Aspects of the Biology, Ecology and Fishery of the Beaked Clam *Eumarcia paupercula* (Holten, 1802), in Maputo Bay

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For Domingos Mugabe and Felismina Sitoi

"My dearly beloved parents... my major strength"

Declaration

I, **Eulália Mugabe**, hereby declare that I know the meaning of plagiarism and that all of the work presented in this thesis is my own, except where otherwise stated and acknowledged in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed: Signed by candidate

Signature removed

Date:

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Abstract

Clam populations globally have declined, or been depleted, with one of the major causes being uncontrolled human exploitation. This thesis investigates the population structure, growth, reproduction and exploitation of the beaked clam *Eumarcia paupercula* in Maputo Bay. The substantial commercial harvesting of this clam may lead to overexploitation of the resource. In this regard, some fundamental knowledge is necessary for the management of future exploitation. The data collection was based on an 18-months (November 2012 – April 2014) sampling for population structure across a tidal flat. The growth analysis was performed on FiSAT II, using mark-recapture experiments and length-frequency data. Monthly reproduction analysis was based on the fluctuation of body weight and gonad smear analysis. Furthermore, interviews were used to ascertain the importance of the resources for collectors and estimate landings of *E. paupercula*.

The von Bertalanffy growth function and length-frequency analysis revealed that *E. paupercula* has a fast growth rate and a short life span. *Eumarcia paupercula* is a year-round spawner with higher peaks in the summer; recruitment follows a similar pattern, occurring over the year and after the spawning peaks. The clam collectors, the majority of whom are women, have experienced an increase in the effort required to collect clams, resulting in a decline of catches over the season. This study highlights that temporal population dynamics are influenced by collection and reproductive patterns, and that single environmental parameters do not explain the patterns of growth, reproductive cycles and spatial distribution.

Findings of this study have relevance and application for the livelihood of the collectors, as well as the sustainability of the *Eumarcia paupercula* stock, by providing a basis for fishery governance. While recommendations are presented for the management of *E. paupercula* collection, the Ministry of Fishery in Mozambique also has to consider collecting data on bivalves, as they are an important source of income for artisanal fishers. Future research should include monitoring of a less exploited population, so as to understand better how collection impacts on the population dynamics of *E. paupercula.* Furthermore, laboratory studies of the larval cycle are necessary to gain thorough understanding of the species life cycle.

List of Acronyms

ADNAP	National Fisheries Administration
CCP	Fisheries Community Centre
CDS-ZC	Centre for Development of Coastal Zone
CI	Condition Index
CITES	Convention on International Trade in Endangered Species
CMM	Municipality Council of Maputo
CONDES	National Council for Sustainable Development
CPUE	Catch per unit effort
CTIGIZC	Inter-institutional Committee for the Integrated Coastal Management
DNFFB	National Directorate of Forests and Wildlife
EAF	Ecosystems Approach to Fisheries
ELEFAN	Electronic Length–Frequency Analysis
FAO	Food and Agricultural Organisation of United Nations
FiSAT	FAO-ICLARM Stock Assessment Tools
IDPPE	Institute for the Development of Small-Scale Fisheries
IIP	Institute of Fisheries Research
INAM	National Institute of Meteorology
INIPE	National Institute of Fisheries Inspection
IUCN	World Conservation Union
LFA	Length-Frequency Analysis
LFD	Length-Frequency Distribution
MPA	Marine Protected Area
MICOA	Ministry for Coordination of Environmental Affairs
NGO	Non-governmental Organisation
TAC	Total Allowable Catch
VBGF	von Bertalanffy Growth Function
WWF	World Wildlife Fund

The Bivalvia is the second largest class within the Phylum Mollusca, after the Gastropoda, and comprises over 7,500 species of oysters, mussels, scallops and clams. Clams themselves constitute a diverse group, with notable variations visible in the external morphology of shells from one species to the next; nonetheless, what is common is that they burrow into the sea bed (Gosling, 2003). Anatomical variations between species include differences in colour, shape, size and levels of sculpturing of the shell, which can be noted even within a single species (Branch *et al*., 2010). As global fishery statistics consider landings and values in combination for clams, cockles and ark-shells (Food and Agriculture Organization, 2014), these categories will be referred to as clams henceforth when being discussed in relation to fisheries.

In evolutionary terms, the Veneridae family (Rafinesque, 1815) is the most diverse bivalve group; it is also one of the least studied and poorly defined molluscan taxa (Mikkelsen *et al*., 2006). Venerids constitute the largest family of bivalves and include several species that are high in abundance and have significant commercial value. Despite this, their biology is not well understood (Mikkelsen *et al*., 2006).

In southern Africa particularly, very little research has been undertaken with regards to venerids despite the fact that, according to Kilburn and Rippey (1982), about 32 species have been recorded in the region. What has been done, by authors such as Ngqulana *et al*. (2010) and Scarlet *et al*. (2015), was concerned with density and distribution of some venerids along with other infauna. Within the region, studies on clam populations have largely focused on the Donacidae species, particularly the large wedge clam or 'white mussel' *Donax serra*. This species is a dominant component of the fauna of exposed ocean sandy beaches along most of the coastline of South Africa (Lastra & McLachlan, 1996; Schoeman, 1996; Sims-Castley & Hosking, 2003), where it is frequently exploited for both food and bait.

The venerid *Eumarcia paupercula* (Holten, 1802) plays an important role in clam fisheries in Mozambique (Scarlet, 2005; Rosendo, 2008); however, as with other species of this family, there remains a significant gap in understanding of its biological traits. In fact, many aspects of the fishery of *E. paupercula* in Maputo Bay are completely unknown. This thesis aims to contribute to the pool of information concerning this venerid, as this is crucial to the future management of this resource. In doing so, this thesis documents the distribution of *E. paupercula* across shore and describes its growth and reproductive patterns in Maputo Bay, Mozambique. Furthermore, aspects of fisheries are presented and prospective management measures suggested. Following a reconnaissance of the literature discussing venerids, we believe this study is the first to investigate the growth and reproduction of this species.

Introduction to the Veneridae

Classification of Veneridae has been somewhat unstable over the years in terms of taxon placement and arrangement (Mikkelsen *et al*., 2006; Silina, 2014). Mikkelsen *et al*. (2006) presented a detailed phylogeny of the Veneridae, which comprises over 800 existing species dispersed among 170 genera (Mikkelsen *et al*., 2006). Geneticists argue that while the 12 subfamilies presented in *Treatise on Invertebrate Palaeontology* (Keen, 1969) are widely accepted, they are based on morphological traits and do not, therefore, reflect genetic relationships (Canapa *et al*., 2003; Mikkelsen *et al*., 2006). This may be among the reasons for the high species synonymy encountered within this group.

Venerids are globally distributed in temperate to tropical waters, and are able to adapt to a broad range of environmental conditions (McLachlan *et al*., 1996; Gosling, 2003; Nel *et al*., 2012). Venerids burrow in muddy or sandy sediments in mangroves, intertidal flats, bays, estuaries, estuarine lagoons, surf zones and deep sea waters (Harte 1998). They are also known as Venus clams, and include some of the most commonly known bivalves, such as the northern quahog, *Mercenaria mercenaria*; Pismo clam, *Tivela stultorum*; littlenecks, *Protothaca staminea* and *Leukoma staminea*; butter clam, *Saxidomus giganteus;* and Manila clam, *Ruditapes philippinarum*.

The most studied species within the Veneridae is *Mercenaria mercenaria*. It naturally occurs on the Atlantic coast but was introduced into the Pacific coast of the United States (Menzel, 1989) and Europe (Rice, 1992). The second most studied species is *Ruditapes philippinarum*, which has many synonyms, most commonly *Tapes philippinarum*; both of these have been used interchangeably, depending on the study or publication (Goulletquer, 1997). Other names include *Tapes semidecussatus, Venerupis philippinarum, V. semidecussatus and V. semidecussata*

(Howson & Picton, 1997). Other venerid species that have been the focus of academic study include *Ruditapes decussatus* (Borsa & Millet, 1992; Urrutia *et al*., 1999; Delgado & Camacho, 2005; Juanes *et al*., 2012)*; R. bruguieri* (Silina, 2014); and *Meretrix* spp. (Jayabal & Kalyani, 1987; Chung, 2007; Xuan *et al*., 2011; Hashiguchi *et al*., 2014) in Asia, and *Anomalocardia brasiliana* from South America (Barreira & Araujo, 2005; Luz & Boehs, 2011).

As mentioned above, little work has been done on venerids in southern African. The few studies that have been done were species-specific in their approach and sought to describe inter-specific relationships between infauna (Pillay *et al*., 2007), the importance of clam resources for fishing communities, and various population features (Scarlet, 2005). Nonetheless, what has been established is that venerids such as *Meretrix meretrix* and *Eumarcia paupercula* are the main feature of fauna in the tidal flats of the tropical east coast of the region (Balidy, 2003; Nel *et al*., 2012; Vicente & Bandeira, 2014) and are regarded as important sources of food and income for coastal communities in Mozambique (de Boer & Longamane, 1996; Rosendo, 2008; Branch *et al*., 2010).

Nomenclature and taxonomy

The beaked clam *Eumarcia paupercula* (Holten, 1802) belongs to the family Veneridae. Synonyms of the species include *Venus paupercula* (Chemnitz, 1795), *V. kochii* (Philippi, 1843), *Tapes kochii* (Philippi, 1843), *Chione* (*Austrovenus*) *ambigua* (Deshayes, 1853), *Anomalocardia alfredensis* (Bartsch, 1915), and *Marcia paupercula* (Chemnitz, 1795; Kilburn & Rippey, 1982). Previously, studies on the benthos of southern African shores referred to *E. paupercula* as *Eumarcia kochi* (Boltt, 1975) and *Pitaria kochi* (Day, 1974). To avoid ambiguity, this thesis will use only *Eumarcia paupercula* when citing the aforementioned studies. According to the World Register of Marine Species or WoRMS (Rosenberg & Huber, 2014), the taxonomy of *Eumarcia paupercula* (Holten, 1802) is as follows:

Phylum: Mollusca
- Class: Bivalvia
  - Order: Veneroida
    - Family: Veneridae
      - Genus: *Eumarcia*

Geographic distribution

Eumarcia paupercula is distributed along the south coast of South Africa to the east coast as well as in southern Mozambique (Branch *et al*., 2010). The southernmost location in which the occurrence of *E. paupercula* has been documented is Kariega Estuary in the Eastern Cape, South Africa (Hodgson, 1987), where it was predominantly recorded in mud intertidal areas (Teske & Wooldridge, 2003). *Eumarcia paupercula* was previously reported as *Pitaria kochi* (Day, 1974) at Morrumbene Estuary, 400 km to the north of Maputo Bay in Mozambique. It has also been documented in Tanzania, where it is collected for personal consumption and trading purposes (Nordlund *et al*., 2010; Rumisha *et al*., 2015). The beaked clam is widely recognised as a native species of the tropical Western Indian Ocean; even so, in the malacology collection of *The Academy of Natural Sciences (ANSP) – Philadelphia*, occurrence of the beaked clam was also reported in Madagascar (reference number: 258909) (ANSP, 1960). There have also been reports of *E. paupercula* being noted in São Tome and Principe (reference number: 267831 at the Malacology Collection of ANSP) (ANSP, 1915); however, no published reports on the species are available from these two countries. This lack of verified sources of information from the Atlantic coast suggests that these records may have been based on misidentifications. Figure 1.1 reflects current global distribution of *E. paupercula* according to Rosenberg and Huber (2014).

Figure 1.1: Current global distribution of *Eumarcia paupercula* adapted from Rosenberg and Huber (2014) and data from literature cited in the text; the colours distinguish confirmed (□) and dubious records (■).

Biology and ecology

Eumarcia paupercula is a morphologically smooth clam with a posterior end that is shaped like a beak. The external shell colour can vary from cream to shades of brown, and may display brown or grey zigzags, flecks or rays. Individuals from muddy sediments tend to be darker than those inhabiting sandy substrata – this is possibly due to the colour of the sediment. The internal surface of the shell of *E. paupercula* is smooth and is white in colour (Figure 1.2); its siphons are separated across their entire length and have light brownish tips (Figure 1.3). *Eumarcia paupercula* burrows 2-3 cm below the surface of sandy or muddy substrata and can grow to a length of 42 mm (Branch *et al*., 2010).

Figure 1.2: Colour variability of *E. paupercula* shells with external (left) and internal (right) views.

The across-shore distribution of *Eumarcia paupercula* does not seem to be closely related to shore levels at the Morrumbene Estuary in Mozambique (Day, 1974). However, in South Africa, *E. paupercula* was recorded at low densities at the Mfolozi-Msunduzi (1-2 individuals/m^2) and Knysna (4- 12 individuals/m^2) estuaries (Allanson *et al*., 2000; Ngqulana, 2012). Furthermore, a decrease in the number of bivalves, including *E. paupercula,* was noticed after the heavy floods of 1971 in the Swartkops Estuary, South Africa (McLachlan & Grindley, 1974).

Figure 1.3: Colour variability of *Eumarcia paupercula* at Costa do Sol fish market in Mozambique. As seen, the siphons are completely separated.

Distribution patterns of clams

There are three dimensions to the spatial distribution patterns of organisms inhabiting tidal flats (Schoeman & Richardson, 2002). Across-shore distribution is related to vertical height from the high-water mark to the low-water mark (Peterson, 1991); along-shore distribution describes variability along the length of the beach; and vertical distribution is that which is between the sediment surface and further depths (Schoeman & Richardson, 2002). Most authors pool across-shore and vertical distribution as the same pattern, by digging quadrat samples to a specific depth (Yap, 1977; Weiss *et al*., 2007; Fahy *et al*., 2010; Juanes *et al*., 2012; Adkins *et al*., 2014; Ruesink, *et al*., 2014) exceeding that of the deepest clams across the shore from high to low-water mark (Murphy, 1985; Bergonci & Thome, 2008). The ways in which clams are typically distributed across these three dimensions are detailed below.

Across-shore distribution of clams

In tidal flats, spatial and temporal variability is mainly the result of tidal range, but may also be due to changes in sediment composition across the shore (Alexander *et al*., 1993; Rankin *et al*., 1994). Boehs *et al*. (2007) recorded a decrease in the abundance of benthic molluscs, including the venerid *Anomalocardia brasiliana*, towards upper shore areas. The authors suggested that physiological stress caused by exposure during low tide and the ability to tolerate this condition affected the variability.

On the coast of Ireland, Fahy *et al*. (2010) found that density and biomass levels of the venerid *Tapes decussatus* on the lower beach level were 2.5 – 4 times higher than those on the top beach level; changes in sediment grain sizes across shore, which was composed of coarse on the lower beach level, explained this pattern. In an *in situ* experiment, Rankin *et al*. (1994) found that juveniles of the venerid *Gemma gemma* were concentrated on the sandy substrate, rather than on the muddy substrate. At their study site in Little Buttermilk Bay, USA, the sandy area was partially exposed during low tide, and the muddy area was shallow – with a maximum depth of 1.8 m. Sassa *et al*. (2011) discuss the ability of venerids to adjust their burrowing criteria according to the sediment type; they also showed that in order to compensate for energy loss during burrowing activity, *Ruditapes philippinarum* reduce their burrowing angle and burial depth as the hardness of the substrate increases.

Along-shore distribution of clams

Along-shore distribution of clams is often related to physical variability (exposure level, grain size, etc.) or the effect of the predominant physical factors (headland, river mouth, etc.) along a particular tidal flat (Congleton Jr. *et al*., 2006). For example, Rankin *et al*. (1994) conclude that the distribution of juveniles of *Gemma gemma* is influenced by the shear velocity during the formation of an eddy, with these concentrated to where the shear velocity is low. On the other hand, Congleton *et al*. (2006) conclude that strong tidal currents of the coast of Maine affected the along-shore distribution of *Mya arenaria* by dispersing its larvae to grounds far away from their origin.

Vertical distribution of clams

The vertical distribution of clams on tidal flats is often related to variability in the burrowing capacity of individuals in response to the intensity of predation risks (Blundon & Kennedy, 1982; Quijón & Jaramillo, 1996; Griffiths & Richardson, 2006; Gribben & Wright, 2014), the presence of predators – which typically leads to increased burrowing speed and depths (Stanley, 1975; Gaspar *et al*., 2002; (Blundon & Kennedy, 1982; Gaspar *et al*., 2002; Griffiths & Richardson, 2006). This response is described as being related to chemical signals that indicate the presence of predators, either secreted by the predator during the attack or present in the injured prey body (Carriker, 1981; Wisenden, 2000).

Changes in venerids burial behaviour in relation to the type of sediment has been detailed by Sassa *et al*., (2011). The authors conclude that the Manila clam, *Ruditapes philippinarum*, reduces the burial depth in relation to the increase of sediment hardness. These findings may be considered an indication of changes in the vertical distribution of venerids with changes of sediment type.

<u>Abiotic factors affecting size and density variability on clam populations</u>

Spatial and temporal variability in density and size distribution of clam populations inhabiting tidal flats is often reported to be a result of inconsistency in environmental factors (Peterson, 1991; Snelgrove & Butman, 1994; Ngqulana *et al*., 2010). This variability is mainly caused by tidal range (Raffaelli & Hawkins, 1996; de Boer *et al*., 2000), but also changes in sediment composition across or along tidal flats (Snelgrove & Butman, 1994). Temperature (Glude, 1955) and salinity (Hashiguchi *et al*., 2014) are also among the physical factors affecting distribution of clams in tidal flats beaches. Nevertheless, no single driver or mechanism has been sufficient to explain all patterns of benthos distribution on tidal flats (Snelgrove & Butman, 1994; Ryu *et al*., 2011).

Sediment type and particle size

Environments characterized by fine particles, such as those composed of mud sediments, are turbid due to suspended sediment and low levels of dissolved oxygen, particularly when water temperature increases (Schoeman & Richardson, 2002). While such environments are not favourable for the majority of clam species, *Spisula subtruncata* shows no adverse effects due to its adaptation to sediment selection (Kiørboe & Møhlenberg, 1981). The large palp size index, which is proportional to selection efficiency, allows *S. subtruncata* to colonize fine particle sediment (Kiørboe & Møhlenberg, 1981). The composition of sediment is also important, as burrowing capacity can be reduced with, for example, sediment compaction, when fine particles fill the spaces between larger particles (Nel *et al*., 2001). Other effects of sediment on particle size on distribution of clams have been introduced in the across-shore distribution section.

Salinity

Salinity is known to have an effect on the size and density distribution of clams, especially in those species inhabiting estuarine areas or adjacent coastlines (Raffaelli & Hawkins, 1996). Low densities of *Ruditapes philippinarum* due to high mortality, may be related to a decrease in salinity due to heavy rains and flooding (Juanes *et al*., 2012). In fact, areas with little variability of water salinity, such as Jeju Island in South Korea (between 33 – 34.9), are preferred by the venerid *R. bruguieri* (Silina, 2014). Contrary to this, Adkins *et al*. (2014) found no correlation between salinity and either density or size of *Austrovenus stutchburyi* from Canterbury, New Zealand. Instead of a single factor explaining the distribution pattern of this species, a combination of salinity and other stressors factors, such as contamination by metals and silt, were considered.

Temperature

With regards to water temperature, only a few studies consider this to affect across-shore variability in clam population structures in tidal flats (Denadai *et al*., 2005). This scenario may find an explanation on the argument from Peterson (1991) that sediment cover of 10 centimetres is enough to buffer any detectable change in temperature during low tides on intertidal flats except for sites in the extreme high intertidal zone. During rare and extended low tide periods, elevated water temperatures can prompt desiccation, thus resulting in high natural mortality rates of the venerid *Tivela mactroides* (Denadai *et al*., 2005). Conversely, winter temperatures of below 14 °C interfered negatively with the vital functions of the venerid *Ruditapes bruguieri* in Jeju Island (Silina, 2014). Marsden (2004) recorded low densities of *Austrovenus stutchburyi*, due to high mortality, when exposure to low temperatures coincided with low food availability for the population.

Dissolved oxygen and redox potential

Oxygen concentration is considered the main driver for the distribution of benthos, including the venerid *Eumarcia paupercula,* at an intertidal estuarine system in KwaZulu-Natal (Ngqulana *et al*., 2010). The distribution of macroinfauna, including clams, seems to have been affected by the discontinuity of oxidized and reduced substrates, thus affecting the burrowing capacity of the species (Quijón & Jaramillo, 1996). This redox potential discontinuity represents shifts from oxidizing to reducing layers associated with aerobic and anaerobic conditions (Bantan & Abu-Zied, 2014).

In their investigation of benthos density in Chesapeake Bay, Seitz *et al*. (2009) conclude that hypoxia was the main factor affecting this, as records reflect historical mortality in low dissolved oxygen areas. The negative effect of low dissolved oxygen was also tested in *Macoma balthica* by Long *et al*. (2008); the authors found that this species reduced its burial depth in low oxygen conditions by 26 mm. One of the consequences of burrowing in shallow depths is that vulnerability of *M. balthica* to predators is increased, which in turn affects its density and spatial distribution. Nevertheless, venerids such as *Austrovenus stutchburyi* can close their valves during short-term hypoxia and rather use certain enzyme mechanisms for anaerobic energy production (Carroll & Wells, 1995).

<u>Biotic factors influencing clam distribution and density patterns</u>

The most commonly described biological elements affecting density and size distribution of clam populations in tidal flats are predation, which can occur during the larval or adult stages (Glude, 1955; de Boer *et al*., 2002; Hunt *et al*., 2003; Laudien *et al*., 2003); reproductive success from recruitment (Dang *et al*., 2010); interspecific ecological interactions, such as competition and bioturbation (Cardoso & Veloso, 2003; Pillay *et al*., 2007; Takeuchi *et al*., 2013); and positive or negative effects of biological substrates (seagrasses or seaweed coverage) (Tyler, 2007; Ruesink *et al*., 2014).

Glude (1955) assessed the biomass and distribution of the soft-shell clam *Mya arenaria* in New England (USA), and concluded that the prevalence of green crabs in its environment controlled the distribution and density of the species. Green crabs are the principal clam predators in that region (Glude, 1955) and have their highest predation during warmer temperatures, when their survival is high (Beal, 2006). Similarly in Tasmania, the predation of the venerid *Katelysia scalarina* by *Carcinus maenas* resulted in a decline of clam density levels (Walton *et al*., 2002).

Ruesink *et al*. (2014) found that stable habitats such as seagrass stimulate the exclusion of clam predators by changing their way of foraging. Clams may thus also change their burial depths in these habitats. In an *in situ* experiment, Peterson (1982) found that high mortality rates of the venerid *Chione* (*Austrovenus*) *cancelata* were the result of predation by whelks when seagrass was removed from the fine sand sediments of Bogue Sound, in the United States. The seagrass root mats result in sediment binding that may also inhibit some clam predators, such as whelks, by decreasing the penetrability of surface sediments (Peterson, 1982).

