Population structure and growth of the beaked clam *Eumarcia paupercula* (Bivalvia, Veneridae) in Maputo Bay, Mozambique

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The edible beaked clam *Eumarcia paupercula* (Holten, 1802) is an abundant component of the intertidal infauna in Maputo Bay, Mozambique, and is an important source of food and income for local communities. This study investigates the population structure and estimates the growth rate of *E. paupercula* on a highly exploited tidal flat. Between November 2012 and April 2014, population structure was tracked by monitoring monthly length and density distributions, and growth rate was estimated using both mark-recapture experiments and length-frequency analysis (LFA). The population structure can be polymodal, bimodal or unimodal, as new cohorts of clams recruit to the population and older ones are fished or die out. The von Bertalanffy growth function 

\[ L(t) = \frac{L_{\infty}}{1 - e^{-Kt}} \]

where \( L(t) \) is the length at age \( t \), \( L_{\infty} \) is the asymptotic length, \( K \) is the growth rate and \( t \) is the age, was used to estimate growth parameters. The results highlight that temporal population dynamics are strongly influenced by collection and reproductive patterns, and that single environmental parameters do not explain the patterns of growth. Understanding these factors will greatly facilitate development of management measures aimed at ensuring future sustainable exploitation of this species.

**Keywords:** clam fishery, length-frequency, life history, marine invertebrate biology, mark-recapture, size distribution

**Introduction**

Bivalves of the family Veneridae inhabit intertidal sandflats and sandy beaches worldwide, and populations of many species have declined or are depleted (FAO 2016). The main causes of these declines include human exploitation (Urban 1998; Crawford et al. 2010), ecological interactions between benthic groups (Beal and Kraus 2002; Pillay et al. 2007; Polyaakov et al. 2007), changes in the environment (Norkko et al. 2006; McLeod and Wing 2008) and failed recruitment (Borsa and Millet 1992; Caddy and Defeo 2003). Studies on the distribution of clams in Maputo Bay are scarce (Scarlet 2005; Vicente and Bandeira 2014), and no published research on the growth of these clams is available.

Seasonal changes in clam population structure are mostly a result of reproduction and recruitment processes in the case of non-fished populations (Emerson and Grant 1991; Denadai et al. 2005; Fiori and Defeo 2006), and are also strongly influenced by fishery control structures in the case of fished populations (Defeo 1998; Lercari et al. 2018).

Fishery aspects (Defeo 1998; Humphreys et al. 2007) and biotic factors (Lima et al. 2000; Beal 2006; Moura et al. 2017) have an impact on clam population growth, mostly by reducing the asymptotic length owing to the loss of larger individuals to the fishery or the loss of smaller individuals to natural predation. Population density might also indirectly affect clam growth through its negative influence on food supply (Griffiths and Griffiths 1987).

The beaked clam *Eumarcia paupercula* (Holten, 1802) comprises a great part of clam consumption in Maputo (Scarlet 2005; Mugabe 2016; Mugabe et al. 2017, 2019), and estimates of growth parameters and the status of populations are required to better manage exploitation of stocks of this species. This study aims to describe seasonal changes in the population density and size structure, and to characterise the growth pattern, of the beaked clam in its natural habitat in Maputo Bay.

**Materials and methods**

**Study area**

Maputo Bay is located at 32°47′ E, 26°03′ S in the south of Mozambique (Figure 1). The total area of the bay is 1 280 km², of which approximately 774 km² constitutes the sub-littoral zone, with the remainder equally divided between intertidal areas and sand dunes (Lencart e Silva et al. 2010). Sampling for *E. paupercula* took place at Costa do Sol beach, an intertidal sandflat, which is the major fishing centre in Maputo Bay and a major source of harvested *E. paupercula*.

**Density and population structure**

The density and size structure of the *E. paupercula* population were analysed by monitoring the numbers and length-frequency distributions of individuals within a 300-m length of exposed intertidal sandflat at Costa do Sol beach.
Sampling was undertaken during low spring tides during an 18-month study period extending from November 2012 to April 2014. Six transects, perpendicular to the coastline, were used. Transect lines were 240-m long and separated from each other by 50 m, and samples were taken from 0.25-m² (0.5 × 0.5 m) quadrats spaced at 10-m intervals along these lines. A maximum of 30 individuals from each sample, if the sample contained more than 30, were randomly selected and shell length (maximum distance along the anterior–posterior axis) of each was measured to the nearest 0.01 mm using Vernier callipers.

