted here that comparisons in terms of  
409 the intensity of over-harvesting, are limited by the fact that the studies above  
410 use different species and that our limited age-window only provides a sim-  
411 plified view on over-harvesting. With <99% of specimens reaching the stage  
412 of maturity, their frequency distribution patterns are a result of processes  
413 that are disconnected from human harvesting and instead linked to the local



414 environmental conditions. Because these variations influence the majority of  
415 measurements they are worth looking into, which we will do in the following.

#### 416 4.3. Patch selection and nearshore environments

417 An often mentioned but unaddressed aspect of size frequency distribu-  
418 tions of shells is the variability of growth conditions among different collec-  
419 tion areas. Giovas et al. (2010), one of the few studies that systematically  
420 discusses each possible cause for shell size changes, describe changes in patch  
421 selection as “although plausible, [...] largely untestable.” (Giovas et al., 2010,  
422 p. 2795). This problem is linked to most shell midden sites having a po-  
423 tential gathering area of more than a square-kilometer, making it difficult to  
424 be certain exactly where shellfish were collected. This uncertainty increases  
425 with the use of water craft (Andrus and Thompson, 2012), and also at Pleis-  
426 tocene or early Holocene sites, where shorelines are not preserved (Lambeck  
427 et al., 2011; Astrup, 2018) or where sites are too distant from a specific part  
428 of the shoreline to make an obvious inference on patch choice. The Farasan  
429 sites do not suffer this problem, because of the ubiquity of preserved shell  
430 midden sites, the homogeneity of the shore-line processing sites, and the  
431 close distance (10–30 m) between sites (Fig. 2). Under these conditions it  
432 is possible to make some spatial association between gathering patches and  
433 the nearest and most obvious midden on which to process the shellfish. In  
434 short, we assume that any midden from Khur Maadi Bay, Janaba Bay West,  
435 or Janaba Bay East was likely accumulated using shells that were collected  
436 close to the site and thus within their respective bay area. By looking at the  
437 variable habitats and geomorphology of each bay we can better understand  
438 the variation in shellfish size.

439 Table 3 describes the preferred habitats of the dominant and commonly  
440 found species in the analysed shell middens. Based on the fairly similar  
441 species compositions of the sites and the relative abundances of *C. fasciatus*,  
442 we concluded that the gathering areas for all bays mostly consisted of inter-  
443 tidal to subtidal environments made of mixed substrates of sand and corals,  
444 as well as their margins. As expected, these habitats are typically found in  
445 the shallow reefs along shorelines today and are especially representative of  
446 the shallow-water areas of Janaba West and the shallow and protected area  
447 of Khur Maadi Bay (Fig. 8).

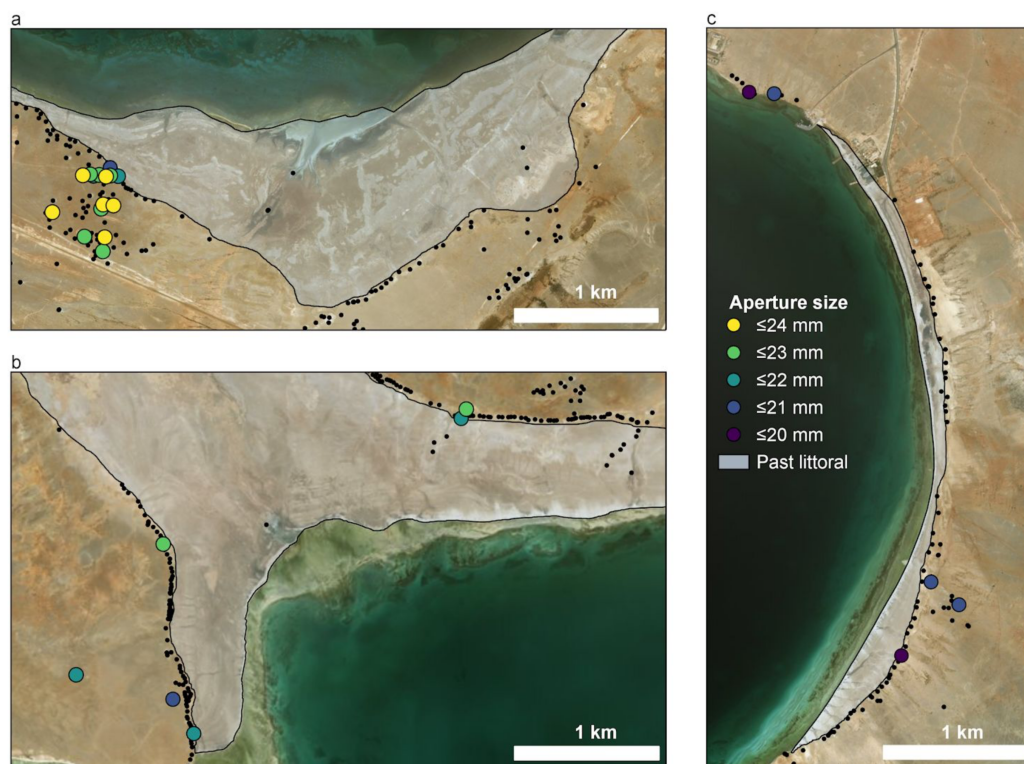


Figure 8: **Farasan bay areas of this study** **a**, Khur Maadi Bay; **b**, Janaba West aperture; **c**, Janaba East. We indicate the potential size of the near-shore littoral zone at the time of higher sea level during the period of shell midden occupation. Colours of sites indicate mean aperture size.

Name of genus/species	Common habitats
<i>Conomurex fasciatus</i>	Littoral to sublittoral sandy, shallow reefs. Often found grazing on seagrass.
<i>Chicoreus</i> sp.	Littoral to sublittoral, sand or rocky/coral on shallow reefs, protected bays and lagoons.
<i>Pinctada</i> sp.	Offshore to littoral –5 to 250 m, mixed and hard substrates to which it is bysally attached. In some cases free living (not attached).
<i>Chama</i> sp.	Low littoral to offshore, cemented to coral and rocks.

<i>Spondylus spinosus</i>	Sublittoral to offshore, cemented to coral and rocks.
<i>Beguinia</i> sp.	Intertidal areas in sand and rocks.
<i>Modiolus</i> sp.	Wide range of habitats, most common in rocky habitats, less often in sandy areas. Often associated with seaward edges of seagrass beds and the landward margin of ridges vegetated with algae.
<i>Tricornis (Strombus) tricornis</i>	Grazes in shallow water, soft substrates and corals
<i>Arca avellana</i>	Littoral to sublittoral (up to −80 m), rocky habitats, corals, or under boulders on sandy substrate.