Competition with other suspension feeders can affect the dynamic of clam populations (Ropes, 1968a; Branch & Pringle, 1987). For example, competition for space with deposit-feeders such as shrimp bioturbators of the genus *Callianassa* have affected distribution of the beaked clam *Eumarcia paupercula* (Pillay *et al*., 2007). Furthermore, activity by bioturbators can transform sediment and increase water turbidity due to suspended solids; this may then obstruct clam feeding apparatus and lead to their death (Tamaki *et al*., 2008).

Fishing activity is also considered a form of predation and can dramatically influence the density and size distribution of clams (Munro, 1989). A population structure survey of *Ruditapes philippinarum* and *R. decussatus* in the Bay of Santander, in Spain, revealed a low occurrence of clams that were larger than the legal harvest size of 40 mm (Juanes *et al*., 2012), showing thus an effect of fishing on the size structure of these species. In contrast, human exploitation of intertidal invertebrates at Saco in Inhaca Island, Mozambique, seems not to have an impact on the size-distribution structure of Veneridae such as *Dosinia hepatica* and *D. lupinus* inhabiting the muddy sediments (de Boer & Prins, 2002). This may be due to the lack of commercial harvest for these venerids, which are only taken for personal consumption at this site (Vicente & Bandeira, 2014).

Clams fisheries globally

Global clam fisheries largely target members of the family Veneridae (Menzel, 1989; Mikkelsen *et al*., 2006; FAO, 2007). Although other families include only a few species that are important for clam fisheries, such as the families Myidae and Cardiidae, their members, like the soft-shell clam *Mya arenaria* and the cockle *Cerastoderma edule*, respectively, may form the basis for very important fisheries at locations in which they occur (Beukema & Dekker, 2006; Hicks & Ouellette, 2011). According to the FAO (2014), 613 475 tons of clams (including cockles and arkshells) were collected in 2012, representing an increment of ca. 10 000 tons compared to 2011.

Hand grabbing is the most commonly used technique to collect clams (Peterson, 2002; Leblanc *et al*., 2005; Scarlet, 2005). In commercial level harvesting though, mechanized harvesting – called clam kicking was introduced for *Mercenaria mercenaria* in North Carolina during the 1970's (Peterson, 2002). Its use led to a decline in clam stocks, as low recruitment rates of *M. mercenaria* were then experienced (Peterson *et al*., 1988)

Table 1.1 characterizes some of the more important venerid fisheries around the world. The table includes the species (local name and scientific name), location of fisheries and an estimation of recent landings. The largest total amount of venerids collected from natural stocks in the period 2009 - 2013 was that of the stripped venus *Chamelea gallina* in Turkey (170 936 tons), followed by *Ruditapes philippinarum* in Japan (13 773 tons). The landings are variable over the five years, for catching of some species declined (e.g.: *R. decussatus* in Portugal), while others did indeed increase (e.g.: *Mercenaria mercenaria* in the USA).

Table 1.1. Landings of venerid fisheries around the world for commercial, industrial, recreational and subsistence purposes. Source: http://faostat3.fao.org

Species	Common Name	Fishery location	Landings (10^3 kg) / Year						
			2009	2010	2011	2012	2013	Total Country	Total spp.
Callista chione	Smooth callista	Croatia	0.00	0.00	1.00	1.00	3.00	5	9964
		France	22.00	62.00	63.00	57.00	34.00	238	
		Italy	1955.00	1679.00	1704.00	1429.00	1493.00	8260	
		Portugal	284.00	319.00	297.00	224.00	136.00	1260	
		Spain	0.00	0.00	0.00	0.00	201.00	201	
Chamelea gallina	Striped venus	Turkey	24574.00	26931.00	30176.00	61225.00	28030.00	170936	386108
		France	262.00	0.00	138.00	121.00	121.00	642	
		Greece	17328.00	19748.00	19668.00	20028.00	14598.00	91370	
		Italy	53.00	20.00	132.00	225.00	255.00	685	
		Portugal	3217.00	2413.00	1161.00	2573.00	3916.00	13280	
		Spain	21572.00	22790.00	21699.00	23606.00	19528.00	109195	
Chione (*Austrovenus*) *stutchburyi*	Stutchbury's venus	New Zealand	1202.00	1202.00	1186.00	1037.00	1089.00	5716	5716
Meretrix lusoria	Japanese hard clam	Korea	1396.00	1146.00	793.00	572.00	132.00	4039	4046
		China (Taiwan)	0.00	0.00	0.00	0.00	7.00	7	
Mercenaria mercenaria	Northern quahog	Canada	839.00	821.00	710.00	682.00	463.00	3515	45133
		USA	4086.00	3615.00	6316.00	10953.00	16175.00	41145	
		France	147.00	184.00	56.00	32.00	1.00	420	
		United Kingdom	4.00	11.00	16.00	19.00	3.00	53	
Meretrix spp.	Hard clam	Indonesia	11844.00	12118.00	10580.00	1058.00	1673.00	37273	37273
Paphia spp.	short neck clam	Philippines	3.00	3.00	2.00	2.00	1.00	11	74380
		Thailand	17763.00	20817.00	12594.00	8713.00	13969.00	73856	
		New Zealand	153.00	120.00	117.00	63.00	60.00	513	

Table 1.1 (cont.)

Protothaca thaca	Taca clam	Chile	15739.00	21591.00	20359.00	11264.00	6299.00	75252	75252
Ruditapes decussatus	Grooved carpet shell	Tunisia	481.00	433.00	0.00	757.00	1 070	1671	5950
		Croatia	1.00	1.00	2.00	2.00	3.00	9	
		France	32.00	18.00	27.00	10.00	23.00	110	
		Portugal	118.00	90.00	65.00	54.00	47.00	374	
		Spain	827.00	807.00	777.00	735.00	640.00	3786	
Protothaca staminea	Pacific littleneck clam	USA	57.00	49.00	33.00	55.00	49.00	243	243
Ruditapes philippinarum	Japanese carpet shell	Japan	31655.00	27185.00	28793.00	27300.00	22800.00	137733	213843
		Korea	22488.00	12818.00	12230.00	12405.00	13565.00	73506	
		France	4.00	0.00	24.00	21.00	15.00	64	
		Ireland	0.00	120.00	0.00	0.00	0.00	120	
		Portugal	9.00	105.00	567.00	889.00	772.00	2342	
		Russia	0.00	22.00	18.00	38.00	0.00	78	
Ruditapes spp.	Carpet shell	Argentina	0.00	346.00	322.00	0.00	0.00	668	2783
		France	395.00	461.00	475.00	367.00	417.00	2115	
Saxidomus giganteus	Butter clam	Canada	612.00	551.00	536.00	425.00	425.00	2549	2776
		USA	109.00	27.00	33.00	22.00	36.00	227	
Tawera gayi	Gay's little venus	Chile	7725.00	9608.00	7494.00	7397.00	4908.00	37132	37132
Tivela mactroides	Triangular tivela	Brazil	1754.00	1652.00	7665.00	1780.00	1495.00	14346	14346
Venerupis pullastra	Pullet carpet shell	France	730.00	712.00	496.00	571.00	1 383	2509	9000
		Portugal	257.00	260.00	135.00	245.00	127.00	1024	
		Spain	1172.00	1184.00	1182.00	983.00	946.00	5467	
Venerupis rhomboides	Banded carpet shell	Portugal	16.00	109.00	75.00	0.00	0.00	200	569
		Spain	0.00	0.00	0.00	0.00	369.00	369	

Clam fisheries management

In response to mounting pressure placed on fishing resources globally, the idea of implementing clam fishery management measures has grown in popularity in the last century (Townsend, 1990). Such measures include the use of harvest size restrictions, setting open/closed seasons for harvesting, placing bag limits, and defining marine protected areas (MPA), among others. These are discussed in greater detail below.

Of the aforementioned measures, the most broadly applied is the introduction of minimum harvest size limits (Hill, 1990; Narasimham, 1991; Appukuttan, 1996; Fisheries and Oceans Canada, 2001; Hicks & Ouellette, 2011; Juanes *et al*., 2012; Bidegain *et al*., 2013; Van Wynsberge *et al*., 2013). Harvest size generally refers to the length of clam animals, which is usually the highest measurement of the antero-posterior orientation (Albridge & McMahon, 1978; Gray, 2016). In fisheries management, the set of a size limit is associated with the reproductive capacity of particular species, where every individual should spawn at least once before it is harvested (Gordon, 1954; Branch & Clark, 2006; Fisheries and Oceans Canada, 2012; Bidegain *et al*., 2013). Van Wynsberge *et al*. (2013) tested the efficiency of different management tools and found that the minimum size limit was the most efficient tool for management of the giant clam *Tridacna maxima* fishery in the French Polynesia Islands.

Apart from limiting the minimum harvest size, another means of control is the establishment of a closed season for clam harvesting (Alagarswami & Narasimham, 1973; Townsend, 1990; Appukuttan, 1996; Fisheries and Oceans Canada, 2001; Hicks & Ouellette, 2011; Juanes *et al*., 2012). In this management approach, the collection season is open long enough to allow clam collectors to take a maximum yet sustainable yield from a particular stock, and then closed until a desirable biomass is reached again (Ciriacy-Wantrup & Bishop, 1975).

The setting of bag limits is a measure in which the amount of clams collected by an individual is controlled (Carpenter & Gunderson, 2001) in order to limit fishing effort on populations that are already showing declines in their catches (Attwood & Bennett, 1995; Lewis, 2015). The bag limits are usually set on a day-to-day basis and are almost exclusively used for recreational fishery (Attwood & Bennett, 1995; Morales-Nin *et al*., 2005; Grafton *et al*., 2006). In terms of its objectives, this measure is in some ways a similar concept to the total allowable catch (TAC) widely used in commercial fisheries over a fishing season for both invertebrates and finfish. While TAC does not place limits on fishing days, both measures aim to reduce the amount collected, particularly in populations with confirmed reduced catch per unit efforts (Bennett, 1991).

In addition, stock management can be maintained with the creation of no-take zones, or marine protected areas (MPAs), for a particular fishery (Pauly *et al*., 2005; Branch & Clark, 2006; Ngowo, 2008; Crawford *et al*., 2010; Van Wynsberge *et al*., 2013). No-take zones are usually rotational; that is, when the fish stocks recover, they can be re-exploited. Alternatively, the same areas are kept closed and are used both as reference sites (demonstrating what an unexploited population should look like) and as a stock reserve for repopulating depleted areas (Caddy & Defeo, 2003).

Lastly, fisheries can be managed by enforcing limited, or controlled, entry to the activity. This is usually done in the form of fishing licences and mostly applies to commercial fishing activity (Townsend, 1990; Ferraz & Goncalves, 2001), but in some cases can apply to subsistence and recreational fisheries (Griffiths & Branch, 1997; Fisheries and Oceans Canada, 2001). In developed countries specifically, clam fisheries have been maintained by limiting new entries – or new licences– to a particular fishery (Townsend, 1990; Fisheries and Oceans Canada, 2012).

Table 1.2 shows a range of management measures applied for clam fisheries globally. Most fisheries use two or more measures, but some have a single measure. The application of the bag limit measure varies among the various clam fisheries presented in Table 1.2. For example, the bag limit for commercial *D. serra* fishery is in the form of a total allowable catch (TAC) per month (Cockcroft *et al*., 2002), while bag limits (number of clams) for the recreational *Venerupis philippinarum* fishery in British Columbia (Fisheries and Oceans Canada, 2012), and *D. serra* (Schoeman, 1996) fishery in South Africa are applied on a daily basis for each collector.

Most management measures across fisheries globally are implemented through a co-management approach. According to McCay and Jentoft (1996), "co-management of fisheries resources is a collaborative and participatory process of regulation and decision-making among representatives of resources users, government agencies and research institutions". The sharing and delegation of measures in a co-management approach is important, as increase chances of success of the practice and can be achieved by empowering the resource users and engaging participatory democracy principles (Jentoft *et al*., 1998). For example, when fishers are not included in the creation of MPAs, it may be that these negatively affect them and can create a situation in which MPA rules are not observed (Mascia *et al*., 2010; Sowman, 2011).

Not all clam management measures are the result of human pressure on clam stocks (Crawford *et al*., 2010), but may be founded on human health concerns and ecological interactions (Fisheries and Oceans Canada, 2001). In British Columbia, Canada, the management plan for clam exploitation determined that the harvest must be closed when contamination of *Mya arenaria, Spisula solidissima, Siliqua patula* and *Mercenaria mercenaria* by marine biotoxins, or by faecal coliform bacteria, is reported (Fisheries and Oceans Canada, 2012).

On the southern African coast, economically constrained fishers in Hout Bay and Elands Bay have been left disadvantaged by restricted access to fishing *Donax serra* (Isaacs, 2006) due to fisher registration (entrance) and commercial licence fees being beyond what they can afford. In Zanzibar, community-based management is applied for highly exploited *Anadara* spp., and no-take zones have been introduced in selected demonstration sites in recent years (Crawford *et al*., 2010). Moreover, establishing a minimum harvest size has proved to be important in ensuring adequate reproduction rates of *Anadara antiquata* and efficient management of the stock (Ngowo, 2008).

Commercial and subsistence fishing of venerids is reported along the Mozambican coastline, where the main species harvested are beaked clam *Eumarcia paupercula* and *Meretrix meretrix* (Balidy, 2003; Scarlet, 2005). The fishery for *E. paupercula* is restricted to Maputo Bay, on the southern coast, while fishing for *M. meretrix* is reported over the southern and central regions. The exploitation of both species is on an 'open-access basis', with no enforced control of the method of collection, amount of collection or sizes of collected individuals. Thus it is estimated that the chances of depletion or collapse of these stocks is high (Griffiths & Branch, 1997).

Along the southern coast of Mozambique, in the Arquipelago de Bazaruto area, the main fishery for *Tridacna maxima* and *T. squamosa* was for both commercial and subsistence purposes (Marshall *et al*., 1999). Some management attempts by the National Directorate of Forests and Wildlife (DNFFB) were made at the Arquipelago de Bazaruto during the 1990s, and included the complete prohibition of clam collection (Marshall *et al*., 1999). During this period, no permits were issued for *Tridacna* spp. – the result was that exploitation of the species ceased, and no trade in *Tridacna* spp. was reported (CITES, 2004).

Social aspects of small-scale clam fisheries

Globally, subsistence clam fishing is primarily practiced by women (Kyle *et al*., 1997; Scarlet, 2005; Kronen *et al*., 2007; Crawford *et al*., 2010; Nordlund *et al*., 2010). To a lesser extent, children in developing countries are also involved in the practice (de Boer & Prins, 2002; Kronen & Vunisea, 2007; Nordlund *et al*., 2010), as they usually accompany their parents or relatives when fishing and learn from an early age how to collect intertidal invertebrates (Kronen *et al*., 2007). On the other hand, children between the ages of 10 – 15 can have same mercenary objectives as adults in invertebrate collection. In Mozambique, this may be partly caused by poverty and high rates of HIV/AIDS in coastal areas, which has meant increased numbers of orphans and child-headed households in the last decade (Conselho Nacional de Combate ao SIDA, 2007).

Small-scale fisheries play an important role in the social, cultural and economic activities of coastal communities in developing countries (Sowman, 2006; Hoguane, 2007). In fisheries co-management, social concerns are always raised, with frequent conflict arising concerning which actors are more important. The group of resource users comprises a broad range of actors, such as boat owners, skippers, crew members, fish processors, fish workers, consumers, and fisher spouses and families. While these actors are to various degrees affected by management decisions, their representation at stakeholder engagements is usually weak (Jentoft *et al*., 1998). According to Sowman (2011), in South Africa, the process of declaration of MPAs is generally conducted by resource conservation scientists targeting fisheries management. During that process, fishery communities are not entirely involved and sometimes their needs are not recognized, causing a negative impact on local communities. The need to incorporate a wide range of knowledge fields to support scientific inputs in fisheries management, primarily local and indigenous knowledge, is gradually being recognized by this sector (de Sá, 2011; Sowman, 2011).

Table 1.2. Management measures applied to selected clam fisheries globally. R, S and C denote recreational, subsistence and commercial fishery, respectively. Numbers denote management measures as follow: 1 – Size limit, 2 – Bag limit, 3 – Closed season, 4 – No-take zone, 5 – Licence limit, 6 – Pollution closure, and 7 – Fishing method restriction. Empty cell denotes absence of any management measure. Some cockles and arks were included in the list, as FAO does not distinguish these groups with clams in the statistics.

Species	**Family**	**Local name**	**Fishery location**	**Fishery type**	**Management measures**	**Literature source**
Anadara antiquata	Arcidae	Cockle, kaikoso	Zanzibar Island, Tanzania	R, S	4	Crawford *et al*., 2010
Cerastoderma edule	Cardiidae	Cockle	Netherlands	C	3, 4, 5, 7	Dijkema, 1997
Donax serra	Donacidae	White sand mussel, wedge clam	South Africa	R, C	1, 2	Schoeman, 1996
D. serra	Donacidae	White sand mussel, wedge clam	West & South coast, South Africa	R, S, C	1, 2, 4, 7	Cockcroft *et al*., 2002
Mesodesma mactroides	Mesodesmatidae	Yellow clam	Barra del Chuy, Uruguay	S	3	Brazeiro and Defeo, 1999
M. donacium	Mesodesmatidae	Surf clam	Chile	C	1	Defeo, 2003
M. donacium	Mesodesmatidae	Surf clam	Peru	S, C	1, 2	Defeo, 2003
Mya arenaria	Myidae	Soft-shell clam	Maine, USA	C	1, 5, 6	Congleton Jr. *et al*., 2006
M. arenaria	Myidae	Soft-shell clam	Eastern New Brunswick, Canada	R, C	2[1], 3, 5, 6	Hicks and Ouellette, 2011
Gari solida	Psammobiidae	Pacific clam	Peru	S		Urban, 1998
Anomalocardia brasiliana	Veneridae	Berbigão	Barra Grande, Piaui, Brazil	R, C	1	Freitas *et al*., 2012
Leukoma staminea *Saxidomus gigantea* *Venerupis philippinarum*	Veneridae	Native littleneck clam Butter clam Manila clam	British Columbia, Canada	R, C	1[2], 2, 5	Fisheries and Oceans Canada, 2012

[1] For fishery (R) only

[2] For fishery (C) only

Table 1.2: (continued)

Species	Family	Local name	Fishery location	Fishery type	Management measures	Literature source
Megapitaria squalida	Veneridae	Chocolate clam	Baja California Sur, Mexico	R, C	1	Schweers *et al*., 2006
Meretrix meretrix	Veneridae	Great clam	Kakinada Bay, India	R, C		Alagarswami and Narasimham, 1979
Ruditapes philippinarum	Veneridae	Manila clam	Chiba, Japan	C	1	Toba, 2004
R. philippinarum *R. decussatus*	Veneridae	Manila clam Carpet shell clam	Bay of Santander, Spain	S, C	1, 4	Juanes *et al*., 2012
R. philippinarum	Veneridae	Manila clam	Arcachon Bay, France	R, C	1	Dang *et al*., 2010
Tapes decussatus	Veneridae	Ameijoa	Azores, Portugal	S	1, 2, 3, 5	Ferraz and Goncalves, 2001
Venerupis senegalensis	Veneridae	Amêijoa-macha	Rio Tejo, Portugal	C	1, 2, 5	Ramajal, 2012

Non-compliance with management regulations is common in fisheries (Schoeman, 1996; Viswanathan *et al*., 1997; Morales-Nin *et al*., 2005; Humphreys *et al*., 2007; Rosendo, 2008; Fisheries and Oceans Canada, 2012; Juanes *et al*., 2012; Lewis, 2015) and puts at risk the success of the management program (Pitcher *et al*., 2002). Schoeman (1996) and Martins and Souto (2006) have found that individuals smaller than the legal size were included in the landings of *D. serra* in St Francis Bay, South Africa, and of *Anomalocardia brasiliana* in Bahia, Brazil. Fishing within protected areas or closed seasons has also been reported (Viswanathan *et al*., 1997; Morales-Nin *et al*., 2005; Humphreys *et al*., 2007; Rosendo, 2008; Juanes *et al*., 2012; Lewis, 2015).

Review of some biological aspects of clams

Growth rates of clams

Growth in bivalves is usually measured as change in the largest dimension, whether this is the actual length, such as in oysters, clams and mussels (Spencer, 2002), or the height, as in scallops (Pedersen, 1994). Growth rate in clams can be measured as an absolute or an allometric parameter (Beverton & Holt, 1993). For absolute growth, the size of the individual is expressed relative to age, whereas allometric growth is a measure of a particular variable expressed in relation to another, giving an indication of shape change (Eleftheriou & McIntyre, 2005). Commonly used methods for studying absolute growth rates in clams include analysis of size-frequency distributions and the tracking of the mean size of cohorts over time. The latter is considered an ideal method for undisturbed populations (Pauly & Munro, 1984), but can become problematic when high fishing mortality depletes larger size classes.

Alternatively, the annual growth ring method can be used. This is most appropriate for species from temperate zones, where a distinct annual ring is formed in the shell valve when the growth is reduced during winter (Van der Meer *et al*., 2005), but is often inappropriate for tropical species, where growth is continuous. The annual increase in ring numbers can be confirmed by tagging-recapture. For allometric growth, equations are used to express a relationship between two growth variables, e.g. length vs width (Munro, 1982). Details of commonly-used equations are presented in Chapter 6.

Factors affecting growth rates in clams

Many factors affect growth in clams, with several authors agreeing that food concentration is the most influential of these (Thompson & Nichols, 1988; Nakaoka, 1992; Weiss *et al*., 2002). A number of studies rank food concentration at the same level of importance as temperature and tidal or aerial exposure (or water depth), which are then followed by salinity as a less significant factor (Laing *et al*., 1987; Beverton & Holt, 1993). Other drivers not discussed in this review, such as high population density (Weinberg, 1998), low oxygen concentration (Belanger, 1991), high concentration of pollutants (Bayne *et al*., 1979; Zhao *et al*., 2014), and storms (Turner & Miller, 1991), can also negatively influence growth rates in clams.