**Growth-data collection**

Length-frequency analysis (LFA) of data obtained from the 18-month study of population structure, and monthly length-increment data obtained from mark-recapture measurements from an *in situ* experiment that lasted 12 months, were both used to study the growth of *E. paupercula*. Two hundred individuals were tagged with plastic colour-coded geometric forms (1-mm thick) and marked with a waterproof pen. Their initial sizes ranged from 15 to 30 mm shell length.

For the LFA, marked clams were released at a density of 50 ind. m⁻² at the experimental station located within the

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**Figure 1:** Map of Maputo Bay showing rivers that discharge into the bay. The oval outline marks the study site at Costa do Sol beach.
sampling area, at 150 m from the highwater mark, and were buried directly in the sediment at a depth of 3–4 cm, without any fencing. The geographical coordinates of the site were recorded, and signs were placed in the area requesting other collectors not to exploit the site.

To relate population parameters to ambient environmental conditions, three replicate measurements of water temperature (°C) and salinity were made in situ on each day of sampling. A handheld digital thermometer and a refractometer were used to record temperature and salinity, respectively. Total monthly rainfall data for the study period were obtained from the Mozambique National Institute of Meteorology.

Data analysis
Analysis of variance (ANOVA) was performed to compare seasonal variation in the density and mean length of *E. paupercula*. Levene’s test was used to test the homogeneity of variances between seasons (winter: April–September; summer: October–March).

The von Bertalanffy growth function (VBGF; Eqn 1) was used to describe the growth rate of *E. paupercula*, where \( L_t \) is the length at time \( t \), \( L_\infty \) the asymptotic length, \( K \) the growth constant, and \( t_0 \) the constant representing time when \( L_t \) equals zero.

\[
L_t = L_\infty [1 - e^{-K(t-t_0)}] \quad (1)
\]

Monthly length-frequency distributions were plotted per 1-mm-size-class for growth estimation. These data were fitted to a VBGF curve, applying the nonparametric electronic length-frequency analysis (ELEFAN I) routine of the FAO-ICLARM Stock Assessment Tools II (FiSAT II 1.2.2) program package (Gayanilo et al. 2005).

In addition, the monthly growth rate (\( \Delta L \) per month) was assessed following one cohort (cohort II), by analysing a curve fitted by eye for this cohort. After constructing length-frequency histograms for the entire population, an inverse of the von Bertalanffy equation was then used to estimate the lifespan of *E. paupercula*. The theoretical lifespan (\( t_{\text{max}} \)) was estimated according to Eqn 2, which considered the maximum shell length as being 95% of \( L_\infty \) (Taylor 1958):

\[
t_{\text{max}} = \frac{\ln L_\text{95\%} - \ln (L_t - L_\text{95\%})}{K} \quad (2)
\]

where \( K \) is the growth constant, \( L_\infty \) the asymptotic length, and \( L_\text{95\%} \) equals 95% of the maximum shell length recorded from the LFA used to fit the VBGF.

The same growth function (VBGF) was used to describe clam growth, using the data from the mark-recapture experiment and applying Munro’s method (Munro 1982) in FiSAT II.

The growth curves obtained from the mark-recapture experiment and LFA were linearised using the Ford–Walford method, and an F-test was performed to compare the regression coefficients, with the null hypothesis \( b_{\text{LFA}} = b_{\text{mark-recapture}} \), where \( b \) is the slope of the regression.

The growth performance index (\( \Phi' \)) was estimated according to Eqn 3 (Pauly and Munro 1984) from the average growth parameter estimates:

\[
\Phi' = \log K + 2 \log L_\infty \quad (3)
\]

Results
Seasonal density variability and population structure
The highest overall mean density of *Eumarcia paupercula* at Costa do Sol (237.50 ind. m\(^{-2}\)) was recorded during October 2013, whereas the lowest density (76.17 ind. m\(^{-2}\)) was found during February 2013 (Figure 2). Analysis of seasonal variation in mean density showed no significant differences (\( p > 0.05 \)) between summer (October to March) and winter (April to September).

A total of 39 920 individuals of *E. paupercula* were collected at Costa do Sol beach over the duration of the study, of which 9 982 individuals were used for length-frequency analysis. A large size range was sampled, with the smallest individual measuring 2 mm and the largest 38 mm. The largest size class of clams (\( >31 \text{ mm} \)) was estimated according to Eqn 2, which considered the maximum shell length as being 95% of \( L_\infty \) (Taylor 1958):

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t_{\text{max}} = \frac{\ln L_\text{95\%} - \ln (L_t - L_\text{95\%})}{K} \quad (2)
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![Figure 2: Monthly variation in mean density of *Eumarcia paupercula* (±SD) at Costa do Sol beach, Maputo Bay, Mozambique, over the period November 2012–April 2014](image-url)
was scarce, with the proportion in the population ranging from 0.33% in May 2013 to 4.90% in February 2013. The most-intensively harvested size class of clams (21–30 mm) (Mugabe 2016) ranged from a maximum proportion of 53.01% during October 2013 to a minimum proportion of just 1.17% in May 2013. Smaller clams of between 11 and 20 mm attained their highest proportion in August 2013 (76.96%) and lowest proportion in April 2013 (early winter) (8.15%). Juvenile clams (2–10 mm) comprised a high percentage of the population in April 2013 (86.52%) and March 2014 (64.92%), but were less than 5% of the population in September 2012.