**Table 3: Commonly found species in Farasan shell middens and their preferred habitats**

450 Comparing the shorelines of the three areas shows that these shallow  
451 water areas of the littoral in Khur Maadi and Janaba West are more extensive  
452 than the ones in Janaba East. We further need to take into account the  
453 changes in sea-level since the shell midden occupation (Lambeck et al., 2011;  
454 Hausmann et al., 2019b). With the sea-level highstand at around 6,000 cal  
455 BP being 2 m higher than today and the palaeoshorelines of Khur Maadi and  
456 Janaba West mirroring these changes, we can conclude that their respective  
457 shallow-water areas were more extensive than they are today. In comparison  
458 Janaba East would have featured a similarly narrow band of shallow water  
459 as it does today, with the sites JE0004 and JE0003 being located close to  
460 an even narrower area than the more southern sites (JE0078, JE0087, and  
461 JE5642).

462 These groupings of extensive (KM and JW) and narrow (JE) shallow wa-  
463 ter areas with their sandy substrates and favourable conditions for seagrass,  
464 fit well with the different sizes of *C. fasciatus* (Fig. 5). The preferred habitats  
465 of this species are found in the upper littoral where it can graze on seagrass  
466 (Table 3). That said, the sizes of shells from Khur Maadi and Janaba West  
467 are still quite different from each other, despite the similar geomorphology  
468 of the bays. It is possible that the more sheltered location of Khur Maadi,  
469 between the two larger islands (Fig. 1), provides it with a more sheltered  
470 environment than the exposed shorelines of Janaba Bay. Ultimately, it is dif-  
471 ficult to reconstruct past shoreline environments without a detailed analysis  
472 of local geomorphology and further analyses of other represented species (not

473 exclusively molluscan) that have lower relative abundances in shell middens.  
474 In the future, this information will no doubt provide a more detailed pic-  
475 ture of the spatial variability in species composition along shorelines. How  
476 much the different shell sizes actively influenced patch-choice by humans is  
477 questionable. Figures 6b and 6c indicate for example that the beginning of  
478 shellfish gathering in Janaba East was not triggered by a decline in shellfish  
479 size in other bay areas. Moreover, both parts of Janaba Bay were harvested  
480 substantially and over a long term, despite shell sizes in Khur Maadi being  
481 higher and the economic return likely higher as well. We can thus assume  
482 that patch-choice by humans was not chiefly controlled by the minute (yet  
483 statistically significant) differences in shell sizes, as they hardly translate in  
484 practical differences for gatherers, but are a product of several factors such  
485 as general availability, accessibility, as well as social factors.

#### 486 4.4. *Implications for the southern Red Sea*

487 The shorelines of the southern Red Sea are variable and have experienced  
488 dynamic shifts and geomorphological transformations in the past (Lambeck  
489 et al., 2011). These likely influenced the local ecologies of marine molluscs.  
490 The variety of impacts that the geomorphology of the shoreline has on shell-  
491 fish abundance has been shown before in the context of reconstructing past  
492 human coastal ecologies (Fa, 2008; De Vynck et al., 2016; Chakroun et al.,  
493 2017; De Vynck et al., 2019). In our dataset, we see similar importance  
494 for growth rates of grazing molluscs, with larger specimens (and thus larger  
495 caloric value) in areas of extensive shallow water areas. However, we also  
496 found that in the areas where shorelines were less extensive (Janaba East)  
497 and comparatively steep (the north of Janaba East), and where shell-sizes  
498 were the smallest and least profitable (JE0004), shellfish harvesting was still  
499 carried out over long periods without signs of over-harvesting.

500 On a temporal scale, the shell midden use seems to happen in parallel  
501 for multiple sites for some centuries, pointing to continuous external stresses  
502 for *C. fasciatus* populations. But the temporal resolution would still allow  
503 for some gaps and for individual patches of shellfish populations to recover  
504 before long-lasting ecological perturbations take effect. More information  
505 on *C. fasciatus* mobility and population structure would help to disentangle  
506 the impact of an individual site on the 'midden's local patch', which could  
507 be dramatic and difficult to recover from in the short-term, and the impact  
508 on the population of *C. fasciatus* across one bay or the archipelago as a

whole, which might have been much less dramatic but could still cause some long-term perturbations currently invisible to us.

Evidence of shell fish populations in upper parts of the littoral being replenished by the population occupying the lower parts, which are not being harvested by humans (De Vynck et al., 2019), could explain the long-term resilience of *C. fasciatus* that we see on Farasan.

A potentially small impact that prehistoric humans had on mollusc populations in general could also be the base for a sustainable harvesting strategy. Seasonal structuring of layers using oxygen isotope sequences in one layer of JW1727 indicated a continuous occupation over 6-7 months (Hausmann and Meredith-Williams, 2017a). The volume of shells in the layer would represent 1 kg of shellfish meat per day. Given the various date ranges of sites along the west of Janaba Bay (Table 1) and the probability of a less continuous occupation of JW1727 at other times, these values are difficult to extrapolate to other sites, but are in a similar range as ethnographic accounts of sustainable shellfish harvesting (Bird, 1997).

How these practices of sustainable shellfish gathering and coastal subsistence could translate to Pleistocene periods of human migration out of Africa has only recently been explored (Inglis et al., 2014, 2019; Bailey et al., 2015, 2019; Sinclair et al., 2019). The Farasan shell midden dataset derived from a more than 2,500 year long occupation represents a Holocene reference point of what was possible given the arid environmental conditions overall. Importantly, whilst research of southern Red Sea coastal subsistence has been heavily biased towards the Farasan shell middens, similar sites have also been found on the other side of the Red Sea, showing similar clustering and preservation (Meredith-Williams et al., 2014; Beyin et al., 2019). Coastal sites dating further back into the Pleistocene are not uncommon and the use of shellfish dates back to 164,000 BP (Marean et al., 2007). For the major migration periods of 65 to 55 ka BP (Nielsen et al., 2017), we can assume that these practices could have been employed without difficulty by anatomically modern humans and that molluscs were likely consumed where available. Moreover, open-air shell middens on shorelines can act as visible landscape features that indicate a local food resource (Gonçalves et al., 2014) and can aid human migrations that follow previous shell midden users along tested corridors. However, the necessary size, quantity, and efficiency of middens which guide these followers is only possible due to the resilience of the local mollusc population.

The implications of having a resilient, abundant, predictable and easily

547 accessible coastal resource at one of the important nodes of human mobility -  
548 the southern Red Sea - adds an extra dimension to the study of Out Of Africa.  
549 The fact that these resources are also unaffected by arid conditions adds an  
550 additional complicating factor to arguments that past dispersal events were  
551 limited to periods of greater moisture availability.