Food availability

Food supply, both in terms of quality and quantity, has been considered the most important factor in defining bivalve growth rates (Bayne & Worrall, 1980; Beverton & Holt, 1993; Marsden, 2004). In studying annual growth rates of *Meretrix lyrata* at the Bach Dang Estuary in Vietnam, Xuan *et al*. (2011) recorded faster growth rates during the months of high nutrient flow into the system, namely July – September. In addition, in laboratory conditions, a reduction in the soft tissue mass of *Austrovenus stutchburyi* was recorded in low food quantity scenarios (Marsden, 2004). In that study, the nutrient flow was from the continent and caused by the rainy season. Thus, the behavioural ability of species to adapt in adverse conditions has to be considered – and tested– to avoid erroneous conclusions about the effect of food supply on the growth of clams. For instance, to conserve energy, the Antarctic clam *Laternula elliptica* reduce its metabolism during periods of low food supply in summer (Ahn & Shim, 1998). Also, although the process of poor-quality particle rejection is not totally efficient, particularly when suspended matter content is high, is important for bivalves for feeding efficiency (Ward & Shumway, 2004).

Temperature

Temperature is considered the dominant driver of growth in bivalves (Davenport, 1938; Goodwin *et al*., 2001). Generally, clam growth rates are positively correlated with water temperature, until a maximum tolerated temperature is reached, of course (Ansell, 1968; Mann, 1979; Goodwin *et al*., 2001). Fluctuations in growth are usually the result of seasonal temperature cycles (Griffiths & Griffiths, 1987), particularly for temperate species. Goodwin *et al*. (2001) recorded optimal growth rates of the venerid *Chione* (*Austrovenus*) *cortezi* at water temperatures between 23 – 26 °C, and found that the temperature boundary for growth of this species in the Gulf of California was 17 – 31°C. The recorded temperature boundary for growth may partly be the result of changes in energy acquisition as influenced by feeding rates and assimilation with temperature (Griffiths & Griffiths, 1987).

Some studies used the temperature coefficient Q_{10} to understand the growth patterns through a physiological process in venerids (Sobral & Widdows, 1997; Marsden, 1999; Portner *et al*., 1999; Baojun *et al*., 2005; Jansen *et al*., 2007). Sobral and Widdows (1997) found a negative scope for growth in *Ruditapes decussatus* with increase of temperature to the highest Q_{10}=1.13 (20-32 °C), which resulted from low clearance rates. On the other hand, an increase in respiration rate of *Meretrix meretrix* was recorded in the higher temperature (25 °C) compared to lower (10-15 °C) in the Q_{10} tests; this makes *M. meretrix* to reallocate the conserved energy for growth. Nevertheless, most of clams undergo seasonal adjustments in physiological process such as clearance and excretion rates, and oxygen uptake to compensate for seasonal changes in water temperature (Marsden, 1999; Jansen *et al*., 2007; Peck *et al*., 2007).

Seasonal fluctuations in temperature can, similarly, determine whether growth is consistent or strongly seasonal. If the former applies, annual growth rings may not form on shells; while if the latter is the case, this may result in distinct annual growth rings (Ansell, 1968; Ringwood & Keppler, 2002). For example, in the Beagle Channel, slow or no growth of *Eurhomalea exalbida* was recorded during autumn and winter, as compared to fast growth during spring and summer months (Lomovasky *et al*., 2002). Likewise in Tokyo Bay, *Ruditapes philippinarum* showed rapid growth rates during the warm season (Nakamura *et al*., 2002); conversely, Goodwin *et al*. (2001) and Schöne *et al*. (2002) recorded a halt or extraordinary decline in growth performance of *Chione* (*Austrovenus*) *cortezi* during the hottest time of the year.

Tidal exposure and water flow

Intertidal bivalves are known to generally close their valves and cease feeding during low tide (Peterson, 1991). Thus, it is expected that individuals from high intertidal areas will exhibit lower growth rates compared to those from the middle and low intertidal areas, as they experience both shorter feeding times and greater physiological stress (Peterson, 1991). The ability to tolerate exposure to high temperatures and desiccation among intertidal bivalves may also affect their growth pattern across shore (Whomersley *et al*., 2010); hence growth is faster for mussels that occur in high water circulation environments than those in limited circulation (van Erkom Schurink & Griffiths, 1993). Xuan *et al*. (2011) found that the Asian hard clam *Meretrix lyrata* from a high tidal flat of the Bach Dang Estuary in Vietnam has a slower growth rate than *M. lyrata*, which is from a lower tidal flat. Similarly, a decrease in water flow was accompanied by a decline in the growth rate of *M. lyrata* in the same estuary (Xuan *et al*., 2011). Contrary to this pattern, however, is the pattern of *R. philippinarum* in Tokyo Bay, which was found to not correlate with tidal exposure (Nakamura *et al*., 2002).

Salinity

A comparison by Marsden & Pilkington (1995) of growth rates of *Austrovenus stutchburyi* from New Zealand showed that individuals from low salinity areas had slower growth, while areas with marine salinity (34) sheltered individuals with higher growth rates. While the authors did not explain the physiological effect of low salinity, they considered their result as an indication of low productive output. The effect of salinity on clam growth can be indirectly explained by considering behavioural changes, which include reducing food intake or respiration rates (Arnold *et al*., 1996; Carmichael *et al*., 2004; Marsden, 2004). The negative effect of low salinity on growth may be more pronounced in conditions of low food availability, as clams feed only for few hours to prevent the effects of low salinity (Marsden, 2004).

A single driver may correlate (positive or negatively) with growth of clams, but the interaction of two or more environmental factors is what ultimately determines the realised rate of growth of clams (Marsden & Pilkington, 1995). There are other factors influencing growth in clams that are not discussed herein. One of these is pollution (chemical and biological), which may affect growth by indirectly influencing the inhibition of food intake or causing diseases in clams through reduction of immune response (Munari & Mistri, 2007). This thesis focuses on detailing effects of temperature and salinity on growth of *E. paupercula*.

Reproductive patterns of clams

Sexes in venerids are separate; however, males and females cannot be distinguished by gonadal appearance or by shell morphology. Most venerids exhibit sex ratios of 1:1 (Ponurovsky & Yakolev, 1992; McLachlan *et al*., 1996; Drummond *et al*., 2006; Gab-Alla *et al*., 2007; Jagadis & Rajagopal, 2007a; Tirado *et al*., 2011). In rare situations, males represent less than 45% of the population (Shafee & Daoudi, 1991; Hamasaki *et al*., 2014). Reasons for sex ratio deviating from 1:1 in clams include triploidism (Allen Jr. *et al*., 1986) and protandric type of reproductive development (Afiati, 2007). For instance, the proportion of males in the population of *R. philippinarum* at Tokyo Bay in Japan reached 0.75 (3:1) (Hamasaki *et al*., 2014), while in Drumcliff Bay in Ireland, *R. philippinarum* exhibited a male:female ratio of 1:1 (Drummond *et al*., 2006). Hermaphroditism is recorded in very low percentages (< 2%) in the population (Ponurovsky & Yakolev, 1992; Drummond *et al*., 2006; Gab-Alla *et al*., 2007). Sex could not be identified when *Tapes philippinarum* and *Anomalocardia brasiliana* individuals were castrated due to infection by parasitic trematodes (Ponurovsky & Yakolev, 1992; Luz & Boehs, 2011).

While spawning, males continuously produce a stream of milk-like sperm, while females shed granular clumps of eggs (Spencer, 2002) for external fertilization (Gosling, 2003). Sexually undifferentiated clams (recovery stage) are often recorded after total spawning events (Morriconi *et al*., 2002; Drummond *et al*., 2006; Hamasaki *et al*., 2014). Most venerids exhibit synchronous spawning (Laruelle *et al*., 1994; Rodrıguez-Moscoso & Arnaiz, 1998; Morriconi *et al*., 2002; Luz & Boehs, 2011), but minor numbers of asynchronous spawning were noted for *Venux nux* in Spain (Tirado *et al*., 2011).

Variability in reproductive patterns also depends on geographic distribution of species from temperate or tropical zones. Species from temperate waters usually exhibit one seasonal spawning event per year during late spring or summer, and recover during winter (Laudien *et al*., 2001; Yan *et al*., 2010; Calderon-Aguilera *et al*., 2014). In contrast, species inhabiting tropical systems have multiple and continuous spawning events, but also exhibit peaks, especially when water temperatures increase (Morriconi *et al*., 2002; Barreira & Araujo, 2005). Moreover, the duration of maturation and of spawning events, as well as the number of spawning events, can differ geographically (Laruelle *et al*., 1994; Drummond *et al*., 2006). In the Morbihan Gulf, *Ruditapes philippinarum* matures speedily over three short spawning events, each of which lasts a month (Laruelle *et al*., 1994). At Drumcliff Bay in Ireland, the same species has one prolonged spawning event which extends to roughly four months (Drummond *et al*., 2006). Differences in local environmental factors such as temperature may be causing this variation (Newell *et al*., 1982); while Laruelle *et al*. (1994) did not record temperature in their study, Drummond *et al*. (2006) recorded temperatures above 8 °C, which is the minimum for gonadal activation in the species (Mann, 1979).

<u>Factors affecting reproduction and recruitment in clams</u>

The role of salinity in the reproduction of clams is not entirely clarified, particularly when there is a single factor analysis (Marsden & Pilkington, 1995; Luz & Boehs, 2011). For instance, the prolonged spawner *Meretrix meretrix* from Korampallam Creek in India did not spawn during periods of very low salinity (10) (Narasimham *et al*., 1988). Salinity differences in the habitats of two populations of *R. philippinarum* from the north-west of Ireland did not reflect any variability in reproductive pattern between the populations (Drummond *et al*., 2006). The only differences of salinity between these two populations (3.3 in the lower and 2.6 in higher values) were minor and probably not sufficient to result in differences in the reproductive cycle. Nevertheless, in the tropics, salinity may have a greater effect on growth than temperature, as the latter remains fairly consistent year-long (Bayne & Worrall, 1980; Jayabal & Kalyani, 1987; Spencer, 2002).

Researchers seem to agree that temperature is a prime environmental factor controlling the timing of bivalve spawning. As with other bivalves, spawning in clams is often observed when water temperature increases (Morriconi *et al*., 2002; Jagadis & Rajagopal, 2007a; Calderon-Aguilera *et al*., 2014). Mild-low water temperatures (12-16 °C) are a potential reason for the lack of a resting stage in the reproduction of *Venux nux* in southern Spain (Tirado *et al*., 2011). Gametogenesis of the venerid *Cyclina sinensis* in Yellow River in China started when the water temperature was low (Yan *et al*., 2010). Spawning of *Meretrix meretrix* in India was recorded for the greater part of the year, when temperature variation is minimal (Narasimham *et al*., 1988). Mann (1979) showed that *Tapes philippinarum* individuals matured (ripened) at all rearing temperatures, but spawning took place only in high temperature conditions.

Along with temperature, food availability is also considered in important exogenous factor regulating reproduction in bivalves (Mann, 1979; Sastry, 1979; Calderon-Aguilera *et al*., 2014). During gametogenesis, food availability not only affects the periodicity of gonadal maturation, but also the amount of gonads generated by the Manila clam *Ruditapes decussatus* (Delgado & Camacho, 2005). Delgado and Camacho (2005) also concluded that retardation in gonadal recovery was related to low food availability. Similarly, a retarded gametogenesis was recorded in *R. philippinarum* in a tidal flat with low food availability and poor quality in Korean waters (Baek *et al*., 2014).

Other exogenous factors, such as physical stimulation (Ropes, 1968b) and dissolved oxygen (Marroquin-Mora & Rice, 2008; Calderon-Aguilera *et al*., 2010), have been less studied in clams, but are known to affect the spawning of bivalves positively.

Outline of chapters

In the above review of clam fisheries and the management thereof, it is evident that fisheries need to be exploited in a sustainable way in order. By doing so, there is at least some guarantee that the ecosystem will continue to provide clams for communities. Management of clam fisheries is weak in most developing regions; in Mozambique, particularly, management is almost entirely absent. Basic biological information regarding population structure, stock size and exploitation status that may affect the dynamics of each target species is needed prior to the implementation of relevant fishery control measures.

This thesis includes a series of studies based on field observations, interviews and an *in situ* experiment. Chapter 1 features a background and literature review of clam fisheries, with emphasis on those targeting clams of the family Veneridae. The biological aspects presented in this chapter focus on growth and reproduction of clam species important for fisheries worldwide. This chapter also describes clam fisheries and various management practices applied to resource management and social aspects of the fisheries.

Chapter 2 describes the study site of Maputo Bay and general methods used in subsequent chapters. The description comprises hydrodynamic features and itemizes the ecosystems of the Bay. Moreover, fisheries and social aspects of the surrounding communities are included. In addition, the sampling area is shown with the sampling design and experimental set up with a general description of methods.

Chapter 3 details the distribution patterns of the natural population of beaked clams. This includes analyses of length-frequency distribution and density distribution. Seasonal population data are also analysed according to tidal exposure or across-shore variability. Recruitment aspects are also addressed across-shore and seasonally.

Chapter 4 describes the status of exploitation and some socio-economic aspects of the *Eumarcia paupercula* fishery. The analyses are based on interviews carried out with collectors and on estimations of landings. Comparisons between sizes collected by harvesters and those from the sampled population in Chapter 3 are presented.

Chapter 5 outlines the reproductive pattern of the beaked clam in Maputo Bay. The reproductive cycle is presented with analysis of seasonal changes in the body condition of a standard-sized individual. In addition, analysis of fresh gonad smears of *Eumarcia paupercula* support the determination of spawning peaks in Maputo Bay.

Chapter 6 describes the growth rates of *Eumarcia paupercula*. Growth rates are derived from the length frequency distributions using cohort analysis as well as by estimation of growth curves by following individual length increments of tagged animals. An *in situ* experiment was undertaken to collect individual growth data in order to estimate growth parameters successfully. The use of both methods provide a bigger picture of both population and individual growth.

The final chapter, Chapter 7, provides a synthesis of the main findings of the study and details recommendations for the management of the resource. These are followed by a brief section on future research perspectives and a reference list of literature cited throughout the thesis.

Chapter 2: Maputo Bay, study site and general methods

INTRODUCTION

Mozambique is located on the south-eastern coast of Africa, between latitudes 10º20'S and 26º50'S. The coastline is about 2,770 km long (Hoguane, 2007). The climate is sub-tropical to tropical and humid, with two distinct seasons: the wet season or summer from October to March, and cold and dry season or winter from April to September. The annual average atmospheric temperatures are about 23 °C and 26 °C for the coastal zones of southern and northern Mozambique respectively (Chemane *et al*., 1997). The average annual rainfall is about 1200 mm (Saide, 2000; Canhanga & Dias, 2014). The Mozambique coast is divided into three administrative divisions; south, central, and north, all areas comprising ecosystems with high levels of biodiversity and endemism, and containing many endangered species (Hoguane, 2007). Hoguane (2007) estimated that natural resources, including fisheries, and coastal and marine fauna and flora, sustain about half of the population of Mozambique living in the coastal areas.

Maputo Bay

Oceanographic conditions

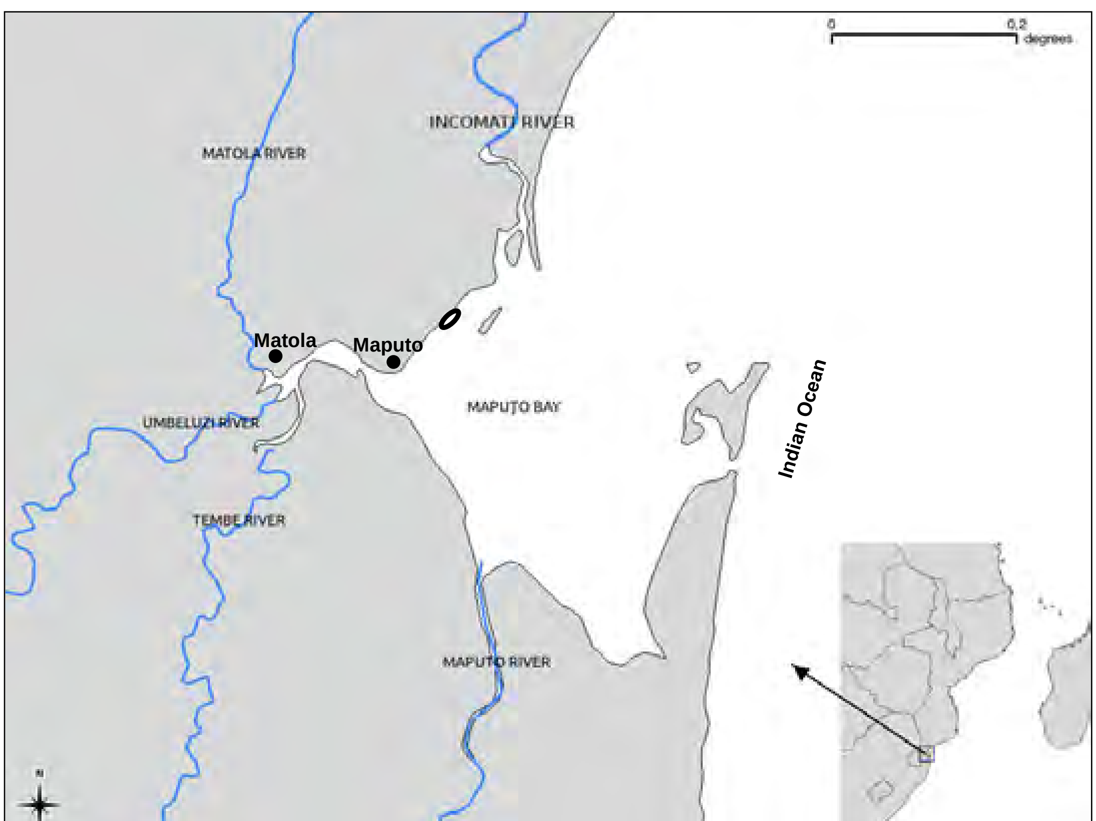
Maputo Bay is located in southern Mozambique, between 25º55' and 26º10'south and 32º40' and 32º55' east (Figure 2.1). On the western side of the Bay is the city of Maputo and the Bay joins the Indian Ocean on the northern side. To the south and west of Maputo Bay is the Machangulo Peninsula, while Inhaca Island lies in the east (Saide, 2000). Two distinct seasons occur in Maputo Bay, a wet warm season from October-March and a dry cold season from April-September, respectively. The average annual rainfall is about 1000 mm. The average daily air temperature varies from 17-27 °C (Saetre & da Silva, 1982), with sea temperatures reaching a maximum of 29 °C in January-March and minimum of 22 °C between July-August (Sete *et al*., 2002). The air humidity ranges from 59-82% (Lencart *et al*., 2010).

The area of Maputo Bay is 1280 km^2, of which approximately 774 km^2 constitutes the sub-littoral zone, while the remainder is equally divided between intertidal areas and sand dunes (Lencart *et al*., 2010). Maputo Bay is a shallow bay, its depth varies from 1-20 m, with most parts of the Bay not exceeding 10 m (Hoguane, 1996). Vertical profiles of salinity and water temperature showed that the Bay is homogeneous, with salinities from 30-39 and water temperatures from 20-29 °C (Hoguane, 1996).

Two distinct water masses prevail in the Bay during the rainy season - estuarine on the west and oceanic on the east. Tides are semidiurnal, with minimum (0.17 m) and maximum (3.9 m) amplitudes varying among different locations (Canhanga & Dias, 2005). The environment in Maputo Bay is strongly influenced by the Mozambique Channel and by rivers discharge. Five rivers discharge into Maputo Bay, namely the Incomati from the north, the Umbeluzi, Tembe and Matola from west and the Maputo River from the south (Figure 2.1). Total discharge rates of these rivers are circa 190 m^3/s (Canhanga & Dias, 2005), with highest contribution of Incomati and Umbeluzi rivers for this total discharge. Nutrients from river discharge, combined with the productivity of the mangrove and seagrass ecosystems, make Maputo Bay a productive environment (Bandeira & Paula, 2014). Consequently, there is a large variation in water visibility between neap and spring tides in the area, caused by sediment discharge by rivers and subsequent transport by tidal currents (de Boer *et al*., 2000).

Maputo Bay habitats and biodiversity

The substrates of Maputo Bay are principally sand, with mud in the southern and western areas. Rocky substrates also occur in some areas of the Bay, particularly on the eastern and northern



shores of Inhaca Island. Maputo Bay is a habitat mosaic of mangroves, seagrass beds, coral reefs and sandy beaches (Figure 2.2) and is known for its rich and diverse fauna and flora, which form important sources of food and building materials, and provide income for the local communities (de Boer & Longamane, 1996; de Boer & Prins, 2002). Ecological studies in the region often tended to focus on Inhaca Island (where there is a marine laboratory), and this may have led to an underestimation of biodiversity in the Bay as a whole (Kalk, 1995; Bandeira *et al*., 2002).

Figure 2.1 Maputo Bay, with rivers discharging into the Bay and main cities marked as black dots (Matola and Maputo). The black oval shape represents the study site at Costa do Sol beach.

The mangroves of Maputo Bay comprise the largest mangrove habitat in southern Mozambique (Barbosa *et al*., 2001). Six species of mangrove occur in the Bay and the mangrove habitat covers three continuous estuarine systems in Maputo Bay, from the mouth of the Maputo River to Inhaca Island. The mangrove habitat in Maputo Bay covers 176 km^2, and can extend up to 50 km upstream in some areas (Ferreira & Bandeira, 2014). Deforestation rates of Maputo Bay mangroves are amongst the highest in Mozambique (Barbosa *et al*., 2001). Conversely, on Inhaca Island, mangrove cover increased by 5% from 1990 to 2002 (Fatoyinbo *et al*., 2008).

Submerged vegetation in the Bay consists of seaweed and about 38 km^2 of seagrass beds, mainly in the shallow inlets bordering Inhaca Island. As stated earlier, the sediment type influences the habitat distributions. Thus, seagrasses are restricted to the eastern and northern part of the Bay, where the sediments are fine, and the habitat unaffected by river discharge (Bandeira *et al*., 2014). Nine seagrass species (Bandeira *et al*., 2014) and eight macroalgae species (Ferreira & Bandeira, 2014) have been recorded in the Bay. Similar to mangrove habitats, the seagrass meadows are important to the fishing communities; as seagrass habitats are exploited for both invertebrates and fish species (de Boer & Prins, 2002; Vicente & Bandeira, 2014).

Only 0.4 km^2 of Maputo Bay is comprised of rocky substrates, much of which is sandstone (Ferreira & Bandeira, 2014). The older sandstones occur in Inhaca Island in the northern and north-eastern areas. Coral reefs in Maputo Bay are limited to Inhaca Island and are associated with over 300 fish species (Schleyer & Pereira, 2014). The number of coral species reported varies among studies. Boshoff (1981) recorded 160 coral species in Inhaca Island. In general, the remainder of Maputo Bay is turbid, with large amounts of sediment and seasonal changes in salinity, which are not favourable for coral growth (Schleyer & Pereira, 2014).