An overview of the monthly length-frequency distribution of *E. paupercula* during the sampling period is provided in

![Figure 3: Monthly length-frequency distributions of the *Eumarcia paupercula* population at Costa do Sol beach during the period November 2012–April 2014. Sample sizes (n) are shown above each chart. Overlaid on the figure are von Bertalanffy growth function (VBGF) growth curves (grey lines) estimated from length frequency analysis (LFA). The VBGF parameters used to fit the curves were $L_\infty = 41$ mm and $K = 1.01$ y$^{-1}$ for the growth rate estimated from cohort II, the major cohort tracked though most of its life cycle](image-url)
Figure 3. The monthly length-frequency histograms were unimodal for April to October 2013. Bimodal distributions were found in November 2012, March and November 2013, and March and April 2014, whereas a multimodal distribution characterised both December–February periods.

**Growth analysis**

Figure 3 shows how the length-frequency distributions of the *E. paupercula* population varied over the entire study period. By analysing these histograms, it was possible to identify three cohorts of *E. paupercula* as present during the study period. These cohorts, defined according to when they were first sampled, are termed cohort I (November 2012), cohort II (April 2013) and cohort III (March 2014). Cohort II exhibited higher recruitment rates than either cohorts I or III, and consequently was designated as the major cohort to be used to estimate the growth rates.

The VBGF parameters estimated from the LFA of cohort II were $L_\infty = 41.0$ mm and $K = 1.01$ y$^{-1}$, with $t_0$ defaulted to zero. The lifespan ($L_\infty$) was estimated as 1.97 years.

Of the 200 individuals initially marked, 126 (63%) were recaptured in at least one pair of successive monthly samples. These recaptures resulted in 527 growth-increment data pairs computed for growth analysis using Munro's method. However, of these 527 observations, only 352 were used by the model to generate the VBGF parameters, as the remaining 175 observations resulted in recapture lengths equal to the marked lengths (no growth observed). The mark-recapture experiment indicated significant and strong seasonal growth oscillations (i.e. $C < 0.80$), with the lowest growth rates observed in July, and the highest in January.

The VBGF parameters estimated from mark-recapture were $L_\infty = 40.50$ mm and $K = 1.65$ y$^{-1}$. Thus, the VBGF for *E. paupercula* in Maputo Bay, as obtained from the mark-recapture experiment, was:

$$L_\infty = 40.5 \left[1 - e^{-1.65(t-0.03)}\right]$$ (4)

Comparisons of linear-transformed growth curves showed significant differences ($p < 0.05$) between the regression equations from the LFA ($y = 0.36x + 41.0$) and the mark-recapture experiment ($y = 0.19x + 45.0$); the respective VBGF curves are presented in Figure 4.

**Discussion**

**Density and population structure**

Much higher densities of *Eumarcia paupercula*, of up to 500 ind. m$^{-2}$, were recorded in the present study, compared with only 15 ind. m$^{-2}$ found by Scarlet (2005) in other tidal flats of Maputo Bay. Similarly high densities of other clam species have been reported not only in southern African beaches (e.g. the surf clam *Donax serra* reaches 1 900 ind. m$^{-2}$ at Port Elizabeth, South Africa: Lastra and McLachlan 1996) but also elsewhere (e.g. the yellow clam *Mesodesma mactroides* in Uruguay reaches densities of up to 900 ind. m$^{-2}$: Brazeiro and Defeo 1999).

From the initiation of sampling in November 2012 until March 2013 and again from October 2013 to March 2014, the clam population structure showed a polymodal or bimodal distribution, and both a diminishing adult cohort and growing new cohort(s) were present. These periods corresponded with the high collection season as well as with an addition of new cohorts of settling juveniles, and thus with periods of replenishment of one cohort by the next. However, April to September was a period of population recovery during which time exploitation was at its minimum and the distribution pattern was unimodal, with higher frequencies of smaller clams (<20 mm) in the beginning of the season, and these grew progressively bigger over time. Therefore, this pattern is a consequence of the reproductive cycle plus the seasonal collection of larger adults by artisanal fisheries.