552 In the future it will be important for archaeologists to quantify which  
553 marine resources were available, to better supplement these claims and to  
554 provide a more nuanced view on which marine environments would be pre-  
555 ferred, rather than a one-size-fits-all approach. To gain such a comprehensive  
556 view on the variety of past coastal ecologies, it is necessary to reconstruct  
557 submerged littorals and their past ecological potential. Although traces of  
558 human activity along palaeoshorelines may be difficult to find due to obvious  
559 taphonomic reasons resulting from sea-level change, it may be possible to find  
560 evidence that indicates what marine resources were potentially available.

561 Uplifted fossilised coral reefs are an opportunity to gain such ecological  
562 information and study past near-shore environments as well as the species  
563 which would have been available for exploitation (Khalil, 2012; Almalki et al.,  
564 2015; Almalki and Bantan, 2016; Bantan and Abu-Zied, 2014; Bantan et al.,  
565 2015; Abu-Zied and Bantan, 2018).

566 Information from these reefs show that many of the species found in the  
567 Farasan shell middens (e.g. *C. fasciatus*) were also available in the Red Sea  
568 during the Pleistocene (Khalil, 2012; Abu-Zied and Bantan, 2018; Almassari  
569 and Gameil, 2019) and *C. fasciatus* was even abundant during MIS5e (Abu-  
570 Zied and Bantan, 2018). This long population history indicates that not only  
571 was there a permanent connection to the Indian Ocean providing access to  
572 important nutrients, but also that the response of near-shore environments to  
573 sea-level change was mainly shifting spatial distribution locally, rather than  
574 a wholesale change in species composition. Currently most datasets focus on  
575 present day exposed reefs that were either uplifted, or date to times of higher  
576 sea-level (i.e. MIS5); it is up to future research to fill the gap between these  
577 and Holocene populations and expand these datasets to submerged reefs.

## 578 5. Conclusions

579 With the analysis of shell remains from the Farasan Island shell midden  
580 complex, this paper provides insights into southern Red Sea shellfish harvest-  
581 ing in prehistory. The data demonstrate that even with intensive year round  
582 harvesting over long periods, the shellfish beds were not negatively impacted

583 and remained available despite arid conditions on land, supposedly making  
584 the landscape inhospitable.

585 This paper demonstrates that there are spatial variations in shellfish  
586 growth rates that occur prior to human harvesting, which are thus more  
587 likely to be linked to environmental conditions controlling the growth rates  
588 of molluscs in different patches. We also show that these spatial variations  
589 can produce pseudo patterns of changes in shellfish size through time. Thus  
590 changes in patch selection, visible both because of the high spatial resolution  
591 of shell midden sites in this case study and the morphology of *C. fasciatus*,  
592 can equally affect shell sizes of other species in other studies. This aspect  
593 especially should be considered when analysing shells from sites that cannot  
594 be confidently linked to a single shoreline. For these sites, it needs to be  
595 considered that size changes through time might be linked to changes in har-  
596 vesting patches (i.e. harvesting from a different local habitat), rather than  
597 the harvesting itself impacting on shellfish communities as a whole.

598 With the data presented here we start to address the gap in quantify-  
599 ing the potential of marine resources in this key gateway of human dispersal  
600 through time. The shellfish diversity and abundance found in the shell mid-  
601 den datasets indicate a rich ecological environment that is unaffected by the  
602 arid conditions of the terrestrial environment, providing sustainable resources  
603 to complement a mixed diet.

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## 636 References

- 637 Abbott, R. T., S. P. Dance, and T. Abbott  
 638 1983. *Compendium of seashells*. EP Dutton New York.
- 639 Abu-Zied, R. H. and R. A. Bantan  
 640 2018. Late pleistocene gastropods from the raised reefal limestone of jed-  
 641 dah, saudi arabia: taxonomic and palaeoenvironmental implications. *PalZ*,  
 642 92(1):65–86.
- 643 Allen, M., D. Poggiali, K. Whitaker, T. R. Marshall, and R. Kievit  
 644 2018. Raincloud plots: a multi-platform tool for robust data visualization.  
 645 *PeerJ Preprints*, 6:e27137v1.
- 646 Almalki, K. A., L. Ailleres, P. G. Betts, and R. A. Bantan  
 647 2015. Evidence for and relationship between recent distributed extension  
 648 and halokinesis in the Farasan Islands, southern Red Sea, Saudi Arabia.  
 649 *Arabian Journal of Geosciences*, 8(10):8753–8766.
- 650 Almalki, K. A. and R. A. Bantan  
 651 2016. Lithologic units and stratigraphy of the Farasan islands, southern  
 652 Red Sea. *Carbonates and Evaporites*, 31(2):115–128.



- 653 Almassari, A. M. and M. Gameil  
654 2019. A Comparison of Pleistocene Gastropod Distribution in Both Open  
655 Shore and Lagoon at Ash Shaibah South Jeddah, Western Saudi Arabia.  
656 *International Journal of Innovative Technology and Exploring Engineering*,  
657 8(7C2).
- 658 Alvarez, M., I. Briz Godino, A. Balbo, and M. Madella  
659 2011. Shell middens as archives of past environments, human dispersal  
660 and specialized resource management. *Quat. Int.*, 239(1):1–7.
- 661 Andersen, S. H.  
662 2000. Køkkenmøddinger (shell middens) in denmark: a survey. In *Pro-*  
663 *ceedings of the Prehistoric Society*, volume 66, Pp. 361–384. Cambridge  
664 University Press.
- 665 Andrus, C. F. T. and V. D. Thompson  
666 2012. Determining the habitats of mollusk collection at the sapelo island  
667 shell ring complex, georgia, USA using oxygen isotope sclerochronology. *J.*  
668 *Archaeol. Sci.*, 39(2):215–228.
- 669 Arz, H. W., F. Lamy, J. Pätzold, P. J. Muller, and M. Prins  
670 2003. Mediterranean moisture source for an Early-Holocene humid period  
671 in the northern Red Sea. *Science*, 300(5616):118–121.
- 672 Astrup, P. M.  
673 2018. Sea-level change in mesolithic southern scandinavia: long-and short-  
674 term effects on society and the environment. *Jutland Archaeological Society*  
675 *Publications*, Vol. 106.
- 676 Bailey, G.  
677 2004. World prehistory from the margins: the role of coastlines in human  
678 evolution. *Journal of Interdisciplinary Studies in History and Archaeology*,  
679 Pp. 39–50.
- 680 Bailey, G., J. Barrett, O. Craig, and N. Milner  
681 2008. Historical ecology of the North Sea basin. *Human impact on ancient*  
682 *marine ecosystems: a global perspective*, Pp. 215–242.
- 683 Bailey, G. N., M. H. Devès, R. H. Inglis, M. G. Meredith-Williams,  
684 G. Momber, D. Sakellariou, A. G. M. Sinclair, G. Rousakis, S. Al Ghamdi,