Sand flats dominate the coastline of Maputo Bay, with the exception of the muddy areas on the south-east side. Wind and wave action contribute to sand deposition in the Bay; this phenomenon led to formation of a small island in the northern area – Banco Sangala. Sandy beaches are an important nesting ground for sea turtles (Ferreira & Bandeira, 2014) and shelter several invertebrate species, some of them edible and hence important to coastal communities (de Boer & Longamane, 1996). Macnae and Kalk (1962) listed over 350 species of invertebrates on Inhaca Island sand flats. Given that sand flats extend to other areas of the Bay (and not just Inhaca), and that the study by Macnae and Kalk (1962) is over 50 years old, the number of invertebrate species in Maputo Bay sand flats is likely higher than 350. For example, at least three clam species that occur in the north-west region do not occur in Inhaca Island according to Macnae and Kalk (1962). Moreover, the bivalve species considered dominant by Macnae and Kalk (1962) did not include species such as *Eumarcia paupercula* and *Meretrix meretrix* (Scarlet, 2005; Vicente & Bandeira, 2014) and *Solen cylindraceus*, *Pinna muricata*, *Dosinia hepatica* and *Macoma litoralis* (Vicente & Bandeira, 2014), all of which are dominant in other regions of the Bay.

The marine megafauna of Maputo Bay include sea turtles, dolphins, dugongs, and whales (Guissamulo, 2014). Five species of sea turtles have been recorded from Inhaca Island by Guissamulo (2014). Dugongs, two dolphin species and two whale species have also been recorded in the Bay, although some are transient. Also, seals were recorded after the sporadic winter storms, but soon succumbed to the warmer water environment (Guissamulo, 2014).

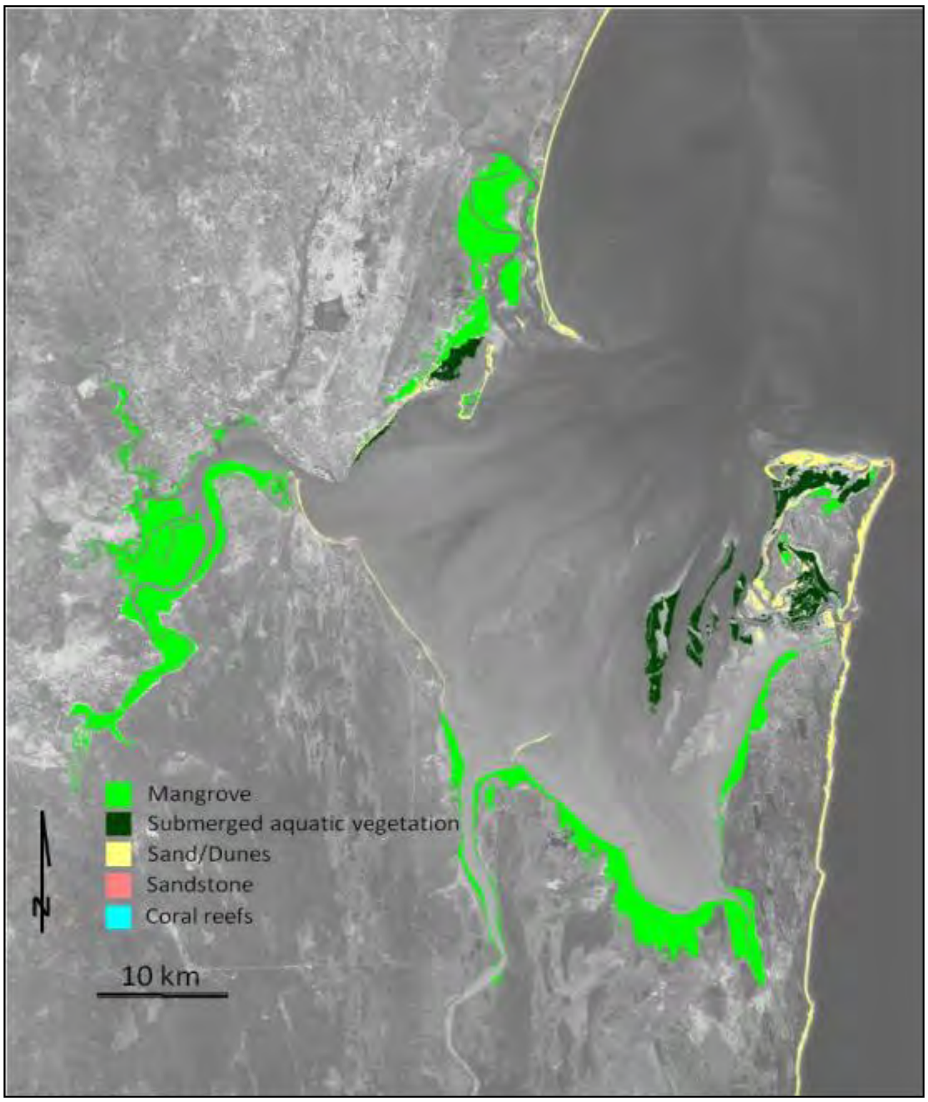


Figure 2.2: Main habitats of Maputo Bay. Source: Ferreira and Bandeira, (2014)

Thirty-three percent of all the marine bird species recorded in Southern Africa occur in the eastern part of Maputo Bay, comprised of migrant and resident shore birds and forest birds (de Boer & Bento, 1999). Furthermore, most of the Maputo Bay avifauna is concentrated in the littoral area of Inhaca Island and is composed of Palearctic migratory birds, the area representing an important ecosystem for such birds (de Boer & Bento, 1999).

Ferreira and Bandeira (2014) developed a strengths, weaknesses, opportunities, and threats (SWOT) analysis on management of the natural resources of Maputo Bay. Among the main strengths was the high level of research about natural marine resources of the region (which is the most studied in the country). Opportunities included the potential to involve coastal communities in conservation and co-management of resources in the area, including enhancing fisheries management and general livelihood improvement. Major threats include pollution and ecosystem destruction. Similar to other coastal cities of the country, coastal erosion constitutes a serious concern for Maputo (Langa, 2007). Urban sewage from industry, households and agriculture is also a significant constituent of land-based pollution, which impacts on Maputo Bay (Scarlet & Bandeira, 2014). Although Maputo has a sewage system, it was built during the colonial period and is now obsolete; it discharges directly into several different areas of Maputo Bay through ten pipes, without any effective treatment (van Buuren & van der Heide, 1995). The sewage contains a mixture of organic and inorganic components, microorganisms and heavy metals (Scarlet & Bandeira, 2014).

Fisheries resources in Maputo Bay

In Mozambique, fisheries are divided into three sectors: industrial, semi-industrial and artisanal (de Sá, 2011). Aquaculture was recently added as a fourth fishing sector (MOZPESCA, 2014). Among these sectors, the artisanal fishery (inland and marine) is the largest in terms of landings; the 2012 catch totalled 186 214 tons, representing 87.25% of the total fish caught (MOZPESCA, 2014). Artisanal (small scale) fishing is conducted along the entire coastline, targeting fish, shrimp and molluscs, using various fishing methods (Hoguane, 2007).

In Maputo, the Ka Mavota municipal district, which include the Costa do Sol fishing centre, landed a total of 1109 tons of marine fish; however, this figure does not include bivalve catches, as the Ministry of Fishery does not record bivalve catch data. In any event, the fisheries catch data that are supplied by the Mozambican fisheries sector to the Food and Agricultural Organisation (FAO) are likely underestimated or incomplete. For instance, Jacquet *et al*. (2010) used reconstructed data from marine catches and estimated that actual catches are over six times greater than those provided to FAO by Ministry of Fisheries.

The country fish consumption per capita is still low (10.4 kg/year) and is confined to the coastal areas (MOZPESCA, 2014). High market-value species, such as prawns, are exported, mainly to Europe. Spain is the principal destination for *Penaeus* spp. Other countries in southern Africa (mainly South Africa) also import Mozambican marine fish products (MOZPESCA, 2014).

Fisheries in Maputo Bay include a semi-industrial sector, whose vessels have inboard freezing systems and ice for storing shallow-water shrimp and fish. In the semi-industrial fisheries, the vessels are small (8-20 m long, with 350 hp inboard or outboard engines) (REPMAR, 2003). There are also artisanal fisheries for shrimp and other invertebrates, fish and shellfish. The artisanal fishers usually target multi-species, using small vessels, up to 10 m long, driven by paddle, sail or outboard engines (up to 100 hp or 75kW). The catches are sold in local markets (REPMAR, 2003; ADNAP, 2013).

The Ministry of Fisheries undertakes the monitoring and enforcement of fisheries regulations through its Provincial Directorates and District Services for Economic Activities. Statistics on artisanal fisheries are collected by the Mozambique National Fisheries Research Institute (IIP), but are limited to a few, important species of fish, lobster, crabs, squids and shrimp. No bivalve catch data are collected (ADNAP, 2013). The National Institute of Fisheries Inspection (INIPE), under the Ministry of Fisheries, is the authority responsible for inspection, testing and certification of fishing products. The Institute for the Development of Small-Scale Fisheries (IDPPE) handles promotion and outreach of the artisanal fisheries.

In Maputo Bay, there are more than 30 artisanal fishing centres. The main fishing centres include Inhaca, Catembe, Matola, Costa de Sol and Muntanhana (EU SADC MCS Programme, 2004). During the wet season, the Ministry of Fisheries applies a closed fishing season for shrimp through a ministerial decree. The dates of the beginning and end of the closed season vary each year, but it is always approximately 4-5 months long (Palha de Sousa *et al*., 2011). A recent and detailed record of the artisanal fishing centres of Maputo Bay was presented by the IDPPE, (2009) (Figure 2.3).

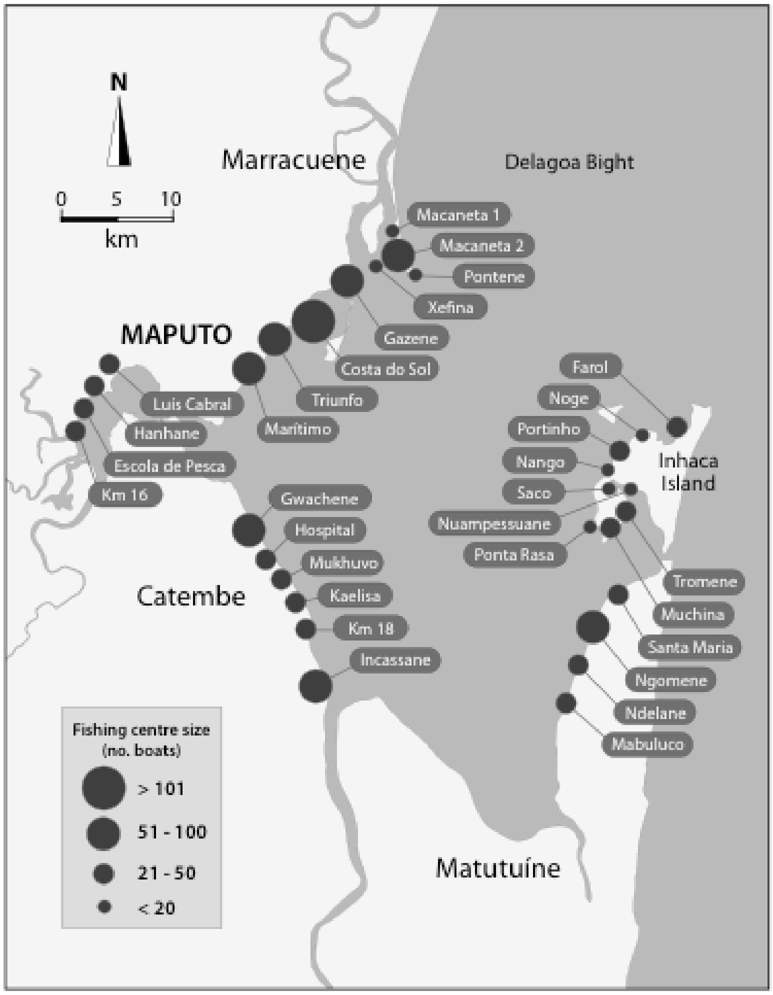


Figure 2.3: Artisanal fishing centres of Maputo Bay. Source: Inacio *et al*. (2014).

The report shows Costa do Sol as the major fishing centre in Maputo Bay. In contrast to many other artisanal fishing communities along the Mozambique coast, where the fishers are nomadic, the fishing community of Costa do Sol is comprised mostly of fishermen living in the village, or around the urban area of Maputo. This fishing centre is composed of many stakeholders, namely net makers, naval mechanics, fish traders and processors (de Sá, 2011). In this area, it is rare to see a fishing camp, while these are commonly seen in rural areas. Most of fish trading for the artisanal fleet takes place on the beach, after the boats have landed (Figure 2.4).

Fig 2- Fish farming at Bairro dos Pescadores

More than 70% of the Mozambican population live in rural areas, and 89% are involved in small-scale farming. Demographic and health surveys from 2013 revealed low levels of education of working-age household members, particularly women; for example, only 13.2% of women between 20-50 years old have completed high school nationwide (INE, 2013). The 1996/7 population surveys highlighted low productivity in the family agriculture sector and poor infrastructure as some of the factors contributing to poverty, especially in rural areas.

Figs 3- Tourism activity at Costa do Sol

Maputo, which is located on the western shore of Maputo Bay, is the capital and biggest city in Mozambique, and houses all the ministries and government departments. The total area of the city is 347.69 km^2, and the total population is 1 177 798, which according to CMM (2013) has increased by 10% in the last ten years leading up to 2011. The administrative divisions of Maputo and their populations are shown in Figure 2.5 and Table 2.1, respectively.

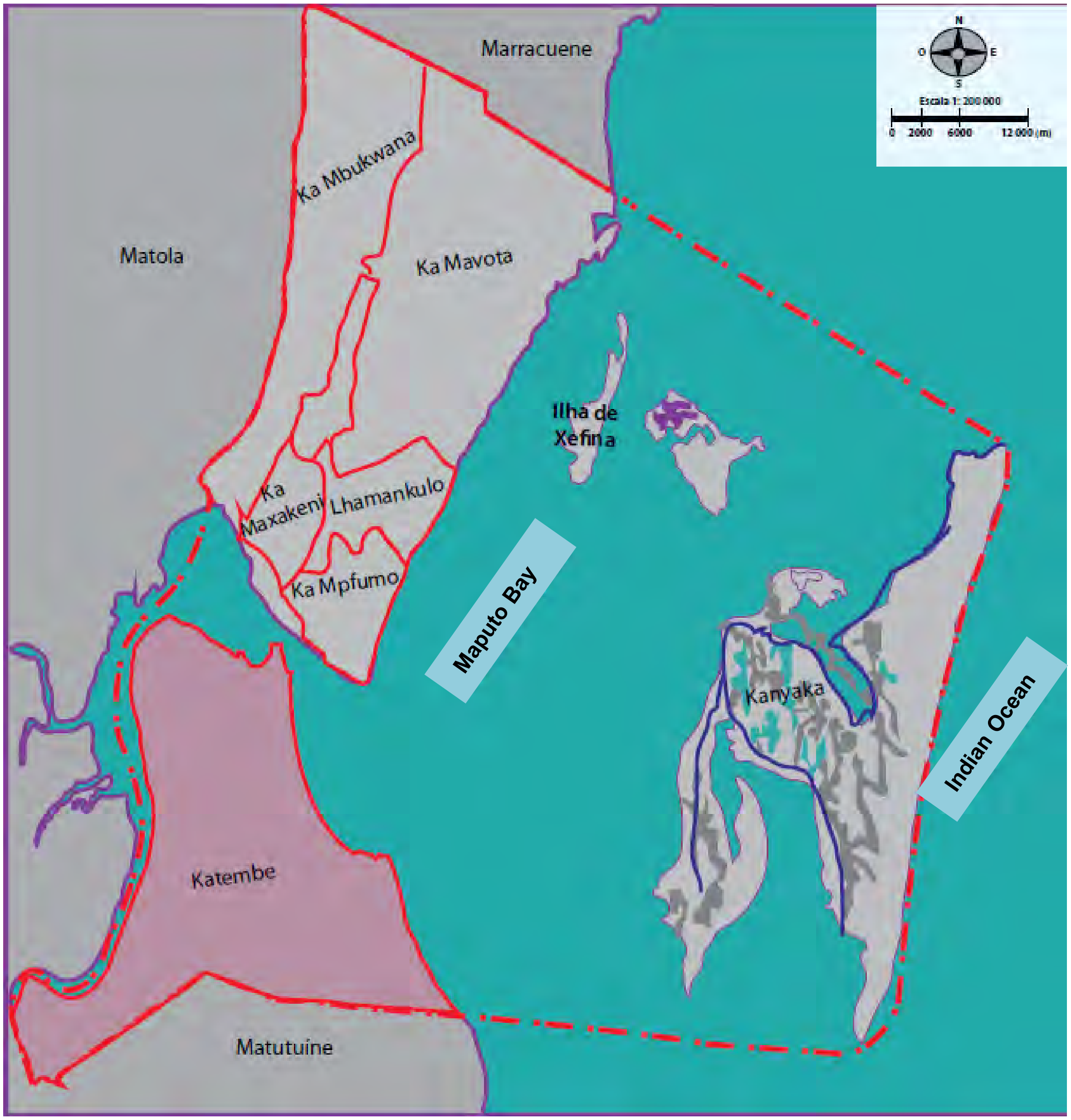


Figure 2.5: Administrative division. The limits of Maputo Municipal area are in dashed line and continuous lines delimit the municipal districts. Source: CMM (2013).

The study area, the Costa do Sol beach, is located in the suburb of Costa do Sol, which is situated in the municipal district of KaMavota. This is one of the most populated districts in the municipality, with a total population of 323 394. Costa do Sol village itself has a population of 16 828 (CMM, 2013).

Table 2.1. Lead demographics of Maputo for 2011. Source: CMM (2013).

Municipal District	***Total Population***	***Men***	***Women***
KaMpfumo	110 285	53 607	56 678
Nlhamamkulo	158 323	77 375	80 949
KaMaxakene	230 751	112 929	117 822
KaMavota	323 394	155 270	168 124
KaMubukwana	328 913	157 659	171 254
KaTembe	19 371	20 975	10 090
KaNyaka	5 473	2 616	2 857

Some socio-economic aspects of Maputo Bay

The industrial activities in Maputo Bay include large plants that cause environmental degradation due to the lack of an effective effluent treatment system. These companies are concentrated in Matola and include the Companhia Industrial da Matola (CIM, a flour mill), Mozambique Aluminium (MOZAL, an aluminium smelter) and Cimentos de Moçambique (CM, a cement factory). Maputo Harbour is an important economic provider for the region. Also, both artisanal and industrial salt production contribute to the economy and take place in the western area of the Bay. In addition to the industrial activities, the tourism sector plays an important role in the economies of Maputo and Matola. Tourism in these cities contributed over USD 57 million to the national budget in 2010 (Nhabinde *et al*., 2014). At Costa do Sol village, most activities and occupations are related to the beach and fisheries. Apart from catching and selling fish, other fishing-related businesses include naval carpenters, fish processors, fishnet manufacturers, boat painters, and sellers of fishing gear. Figure 2.6 shows the selling of clams at the fish market of Maputo. The collection of marine invertebrates is also an important activity for women. Recreational activities are also important at Costa do Sol beach, as it is the main beach of Maputo (Figure 2.7). Hence, food and drinks are sold on the beach. Other small-scale business activities also take place there, such as the selling of second-hand clothes, fruits and vegetables, and groceries.

Figure 2.6: Clams being sold at Maputo fish market. The darker clams (foreground) are *Eumarcia paupercula* and lighter ones are *Meretrix meretrix* (background).

Figure 2.7: Costa do Sol beach during summer. Photo: Olavo Aires.

Costa do Sol and its environs have a developed basic infrastructure. This includes a hospital with a maternity ward, two primary schools that teach up to grade seven, and a secondary school that goes up to grade 10. One shopping mall and three markets, including the biggest fish market in the province, are located in the study area. The suburb has some of the richest areas and prime beach real estate, as well as some of the poorest areas (made up of communities of subsistence fishermen) in Maputo.

Similar to most Mozambican coastal cities, Maputo is comprised of a mix of cultures from Africa, Asia, and Europe. It is multi-religious, but Christianity and Islam are dominant. Furthermore, migrations resulting from the 16-y civil war, which ceased in 1992, have added to the mixture of cultures and religions found in Maputo (Hoguane, 2007). The majority of artisanal fishers at Costa do Sol Beach speak Rhonga, and Changana (major southern Mozambique tribes) as their primary language and Portuguese as their secondary one. Other common local languages include Copi and Tonga (Ngunga, 2011).

Legislation is available for effective management of the Maputo Bay natural resources, from the fisheries sector to general coastal management, and further conservation influence is provided by several international conventions to which Mozambique is a cosignatory. For example, Mozambique is a cosignatory of the Ramsar Convention and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Also, local initiatives have been developed for the better management of the coastal zones in general. Locally, the creation of the Centre for Development of Coastal Zone (CDS-ZC) by a Ministry decree in 2003 and the Inter-institutional Committee for the Integrated Coastal Management (CTIGIZC) have been designated to lead the process of coastal zone management. These institutions are governed by the Ministry of Coordination of Environmental Affairs (MICOA) and National Council for Sustainable Development (CONDES – represented by all ministries), respectively.

Application of the legislation, or law enforcement, is weak, partly caused by tenuous links between inter-institutional networks (e.g. government and research institutions), although some improvement has been made, since research outputs are now used for policy making. For instance, in order to improve the management of the region, Rosendo, Celliers and Mechisso (2014) advised that Maputo Bay has to be recognized as an independent management area with particular needs, and better coordination between institutions (decision makers) and communities.

GENERAL METHODS

The methods presented in this section are those for sample site selection, including a description of the study site, as well as the methods used for the measurement of environmental parameters. Also included is a description of the basic methods of sampling of *Eumarcia paupercula* for population structure analyses.

Sampling site selection and description, and sampling design

Informal meetings with clam dealers took place to find out from where they purchased clams, and then the collectors supplying them were followed to see where they were doing their collection. These meetings took place with the assistance of the Fishing Community Council (CCP) of Costa do Sol, which is approved by a dispatch of the Ministry of Fisheries, dated 23 May 2008. Collection was taking place mainly at Gazene, Luis Cabral, Macaneta, Maritimo, Pescadores and Costa do Sol fishing centres. From the landings of bivalves in these fishing centres, the only sites in which *Eumarcia paupercula* individuals were not recorded were in Matola (Escola de Pesca and Hanhane). According to these preliminary findings, over 80% of beaked clams sold in Maputo markets were collected in Costa do Sol. On this basis Costa do Sol beach, which is located on the north-western side of Maputo Bay, was selected as the most appropriate study site.