**Growth rates from LFA**

Analysis of the growth rates of cohort II showed that highest shell growth occurred in April and September, at the rate 5.94 mm month$^{-1}$. Although evidence of predation was present (drilled shells in marked individuals), the impact of predation on these calculated growth patterns of *E. paupercula* was not tested. The selective removal of larger, faster-growing individuals by predators that select for larger prey can artificially depress calculated growth rates. Also, the presence of predators might result in actual decreases in the growth rates of surviving clams (Beal 2006). For example, some clam species might burrow deeper to evade foraging crabs (Blundon and Kennedy 1982; Beal and Kraus 2002), leading to reduced growth rates as feeding in the deeper sediment layers is restricted.

Bird predation in the tidal flats at Maputo Bay might also be a significant factor contributing to the removal of intertidal organisms, although to a far lesser extent than the contribution by fishing mortality. Scarlet (2005) and Gribben and Wright (2014) found white-faced herons *Egretta novaehollandiae* and little egrets *E. garzetta*, among other birds, foraging during their surveys and they concluded that these birds were the main avian predators of the venerids *Katelysia scalarina* and *E. paupercula*, respectively. Rates of mortality due to bird predation at this site have not, however, been measured.
The lowest growth rates were recorded in July 2013 (0.09 mm month$^{-1}$) and February 2014 (0.67 mm month$^{-1}$). February 2014 corresponded to the period when the growth rate of cohort II was probably slowing, as the clams approached adult size, but the apparent decline in growth rate might also partially be an artefact caused by selective removal of larger individuals by collectors.

Growth patterns of *E. paupercula* from this study are similar to those found in Uruguay by Brazeiro and Defeo (1999) for *M. mactroides*, where the lowest growth rates recorded coincided with peak fishing effort, and vice versa. Low growth rates recorded during November are probably related to spawning events during this period (Mugabe et al. 2017), because most of the energy available for production might be diverted into reproduction (Urrutia et al. 1999).

Although the strong presence of cohort II through most of the study period allowed growth modelling of this cohort using LFA, it is often difficult to estimate appropriate VBGF parameters for an entire population. For example, when age-length equivalents are fitted with insufficient data, an accumulation of error occurs (Hofmann et al. 2006; Vasconcelos et al. 2018). This means that larger numbers of individuals of the same age are required to predict an equivalent length of an individual of that age, and vice versa, and these are not always possible to find within a population. For instance, out of 3 401 individuals used to fit the population growth curve here, only 451 were between 25 and 38 mm.

**Growth rates from mark-recapture data**

The growth curve calculated by this method showed that, following the typical pattern, smaller individuals had a faster growth rate and that slow growth increments were recorded in the last months of the experiment, as the clams were approaching their terminal size. This is the first growth study of this species and the growth rates reported are compared with those of other species listed in Table 1. These studies also applied mark-recapture to estimate the VBGF parameters, thereby allowing the calculation of $\Phi'$ for comparative purposes. This index can also be used for interspecific growth comparisons (Pauly and Munro 1984). Local characteristics, rather than simple latitudinal differences, would better explain the differences of $\Phi'$ (Lercari et al. 2018). When venerids only are considered, *E. paupercula* has the highest growth performance index after that of the great clam *Ruditapes philippinarum* (Chung et al. 1994; Humphreys et al. 2007; Ponurovskii 2008; Dang et al. 2010; Colakoglu and Palaz 2014), *Tivela mactroides* (Arrieche and Prieto 2006; Turra et al. 2014) and *Leukoma antiqua* (=*Venus antiqua*, Clasing et al. 1994).

The index $P$ assumes that the slope of the growth curve has one maximum value of growth rate, and therefore $P$ is proportional to the size increase at the inflexion point of the VBGF:

$$P = \log(KL_\infty)$$

Although there is no clear distinction in terms of $P$ between the subtropical/tropical and temperate species, it appears that the growth performance of venerids increases with latitude. Moreover, differences in seawater temperature and food supply between the studied areas are the major drivers of differences in growth patterns in clams (Purroy et al. 2018).

**Analysis of growth from length-frequency versus mark-recapture data**

The LFA method appeared to be sensitive to the season of collection and clam recruitment. The small frequency of large size classes during and after the collection season might have led to a smaller estimated $L_\infty$ than that estimated from the mark-recapture analysis. The relatively fast growth rates and the year-round spawning pattern of *E. paupercula* (Mugabe et al. 2017) created overlapping cohorts, which might have led to a biased estimation of growth parameters using computed LFA (Sparre and Venema 1998).

