Shellfish resilience to prehistoric human consumption in the southern Red Sea: Variability in *Conomurex fasciatus* across time and space

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A B S T R A C T

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 7360 and 4780 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 the potential of shellfish as a reliable food source during Palaeolithic migrations out of Africa.

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 a 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 sites that illustrate some of the activities and commonalities that both shores have shared (Khalidi, 2007, 2010; Mayer and Beyin, 2009; Meredith-Williams et al., 2014; Hausmann et al., 2019a; Beyin et al., 2019). Archaeological surveys show that marine resources were an important component of coastal subsistence, evidenced by over 4000 sites spread along both sides of the Red Sea (Meredith-Williams et al., 2014). These sites have shell remains as their main component and are thus referred to as 'shell middens' or 'shell matrix deposits'. The quantity of sites, the rapid accumulation of some shell deposits (Hausmann et al., 2019b), and the increased consumption during the more arid seasons of the year (Hausmann and Meredith-Williams, 2017b), indicate the repeated and systematic collection of shellfish with potentially detrimental impacts on their populations.

The resilience (i.e. the ability to sufficiently recover from or respond to outside damage or disturbance) of shellfish populations to human consumption strongly influences their attractiveness as long term resources. Their predictability is a main factor explaining why, in many cases, they came to be relied on as an important part of the diet during the Holocene (Andersen, 2000; Alvarez et al., 2011; Gutiérrez-Zugasti et al., 2011; Habu et al., 2011; Bailey et al., 2013; Biagi et al., 2013; Villagran and Giannini, 2014), and also Pleistocene sites frequently exhibit shells within their deposits (e.g. (Barker et al., 2012; Gutiérrez-Zugasti, 2011; Jerardino, 2016; Colonese et al., 2018). In addition to their predictability, shellfish are easily accessible in the intertidal zone and can be gathered by most members of a community, providing them with a means of feeding themselves and acquiring tradable resources (Meehan, 1977; Waselkov, 1987; Erlandson, 1988; Bird, 1997; Thomas, 2015; Hardy et al., 2016; Jerardino, 2016). Despite their frequent occurrence through time, molluscs can be adversely impacted by human harvesting activity, and it is unlikely that they remain viable as long term resources if they are not resilient to such activity (Seeto et al., 2012; Morrison and Allen, 2017). While coastlines are attractive for many other reasons (e.g. high terrestrial as well as marine biodiversity, increased connectivity across water (Bailey, 2004),) a drop in shellfish abundance specifically could have had some negative impact on the attractiveness of the coastal near-shore environment as a source for easily gathered food. The resilience of shellfish species to human harvesting is commonly discussed in coastal archaeology (Botkin, 1980; Koike, 1986; Claassen, 1998; Mannino and Thomas, 2002; Mason et al., 1998, 2000; de Boer and Prins, 2002) and the general criteria to recognise the potential effects of unsustainable harvesting of a given species are as follows:

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

With regard to criteria 3 and 4, changes in shell sizes can be deceiving without knowledge of the age structure of a given species (Claassen, 1998; Mannino and Thomas, 2002; Bailey et al., 2008), which can help to rule out environmental effects on the growth rate (e.g. general decline of nutrients over time). Most importantly, age is an indicator of whether specimens are old enough to reproduce. Consuming juvenile specimens before they can spawn a new generation will be more detrimental to the survival of the local population than consuming specimens that have already successfully reproduced. Should harvesting gradually deplete populations until only juvenile specimens are

available, no future generations would be able to grow. A key question arising from this is whether such intensive shellfish harvesting had occurred in the arid-period sites in the Red Sea, and whether this could be used to infer the general attractiveness of coastal environments during periods of aridity. This has implications not only for Holocene exploitation, but also for shellfish consumption back into the Palaeolithic and for advancing the study of Palaeolithic coastal environments.

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

1.1. Background

The southern Red Sea seascape consists of hundreds of islands, scattered along both shorelines together with two major archipelagos, the Farasan Islands and the Dahlak Islands, situated towards the southern end (Fig. 1). The genesis of most islands is linked to the uplift of coral terraces following diapirism as a result of this tectonically very active area (Almalki and Bantan, 2016; Almalki et al., 2015). As such, many islands consist of coral bedrock with little or no topsoil'.