The sampling for the *Eumarcia paupercula* population structure study took place on Costa do Sol beach every other month from November 2012 – April 2014. Six transects, perpendicular to the coastline, were used (Figure 2.8). Clams were only found between 15-250 m from the high water mark, the uppermost 15 m being a steeper section of shore, which was unsuitable habitat for these clams. Thus, transects lines were 240 m long and sampling stations were located at 10 m intervals, making 24 stations per transect line. The transects were separated from each other by 100 m.

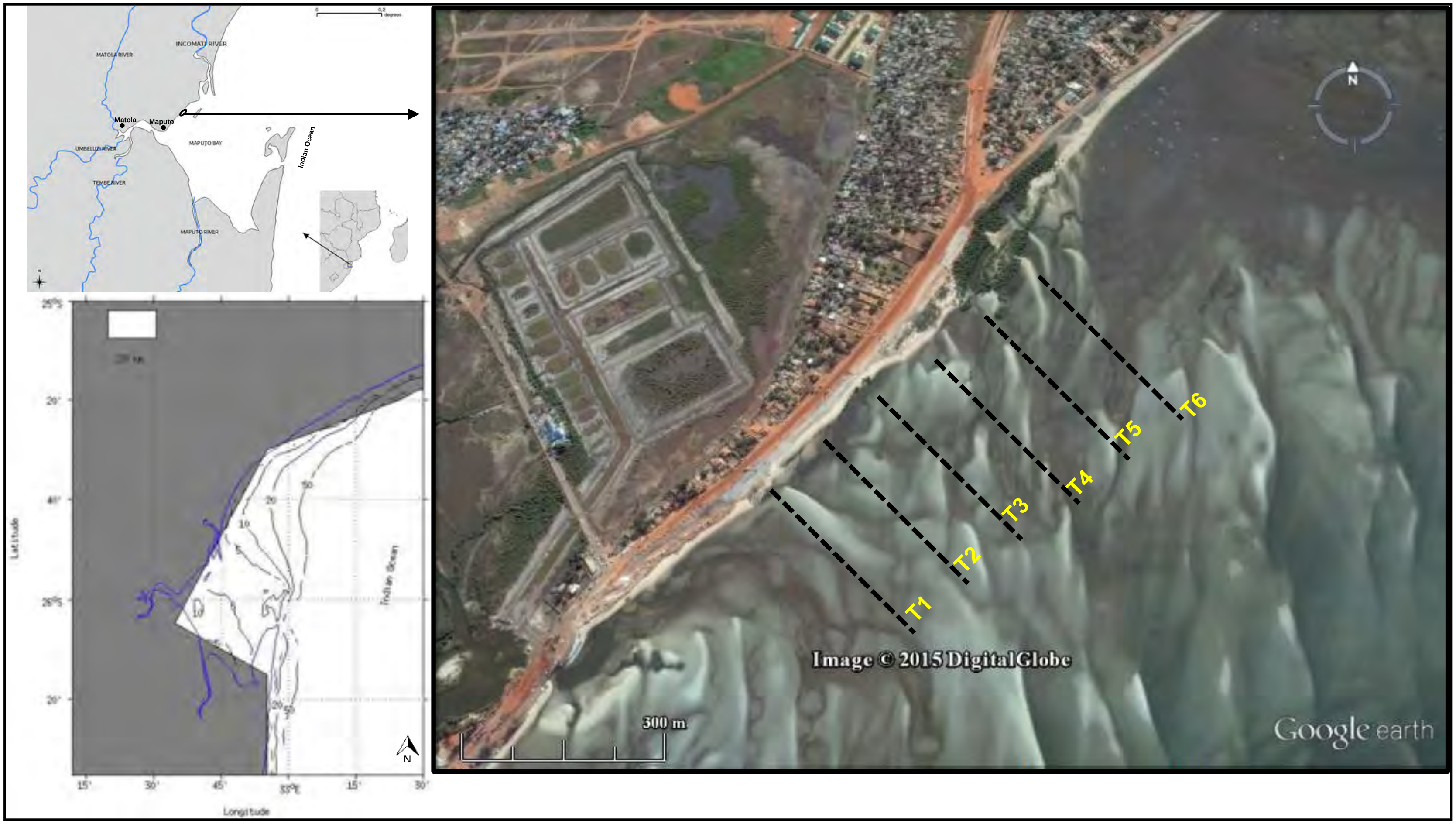


Figure 2.8: The sampling design at Costa do Sol beach, showing transect lines (T1-T6) with bathymetry of Maputo Bay. The blue line in the bathymetry (bottom left) represents the coastline.

The shore across each transect was divided into three shore levels, namely upper (US), middle (MS) and lower (LS) shores. The point of high tide was determined by the level of the drift-line left by the previous high tide, while the lowest level to which the water ebbed was taken as the low tide level. These actual shore levels were not checked against the predicted range of tide on each sampling day, as given by tide tables. The beach slope was not measured, it was assumed to be fairly uniform (Figure 2.9), and the maximum error would probably be less than 10 cm. Thus, stations 1-8 were considered upper shore, followed by the middle shore stations (9-16) and the lower shore stations (17-24), each of these levels comprising an 80 m section along the transect line. The length of transects did not effectively vary along the shore, and although it was sometimes necessary to jump some 2-5 m wide water channels, the 10 m between stations ensured this was not a sampling constraint.

Sampling in the shallow channels (< 50 cm) was avoided. A 0.25 m^2 (0.5 x 0.5 m) quadrat was used to sample at each station, and sediment to 10 cm depth was taken and washed through a sieve with 1 mm mesh size, from which all *Eumarcia paupercula* were collected. The quadrat was thrown alternately between the left and right sides over the stations along each transect. Each transect station was sampled once per survey and each transect was sampled three times at low tide during the study. Data obtained from this sampling were used for growth analysis via length-frequency distribution (Chapter 6) and for assessing population structure (density and size distribution) and recruitment, as presented in Chapter 3.

Figure 2.9: Sampling site overview as it appears during low spring tide.

Environmental parameters

Water temperatures (˚C) and salinity were measured *in situ* on each day of sampling. A hand-held digital thermometer and refractometer were used to record temperature and salinity, respectively. Data were collected three times a day, and every two weeks during sampling. Measurements were taken during the ebbing tide (usually on time of arrival for sampling), the low tide (during sampling) and on the flooding tide (at the end of sampling) in the channel closest to a transect area, between 0.5-1 m deep. Daily sampling times varied depending on the tide table; but readings were usually between 10:00 and 16:00, with the low tide reading being after three hours. Total monthly rainfall data for the study period were obtained from the Mozambican National Institute of Meteorology (INAM) for Maputo. Results of the environmental parameters are presented in the next chapter, and discussed in all relevant chapters.

Chapter 3: Spatial and temporal patterns in density and size distribution of *Eumarcia paupercula* in Maputo Bay

INTRODUCTION

Clam populations around the world have declined or been depleted (FAO, 2014, 2016). The main causes of these declines include human exploitation (Yap, 1977; Urban, 1998; Crawford *et al*., 2010), ecological interactions between benthic groups (Ropes, 1968a; Beal & Kraus, 2002; Pillay *et al*., 2007; Polyakov *et al*., 2007), changes in the environment (Toba, 2004; Norkko *et al*., 2006; McLeod & Wing, 2008) and failure of recruitment (Borsa & Millet, 1992; McLachlan *et al*., 1995; Caddy & Defeo, 2003). Occasionally, the origin of the decline in clam resources is the combination of different environmental factors, such as salinity, food availability and temperature (Blundon & Kennedy, 1982; McLeod & Wing, 2008; Kandeel, 2013), which in turns may affect the reproductive output (Newell *et al*., 2009).

Factors affecting distribution of clams

There are three well-documented factors controlling the dynamic of clam populations, namely intensity of wave action (Brazeiro & Defeo, 1996), sediment composition (Lastra & McLachlan, 1996; Hunt *et al*., 2003; Kandeel, 2013) and tidal range and currents (Paul & Feder, 1973; Hunt *et al*., 2003). Other documented factors include food availability (McLachlan, 1990; Denadai *et al*., 2005). The effects of the main distribution and density drivers have been presented in Chapter 1.

Complex interactions between these primary distribution drivers turns the single factor effects into a set of interactions of many elements that ultimately determine the density and distribution patterns of clams (Bally, 1983; Adkins *et al*., 2014). Water depth was found to affect the size distribution of the venerid clam *Megapitaria squalida* in Magdalena Bay, Mexico, where larger clams were predominantly in deeper waters (Schweers *et al*., 2006). The distribution pattern of two clam species, namely the venerid *Austrovenus stutchburyi* and the mesodesmatid *Paphies australis* along a New Zealand estuary were found to be related to fluctuations in salinity levels; the small population size in inner estuarine areas partially resulting from low salinity levels (McLeod & Wing, 2008). In Australia, the increase in abundance of the clam *Sanguinolaria* *donaciodes* accompanied increasing protection from wave action (Dexter, 1983). Fiori and Defeo (2006) observed a decrease in density of *Mesodesma mactroides* with latitude in South America.

An interaction between biotic and abiotic influences may regulate the density and distribution patterns in clams (Breitburg *et al*., 1997; Taylor & Eggleston, 2000). Stress and mortality of *Macoma balthica* occurred in hypoxia conditions (<2 $mgO_2.l^{-1}$), as in these conditions *M. balthica* move to shallower burial depths and become available to crab predators (Seitz *et al*., 2003). This is a typical example of the interaction of biotic and abiotic factors in the distribution of clams.

Fishery can also control the density and size distribution of clams. Some examples of the probable consequences of human exploitation include lower total density of the exploited species, and hence lower total biomass and decrease in the predator-prey ratio (de Boer *et al*., 2002). Also, the higher abundance of species with relatively small biomass can also be a consequence of anthropogenic activities (Griffiths & Branch, 1997); however, de Boer and Prins (2002) did not find any of these predicted effects in their study of the impact of human exploitation on the benthic community of Maputo Bay. Fishing effort negatively affected the density and age distribution of *Mesodesma mactroides* in Uruguay (Brazeiro & Defeo, 1999). In their study, fishing contributed to the mortality rates of recruits because of the hand-gathering technique applied, by disturbing the sediment, which restricts the movement of *M. mactroides*.

Role of settlement and recruitment in distribution of clams

Seasonal changes in clam population structure are mostly a result of reproduction and recruitment processes, particularly in non-fished populations (Ricker, 1954; Emerson & Grant, 1991; Lima *et al*., 2000; Fiori & Defeo, 2006), as well as of predation (Ropes, 1968a; Beal *et al*., 2001). Clams constitute the group of bivalves that settle in the most variable range of substrates, and a single species can also be found settling in different substrates (Crimaldi *et al*., 2002; Fraschetti *et al*., 2003; Hunt *et al*., 2003). Small clams attach to small pieces of shell or stone using a byssus thread, which can be utilized until the clam reaches 7-9 mm shell length (Menzel, 1989). Since settlement is hard to measure under natural conditions, this is often measured by the success of recruitment. According to Seed and Suchanek (1992), recruitment is defined as the successful process of colonization of certain area after a particular period of time, during which certain mortality of part of this new generation may have occurred. Recruits are considered the first age-class that composes a particular population, after all processes of settlement and mortality have occurred (Keough & Downes, 1982).

Various factors can affect recruitment in clams, but the most important is the size of the parent stock and their reproductive output capacity (Eversole, 1989; Caddy & Defeo, 2003). Kraeuter *et al.* (2005) found that recruitment rates in *M. mercenaria* were strictly dependent on the parental stock density, particularly in high adult density conditions. The age of an individual clam can affect the capacity of egg production, where a predominance of small adults results in low recruitment rates, as the reproduction rate is reduced in the small and also in very old individuals, but adult individuals in general have higher reproduction output (Peterson, 1983).

The success of settlement processes and survival of individuals are influenced by different processes occurring during the planktonic larval stage and settlement processes (Keough & Downes, 1982). The most common factors include hydrography of the area, and weather conditions prior to the settlement process (Borsa & Millet, 1992; Crimaldi *et al*., 2002), as well as food availability (Sastre, 1984; Van Colen *et al*., 2010). For instance, the settlement of the Asian clam *Potamocorbula amurensis* is decreased as their anchoring capacity is reduced during turbulence events (Crimaldi *et al*., 2002). Other elements are the weak swimming capacity of the larvae (Ishii *et al*., 2005), lack of suitable substrates for settlement, mortality by predation in pre- and post-settlement phases (Beal & Kraus, 2002; Hunt *et al*., 2003), and ecological interactions between adult stock and recruits (Caddy & Defeo, 2003).

Peaks of reproductive activity are not always followed by peaks of recruitment, as larval dispersal by tidal currents and water flow can result in recruitment in different grounds from those occupied by the parent stock (Paul & Feder, 1973; Juanes *et al*., 2012). Also, the post-settlement period is found to be crucial for benthic species recruitment, as recruits are subject to high mortality rates (Hunt & Scheibling, 1997). Thus, recruitment rates are not always proportional to the adult stock density. For instance, Borsa and Millet (1992) found significant spatial and temporal variation in recruitment of the venerid *Ruditapes decussatus* at a lagoon in France; however, Bowen and Hunt (2009) did not find any relationship between densities of the new settlers and adult stock in a population of *Mya arenaria*. These findings indicate that local environmental conditions are more likely to regulate the settlement and recruitment patterns.

Across-shore distribution of clams

Intrinsic and extrinsic factors regulate density and size distribution across-shore. Tidal across-shore migrations have been documented for *Austrovenus stutchburyi* (Adkins *et al*., 2014), and *Tivela mactroides* (Denadai *et al*., 2005). In both cases, migration resulted in temporal changes in size distribution across-shore, as recruits and juveniles often migrate from lower to higher tidal levels. For instance, the migration of juveniles *T. mactroides* from the lower to upper shores seems to be crucial for the maintenance of the population (Denadai *et al*., 2005). Also the migration of adult clams from upper to lower shore may occur, as documented for *Megapitaria squalida* (Schweers *et al*., 2006), resulting in highest densities of larger clams in the lower areas.

Additionally, predation by star fish, hermit crabs, and blue crabs seems to regulate the across-shore size distribution of *Tivela mactroides* (Denadai *et al*., 2005). Also, during extended low tide periods in regions of high temperatures, massive mortalities of clams from upper shores may occur due to this natural disturbance (McLachlan *et al*., 1996). These findings suggest that not only environmental factors will affect the distribution of clams across-shore, but also some behavioural mechanisms that some species undergo to preserve their lives in the intertidal areas (Breitburg *et al*., 1997; Seitz *et al*., 2003), including active shore movements and enhancement of their burrowing capacity.

Extent of *Eumarcia paupercula* grounds in Maputo Bay

Studies on the distribution of clams in Maputo Bay are scarce. A schematic attempt to illustrate the distribution of *Eumarcia paupercula* in Maputo Bay is presented in Figure 3.1. This distribution was based on prior personal observations made for site selection for the project. Results from the studies by Scarlet (2005) and Vicente and Bandeira (2014) were also used, where both described the occurrence of this species in four areas. Since this species is extensively sold in Maputo markets, the personal observations consisted of accompanying invertebrate collectors and recording landings in the main fishing centres during four spring tides, in August and September 2013. In other areas shown in the map than Costa do Sol, *E. paupercula* individuals may occur in very low densities.

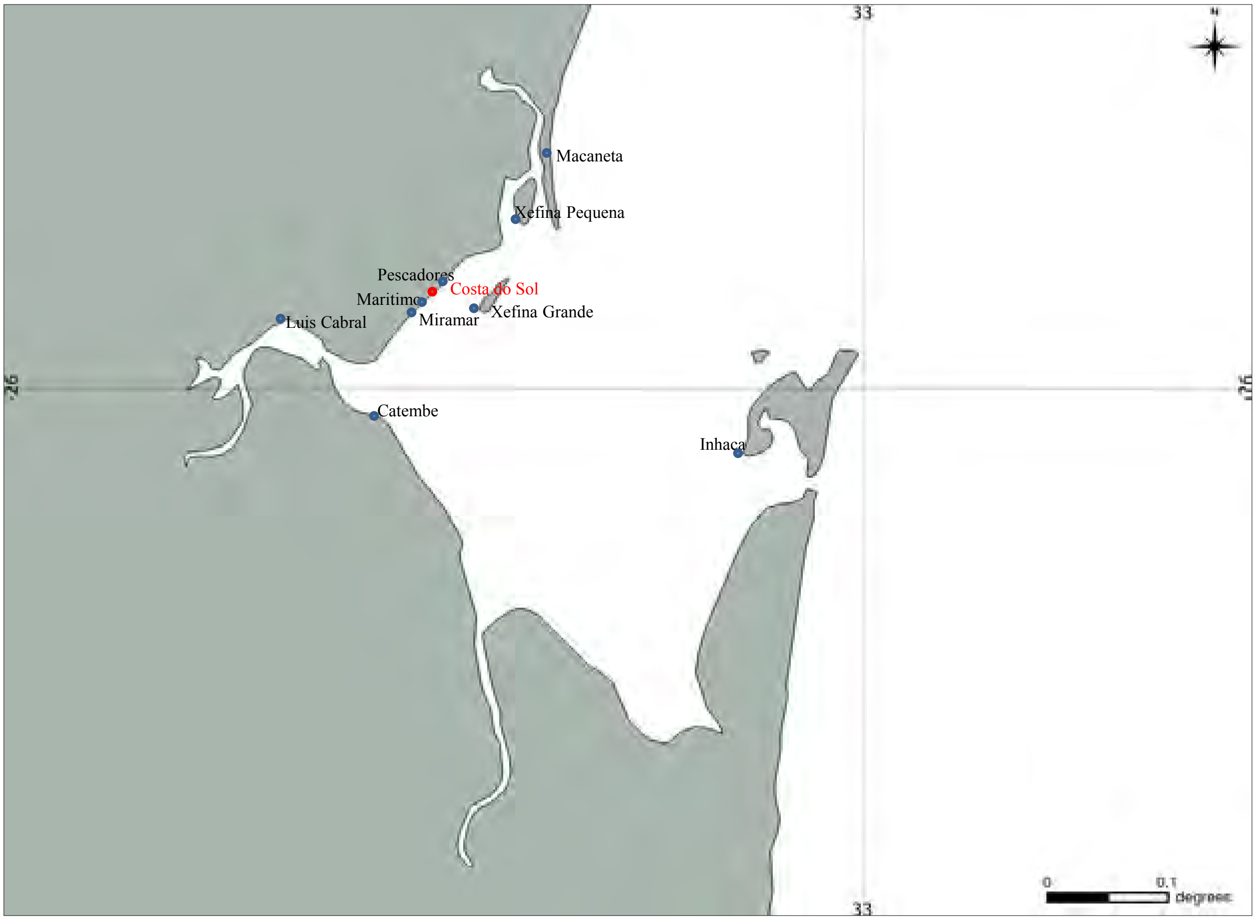


Figure 3.1: Locations in Maputo Bay where *Eumarcia paupercula* have been recorded, with the highlight of Costa do Sol Beach (red outline). During the study period, the main collection was the Costa do Sol beach. In other areas, low densities of *E. paupercula* were recorded during the site selection survey. Illustration based on personal observations and findings of Scarlet (2005) and Vicente and Bandeira (2014).

The beaked clam comprises a great part of clam consumption in Maputo. Little is known about the stock of *Eumarcia paupercula*, or the capacity of the population to recover naturally and sustains the harvest for future generations. The aim of this chapter is to determine the distribution, density and size composition of *E. paupercula* population in Maputo Bay, and also determine the standing stock of *E. paupercula*.

The following questions were posed:

1) What is the density and size distribution of *Eumarcia paupercula* in Maputo Bay?
2) How are densities and size distributions of *E. paupercula* related to vertical zonation?

3) Is there any seasonal variation in the density and size distribution of *E. paupercula* in Maputo Bay?

4) What is the recruitment pattern of *E. paupercula* in Maputo Bay?

5) Does the recruitment of *E. paupercula* follow the spawning peak periods?

METHODS

The size structure of the *Eumarcia paupercula* population was analysed by recording the length-frequency distribution of individuals along the coastline of Costa do Sol beach. The intertidal zone, where sampling took place, is a sand flat with approximately 300 m width of exposed area during low spring tides. Sampling design and description of the site was presented in Chapter 2 (study site description and general methods).

It was noted that the peak collection period for the beaked clam in Maputo Bay was during summer. Thus, there was a need to test if harvesting of clams affects population densities throughout the year. Hence, assessment of seasonal changes in the mean density was done by comparing the mean density per transect in each sub-season. Four seasons were defined: early summer (ES – from October to December), late summer (LS – from January to March), early winter (EW – from April to June) and late winter (LW – from July to September). There are two factors that may regulate the size distribution in this population, the population growth (including recruitment) and the harvesting, which selectively targets larger individuals. The time series measure combined these effects, but the discussion is provided later.

The definition of the sizes of *Eumarcia paupercula* individuals that were considered recruits, juveniles or adults follows similar studies of other venerids (Boehs *et al*., 2007; Kandeel, 2013; Hashiguchi *et al*., 2014). The classification is also based on maximum length, growth rates and global distribution, with preference for tropical and sub-tropical waters studies. Similar studies on clam recruitment included species such as *Tivela mactroides* (Denadai *et al*., 2005) and *Anomalocardia brasiliana* (Monti *et al*., 1991). Recruitment data emerged from the same sampling of population structure previously described. Recruits are considered clams that match the first length classes (Keough & Downes, 1982). Thus, all clams below 10 mm were considered recruits for the present study. Juveniles were those individuals between 11-20 mm and adults all individuals over 20 mm in shell length.

Long time-series data for stock-recruitment relationship analysis are not available for Maputo Bay. The present study presents the longest data series of 18 months; however, these data are not adequate for stock-recruitment relationships (SRRs) using standard models by Ricker (1954) and Beverton and Holt (1957). Thus, the stock-recruitment relationship presented was determined by plotting density of recruits against the density of adult, to find a logarithmic relationship using the Pearson correlation analysis.

The same assumptions of those models by Ricker (1954) and Beverton and Holt (1957) were taken into account: the mortality rate of larvae and juveniles is assumed to be proportional to the initial density. Moreover, environmental changes and fishing mortality can also mask the actual relationships (Kandeel, 2013; Maunder & Piner, 2014). Thus, results on the distribution patterns are often specific to the study area.