The use of LFA to fit the von Bertalanffy growth curves might also have led to our smaller value of $L_\infty$ (41.00 mm). This length is smaller than the largest individual (42 mm) recorded for the species (Branch et al. 2010). The small value of $L_\infty$ was probably affected by temporal changes in size frequencies, with certain months having low densities of bigger clams (>20 mm) as an outcome of fishing. For the mark-recapture experiment, only individuals greater than 20 mm were used (owing to the difficulty of tagging and recovering smaller individuals), and these would already be showing slowed rates of growth as they approached adult size, leading to the significantly smaller growth constant for mark-recapture data, but with a comparable $L_\infty$.

**Growth in relation to environmental parameters**

The growth performance index ($\Phi'$) of *E. paupercula* showed no significant correlation with any of the environmental parameters tested ($p > 0.05$). Grizzle et al. (2001) noted that other venerids have high tolerance to many environmental factors, including those recorded in this study. In any event, the small temperature variations found in tropical ecosystems, such as the one studied here, are likely to have little effect on the growth patterns of clams, in comparison with those from temperate regions, which are subject to much larger seasonal temperature variations, which dramatically influence seasonal growth patterns (Broom 1982).

**Lifespan**

*Eumarcia paupercula* is a fast-growing species (Table 1); theoretically, it would take only 17 months for a clam to reach the maximum size of 42 mm recorded by Branch...
Table 1: Comparison of the growth parameters of several venerids. Present study shown in bold

| Species                  | Location (latitude) | Water temperature (°C) | $L_{\text{max}}$ (mm) | Lifespan (years) | $\Delta L$ (mm month$^{-1}$) | $\Phi'$ | Reference                      |
|--------------------------|---------------------|------------------------|------------------------|-----------------|------------------------------|--------|-------------------------------|
| Anomalocardia flexuosa   | Brazil (23°49′ S)   | 19.8–29.0              | 39.00                  | 3.41            | –                            | 2.89   | Corte et al. (2017)            |
| Eumarcia paupercula      | Mozambique (25°54′ S) | 22.2–30.9              | 38.00                  | 1.97            | 0.24–6.30, 0.14–4.96         | 3.43   | Present study                 |
| Tivela mactroides        | Brazil (25°54′ S)   | –                      | 32.47                  | 2.4             | –                            | 3.22   | Turra et al. (2014)           |
| Gafarium pectinatum      | India (8°35′–9°25′ N) | –                      | 37.70                  | 3               | 0.38–2.24                    | 2.93   | Jagadis and Rajagopal (2007)  |
| Meretrix meretrix        | India (8°45′ N)     | 25.0–31.0              | 91.00                  | 7.8             | 0.15–2.20                    | 3.50   | Narasimham et al. (1988)      |
| Mercenaria mercenaria    | USA (37°15′ N)      | 4.0–27.0               | 84.00                  | 9               | –                            | 3.17   | Harding (2007)                |

Figure 5: Auximetric grid (after Pauly 1979) comparing the overall growth performance ($P$) of several venerids from subtropical/tropical regions (open circles) and temperate regions (solid circles) with Eumarcia paupercula from Maputo Bay (solid square). Diagonal lines indicate equal values of $P$.

et al. (2010). This is consistent with the lifespan of 1.97 years estimated for this species in Maputo Bay.

Lifespan and growth rate of different species of venerid clams are presented in Table 1. As growth rates are determined using various indicators ($K$, $\Phi'$ and $\Delta L$), this table includes only those studies that used $\Delta L$ and $\Phi'$. The lifespan for E. paupercula (1.97 years) for the recorded $L_{\text{max}}$ of 38 mm is shorter than that estimated for the venerid Ruditapes bruguieri (6.6 years), although the $L_{\text{max}}$ (36 mm) of that species was smaller (Salina 2014); this suggests a latitudinal variability in the growth parameters and lifespans within the Veneridae, under growth-favourable local environmental conditions. Urrutia et al. (1999) found that the growth of R. decussatus was slower than that reported by previous studies from similar latitudinal ranges, due to a low food concentration. Also, Turra et al. (2014) found that, for Tivela mactroides, a smaller maximum size was associated with a lifespan longer than the lifespan of a larger maximum size recorded in the same area three years later.

The lifespans of clams can vary from one year to hundreds of years (Cardoso and Veloso 2003; Brix 2013). The lifespan of E. paupercula is consistent with the shorter duration associated with clams recorded from tropical regions (Turra et al. 2014) compared with those of temperate species (Harding 2007). The relatively high growth rates and the short lifespan of E. paupercula in Maputo Bay are favourable characteristics for an exploited population, since they facilitate rapid recovery of the population.

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