The sites in this study are all located on the Farasan Islands (Fig. 1b), which are on the Arabian side of the Red Sea, about 40 km off-shore but inter-connected through smaller islands less than a dozen kilometres apart from each other. The landscape is generally arid with an annual precipitation of only around 100 mm of rain. Holocene climate records indicate that this arid period started around 8000 years ago (cal BP) (Arz et al., 2003) and thus covers the timing of shell midden accumulation (Hausmann et al., 2019b). Earliest evidence of occupation of the Farasan middens dates to 7360–7030 cal BP (OxA-31167, uncalibrated date: 6870±38), but the majority of contexts dates to between 6000 and 4800 cal BP, which is a result of the inundation of older shorelines and their sites dating to before 6000 cal BP (Lambeck et al., 2011). The similar aridity of the mid-Holocene to today suggests that only a few plants populated the islands, supported by groundwater (Mutairi et al., 2012). However, enough localised vegetation persisted to maintain a population of gazelle (*Gazella arabica*). Gazelles likely relied on food sources such as foliage, fruits, flowers, and also, to a lesser extent, annual and perennial herbs (Wronski and Schulz-Kornas, 2015). Given that these food sources are available for gazelle, it is likely that prehistoric humans also made use of them, as well as hunting the gazelle itself, bones of which are occasionally found in shell middens (Bailey et al., 2013). Seasonality data on shellfish has demonstrated that shellfish was eaten year round, but that their consumption during arid seasons was more frequent, indicating that during these months they were used to compensate for the lack of other food sources (presumably plant foods) (Hausmann and Meredith-Williams, 2017b). The shell midden data thus needs to be interpreted in conjunction with an unknown, but significant amount of caloric intake from terrestrial flora and fauna as part of a mixed diet. The Farasan Island shell midden sites have been excavated in multiple seasons from 2009 to 2013. Obtaining a good understanding of the cluster of over 3000 sites as a whole meant being selective about which sites to excavate and how to use information from one site to make inferences about neighbouring sites (Fig. 2).

Sites were selected to cover multiple different bays, representing subtly different local environments. These bay areas are called Khur Maadi (KM) and Janaba Bay, which is separated into Janaba West (JW) and Janaba East (JE). Each site was given a 4-digit number following the bay area code (e.g. KM1234). The results of the taxonomic analysis from 3 of these 19 sites have already been published: KM1057 and JE0004 (Williams, 2010) as well as JW1727 (Hausmann and Meredith-Williams, 2017b), with the latter also including information on changes in size for
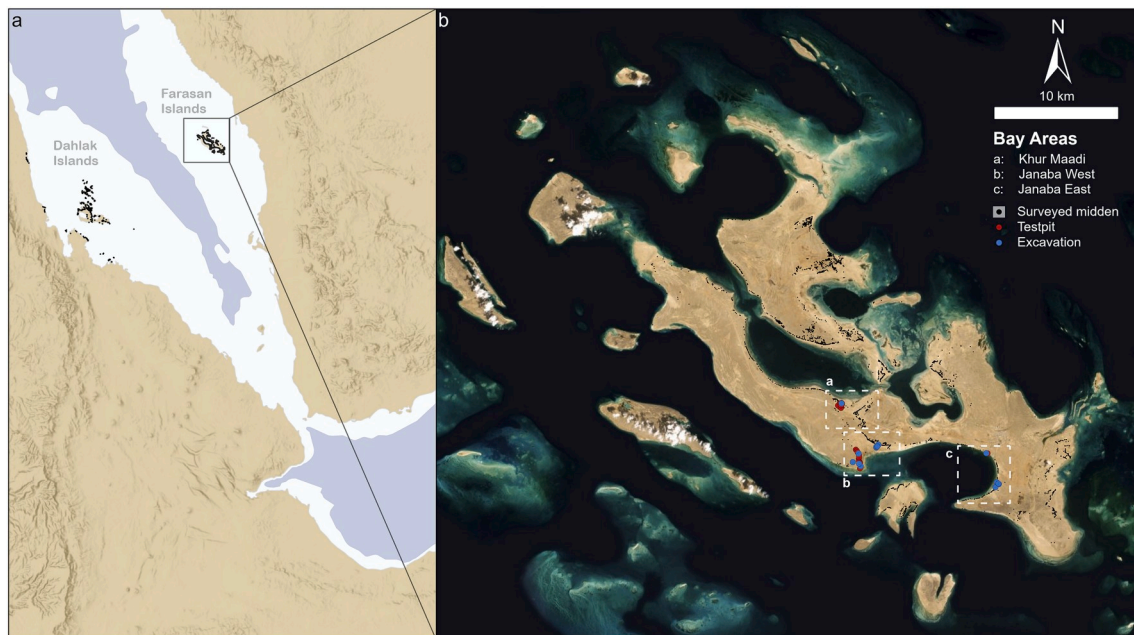
Fig. 1. Overview of the Farasan Island shell midden cluster. a) Map of southern Red Sea. Black dots indicate shell midden sites in the Red Sea. b) the Farasan Island shell midden cluster. White rectangles indicate the three research areas where sites have been excavate, blue dots: excavations, red dots: test pits, small black dots: surveyed sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 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.

the marine gastropod *C. fasciatus*.