The standing stock of *Eumarcia paupercula* in Costa do Sol was estimated in terms of the present biomass (whole live weight). The biomass in each month was calculated by multiplying the mean individual fresh weight of each clam size class by the number of individuals of the same class per m^2. The monthly biomass per m^2 was the sum of the biomass of each size class in that month. The total was extrapolated for the total area of the study, which is approximately 144 000 m^2 of clams bed. A similar approach was used to estimate the biomass of the hard clam *Mercenaria mercenaria* (Mann *et al*., 2005), and Manila clam *Ruditapes philippinarum* (Thompson, 1995; Juanes *et al*., 2012). Special attention was given to the stock biomass of the harvestable clams (≥ 22 mm), to discuss the impact of the *E. paupercula* fishing on the standing stock.

Data analysis

Analysis of variance was performed to compare the seasonal and shore variation in the density and the mean length of *Eumarcia paupercula*, considering Mozambique summer between October and March and winter between April and September. Levene test was conducted to test the homogeneity of variances between seasons and also between shore levels. When it was found that there were no differences in mean density between seasons, then sub-seasons (early and late winter, and early and late summer) were tested and the same analysis performed for density.

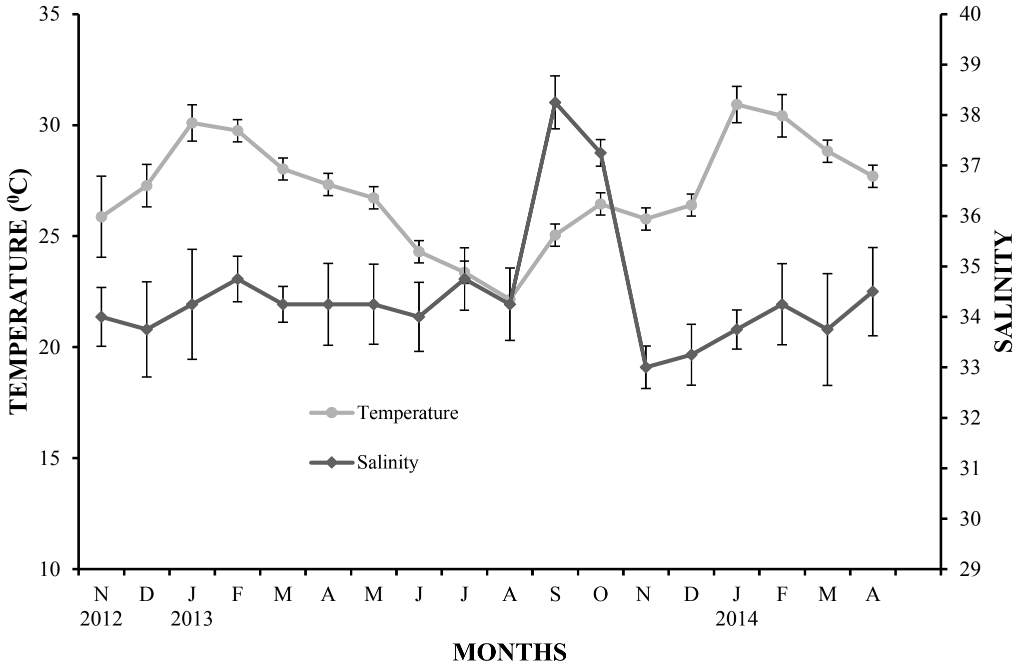
Data for stock-recruitment relationship analysis were log transformed due to the inequality of variance in the number of recruits along the sampling period. Correlation analysis was then compared for four length-classes, through one-way ANOVA. All statistical analyses were performed in SPSS 22.0 at a significance level of 0.05.

RESULTS

Environmental Parameters

The mean monthly sea temperature and salinity readings in the study area are presented in Figure 3.2. Average monthly temperature (mean ±SD) ranged from a minimum of 22.15±0.26 ^{0}C in August 2013 to a maximum of 30.93±1.11 ^{0}C in January 2014. The salinity changed from a low of 33.0±0.8 in November 2013 to a high of 38.2±0.5 in September 2013. Monthly rainfall is presented in Figure 3.3. There was no rainfall in June and July 2013, nor in March and April 2014. The maximum rainfall was recorded in January 2013 (262.1 mm). The sea surface Chl a concentration in Maputo Bay (Figure 3.3) varied from 4.28 mg m^{-3} recorded during December 2013 to 8.31 mg m^{-3} during February 2013. Despite some irregular seasonal fluctuations, the Chl *a* was lower in summer and higher in winter.

Effects of environmental parameters are discussed in other relevant chapters, to understand their possible effect on reproduction (Chapter 5), or growth (Chapter 6) of *Eumarcia paupercula* in Maputo Bay.



from November 2012 to April 2014.

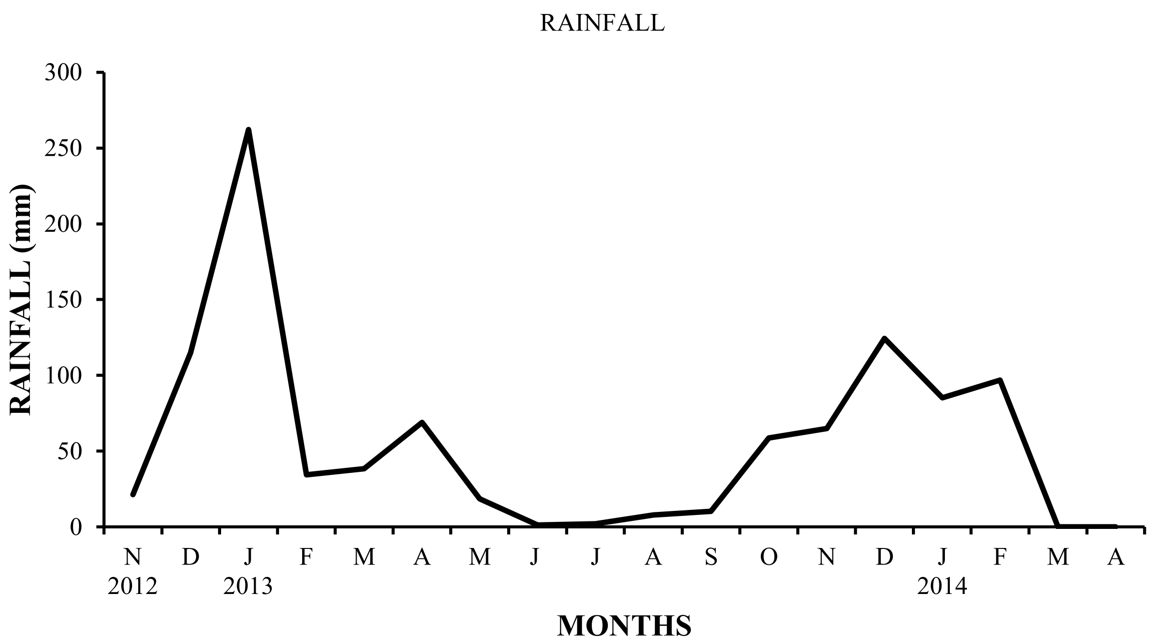


Figure 3.3: Monthly rainfall (mm) recorded for Maputo Bay from November 2012 to April 2014.

Seasonal density variability

The highest overall mean density (237.50 clams/m^2) of *Eumarcia paupercula* at Costa do Sol was found during October 2013, while the lowest (76.17 clams/m^2) was found during February 2013 (Figure 3.4). Analysis of seasonal variation in the mean densities of the beaked clam showed no significant differences between summer (October to March) and winter (April to September). As a monthly density from Figure 3.4 shows a strong seasonal pattern, samples were grouped into sub-seasons, based on the harvest seasonality, to test for any seasonal differences. In the sub-seasonal analysis, density during early-summer (ES) was significantly greater than during late-summer (LS) ($P < 0.05$), and no significant differences were obtained between the other sub-seasons. Further, it was found that density during LS-12 was not significantly different ($P > 0.05$) with densities recorded in late-winter (LW)-13, LS-13 and early-winter (EW)-14, but it was significantly lower than the remaining three sub-seasons. Further, the density in the EW-14 was significantly lower ($P < 0.05$) than that recorded in ES-13 (Figure 3.5).

The mean density of harvestable sizes against the overall population by sub-seasons is also plotted in Figure 3.5. When the density of sizes targeted for collection (≥ 22 mm) was analysed, the density variability showed a dissimilar pattern of that of the whole population in EW-13, where the density of the fished population decreased, while that of the overall population was increasing. This size fished was defined according to the smallest clam recorded in collectors samples (Chapter 4). In the remaining sub-seasons, the pattern of density variations was similar to that of the entire population. Figure 3.5 shows that densities of harvestable sizes can fall to 80 times less than the density of the non-target sizes in EW-13.

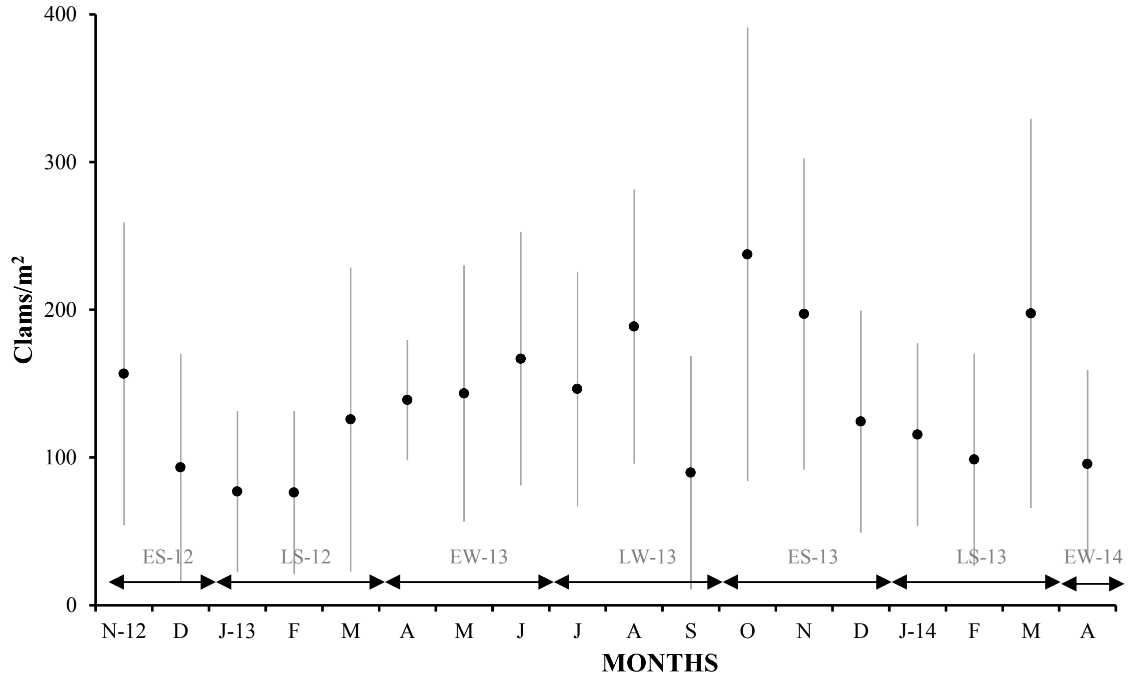


Figure 3.4: Monthly variation in the mean density of *E. paupercula* (±SD) during the period of November 2012 – April 2014.

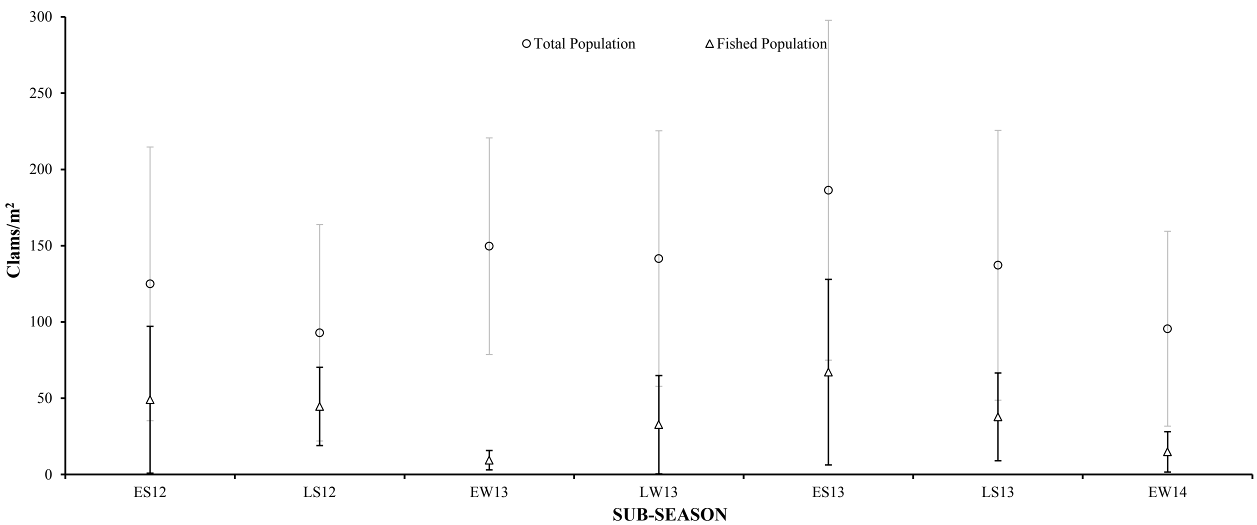


Figure 3.5: Sub-seasonal variation in the mean density (±SD) of *E. paupercula* population at Costa do Sol beach. Showing variation between densities of clams suitable for collection (triangles) and the entire population (circles), during early summer (ES12, ES13), late summer (LS12, LS13), early winter (EW13, EW14) and late winter (LW13).

Across-shore density variability

Analysis of the effect of exposure time on the density across-shore showed no significant differences ($P > 0.05$) between densities from lower and middle shores, from which 167.55 and 156.28 clams/m^2 were recorded, respectively. Those densities were significantly higher ($P < 0.05$) than that recorded in the upper shore (105.95 clams/m^2). Also, the combined effect of shore zone and sub-seasonality showed no significant differences in the density of *E. paupercula* in Costa do Sol Beach (Figure 3.6).

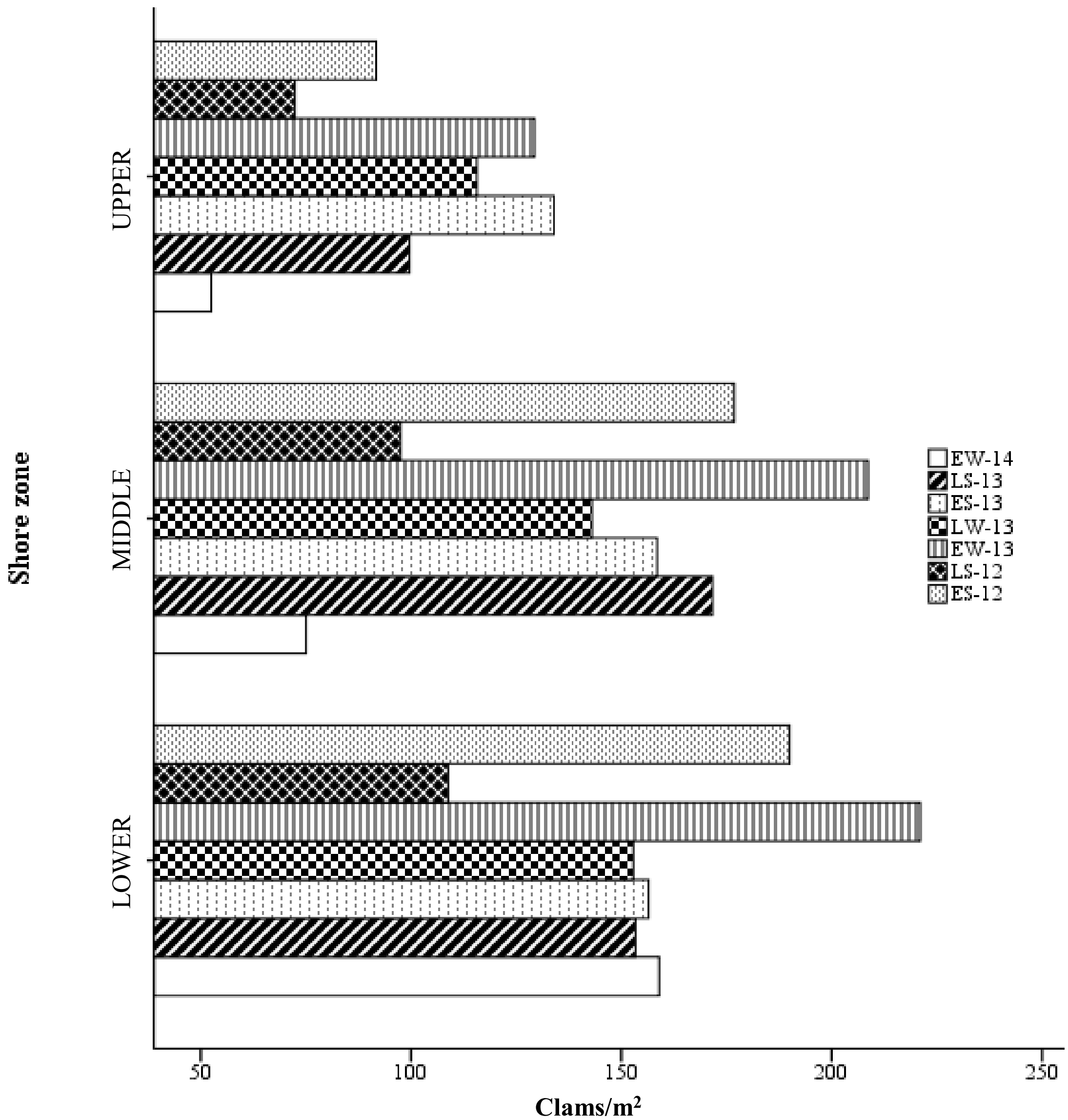


Figure 3.6: Differences in sub-seasonal and vertical mean density of *E. paupercula* population at Costa do Sol beach. Different letters show significant differences in the mean density along the shore ($P < 0.05$).

Seasonal length-frequency distribution

A total of 39 920 individuals of *Eumarcia paupercula* were collected at Costa do Sol beach, and 9982 individuals were used for length-frequency analysis. All four size-classes (2-10, 11-20, 21-30, 31-40 mm), defined according to the population size-distribution, were present throughout the sampling months (Figure 3.7). Collection of *E. paupercula* by fishers in Maputo Bay takes place during summer, but sometimes starting in the late winter (September) and running until the beginning of the winter of the next year (April) (Chapter 4). Consequently, it was expected that the collection would affect the length-frequency distribution, thus sub-season were used instead of standard seasons.

The clams in the largest size class (31 – 40 mm) were scarce, and reached lowest (0.33%) and highest values (4.90%) in May (EW) and February 2013 (LS), respectively. The class of mostly harvested clams (21 – 30 mm; Chapter 4) reached the maximum frequency of 53.01% during October 2013 (LS) and minimum of just 1.17% in May 2013 (EW). On the other hand, clams between 11 – 20 mm attained the highest peak in late winter (76.96% in August) and lower peak in early winter (8.15% in April 2013). Smaller clams (2 – 10 mm) comprised a high percentage of the population during EW (86.52% in April 2013) and LS (64.92 in March 2014), but during LW densities could drop to less than 5% of the population (September 2012). When considering only the fishable stock, which consists of the two largest size-classes, in general, the highest frequencies were recorded during the summer and the lowest during the winter. During October 2013, the fishable stock was over 50% (53.79%), as it was in September 2013 (50.85%). In the remaining months the fishable sizes formed less than 50% of the total population and the lowest frequency was found in May 2013, when the fishable clams comprised only 1.51% of the total stock.

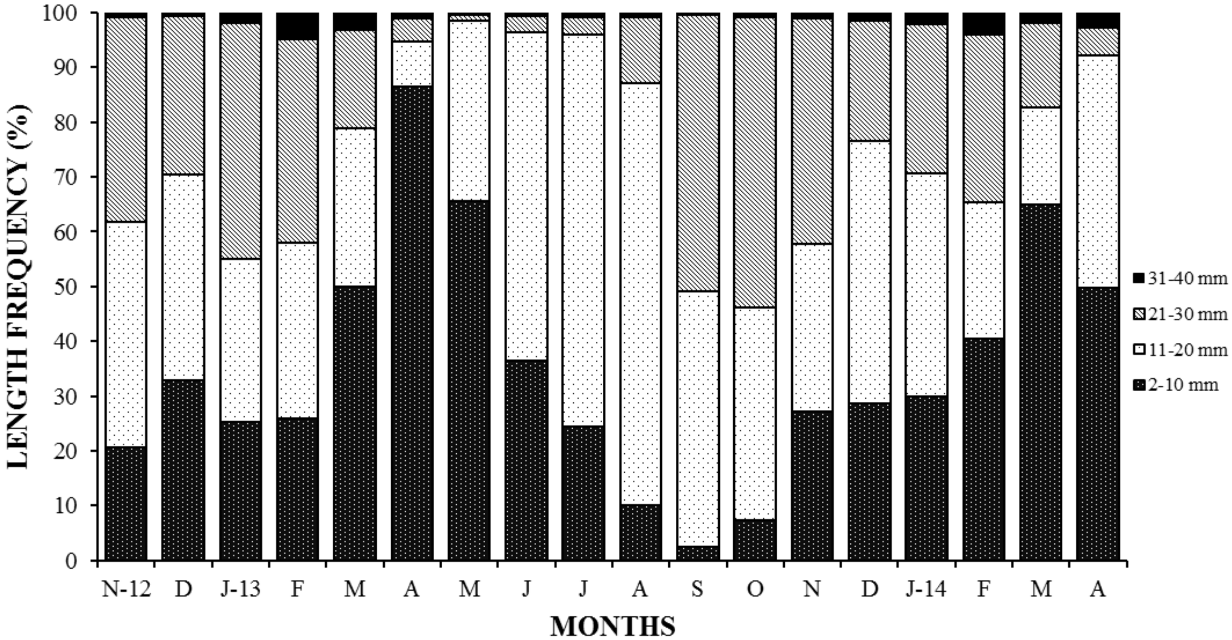


Figure 3.7: Population length-frequency classes expressed as a percentage of *E. paupercula* at Costa do Sol beach over the period November 2012 - April 2014.

An overview of the length frequency distribution of *Eumarcia paupercula* during the sampling period is provided in Figure 3.8. The monthly length-frequency histograms were highly unimodal from April to October 2013. Bimodal distributions were found in November 2012, March and November 2013 and in March and April 2014, while the multimodal pattern characterized December to February of both 2012 and 2013.