- 685 and A. M. Alsharekh  
686 2015. Blue arabia: Palaeolithic and underwater survey in SW Saudi Arabia  
687 and the role of coasts in Pleistocene dispersals. *Quat. Int.*, 382:42–57.
- 688 Bailey, G. N. and N. C. Flemming  
689 2008. Archaeology of the continental shelf: Marine resources, submerged  
690 landscapes and underwater archaeology. *Quat. Sci. Rev.*, 27(23-24):2153–  
691 2165.
- 692 Bailey, G. N., M. Meredith-Williams, A. Alsharekh, and N. Hausmann  
693 2019. The archaeology of pleistocene coastal environments and human  
694 dispersals in the red sea: insights from the farasan islands. In *Geological*  
695 *Setting, Palaeoenvironment and Archaeology of the Red Sea*, Pp. 583–604.  
696 Springer.
- 697 Bailey, G. N., M. G. Meredith-Williams, and A. M. Alsharekh  
698 2013. Shell mounds of the Farasan Islands, Saudi Arabia. *Shell energy:*  
699 *mollusc shells as coastal resources*. Oxbow Books, Oxford, Pp. 241–254.
- 700 Bantan, R. A. and R. H. Abu-Zied  
701 2014. Sediment characteristics and molluscan fossils of the Farasan Is-  
702 lands shorelines, southern Red Sea, Saudi Arabia. *Arabian Journal of*  
703 *Geosciences*, 7(2):773–787.
- 704 Bantan, R. A., R. H. Abu-Zied, and R. A. Haredy  
705 2015. Lithology, fauna and environmental conditions of the Late Pleis-  
706 tocene raised reefal limestone of the Jeddah coastal plain, Saudi Arabia.  
707 *Arabian Journal of Geosciences*, 8(11):9887–9904.
- 708 Barker, G., P. Bennett, L. Farr, E. Hill, C. Hunt, G. Lucarini, J. Morales,  
709 G. Mutri, A. Prendergast, A. Pryor, R. Rabett, T. Reynolds, P. Spry-  
710 Marques, and M. Twati  
711 2012. The cyrenaican prehistory project 2012: the fifth season of investi-  
712 gations of the hua fteah cave. *Libyan Studies*, 43:115–136.
- 713 Beyin, A., P. R. Chauhan, and A. Nassr  
714 2019. Reconnaissance of prehistoric sites in the Red Sea Coastal Region  
715 of the Sudan, NE Africa. *J. Field Archaeol.*, 44(3):147–164.
- 716 Biagi, P., T. Fantuzzi, and C. Franco  
717 2013. The shell middens of the Bay of Daun: environmental changes and

- human impact along the coast of Las Bela (Balochistan, Pakistan) between the 8th and the 5th millennium bp. *Eurasian Prehistory*, Pp. 1–21.
- Bird, D. W.  
1997. Behavioral ecology and the archaeological consequences of central place foraging among the Meriam. *Archeological Papers of the American Anthropological Association*, 7(1):291–306.
- Bosch, D. T., S. P. Dance, R. Moolenbeek, P. Oliver, et al.  
1995. *Seashells of eastern Arabia*. Dubai Motivate Publishing.
- Botkin, S.  
1980. Effects of human exploitation on shellfish populations at Malibu Creek, California. *Modeling Change in Prehistoric Subsistence Economies*, Academic Press, New York, 1980:121–139.
- Chakroun, A., D. Chahid, L. Boudad, E. Campmas, A. Lenoble, R. Nespolet, and M. A. El Hajraoui  
2017. The Pleistocene of Rabat (Morocco): Mollusks, coastal environments and human behavior. *African Archaeological Review*, 34(4):493–510.
- Claassen, C.  
1998. *Shells*. Cambridge University Press.
- Claassen, C.  
2000. Quantifying shell: comments on mason, peterson, and tiffany. *American Antiquity*, 65(2):415–418.
- Coleman, N.  
2002. Sea shells: Catalogue of indo-pacific mollusca. *Neville Coleman's Underwater Geographic Pty Ltd., Australia*.
- Colonese, A. C., D. Lo Vetro, W. Landini, Z. Di Giuseppe, N. Hausmann, B. Demarchi, C. d'Angelo, M. J. Leng, A. Incarbona, A. C. Whitwood, and F. Martini  
2018. Late Pleistocene-Holocene coastal adaptation in central Mediterranean: Snapshots from Grotta d'Oriente (NW Sicily). *Quat. Int.*, 493:114–126.

- 748 de Boer, W. F. and H. H. T. Prins  
749 2002. The community structure of a tropical intertidal mudflat under  
750 human exploitation. *ICES J. Mar. Sci.*, 59(6):1237–1247.
- 751 De Vynck, J., M. Difford, R. Anderson, C. Marean, R. Cowling, and K. Hill  
752 2019. The resilience to human foraging of intertidal resources on the south  
753 Cape coast of South Africa and the implications for prehistoric foragers.  
754 *Quaternary Science Reviews*, P. 106041.
- 755 De Vynck, J. C., R. Anderson, C. Atwater, R. M. Cowling, E. C. Fisher,  
756 C. W. Marean, R. S. Walker, and K. Hill  
757 2016. Return rates from intertidal foraging from Blombos Cave to Pin-  
758 nacle Point: Understanding early human economies. *Journal of human*  
759 *evolution*, 92:101–115.
- 760 Debelius, H.  
761 2000. *Red Sea Reef Guide: Egypt, Israel, Jordan, Sudan, Saudi Arabia,*  
762 *Yemen, Arabian Peninsula (Oman, UAE, Bahrain)*. Dive International  
763 Pub.
- 764 Drake, N. A., R. M. Blench, S. J. Armitage, C. S. Bristow, and K. H. White  
765 2011. Ancient watercourses and biogeography of the Sahara explain the  
766 peopling of the desert. *Proc. Natl. Acad. Sci. U. S. A.*, 108(2):458–462.
- 767 Durrani, N.  
768 2001. *The Tihamah coastal plain of South West Arabia in its regional*  
769 *context: c. 6000 BC-AD 600*. PhD thesis, University College London  
770 (University of London).
- 771 Erlandson, J. M.  
772 1988. The role of shellfish in prehistoric economies: A protein perspective.  
773 *Am. Antiq.*, 53(1):102–109.
- 774 Erlandson, J. M., T. J. Braje, T. C. Rick, N. P. Jew, D. J. Kennett, N. Dwyer,  
775 A. F. Ainis, R. L. Vellanoweth, and J. Watts  
776 2011. 10,000 years of human predation and size changes in the owl limpet  
777 (*Lottia gigantea*) on San Miguel Island, California. *Journal of Archaeolog-*  
778 *ical Science*, 38(5):1127–1134.