2. Materials and methods

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

C. fasciatus (previously referred to as *Strombus fasciatus*) (Fig. 3) is a small, herbivorous true conch (Family Strombidae) that grazes on detritus and algae in tropical waters. Earlier research on this species is scarce and its ecology has only been touched on briefly when its use as an environmental proxy for sea surface temperature was tested (Hausmann et al., 2017, 2019a). The species favours shallow water habitats in and around reefs, including clean sand, seagrass beds, sand patches on reef flats, and sandy to muddy sand bottoms of lagoons and inshore waters (Liverani, 2013; Horton et al., 2019). *C. fasciatus* possesses a strong foot, allowing it to be very mobile by jumping short distances of about 30–40 cm depending on the prevailing currents. Live specimens

have been seen to congregate by the hundreds in some locations of the archipelago (G. Bailey pers. comm.). The shell reaches a maximum of c. 80 mm in length, with most adult specimens being between 25 and 50 mm. There is a slight degree of sexual dimorphism with adult females being larger than males. There is no information on the lifespan of *C. fasciatus* specimens, but it is safe to assume they have a short life span of only a few years, similar to other smaller Strombid species (Walls, 1980).

Different to other mollusc species commonly found in shell middens, *C. fasciatus* grows the majority of its shell during the first year (Hausmann et al., 2017), a feature among strombids (Radermacher et al., 2009). Maturation occurs at the end of this growth period, and is visible by the development of a distinct thickening of the lip. Over what period of time and how fast this thickening takes place is unclear and oxygen isotope sequences indicate that lip growth rates are anywhere between 3 and 10 mm per year (Hausmann, 2015; Hausmann et al., 2017). Thus measuring the lip thickness to further determine age classes, as was done
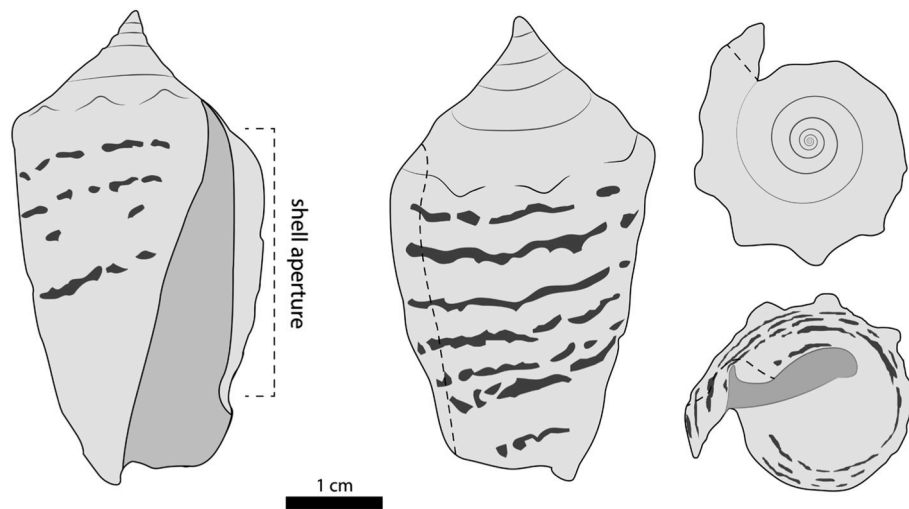
Fig. 3. Drawing of mature *C. fasciatus* shell and the location of the 'shell aperture' measurement between the shoulder of the shell and the stromboid notch. Dashed line on drawings in the centre and on the right indicate the location of the developing lip at the beginning of maturity.

for other species (Ulm et al., 2019), is not possible here. The proxy for shell size used in this study, which we call the 'aperture size', is the length measured between the stromboid notch, the location where the eye-stalk protrudes and leaves an indentation in the lip, and the upper shoulder of the shell. This length remains identical throughout maturity and will thus resemble the size at maturation. By measuring the shell size at maturation we thus measure the cumulative result of shell growth-rates during youth. These growth rates are dependent on internal as well as external factors, including nutrient availability and habitat suitability but also predation by other animals or harvesting by humans, provided that gathering extended to juvenile specimens (McCarthy, 2007; Giovas et al., 2010). On the one hand this limited time-frame prevents the use of size/age-frequency distributions to detect human impact on the mature molluscs beyond the point when specimens mature and thus also means that the impact of harvesting by humans remains undetectable, unless the harvest makes inroads into juvenile specimens at the last stage of resource depletion. On the other hand, where human influence can be ruled out (i.e. in the absence of juvenile specimens), patterns in size-frequency distributions can be linked directly to environmental conditions (e.g. habitat suitability) controlling the growth rates, providing insight into environmental variation that would otherwise be difficult to achieve.