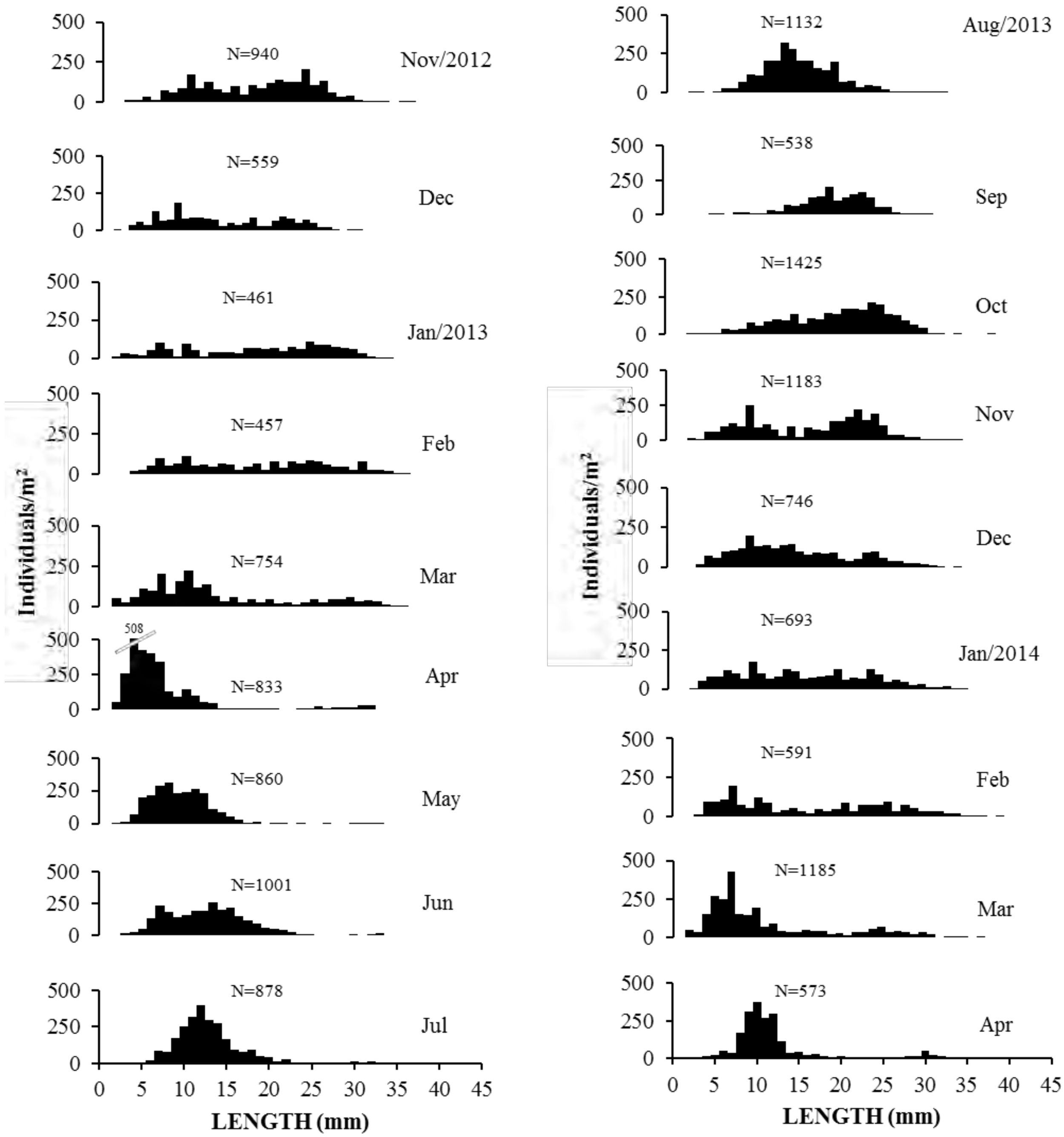


Figure 3.8: Monthly length-frequency distribution of *E. paupercula* population during November 2012 - April 2014 period. Number of observations (*n*) used to plot the histograms are above each chart.

Across-shore length-frequency distribution

Figure 3.9 shows the across-shore length-frequency distribution histograms over the sampling period. The same cohorts identified in growth analysis (Chapter 6) are described to explain the dynamics of the population across-shore. Cohort I was represented at all shore levels and was followed until January 2013 (three months) only on the middle shore. At the other shore levels, cohort I was distinctive only during November and December 2012.

Analysis of variance showed that in the middle shore mean length was statistically higher (15.1 mm) than the mean length of clams found in the lower (14.2 mm) and upper (13.6 mm) shores. On the other hand, clams from the lower and upper shores did not show any differences in mean length. There were no significant differences between mean lengths among seasons (analysis performed within the shore zone).

On the upper shore, from December 2013 to February 2014 it was not possible to distinguish between cohorts I and II, until the appearance of cohort III in March 2014. Cohort III occurred simultaneously with a low density of cohorts II until April 2014. A similar pattern was found on the middle shore, although cohort II and III were also detectable during December 2013. This differed in the lower shore, where cohort III appeared in October 2013. Similar to the middle shore, Cohort III appeared a month earlier (February) on the lower shore and occurred simultaneously with cohort II (although in low densities) up to April 2014.

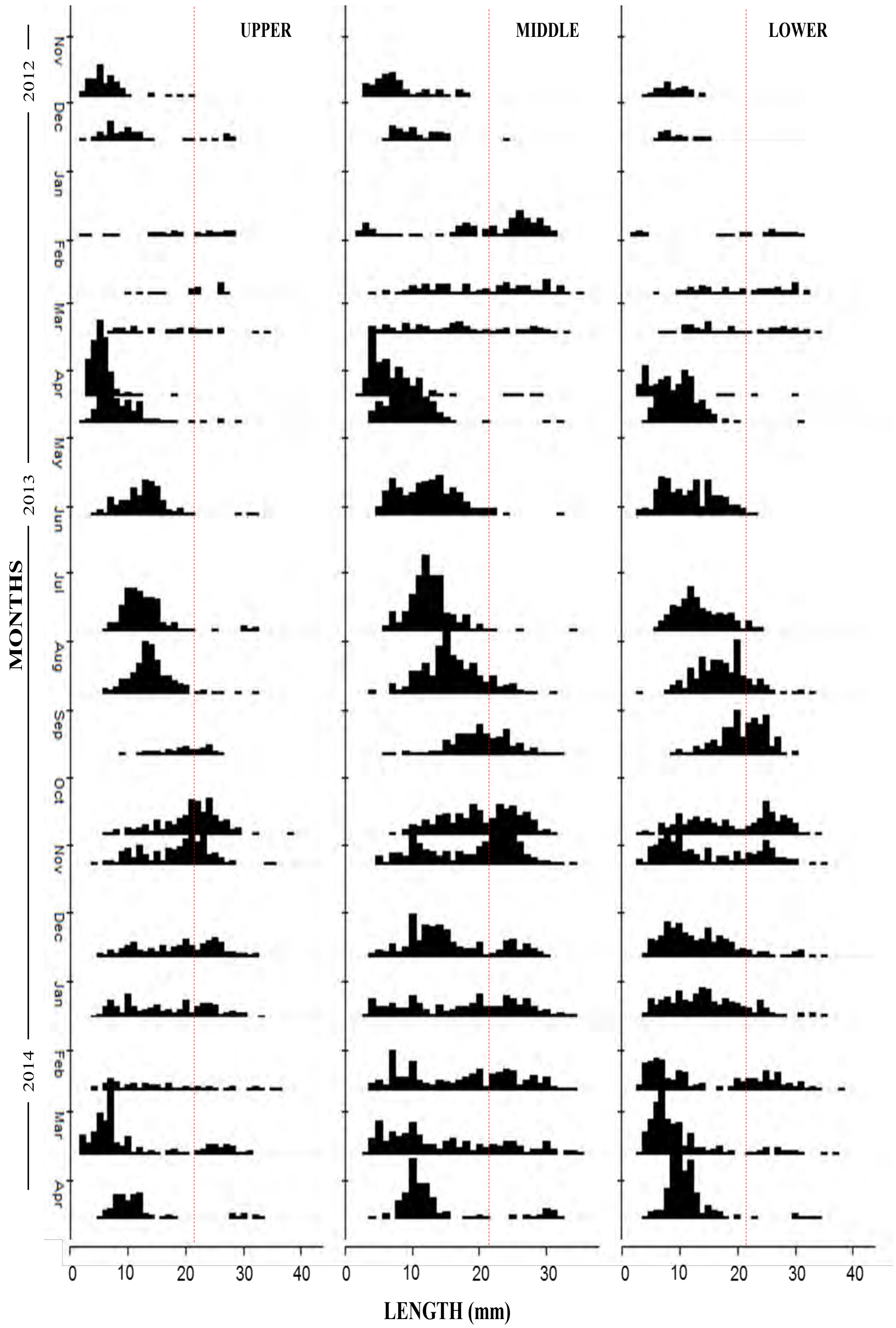


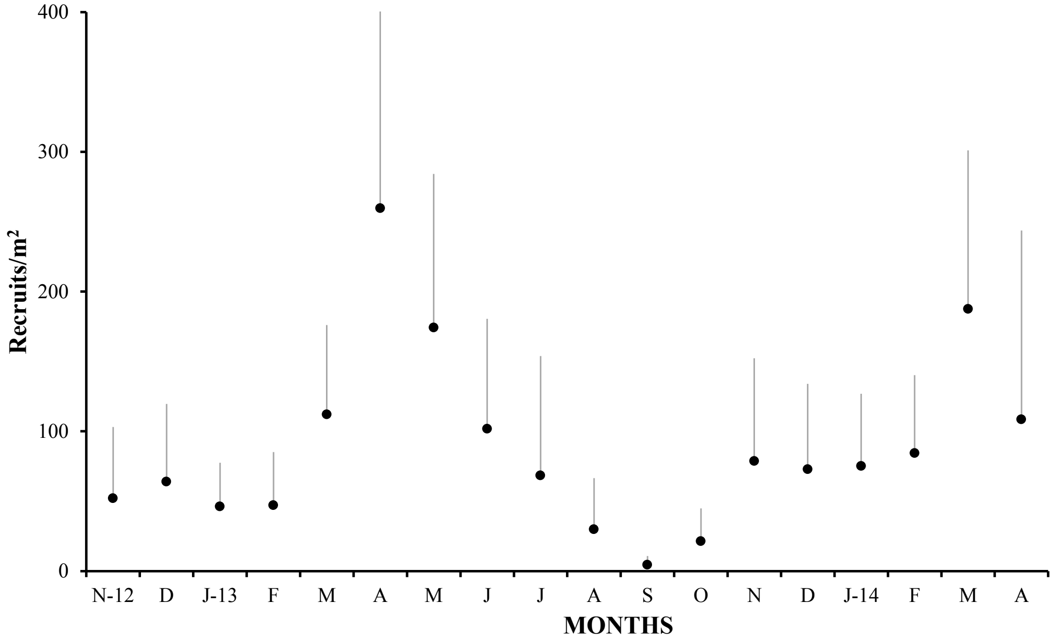
Figure 3.9: Overall length-frequency distributions of the upper, middle and lower shore levels. The dashed red vertical line indicates the size of first harvest of *E. paupercula*.

Recruitment patterns

The new cohorts from winter (March 2013 and 2014) were conspicuous. High densities of new settlers (2 – 10 mm) were detected in the following months and were clear and easy to follow with the unimodal pattern. The density of these cohorts reached over 250 individuals/m^2. On the other hand, new cohorts noticed during the summer (December 2012 and November 2013) were of lower intensity as those from the winter, and not easy to follow with a multimodal distribution. The densities of the winter cohorts were below 20 individuals/m^2.

The highest mean density of 260 recruits/m^2 (clams < 10 mm) was recorded in April 2013, and the lower of 4 recruits/m^2 was found in September of the same year (Figure 3.10). During a great part of summer (November - February), the density of recruits showed little variation throughout the sampling period, but lower recruitment rates were recorded in the summer of 2012. Figure 3.10 also illustrates that highest densities of recruits were found during EW (March - May 2013 and March - April 2014). This result was also shown by the significantly greater densities ($P < 0.05$) of recruits during winter, compared to summer. This pattern suggests a seasonal pattern in the recruitment of *E. paupercula* in Maputo Bay.

The negative correlation ($a = -1.26$) between stock and recruit density produced a determination coefficient of 0.48 between the density of spawning stock and recruits. Consequently, this coefficient indicated a negative stock-recruitment relationship for *Eumarcia paupercula*, where the high recruitment rates were not correlated with high densities of adults (Figure 3.11).



Figure

2012-April 2014 period.

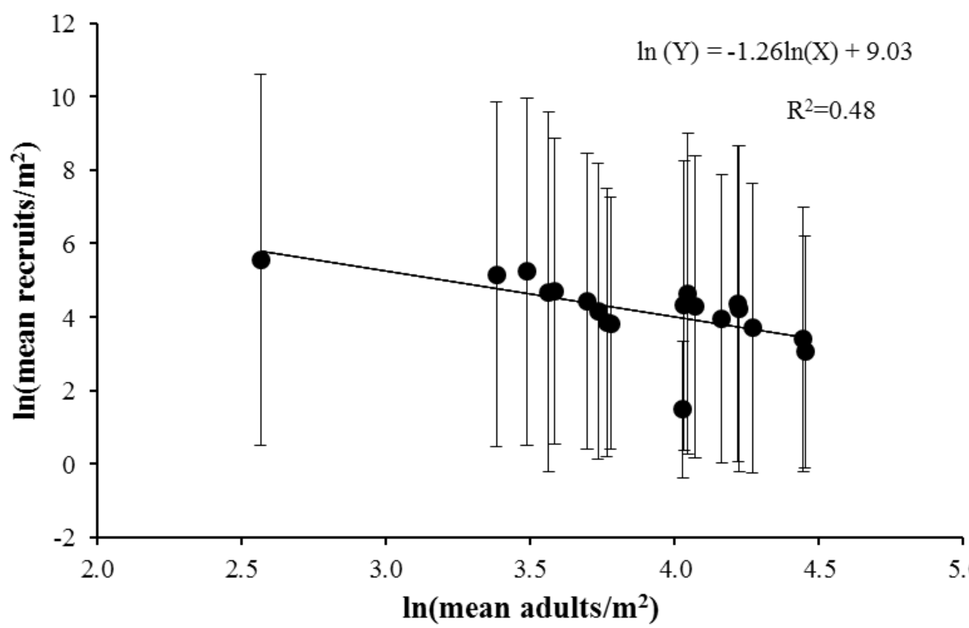


Figure 3.11: Correlation between the mean abundance (±SD) of adults and recruits for monthly samples of *E. paupercula* collected during November 2012-April 2014 period.

Eumarcia paupercula standing stocks

The estimated mean biomass of *Eumarcia paupercula* at Costa do Sol ranged from a minimum of 48.25 g/m^2 in May 2013 to a maximum of 273.55 g/m^2 in November 2013, respectively, in a total area of approximately 144 000 m^2 of surveyed area. The average biomass of beaked clams at Costa do Sol is estimated at approximately 24 200 kg (based on the results for the 2013 year only). The average total standing stock, regardless the collection effect, in the study area is estimated to be approximately 25 300 kg and the total fishable stock (≥ 22 mm) at nearly 13 000 kg over the study period. The biomass of the fishable stock was highest (30 800 kg) during November 2013 and lowest (1 100 kg) during May 2013. The fluctuations in the fishable stock biomass followed the same pattern as that of the total stock (Figure 3.12). The result of the stock size is fully discussed in the next chapter when the impact of fishery on the beaked clam standing stock is addressed.

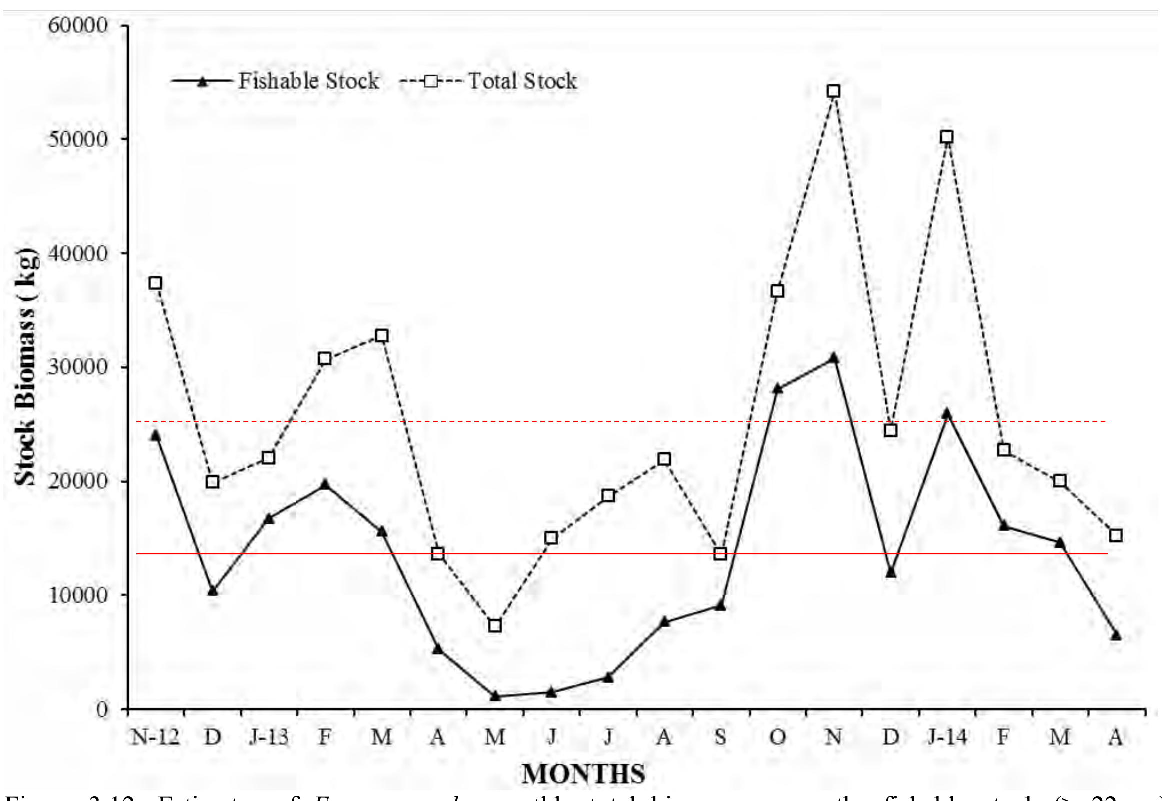


Figure 3.12: Estimates of *E. paupercula* monthly total biomass versus the fishable stock (≥ 22mm) during November 2012-April 2014. The red horizontal lines indicate the average of the biomass from total (dashed) and fishable stocks (continuous).

DISCUSSION

Seasonal density variability

Relative higher densities of *Eumarcia paupercula* were recorded in the present study, up to 500 individuals/m^2, comparing with the densities of 15 individuals/m^2 found by Scarlet (2005) in other tidal flats of Maputo Bay. High densities, such as those found in this study, are expected in Southern African beaches. Contrary to the present study, densities of *Mercenaria mercenaria* were low (maximum of 20 individuals/m^2) in Chesapeake Bay (Mann *et al*., 2005). In their study, not only the harvest influenced the low density recorded, but mainly the low reproductive output and mortality of recruits by predation. In the present study, it seems that harvest is the main driver for density oscillation.

Distribution of animals in tidal flats, such as the Costa do Sol, is mostly influenced by physical factors (McLachlan, 1990) and clam species have variable degrees of connectivity between local populations through larval dispersal (Defeo & McLachlan, 2005). Besides the physical factors, another population of the beaked clam inhabits sea grasses 4-5 km from the studied population and may have affected the dynamic of the Costa do Sol population, particularly by adding recruits to this population. Study of effects of tidal currents movements on larval dispersal would assist in understanding whether the clams from that nearby population contribute in increasing the size of the studied population.

Temperature and salinity recorded during the sampling period were typical for Maputo Bay (Scarlet, 2005; Canhanga & Dias, 2014). The mean monthly temperature was 22.2 – 26.7 °C during winter and 25.8 – 30.9 °C during summer. Mean monthly salinity was between 34.3 – 38.3 and 33.0 – 37.3 during winter and summer, respectively. The level of variations recorded for these parameters may not affect the physiological activities for *E. paupercula*, such as food intake and regular reproduction pattern. The assumptions about water temperature and salinity limits agree with the findings of Scarlet (2005). At Espirito Santo Estuary, approximately 10 km from the study site, individuals of *E. paupercula* were recorded at low densities (maximum of 5 clams/m^2) during 12 sampling months. The water temperature at Espirito Santo Estuary, which is formed by Maputo Bay salt waters, was 18 – 35 °C, and salinity was 32 – 45.

Since there are no data available for tolerance of *Eumarcia paupercula* to temperature and salinity, the annual variability in these parameters can be considered within the range of tolerance for the species. Nonetheless, although in lower density and smaller sizes than in the present study, *E. paupercula* is also found in estuarine areas of Maputo Bay, where salinity is lower (Scarlet, 2005). Further, as temperatures recorded in this study were similar to those recorded by Scarlet (2005), the minimum temperature tolerance can be set at around 20.5 °C (temperature obtained by Scarlet, 2005) and the maximum at 31 °C. For salinity, the lower tolerance limit can be at below the 32 recorded in this study, as the species has been recorded in estuarine habitats (Day, 1974; Ngqulana, 2012), while the upper is at about 39. Therefore, within these boundaries, this species can exist without compromising the physiological activity. Nevertheless, venerids are known to tolerate a broad range of salinities (Marsden, 2004).

Across-shore density variability

In the present study, the significantly lower density in the upper shore, compared to the middle and lower shores, suggests that exposure time has some influence in the distribution of *E. paupercula* in Maputo Bay. Clearly this was expected, as filter feeders can only feed when submerged and this might be the major forcing factor for this difference in densities (Griffiths & Griffiths, 1987).

The findings of the present study are similar to those obtained in Galena Bay for *Protothaca staminea* (Paul & Feder, 1973). Those authors recorded highest densities in the intermediate tide height, while lowest densities were recorded at high and low tide heights, referred in our study by upper and lower shores, respectively. High densities of *Donax serra* were also found in the mid-tidal area of the west coast of South Africa (Bally, 1983). Relatively high densities of clams are found in the central intertidal zone, and low densities in upper and lower zones (Defeo & McLachlan, 2005).