- 779 Evans, A. M., J. C. Flatman, and N. C. Flemming  
780 2014. *Prehistoric Archaeology on the Continental Shelf: A Global Review*.  
781 Springer.
- 782 Fa, D. A.  
783 2008. Effects of tidal amplitude on intertidal resource availability  
784 and dispersal pressure in prehistoric human coastal populations: the  
785 Mediterranean–Atlantic transition. *Quaternary Science Reviews*, 27(23–  
786 24):2194–2209.
- 787 Faulkner, P.  
788 2009. Focused, intense and long-term: evidence for granular ark (*Anadara*  
789 *granosa*) exploitation from late Holocene shell mounds of Blue Mud Bay,  
790 northern Australia. *Journal of Archaeological Science*, 36(3):821–834.
- 791 Faulkner, P.  
792 2011. Quantifying shell weight loss in archaeological deposits. *Archaeology*  
793 *in Oceania*, 46(3):118–129.
- 794 Flemming, N. C., G. N. Bailey, V. Courtillot, G. King, K. Lambeck, F. Ry-  
795 erson, and C. Vita-Finzi  
796 2003. Coastal and marine palaeo-environments and human dispersal points  
797 across the Africa-Eurasia boundary. *Maritime Heritage*, Pp. 61–74.
- 798 Giovas, C. M., S. M. Fitzpatrick, M. Clark, and M. Abed  
799 2010. Evidence for size increase in an exploited mollusc: Humped conch  
800 (*Strombus gibberulus*) at Chelechol ra Orrak, Palau from ca. 3000–0 BP.  
801 *Journal of Archaeological Science*, 37(11):2788–2798.
- 802 Glassow, M. A.  
803 2000. Weighing vs. counting shellfish remains: A comment on mason,  
804 peterson, and tiffany. *Am. Antiq.*, 65(2):407–414.
- 805 Gonçalves, C., J. Cascalheira, and N. Bicho  
806 2014. Shellmiddens as landmarks: Visibility studies on the mesolithic of  
807 the muge valley (central portugal). *Journal of Anthropological Archaeology*,  
808 36:130–139.
- 809 Gutiérrez-Zugasti, I.  
810 2011. Coastal resource intensification across the Pleistocene–Holocene

- 811 transition in Northern Spain: Evidence from shell size and age distribu-  
812 tions of marine gastropods. *Quat. Int.*, 244(1):54–66.
- 813 Gutiérrez-Zugasti, I., S. H. Andersen, A. C. Araújo, C. Dupont, N. Milner,  
814 and A. M. Monge-Soares  
815 2011. Shell midden research in Atlantic Europe: State of the art, research  
816 problems and perspectives for the future. *Quat. Int.*, 239(1):70–85.
- 817 Habu, J., A. Matsui, N. Yamamoto, and T. Kanno  
818 2011. Shell midden archaeology in japan: Aquatic food acquisition and  
819 long-term change in the jomon culture. *Quat. Int.*, 239(1-2):19–27.
- 820 Harding, J. M., R. Mann, and M. J. Southworth  
821 2008. Shell length-at-age relationships in James River, Virginia, oysters  
822 (*Crassostrea virginica*) collected four centuries apart. *Journal of Shellfish*  
823 *Research*, 27(5):1109–1116.
- 824 Hardy, K., A. Camara, R. Piqué, E. Dioh, M. Guèye, H. D. Diadhiou,  
825 M. Faye, and M. Carré  
826 2016. Shellfishing and shell midden construction in the Saloum Delta,  
827 Senegal. *Journal of Anthropological Archaeology*, 41:19–32.
- 828 Hausmann, N.  
829 2015. *The shell mounds of the Farasan Islands - An isotopic study of*  
830 *seasonality and coastal exploitation*. PhD thesis, University of York.
- 831 Hausmann, N., A. C. Colonese, A. de Lima Ponzoni, Y. Hancock,  
832 M. Meredith-Williams, M. J. Leng, and G. N. Bailey  
833 2017. Isotopic composition of *conomurex fasciatus* shells as an environ-  
834 mental proxy for the red sea. *Quat. Int.*, 427:115–127.
- 835 Hausmann, N., O. Kokkinaki, and M. J. Leng  
836 2019a. Red Sea Palaeoclimate: Stable isotope and Element-Ratio analysis  
837 of marine mollusc shells. In *Geological Setting, Palaeoenvironment and*  
838 *Archaeology of the Red Sea*, N. M. A. Rasul and I. C. F. Stewart, eds.,  
839 Pp. 725–740. Cham: Springer International Publishing.
- 840 Hausmann, N. and M. Meredith-Williams  
841 2017a. Exploring accumulation rates of shell deposits through seasonality  
842 data. *Journal of Archaeological Method and Theory*, 24(3):776–795.