2.2. Site sampling

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

Each bulk sample was sieved using 1 mm, 2 mm and 4 mm mesh sizes. However, any residue smaller than 4 mm was not analysed in great detail due to the significant investment in time needed to identify these tiny shell fragments. Less than 1 mm size residue was bagged and labelled 'Unsorted Residue'. Residue that was larger than 1 mm but less than 2 mm was briefly sorted to extract small shells or fish bone; the remainder was added to the 'Unsorted Residue' for potential later re-examination. Residue that was larger than 2 mm but less than 4 mm

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

Area	Site	Start Date [calBP]	End Date [calBP]	Total analysed shell weight [g]	n = apertures
Khur Maadi	KM1057	5250	5030	56,967.00	3064
	Test Pits	/	/	25,675.89	1058
Janaba West	JW1705	7360	2820	6,024.82	211
	JW1727	4780	4700	40,647.10	2013
	JW2298	5710	4810	17,139.75	251
	JW1807	5420	4910	16,106.75	1203
	JW1864	5940	5480	47,451.25	1978
	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	1208
	JE0078	5600	4950	28,548.70	1585
	JE0087	5970	5850	46,493.00	2156
	JE5642	6160	5730	8,235.00	210

was sorted to extract all small shells, fish bone, or anything that appeared noteworthy. However, this was not an exhaustive process and this residue (2–4 mm) was therefore bagged separately and labelled 'Rough Sorted Residue', indicating that some material may have been missed and require further investigation at a later date in order to extract more detailed information. Lastly, residues over 4 mm in size were fully sorted and the only remaining materials that were not identified to species were small pieces of shell, stone and breccia which were bagged and labelled as 'Sorted Residue'. Whole and partial shells were sorted into species using a range of references (Bosch et al., 1995; Abbott et al., 1983; Coleman, 2002; Debelius, 2000; Lieske et al., 2004; Mordan, 1980, 1986; Neubert, 1998; Oliver, 1992; Oliver et al., 2004; Sharabati, 1984; Vine, 1986; Zuschin and Oliver, 2003). If a partial shell could not be individually identified but could be identified to its genus it was labelled as that (e.g. 'Arca species' or 'Chama species'). Burnt shell as either whole or fragments was separated out and recorded as 'Burnt Shell'. This amounted to only a small total of 3362 g, with an average of 1% of relative abundance per site.

During the shell sorting we encountered some problems that related primarily to shell degradation and a lack of reference material. These were sorted out in the following manner: The *Chama* species were frequently colourless with heavy erosion particularly of the exterior

surface and many were identified as *Chama pacifica* (Broderip, 1835); this may in some cases have been a wrong identification. Some of the smaller shells were also identified as *Chama pacifica* but may be different species such as *Chama asperella* (Lamarck, 1819) and *Chama aspersa* (Reeve, 1846). Consequently in the later identifications all *Chama* were often identified generically as '*Chama* Species'. It was decided that it would not be necessary to retrace and reclassify for this particular analysis but it may be necessary in the future if a different kind of analysis is required.

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

The third possible misidentification relates to the *Chicoreus* species where some shells identified as *Chicoreus ramosus* (Linnaeus, 1758) may in fact be *Chicoreus virgineus* (Röding, 1798). Again it was not necessary to re-examine this distinction for the present analysis as these two species occupy very similar ecological niches. For a similar discussion regarding the difficulties in analysing mollusc remains and the potential for over-identification see Szabó (2009).

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

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

All records were made on paper and subsequently transferred to digital media. All analyses were carried out in R (Team R, 2013) and site specific data can be accessed in the Supplementary Materials as well as online (Hausmann et al., 2020). For the comparison of mean aperture sizes through time, we were restricted by the number of radiocarbon-dated layers and sites, meaning that some sites were not considered (see Table 1) and that layers were assigned dates based on the interpolation of minimum and maximum ranges of the individual sites at a high degree of chronological resolution. This method is not sufficient to reveal synchronicities between sites, but was deemed sufficient to structure the mean aperture size data for an overview of intra-site changes and a general comparison between bay-areas.

3. Results

3.1. Species composition

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

While these other species are not the main edible species and their 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, showing little or no long-term trends through the individual site stratigraphies.

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). Fig. 6b also reveals that the potential biases from the 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 (6250–5800 cal BP) and later (5000–4800 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 Fig. 7 clearly describes a trend towards smaller sizes, while in Janaba West this trend is not quite as obvious due to a

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.