- 843 Hausmann, N. and M. Meredith-Williams  
844 2017b. Seasonal patterns of coastal exploitation on the Farasan Islands,  
845 Saudi Arabia. *The Journal of Island and Coastal Archaeology*, 12(3):360–  
846 379.
- 847 Hausmann, N., M. Meredith-Williams, K. Douka, R. H. Inglis, and G. Bailey  
848 2019b. Quantifying spatial variability in shell midden formation in the  
849 Farasan Islands, Saudi Arabia. *PLoS One*, 14(6):e0217596.
- 850 Hausmann, N., M. Meredith-Williams, and E. Laurie  
851 2020. Farasan-Shell-Data: Shellfish Resilience to Prehistoric Hu-  
852 man consumption in the southern Red Sea (Version v1.0). *Zenodo*,  
853 <https://doi.org/10.5281/zenodo.3736543>.
- 854 Horton, T., A. Kroh, S. Ah Yong, N. Bailly, C. B. Boyko, S. N. Brandão,  
855 S. Gofas, J. N. A. Hooper, F. Hernandez, O. Holovachov, J. Mees, T. N.  
856 Molodtsova, G. Paulay, W. Decock, S. Dekeyser, T. Lanssens, L. Van-  
857 depitte, B. Vanhoorne, R. Adlard, P. Adriaens, S. Agatha, K. J. Ahn,  
858 N. Akkari, B. Alvarez, G. Anderson, M. V. Angel, D. Antic, C. Arango,  
859 T. Artois, S. Atkinson, R. Bank, A. Barber, J. P. Barbosa, I. Bartsch,  
860 D. Bellan-Santini, J. Bernot, A. Berta, T. N. Bezerra, R. Bieler, S. Blanco,  
861 I. Blasco-Costa, M. Blazewicz, P. Bock, R. Böttger-Schnack, P. Bouchet,  
862 N. Boury-Esnault, G. Boxshall, R. Bray, N. L. Bruce, S. Cairns, J. L.  
863 Carballo, P. Cárdenas, E. Carstens, B. K. Chan, T. Y. Chan, L. Cheng,  
864 M. Churchill, C. O. Coleman, A. G. Collins, G. E. Collins, L. Cor-  
865 bari, R. Cordeiro, A. Cornils, M. Coste, M. J. Costello, K. A. Cran-  
866 dall, F. Cremonte, T. Cribb, S. Cutmore, F. Dahdouh-Guebas, M. Daly,  
867 M. Daneliya, J. C. Dauvin, P. Davie, C. De Broyer, S. De Grave,  
868 V. de Mazancourt, N. J. de Voogd, P. Decker, W. Decraemer, D. De-  
869 faye, J. L. d’Hondt, S. Dippenaar, M. Dohrmann, J. Dolan, D. Domning,  
870 R. Downey, L. Ector, U. Eisendle-Flöckner, M. Eitel, S. C. d. Encarnação,  
871 H. Enghoff, J. Epler, C. Ewers-Saucedo, M. Faber, S. Feist, D. Figueroa,  
872 J. Finn, C. Fišer, E. Fordyce, W. Foster, J. H. Frank, C. Fransen, H. Fu-  
873 ruya, H. Galea, O. Garcia-Alvarez, R. Garic, S. Garnett, R. Gasca,  
874 S. Gaviria-Melo, S. Gerken, D. Gibson, R. Gibson, J. Gil, A. Gittenberger,  
875 C. Glasby, A. Glover, S. E. Gómez-Noguera, D. González-Solís, D. Gordon,  
876 M. Grabowski, C. Gravili, J. M. Guerra-García, R. Guidetti, Guiry, K. A.  
877 Hadfield, E. Hajdu, J. Hallermann, B. W. Hayward, E. Hendrycks, D. Her-  
878 bert, A. Herrera Bachiller, J. s. Ho, M. Hodda, J. Høeg, B. Hoeksema,

879 R. Houart, L. Hughes, M. Hyžný, L. F. M. Iniesta, T. Iseto, S. Ivanenko,  
 880 M. Iwataki, R. Janssen, G. Jarms, D. Jaume, K. Jazdzewski, C. D. Jer-  
 881 sabek, P. Józwiak, A. Kabat, Y. Kantor, I. Karanovic, B. Karthick, Y. H.  
 882 Kim, R. King, P. M. Kirk, M. Klautau, J. P. Kociolek, F. Köhler, J. Kolb,  
 883 A. Kotov, A. Kremenetskaia, R. M. Kristensen, M. Kulikovskiy, S. Kul-  
 884 lander, G. Lambert, D. Lazarus, F. Le Coze, S. LeCroy, D. Leduc, E. J.  
 885 Lefkowitz, R. Lemaitre, Y. Liu, A. N. Lörz, J. Lowry, T. Ludwig, N. Lund-  
 886 holm, E. Macpherson, L. Madin, C. Mah, B. Mamo, T. Mamos, R. Man-  
 887 con, G. Mapstone, P. E. Marek, B. Marshall, D. J. Marshall, P. Martin,  
 888 R. Mast, C. McFadden, S. J. McInnes, T. Meidla, K. Meland, K. L. Merrin,  
 889 C. Messing, D. Miljutin, C. Mills, Ø. Moestrup, V. Mokievsky, F. Monniot,  
 890 R. Mooi, A. C. Morandini, R. Moreira da Rocha, F. Moretzsohn, C. Mor-  
 891 row, J. Mortelmans, J. Mortimer, L. Musco, T. A. Neubauer, E. Neu-  
 892 bert, B. Neuhaus, P. Ng, A. D. Nguyen, Y. Nguyen Thi My, C. Nielsen,  
 893 T. Nishikawa, J. Norenburg, T. O'Hara, D. Opresko, M. Osawa, H. J. Os-  
 894 igus, Y. Ota, B. Páll-Gergely, D. Patterson, H. Paxton, R. Peña-Santiago,  
 895 V. Perrier, W. Perrin, I. Petrescu, B. Picton, J. F. Pilger, A. B. Pis-  
 896 era, D. Polhemus, G. C. Poore, M. Potapova, P. Pugh, G. Read, M. Re-  
 897 ich, J. D. Reimer, H. Reip, M. Reuscher, J. W. Reynolds, I. Richling,  
 898 F. Rimet, P. Ríos, M. Rius, D. C. Rogers, G. Rosenberg, K. Rützler,  
 899 K. Sabbe, J. Saiz-Salinas, S. Sala, S. Santagata, S. Santos, E. Sar, A. Satoh,  
 900 T. Saucède, H. Schatz, B. Schierwater, A. Schmidt-Rhaesa, S. Schneider,  
 901 C. Schönberg, P. Schuchert, A. R. Senna, C. Serejo, S. Shaik, S. Shamsi,  
 902 J. Sharma, W. A. Shear, N. Shenkar, A. Shinn, M. Short, J. Sicinski,  
 903 P. Sierwald, E. Simmons, F. Sinniger, D. Sivell, B. Sket, H. Smit, N. Smit,  
 904 N. Smol, J. F. Souza-Filho, J. Spelda, W. Sterrer, E. Stienen, P. Stoev,  
 905 S. Stöhr, M. Strand, E. Suárez-Morales, M. Summers, L. Suppan, C. Sut-  
 906 tle, B. J. Swalla, S. Taiti, M. Tanaka, A. H. Tandberg, D. Tang, M. Tasker,  
 907 J. Taylor, J. Taylor, A. Tchesunov, H. ten Hove, J. J. ter Poorten, J. D.  
 908 Thomas, E. V. Thuesen, M. Thurston, B. Thuy, J. T. Timi, T. Timm,  
 909 A. Todaro, X. Turon, S. Tyler, P. Uetz, J. Uribe-Palomino, S. Utevsky,  
 910 J. Vacelet, D. Vachard, W. Vader, R. Väinölä, G. Valls Domedel, B. Van de  
 911 Vijver, S. E. van der Meij, T. van Haaren, R. W. van Soest, A. Vanreusel,  
 912 V. Venekey, M. Vinarski, R. Vonk, C. Vos, G. Walker-Smith, T. C. Walter,  
 913 L. Watling, M. Wayland, T. Wesener, C. E. Wetzel, C. Whipps, K. White,  
 914 U. Wieneke, D. M. Williams, G. Williams, R. Wilson, A. Witkowski,  
 915 J. Witkowski, N. Wyatt, C. Wylezich, K. Xu, J. Zanol, W. Zeidler, and



- 916 Z. Zhao  
917 2019. World register of marine species (WoRMS).
- 918 Hunt, C., T. Reynolds, H. El-Rishi, A. Buzaian, E. Hill, and G. Barker  
919 2011. Resource pressure and environmental change on the North African  
920 littoral: Epipalaeolithic to Roman gastropods from Cyrenaica, Libya. *Qua-*  
921 *ternary International*, 244(1):15–26.
- 922 Inglis, R., A. Sinclair, A. Shuttleworth, A. Alsharekh, M. Devès,  
923 S. Al Ghamdi, M. Meredith-Williams, and G. Bailey  
924 2014. Investigating the palaeolithic landscapes and archaeology of the  
925 Jizan and Asir regions, south-western Saudi Arabia. *Proceedings of the*  
926 *Seminar for Arabian Studies*, 44:193–211.
- 927 Inglis, R. H., W. Bosworth, N. M. A. Rasul, A. O. Al-Saeedi, and G. N.  
928 Bailey  
929 2019. Investigating the palaeoshorelines and coastal archaeology of the  
930 Southern Red Sea. In *Geological Setting, Palaeoenvironment and Archaeol-*  
931 *ogy of the Red Sea*, N. M. A. Rasul and I. C. F. Stewart, eds., Pp. 553–581.  
932 Cham: Springer International Publishing.
- 933 Jerardino, A.  
934 2016. On the origins and significance of Pleistocene coastal resource use  
935 in southern Africa with particular reference to shellfish gathering. *Journal*  
936 *of Anthropological Archaeology*, 41:213–230.
- 937 Khalidi, L.  
938 2007. The formation of a southern Red Seascape in the late prehistoric  
939 period: tracing cross-Red Sea culture, contact, interaction, and maritime  
940 communities along the Tihamah coastal plain, Yemen in the third to first  
941 millennium BC. *Natural Resources and Cultural Connections of the Red*  
942 *Sea: Proceedings of Red Sea Project III*, Pp. 35–43.
- 943 Khalidi, L.  
944 2010. Holocene obsidian exchange in the Red Sea region. In *The Evolution*  
945 *of Human Populations in Arabia*, Vertebrate Paleobiology and Paleoan-  
946 *thropology*, Pp. 279–291. Dordrecht: Springer Netherlands.
- 947 Khalil, H. M.  
948 2012. Pliocene–Pleistocene stratigraphy and macrofauna of the Farasan Is-

- 949 lands, South East Red Sea, Saudi Arabia. *Arabian Journal of Geosciences*,  
950 5(6):1223–1245.
- 951 Klein, R. G.  
952 2008. Out of africa and the evolution of human behavior. *Evolutionary*  
953 *Anthropology: Issues, News, and Reviews*, 17(6):267–281.
- 954 Koike, H.  
955 1986. Prehistoric hunting pressure and paleobiomass: an environmental  
956 reconstruction and archaeozoological analysis of a Jomon shellmound area.  
957 *Prehistoric hunter-gatherers in Japan: new research methods*, 27:27–53.
- 958 Lambeck, K., A. Purcell, N. C. Flemming, C. Vita-Finzi, A. M. Alsharekh,  
959 and G. N. Bailey  
960 2011. Sea level and shoreline reconstructions for the Red Sea: isostatic  
961 and tectonic considerations and implications for hominin migration out of  
962 Africa. *Quat. Sci. Rev.*, 30(25-26):3542–3574.
- 963 Lieske, E., K. E. Fiedler, and R. F. Myers  
964 2004. *Coral Reef Guide: Red Sea to Gulf of Aden, South Oman*. Collins.
- 965 Liverani, V.  
966 2013. The superfamily *stromboidea*. addenda and corrigenda. *A Concho-*  
967 *logical Iconography, Supplement*, 1:1–54.
- 968 Mannino, M. A. and K. D. Thomas  
969 2002. Depletion of a resource? The impact of prehistoric human foraging  
970 on intertidal mollusc communities and its significance for human settle-  
971 ment, mobility and dispersal. *World Archaeol.*, 33(3):452–474.
- 972 Marean, C. W., M. Bar-Matthews, J. Bernatchez, E. Fisher, P. Goldberg,  
973 A. I. R. Herries, Z. Jacobs, A. Jerardino, P. Karkanas, T. Minichillo, P. J.  
974 Nilssen, E. Thompson, I. Watts, and H. M. Williams  
975 2007. Early human use of marine resources and pigment in South Africa  
976 during the Middle Pleistocene. *Nature*, 449(7164):905–908.
- 977 Mason, R. D., M. L. Peterson, and J. A. Tiffany  
978 1998. Weighing vs. counting: Measurement reliability and the California  
979 school of midden analysis. *Am. Antiq.*, 63(2):303–324.

- 980 Mason, R. D., M. L. Peterson, and J. A. Tiffany  
 981 2000. Weighing and Counting Shell: A Response to Glassow and Claassen.  
 982 *Am. Antiq.*, 65(4):757–761.
- 983 Mayer, D. E. B.-Y. and A. Beyin  
 984 2009. Late stone age shell middens on the Red Sea Coast of Eritrea. *The*  
 985 *Journal of Island and Coastal Archaeology*, 4(1):108–124.
- 986 McCarthy, K.  
 987 2007. *A review of queen conch (Strombus gigas) life-history*. NOAA Na-  
 988 tional Marine Fisheries Service, Southeast Fisheries Science Center.
- 989 Meehan, B.  
 990 1977. Hunters by the seashore. *J. Hum. Evol.*, 6(4):363–370.
- 991 Meredith-Williams, M., N. Hausmann, R. Inglis, and G. Bailey  
 992 2014. 4200 new shell mound sites in the southern Red Sea. *Internet*  
 993 *Archaeology*.
- 994 Mordan, P.  
 995 1980. Molluscs of Saudi Arabia. land molluscs. *Fauna of Saudi Arabia*,  
 996 2:359–367.
- 997 Mordan, P. B.  
 998 1986. *taxonomic revision of the southern Arabian Enidae sensu lato (Mol-*  
 999 *lusca; Pulmonata)*. British Museum (Natural History).
- 1000 Morrison, A. E. and M. S. Allen  
 1001 2017. Agent-based modelling, molluscan population dynamics, and ar-  
 1002 chaeomalacology. *Quat. Int.*, 427:170–183.
- 1003 Morrison, A. E. and T. L. Hunt  
 1004 2007. Human impacts on the nearshore environment: an archaeological  
 1005 case study from Kaua ‘i, Hawaiian Islands. *Pacific Science*, 61(3):325–346.
- 1006 Mutairi, K. A., M. El-Bana, M. Mansor, S. Al-Rowaily, and A. Mansor  
 1007 2012. Floristic diversity, composition, and environmental correlates on the  
 1008 arid, coralline islands of the Farasan Archipelago, Red Sea, Saudi Arabia.  
 1009 *Arid Land Res. Manage.*, 26(2):137–150.