Area	Site	*Conomurex fasciatus*	*Pinctada sp.*	*Chicoreus ramosus/ virgineus*	*Chama pacifica*	*Spondylus spinosus*	*Tricornis (Strombus) tricornis*	*Plicatula Plicata*	*Arca sp.*	*Pleuroploca trapezium*	*Ostrea sp.*
Khur Maadi	KM1057	**93**			4	2					
Test pits	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				
	JW0006	**92**	1		2		1				
	JW0007	**98**									
	JW0008	**79**	3	2	1		1	1	5		
	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		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	
	JE0004	**64**	8	15	5	4		2			
	JE0078	**86**		9	4						
	JE0087	**98**		1							
	JE5642	**92**	1	2	3	1					
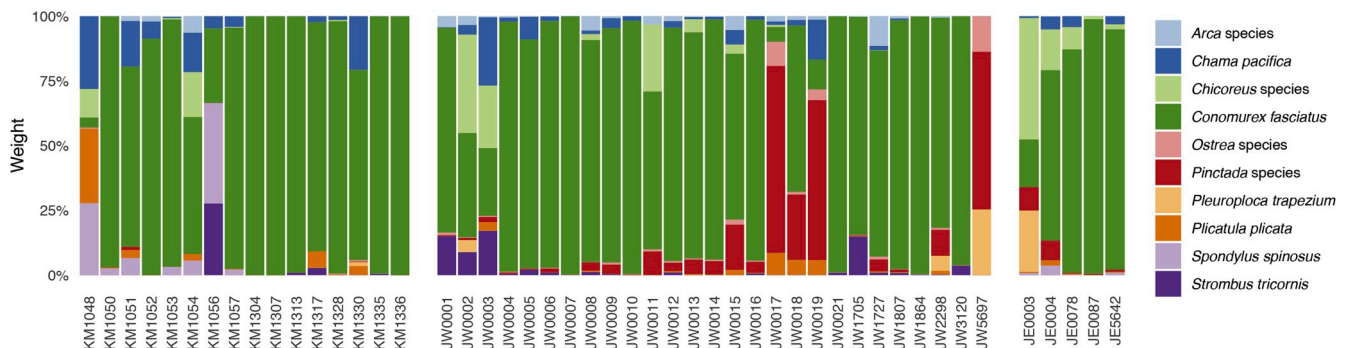
Fig. 4. Species composition by site. Note that the graph only represents the main identified species as listed in Table 2.
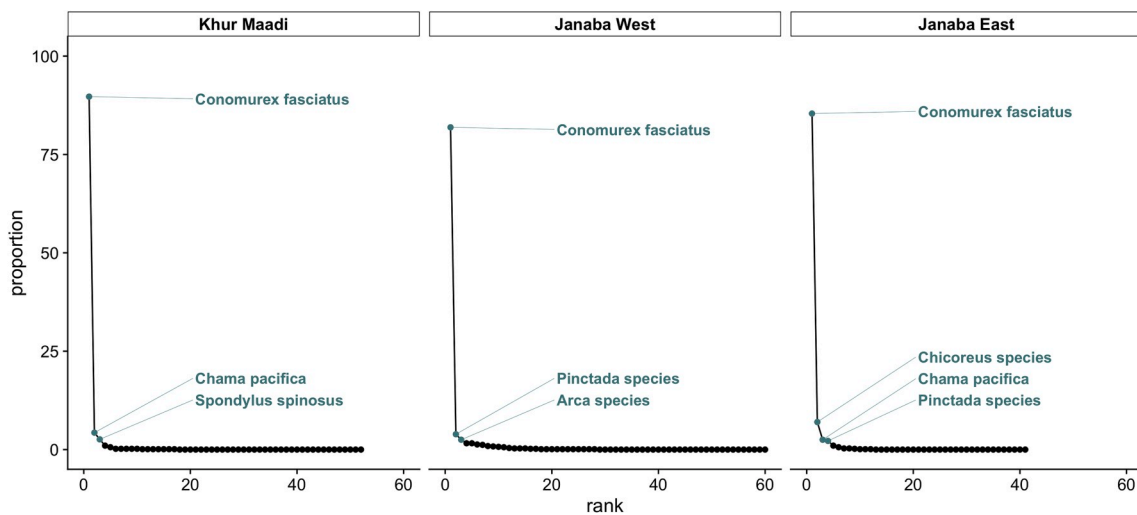
Fig. 5. Dominant species in each bay area shown as weight percentage. Named species represent more than 2% of the overall weight.
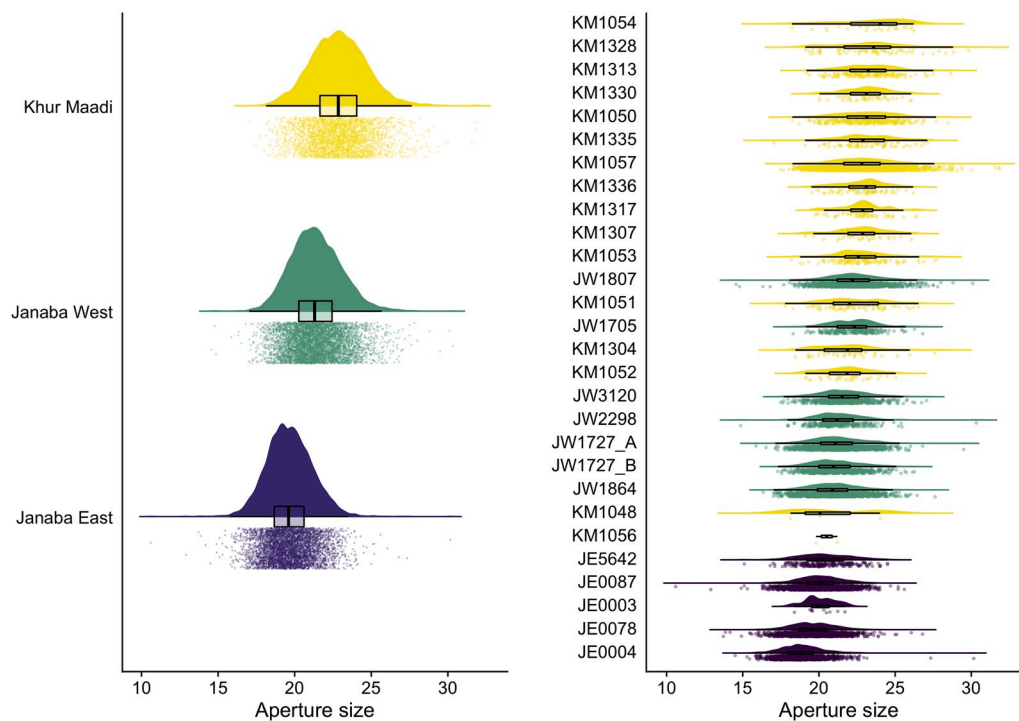
Fig. 6. Raincloud plots of the aperture sizes by area (left) and by site (right) Each raincloud plot consists of a distribution curve on the top, a boxplot indicating the individual quantiles, and each individual measurement as a point within the point cloud at the base. For more information see Allen et al. (2018).

short-lived increase between 5500 and 5000 cal BP. Khur Maadi Bay only features one dated site (KM1057; 5250–5030 cal BP), and exhibits no consistent tendency to size reduction over time. However, when the data are further subdivided into individual site sequences, the consistent time trends disappear (Fig. 7c). Moreover, the intra-site variation is relatively small compared to the range of variation when sites are grouped by bay area. In other words, the long-term time trends apparent in Fig. 7b are largely illusory, resulting from the conflation of short-term individual site sequences, each with its own range of aperture sizes.

4. Discussion

4.1. Species composition

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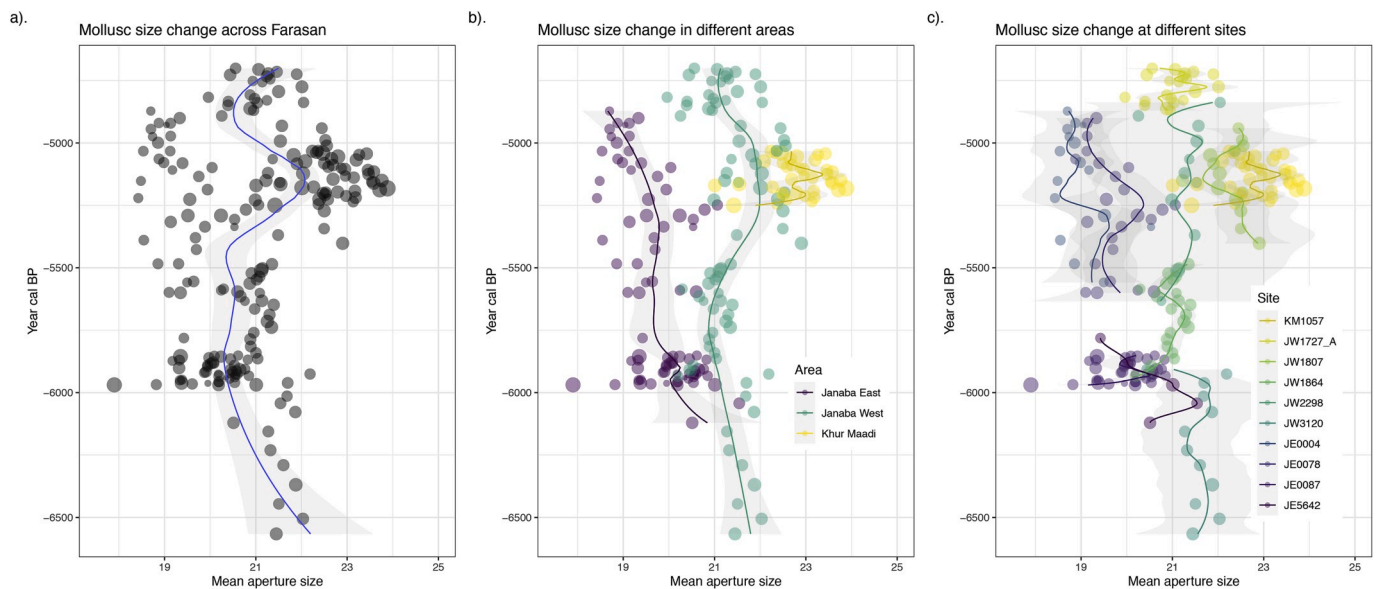
Fig. 7. Mean aperture sizes through time. a, all mean aperture sizes through time without spatial grouping; **b**, mean aperture sizes by bay area; **c**, mean aperture sizes by site. The size of each circle indicates the standard error of the measurements in that sample. Lines describe mean aperture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

instance, this may be the case with *Tridacna* sp. (the giant clam), which was 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 consideration, we are confident that they are not substantial enough to affect our conclusions about the dominance of *C. fasciatus* as the principal target species.