- 1010 Neubert, E.  
1011 1998. Annotated checklist of the terrestrial and freshwater molluscs of  
1012 the Arabian Peninsula with descriptions of new species. *Fauna of Arabia*,  
1013 17:333–462.
- 1014 Nielsen, R., J. M. Akey, M. Jakobsson, J. K. Pritchard, S. Tishkoff, and  
1015 E. Willerslev  
1016 2017. Tracing the peopling of the world through genomics. *Nature*,  
1017 541(7637):302–310.
- 1018 Oertle, A.  
1019 2019. *Time and Relative Dimension in Space: Untangling site formation*  
1020 *and taphonomic processes on archaeological shell from the tropical Indo-*  
1021 *Pacific*. PhD thesis, University of Sydney.
- 1022 Oliver, G. P.  
1023 1992. *Bivalved seashells of the Red Sea*. Hemmen.
- 1024 Oliver, G. P., A. M. Holmes, I. J. Killeen, J. M. Light, and H. Wood  
1025 2004. Annotated checklist of the marine bivalvia of rodrigues. *Journal of*  
1026 *Natural History*, 38(23-24):3229–3272.
- 1027 Petraglia, M. M. D. and J. I. Rose  
1028 2009. *The Evolution of Human Populations in Arabia*, Paleoenvironments,  
1029 Prehistory and Genetics. Springer.
- 1030 Radermacher, P., B. R. Schöne, E. Gischler, W. Oschmann, J. Thébault, and  
1031 J. Fiebig  
1032 2009. Sclerochronology—a highly versatile tool for mariculture and recon-  
1033 struction of life history traits of the queen conch, *Strombus gigas* (*Gas-*  
1034 *tropoda*). *Aquatic Living Resources*, 22(3):307–318.
- 1035 Rick, T. C., L. A. Reeder-Myers, C. A. Hofman, D. Breitburg, R. Lockwood,  
1036 G. Henkes, L. Kellogg, D. Lowery, M. W. Luckenbach, R. Mann, et al.  
1037 2016. Millennial-scale sustainability of the chesapeake bay native amer-  
1038 ican oyster fishery. *Proceedings of the National Academy of Sciences*,  
1039 113(23):6568–6573.
- 1040 Seeto, J., P. D. Nunn, and S. Sanjana  
1041 2012. Human-Mediated prehistoric marine extinction in the tropical pa-  
1042 cific? understanding the presence of *Hippopus hippopus* (linn. 1758) in

1043 ancient shell middens on the Rove Peninsula, Southwest Viti Levu Island,  
1044 Fiji. *Geoarchaeology*, 27(1):2–17.

1045 Sharabati, D.  
1046 1984. *Red Sea shells*. Routledge Kegan & Paul.

1047 Sinclair, A., R. H. Inglis, A. Shuttleworth, F. Foulds, and A. Alsharekh  
1048 2019. Landscape archaeology, palaeolithic survey and coastal change along  
1049 the Southern Red Sea of Saudi Arabia. In *Geological Setting, Palaeoen-*  
1050 *vironment and Archaeology of the Red Sea*, N. M. A. Rasul and I. C. F.  
1051 Stewart, eds., Pp. 533–552. Cham: Springer International Publishing.

1052 Stewart, J. R. and P. B. Fenberg  
1053 2018. A climatic context for the out-of-Africa migration: Comment. *Ge-*  
1054 *ology*, 46(5):e442–e442.

1055 Szabó, K.  
1056 2009. Molluscan remains from fiji. *The early prehistory of Fiji*, Pp. 183–  
1057 211.

1058 Team R, C.  
1059 2013. R: A language and environment for statistical computing.

1060 Thakar, H. B.  
1061 2011. Intensification of shellfish exploitation: Evidence of species-specific  
1062 deviation from traditional expectations. *Journal of Archaeological Science*,  
1063 38(10):2596–2605.

1064 Thomas, K. D.  
1065 2015. Molluscs emergent, Part I: themes and trends in the scientific in-  
1066 vestigation of mollusc shells as resources for archaeological research. *J.*  
1067 *Archaeol. Sci.*, 56:133–140.

1068 Tierney, J. E., P. B. deMenocal, and P. D. Zander  
1069 2017. A climatic context for the out-of-Africa migration. *Geology*,  
1070 45(11):1023–1026.

1071 Timmermann, A. and T. Friedrich  
1072 2016. Late pleistocene climate drivers of early human migration. *Nature*,  
1073 538(7623):92–95.

- 1074 Ulm, S., I. J. McNiven, S. J. Aird, and A. B. J. Lambrides  
 1075 2019. Sustainable harvesting of *Conomurex luhuanus* and *Rochia nilotica*  
 1076 by Indigenous Australians on the Great Barrier Reef over the past 2000  
 1077 years. *Journal of Archaeological Science: Reports*, 28:102017.
- 1078 Villagran, X. S. and P. C. F. Giannini  
 1079 2014. Shell mounds as environmental proxies on the southern coast of  
 1080 Brazil. *Holocene*, 24(8):1009–1016.
- 1081 Vine, P.  
 1082 1986. *Red Sea invertebrates*. Immel.
- 1083 Walls, J. G.  
 1084 1980. *Conchs, tibias, and harps*. Tfh Publications Incorporated.
- 1085 Waselkov, G. A.  
 1086 1987. Shellfish gathering and shell midden archaeology. *Advances in Ar-*  
 1087 *chaeological Method and Theory*, Pp. 93–210.
- 1088 Williams, M.  
 1089 2010. Shell mounds of the Farasan Islands, Saudi Arabia. In *Proceedings*  
 1090 *of the Seminar for Arabian Studies*, Pp. 357–366. JSTOR.
- 1091 Wronski, T. and E. Schulz-Kornas  
 1092 2015. The Farasan gazelle—a frugivorous browser in an arid environment?  
 1093 *Mammalian Biology*, 80(2):87–95.
- 1094 Zuschin, M. and P. G. Oliver  
 1095 2003. *Bivalves and bivalve habitats in the northern Red Sea*. Naturhis-  
 1096 torisches Museum Vienna, Austria.