4.2. Shell sizes

The morphology of the dominant species *C. fasciatus* restricted our window of opportunity for analysing size frequency distributions of juvenile and young adult specimens. Thus any indications of reduced frequencies of older and larger specimens, indicating over-harvesting, are not detectable. Nevertheless, with less than 0.8% of juveniles in our assemblage, we can rule out that juvenile specimens were targeted and that over-harvesting to a degree where specimens were eaten prior to being reproductively active has taken place. One caveat to this is the fragility of juvenile lips in comparison to mature, thicker lips, which provide more protection. It is therefore possible that juvenile specimens are under-represented because of differential preservation. While this bias is difficult to quantify, we do not expect it to significantly shift the proportion of juvenile specimens above a few percent. With the reproduction of specimens being unaffected (not counting the positive effect on fecundity (Harding et al., 2008) of older specimens) and *C. fasciatus* retaining its role as dominant species throughout the midden accumulation period, the resilience of *C. fasciatus* to prehistoric human harvesting can be argued to be substantial. This aspect is especially noteworthy given the large quantities of shellfish represented by the over 3000 midden sites on the Farasan Islands (Meredith-Williams et al., 2014), the year-round collection of shells (Hausmann and Meredith-Williams, 2017b), and shell accumulation rates of up to 1.7 m per century per site (Hausmann et al., 2019b). This puts the Farasan middens apart from other sites, where studies have indicated significant impacts on mollusc populations by prehistoric or pre-contact harvesting (Mannino and Thomas, 2002; Morrison and Hunt, 2007; Klein, 2008;

Faulkner, 2009; Erlandson et al., 2011; Hunt et al., 2011). That being said, evidence of small to no changes (Rick et al., 2016) or even increase in shell size following human harvesting is becoming more common (Giovas et al., 2010; Thakar, 2011). It should be noted here that comparisons in terms of the intensity of over-harvesting, are limited by the fact that the studies above use different species and that our limited age-window only provides a simplified view on over-harvesting. With >99% of specimens reaching the stage of maturity, their frequency distribution patterns are a result of processes that are disconnected from human harvesting and instead linked to the local environmental conditions. Because these variations influence the majority of measurements they are worth looking into, which we will do in the following.

4.3. Patch selection and nearshore environments

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

Table 3 describes the preferred habitats of the dominant and

Table 3

Commonly found species in Farasan shell middens and their preferred habitats.

Name of genus/ species	Common habitats
Conomurex fasciatus	Littoral to sublittoral sandy, shallow reefs. Often found grazing on seagrass.
Chicoreus sp.	Littoral to sublittoral, sand or rocky/coral on shallow reefs, protected bays and lagoons.
Pinctada 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).
Chama sp.	Low littoral to offshore, cemented to coral and rocks.
Spondylus spinosus	Sublittoral to offshore, cemented to coral and rocks.
Beguina sp.	Intertidal areas in sand and rocks.
Modiolus 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.
Tricornis (Strombus) tricornis	Grazes in shallow water, soft substrates and corals
Arca avellana	Littoral to sublittoral (up to −80 m), rocky habitats, corals, or under boulders on sandy substrate.

commonly found species in the analysed shell middens. Based on the fairly similar species compositions of the sites and the relative abundances of *C. fasciatus*, we conclude that the gathering areas for all bays mostly consisted of intertidal to subtidal environments made of mixed substrates of sand and corals, as well as their margins. As expected, these habitats are typically found in the shallow reefs along shorelines today and are especially representative of the shallow-water areas of Janaba West and the shallow and protected area of Khur Maadi Bay (Fig. 8).

Comparing the shorelines of the three areas shows that these shallow water areas of the littoral in Khur Maadi and Janaba West are more extensive than the ones in Janaba East. We further need to take into account the changes in sea-level since the shell midden occupation (Lambeck et al., 2011; Hausmann et al., 2019b). With the sea-level

highstand at around 6000 cal BP being 2 m higher than today and the palaeoshorelines of Khur Maadi and Janaba West mirroring these changes, we can conclude that their respective shallow-water areas were more extensive than they are today. In comparison Janaba East would have featured a similarly narrow band of shallow water as it does today, with the sites JE0004 and JE0003 being located close to an even narrower area than the more southern sites (JE0078, JE0087, and JE5642).

These groupings of extensive (KM and JW) and narrow (JE) shallow water areas with their sandy substrates and favourable conditions for seagrass, fit well with the different sizes of *C. fasciatus* (Fig. 5). The preferred habitats of this species are found in the upper littoral where it can graze on seagrass (Table 3). That said, the sizes of shells from Khur Maadi and Janaba West are still quite different from each other, despite the similar geomorphology of the bays. It is possible that the more sheltered location of Khur Maadi, between the two larger islands (Fig. 1), provides it with a more sheltered environment than the exposed shorelines of Janaba Bay. Ultimately, it is difficult to reconstruct past shoreline environments without a detailed analysis of local geomorphology and further analyses of other represented species (not exclusively molluscan) that have lower relative abundances in shell middens. In the future, this information will no doubt provide a more detailed picture of the spatial variability in species composition along shorelines. How much the different shell sizes actively influenced patch-choice by humans is questionable. Fig. 7b and c indicate for example that the beginning of shellfish gathering in Janaba East was not triggered by a decline in shellfish size in other bay areas. Moreover, both parts of Janaba Bay were harvested substantially and over a long term, despite shell sizes in Khur Maadi being higher and the economic return likely higher as well. We can thus assume that patch-choice by humans was not chiefly controlled by the minute (yet statistically significant) differences in shell sizes, as they hardly translate into practical differences for gatherers, but are a product of several factors such as general availability, accessibility, as well as social factors.
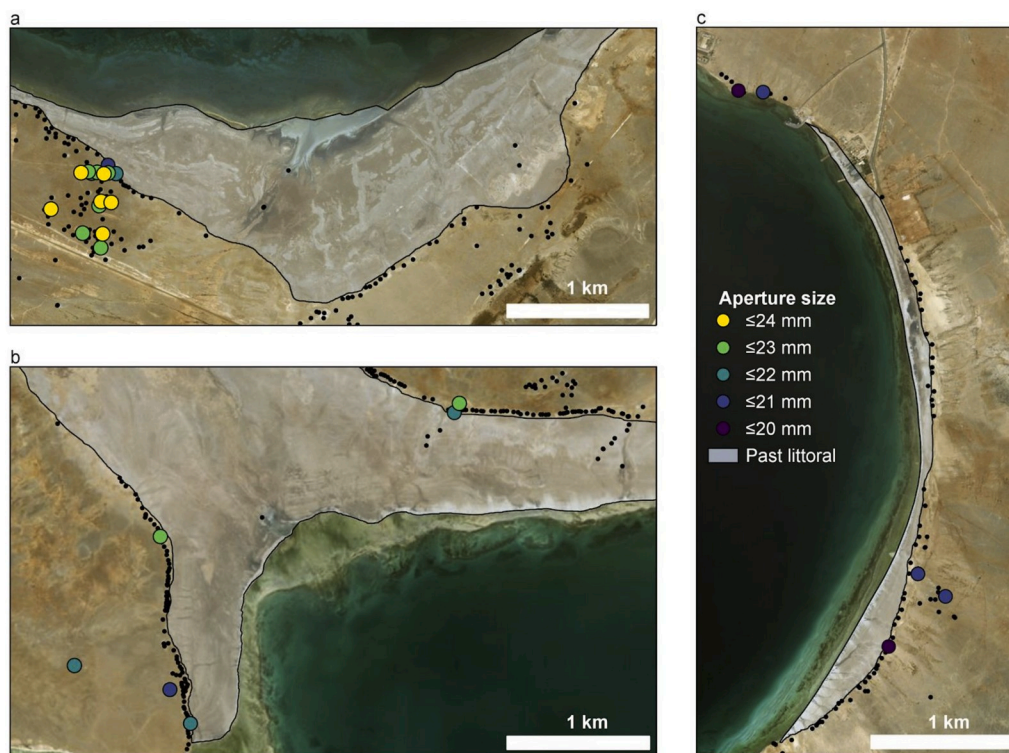
Fig. 8. Farasan bay areas of this study a, Khur Maadi Bay; **b**, Janaba West aperture; **c**, Janaba East. We indicate the potential size of the near-shore littoral zone at the time of higher sea level during the period of shell midden occupation. Colours of sites indicate mean aperture size. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.4. Implications for the southern Red Sea

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

On a temporal scale, the shell midden use seems to happen in parallel for multiple sites for some centuries, pointing to continuous external stresses for *C. fasciatus* populations. But the temporal resolution would still allow for some gaps and for individual patches of shellfish populations to recover before long-lasting ecological perturbations took effect. More information on *C. fasciatus* mobility and population structure would help to disentangle the impact of an individual site on the 'midden's local patch', which could be dramatic and difficult to recover from in the short-term, and the impact 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 JW1727 indicate 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 2500 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 accessible coastal resource at one of the important nodes of

human mobility - the southern Red Sea - adds an extra dimension to the study of Out Of Africa. The fact that these resources are also unaffected by arid conditions adds an additional complicating factor to arguments that past dispersal events were limited to periods of greater moisture availability.

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

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

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

5. Conclusions

With the analysis of shell remains from the Farasan Island shell midden complex, this paper provides insights into southern Red Sea shellfish harvesting in prehistory. The data demonstrate that even with intensive year round harvesting over long periods, the shellfish beds were not negatively impacted and remained available even when arid conditions prevailed on land, supposedly making the landscape inhospitable.

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

With the data presented here, we start to address the gap in quantifying the potential of marine resources in this key gateway of human dispersal through time. The shellfish diversity and abundance found in the shell midden datasets indicate a rich ecological environment that is unaffected by the arid conditions of the terrestrial environment, providing sustainable resources to complement a mixed diet.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2020.04.034.

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