Seasonal length-frequency distribution

As clams grow, the larger individuals are selectively removed by collectors. The relatively low densities of bigger sizes (21 – 30 and 31 – 40 mm) registered between March and August are due, most probably, to the end of the high collection season, which takes place between March-

April. Usually, after the month of March, the clam grounds are often totally grubbed, and a decline in the number of clam collectors is visible along the sandy beaches of Maputo Bay. Although relatively high recruitment rates were recorded, it would be expected that density would decline and affect length distribution of *Eumarcia paupercula*, particularly due the decline of larger individuals. Nevertheless, this effect of density on length distribution is stronger with size increment (Weinberg, 1998), which would be unlikely to occur in this population, as clams are removed as they grow and the density declines. An evidence of the bigger size preference by collectors can be observed during December (2012 and 2013), when after a decline in the harvestable stock, it increased in January. This was probably due the few collectors during December and beginning of January, caused by the festive season and heavy rain, as detailed in the next chapter. Also, the finding that the monthly catches were always greater than 50% of the fishable stock (Chapter 4) is indicative of the extremely high fishing pressure on this stock, as discussed later.

During the period October – March, the length-frequency distribution was mostly multimodal, with all sizes present in low frequencies, but with some bimodal distributions. This period corresponds to the high collection season and also an addition of new cohorts generated this distribution pattern. On the other hand, during the period of population recovery (April – September), the distribution pattern was exclusively unimodal, with higher frequencies of smaller clams (< 20 mm) in the beginning of the season, and bigger sizes at the end of season. This pattern is a consequence of the reproductive cycle plus the seasonal collection by artisanal fisheries. The proportion of larger individuals removed by collectors can reach over 90% in the final months of collection season, namely March and April (Chapter 4). Defeo and McLachlan (2005) concluded that recruitment of macroinfauna tends to lead distribution to a multimodal pattern. During the establishment of new cohorts (e.g. April-September 203) distribution of *E. paupercula* population was mainly unimodal until collection began, or individual differences in growth rates were evidenced.

Across-shore length-frequency distribution

Larger *Eumarcia paupercula* individuals were found in the middle shore. Surprisingly, the greatest mean length was recorded in the middle shore and not in lower shore; probably because there is greater predation of larger clams in the lower shore, and other causes of mortality there that are yet unknown. The low spring water limit is the swash zone, and possible sediment suspension may occur in this area, causing individuals from this area to change their filtration rates. They can stop feeding during a certain period even when submerged, as they are forced to close valves, or may have gills clogged (Malouf & Bricelj, 1989). Further, they may decrease the water clearance rates (Higano, 2004) or produce more pseudofaeces (Griffiths & Griffiths, 1987) resulting in low growth rates. Some filter-feeders from high-sediment load habitats have larger labial palps, which improve their particles selection (Barillé *et al*., 2000); however, particle-feeding bivalves may use both passive and active particle selection, depending upon certain particle regimes and environmental conditions, to cope with high sediment loading (Ward & Shumway, 2004). These physiological responses may become important for species, such as *E. paupercula*, as they inhabit intertidal areas and feed only when they are submerged.

The upper shore is the area where, mainly during spring tides, clams are more exposed to dehydration and predation by shorebirds. The shore birds present in the study area and known as clam predators (Myers *et al*., 1980; Zwarts & Wanink, 1989; Grosholz *et al*., 2000; Petracci, 2002) include the sanderling *Calidris alba*, seagulls *Larus cirrocephalus*, *L. dominicanus*, *L. fuscus* and the African black oystercatcher *Haematopus moquini* (Parker, 1999). Nevertheless, Scarlet (2005) identified 21 seabirds species foraging in the intertidal where she studied *Eumarcia paupercula* distribution in Maputo Bay, but she did not directly correlate their occurrence with clam densities. Over 130 species of waterfowl and seabirds have been described in Maputo Bay (Parker, 1999), and 50% of the benthic fauna is consumed by birds such as *L. cirrocephalus*, the little egret *Egretta garzetta* and the heron *Ardea cinerea* at Inhaca Island (de Boer & Longamane, 1996). Moreover, extended periods of emersion, will reduce growth rates by *E. paupercula* in the upper shore zone. Findings of this study are similar to those of Denadai *et al.* (2005), who also found larger *Tivela mactroides* distributed in the middle shore; however, their population included also a sub-tidal area, which is not the case of *E. paupercula* here, which were sampled only within the intertidal area.

Recruitment patterns

Recruitment, reflected by the presence of *Eumarcia paupercula* less than 10 mm, occurred year round, with highest rates during the end of summer and beginning of winter (March - April). The presence of more than 50% of adults in 15 out of the 19 sampling months does not mean that clams at harvest size, which is from approximately 25 mm, are always present in high densities. Recruitment rates recorded from this study (> 250 recruits/m^2) can be considered high for venerids. According to Donn (1987), the presence of a river mouth around the population of *Donax serra* promoted recruitment of this species. This was not observed for *E. paupercula,* where river input seemed not to contribute to the population of *E. paupercula* in Maputo Bay. At least three rivers discharge close to the study area (Litulo, 2005). Nevertheless, some authors have found that river discharges with fresh water input may prevent recruitment (Defeo & McLachlan, 2005).

Despite the fact that for the present study sediment composition was not analysed, within the sampling area, sediment was characterized by fine sand and shell gravel. Achimo *et al.* (2014) showed that the sediments of this part of Maputo Bay varied from mud (composed of silt and clay) to coarse pebbly-sand. In some areas mud composed more than 50% of the sediment. This sediment composition with small particles is known to be favourable for bivalve settlement (Spencer, 2002). High tidal flow disperses larvae away from their original grounds (Congleton Jr. *et al*., 2006). It has been shown that the tidal currents in Maputo Bay greatly influence plankton dispersal (Paula *et al*., 1998; de Boer *et al*., 2000). Consequently, it is probable that the recruits are not coming from the local parental stock, which is supported by the negative correlation between adult densities and recruitment rates.

There are no data on the larval cycle for *E. paupercula*, but this is expected not to differ largely from that of other venerids. Time to settlement varies among venerids, but mostly it occurs between 15-30 days (Ansell & Trevallion, 1967; Stead *et al*., 1997); however, the settlement process is influenced by the high mortality rates during the post-settlement process and is difficult to measure because of the individuals small sizes. Approximately 40 days after spawning (Chapter 5) a new cohort was established in the *E. paupercula* population. This is a strong indication that recruitment rates follow peaks of spawning in this species, although it seems that recruits may come from a parental stock other than that in the immediate vicinity. In the hard-shell clam *Venus (Mercenaria) mercenaria*, the first settlement was observed 16 days after fertilization (Ansell & Lander, 1967) and after 27 days for *Ruditapes decussatus* (Aranda-Burgos *et al*., 2014). For *Venus antiqua*, first recruits appear in the population 30 days after its main spawning event in a tidal flat in southern Chile (Stead *et al*., 1997). The finding of Mouëza *et al.* (1999) is closer to that of this study as, after three weeks of fertilization, *Anomalocardia brasiliana* reached 1mm, compared to the minimum size in the present sampling of 2 mm.

Highest recruitment rates observed in winter (April) are normal for clams in the subtropical and tropical zones. Similarly, Turra *et al*. (2014) also found the best recruitment of *Tivela mactroides* during winter in Brazil (23°40’). A slight early start of a month was observed on the lower shore in the March 2014 major recruitment process, comparing to the previous year (April 2013). Unfortunately, it is difficult from the data and parameters obtained in this study to understand this pattern. Nevertheless, timing of gametogenic cycles may change among years within the same population (Eversole, 1989).

There was a negative and moderate correlation between the density of adult stock and recruitment rates for the beaked clam in Maputo Bay. These findings suggest that the presence of recruits depends also on other factors, most probably the abiotic factors such as sediment composition (Lastra & McLachlan, 1996; Hunt *et al*., 2003; Kandeel, 2013) and water flow speed (Hunt *et al*., 2003). In the case of *E. paupercula* in Maputo Bay, long time-series data are not available and also the clam stock was never closed to exploitation. Nevertheless, the collectors move from one stock to another, redirecting their effort onto new clam grounds once the previous one is depleted. This was a general communication from the collectors during the meetings held before the beginning of this project.

Predators also play a role in the recruitment of prey species (Ishii *et al*., 2001; Laudien *et al*., 2003). Biotic factors such as predation constitute a cause of the decline in clams density (Glude, 1955; Hunt *et al*., 2003). A total of 17 marked clams were found dead with a tiny hole in the valves throughout the experiment (Figure 3.13). The highest number (eight) was found during May 2013, and the remaining number throughout the year, and holes were present in all the size-ranges. The pattern of the holes is an indication of predation by snails (Carriker, 1981; Morton, 2005). Among other snails inhabiting the study site, the muricids *Murex brevispina* and *Thais carinifera* were recorded as present and abundant species, respectively by Vicente and Bandeira (2014). This is the same family of the snail investigated in the prey-predator interactions, and found to decrease the densities by mortality of the clams, or affecting the structure of communities (Govan, 1994; Lomovasky *et al*., 2002; Morton, 2005; Savini & Occhipinti-Ambrogi, 2006; Munari & Mistri, 2011).

Figure 3.13: Marked shells with small holes in the shells (indicated by the black arrows), suggesting predation by snails.

The study area is also known to shelter large populations of the blue crab *Portunus pelagicus*. This crab is commonly found in shrimp by-catch (Machava *et al*., 2014), and also targeted in artisanal fisheries (Inacio *et al*., 2014). This crab species belongs to the family Portunidae, which is known to include clam predators (Glude, 1955; Byers *et al*., 2010). Glude (1955) found that clam densities decreased 50% when the population of crabs increased. Although portunid crabs are common in the tidal channels of the Bay (de Boer *et al*., 2002), predation rates and prey preferences by these crabs have not been reported for the study area; however, since crabs often forage for smaller clams, because it is easier to break their shells, as found in predation of *C.*

edule by *Carcinus maenas*, also a portunid crab (Sanchez-Salazar *et al*.,1987), it may be possible that this predation occurred in the population studied in Maputo Bay. Yet, none of the clams found dead in the mark-recapture experiment showed patterns of predation by crabs, which is characterized by randomly broken shells, usually on the valve edges.

A long time-series is necessary to produce a consistent relationship between stock and recruitment (Peterson, 2002). Although the landings *E. paupercula* encountered in Chapter 4 are related to a short-time series from October-November 2013 and January-February 2014, the data suggest that clam collection may have led to a bias on stock-recruitment relationship pattern, as the relationship was negative. The fact that collectors are selective for bigger sizes, and also the fact that during these months the frequency of adults was higher than that of recruits, supports this theory. The size preference by collectors (≥ 22 mm, Chapter 4) appears not to be very destructive to the population, as the recruitment rates seem to be high; probably, the collection takes place during or after the spawning stock has released the gametes, or the gametes come from another stock in another site.

Eumarcia paupercula standing stocks

The standing stock of *Eumarcia paupercula* was influenced by the recruitment and removal of adult clams over the study period. The arrival of recruits, which was accompanied by the changes in the LFD histograms over the sampling periods, is clearly critical to sustaining the harvestable stock. Although it was clear that once the clams grow to a certain size, they are being quickly removed (Chapter 4), the major spatfalls were regular in both years (April 2013 and March 2014). The high growth rates of *E. paupercula* may contribute to the harvestable stock in the studied population, as the age at entry into the fishery of *E. paupercula* (clams with 22 mm in length) can be estimated to be only 0.5 year. The highest mean density of recruits of 250/m^2 (April 2013) compared to the highest density of 94/m^2 adults (October 2013), suggests that approximately 38% of recruits reach the fishable size. The study of population dynamics of fished population constitute the source of the management measures to be applied for the sustainability of fisheries and ecosystems (Jennings & Kaiser, 1998).

CONCLUSION

The present study has shown across-shore differences in the density distribution of *Eumarcia paupercula* in Maputo Bay, with highest densities found in the lower and middle areas. Seasonal fluctuations in the density of the beaked clam showed highest densities in early winter of 2012 and lower density in late summer of 2012. Removal of larger individuals via collection and reproduction (by adding new cohorts of small individuals) seem to be the major factors regulating the changing seasonal pattern of length-frequency distribution in this population.

The population size structure switches between polymodal and unimodal, to a bimodal distribution by introduction of new cohorts to the population. Analysis of length distribution along the intertidal area revealed no differences in mean length between seasons; however, there were differences in length distribution across the shore, demonstrating an effect of exposure time on size distribution. Surprisingly, larger clams were found in the middle shore, while smaller clams occurred within both upper and lower shores. Exposure time might not be the only factor influencing size distribution, as largest individuals would then be found on the lower shore.

Recruitment of new individuals takes place all year round. The highest recruitment success takes place during winter, while the lowest recruitment rates were found during the summer. The presence of adult stock seems not to have an influence in the recruitment rates of *E. paupercula* in Maputo Bay. Nevertheless, recruitment events follow spawning peaks recorded in Chapter 5. Other factors, such as sediment composition and currents, have to be tested to understand better the recruitment pattern.

The present study was carried out in the biggest fishing centre of Maputo Bay, where the highest number of invertebrate collectors was documented. Other collection grounds of *E. paupercula* in Maputo Bay, e.g. Maritimo, Luis Cabral, Inhaca Island and Xefina Grande Island, have less human exploitation. Densities found in previous studies in these areas were low (maximum of 20 individuals/m^2), while at Costa do Sol high mean densities were up to 250 individuals/m^2.

Chapter 4: Socio-economic aspects of *Eumarcia paupercula* collection in Maputo Bay

INTRODUCTION

Present marine ecosystems are experiencing the effects of high and increasing levels of fishing pressure. The unprecedented speed and magnitude of those phenomena raise serious concerns about the ability of these ecosystems to sustain services, such as fisheries, to human societies. According to Hoguane (2007), the main threat to the sustainability of marine natural resources in Mozambique is related to the ever-increasing pressure, from anthropogenic and natural origins, such as fisheries overexploitation and climate change, respectively. Also, the coastal area is characterized by conflicts in resource use and destruction of habitats.

Fish resources are important sources of income and protein for traditional inhabitants of coastal zones in this region. The first evidence of exploitation of shellfish around Maputo Bay dates from 8000 BP (Barradas, 1967). This is similar to other coasts of southern Africa (Thackeray, 1988), but the exploitation of intertidal shellfish by coastal communities has increased massively over the last decades, as documented both at this site (de Boer & Prins, 2002) and in other areas of southern Africa (Griffiths & Branch 1997). The survey of Hauck *et al*. (2014) showed that the major source of household monthly income in most coastal communities of southern Mozambique comes from sale of marine resources products. Nevertheless, other occupations, such as temporary employment, small business, and thatch construction also contribute to the household incomes. Clams represent a resource with considerable dietary value and represent a significant source of income for coastal communities along Maputo Bay (de Boer *et al*., 2002; Balidy, 2003; Rosendo *et al*., 2014; Vicente & Bandeira, 2014) and are one of the main seafood sold in Maputo City markets.

According to Scarlet (2005) two venerids important to these fisheries dominate and occupy, together with other species, approximately 19 km^2 of the intertidal area in Maputo Bay, namely the hard clam *Meretrix meretrix* and the beaked clam *Eumarcia paupercula*. While *M. meretrix* has a narrow distribution in the Bay, *E. paupercula* is the dominant clam species. Other clams with significant frequency at Costa do Sol beach are mostly associated with the *Zostera capensis* beds and include *Anadara antiquate*, *Dosinia* spp., *Macoma litoralis*, *Solen cylindraceus*, and

Trachicardium flavum, but these all occur in lower density comparing with *E. paupercula* (Vicente & Bandeira, 2014).

Mozambique has no functioning management system controlling resource exploitation for clams and other bivalves. Intertidal shellfish collection in Maputo Bay is an activity preferred by women and children (de Boer & Prins, 2002). Since there is no regulation and a lack of other sources of income and of animal protein in the coastal communities of Mozambique (Hoguane, 2007), shellfish collection becomes an important source of protein (Kyle *et al*., 1997). Consequently, the potential for overexploitation of resources is high in these areas. Overfishing can change the density and size structure of the population and can affect biological interactions, which may have indirect effects on other animal populations (Griffiths & Branch, 1997).

Different approaches have been discussed for small-scale fisheries management worldwide. Most include equipment, space, and fishing period restrictions (Salayo *et al*., 2008; Crawford *et al*., 2010), setting of minimum size limits (Crawford *et al*., 2010), daily or seasonal catch limits and restrictions on the number of fishers (Salayo *et al*., 2008), all of which aim at decreasing the fishing effort. The fisheries management approach by the Mozambican government is a co-management strategy involving many stakeholders, from the fishermen to academics and government (Figure 4.1). Co-management is a process with distinct stages that take place in different times and modes along certain fishing area and involves institutional relationships that can be horizontal through the geospace and also vertical through the levels of organization (de Sá, 2011). Success in the implementation of co-management varies among various fishing communities in Mozambique (Menezes *et al*., 2009); however, the benefits generated in the fishing communities are directly for the fishers or the surrounding communities. These benefits include social infrastructures and network support that assist in better managing of the adverse social and economic pressures in the coastal zone of the country.

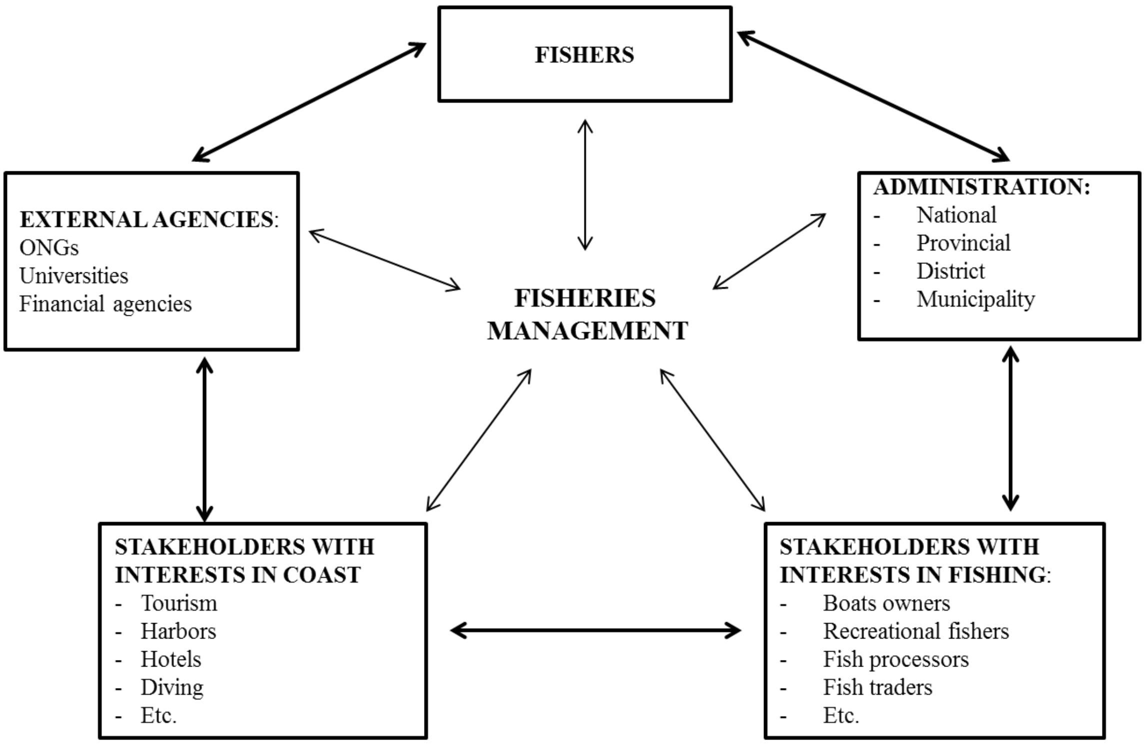


Figure 4.1: Fisheries co-management system in Mozambique (de Sá, 2011).

The community of Costa do Sol is highly dependent on coastal resources, such as mangroves and invertebrates (Crona *et al*., 2009). The only available study on the *E. paupercula* population in Maputo Bay is that by Scarlet (2005) and this focused on distribution patterns and on landings in the main collection ground for the species in that period (*Bairro dos Pescadores*). Though, her study did not include any analysis of the social importance of this resource for the collectors. There is still a lack of information about *E. paupercula* exploitation by coastal communities around Maputo Bay. For example, how this activity is being carried out, what categories of people are involved or use the resource for their livelihood, as well as the amount they are taking from the stock. The aim of this chapter was to describe the socio-economic importance of *E. paupercula* collection for the collectors at Costa do Sol Beach. Also, to determine the amounts and sizes of the collected beaked clam to find out if the collection is being done in a sustainable way.

The beaked clam, *Eumarcia paupercula* is one of the bivalve species that is targeted by lots of collectors on the Maputo Bay beaches and is mostly collected at vicinities of Costa do Sol (Scarlet, 2005). Data on numbers of collectors involved in the activity, how the activity is being carried out, and the importance of this fishery for communities are scarce. Thus, given these facts, an improved understanding of several factors is needed:

1) Who collects the species and what is the final destination of the crop (sell or consume)?

2) What is the range of numbers and sizes of the collected *E. paupercula*?

3) Do clams collected have the same average size as the sampled population?

4) Is there any commercial trade in *E. paupercula* for the coastal communities? If yes, what is the price in the local market?

5) Is there any value chain for this species?

METHODS

Interviews

Preliminary arrangements with the Costa do Sol Fishery Community Council (CCP) were carried out to find out if there is any organization or leadership regarding clam harvesting. This procedure was also necessary to seek possible assistance in the communication with collectors and to decide the best period to carry out the interviews.

A CCP is an organization from a base, i.e., from where the fishing is being done by the fishing communities and is recognized by the Mozambican government through the Ministry of Fisheries. The CCPs participate in the management of fisheries resources. The main tasks of a CCP include the contribution to the conservation of ecosystem in its operational area, as well as problem identification in fisheries resources use. CCPs also contribute to the inclusive management of fisheries together with the fishers, government, and other stakeholders to guarantee a sustainable use of resources. Also, they manage conflicts that arise from fishing, develop activities for the sustainable use of fisheries and help to improve livelihoods by incorporating the community interests in the action plan of the Ministry of Fisheries (de Sá, 2011). Most of the CCPs are focused on artisanal fisheries, where principal activities are the control of the closed season for shrimp fishing, type of boats used, combat the use of mosquito nets and use of safety tools. No CCP was identified, countrywide, working with clams collection and those working in artisanal fisheries appear to have weak actions (de Sá, 2011).

Counting of collectors was carried out during two low spring tide periods (ten days) in the study area in September 2013. An average of 103 clam collectors/day was observed over approximately 300 000 m^2 between transect areas. To determine the number of interviewees per month, it was assumed that the number of collectors would decrease with time, as it was noticed in previous collection season (2012-2013) that the number of collectors reduced over the season, due to the decline in density of clams. To have a significant number of interviewees, 20 collectors were interviewed per month. Also, this number was chosen because it was not expected that all the harvesters would accept to be interviewed. This area was the same used for sampling for distribution patterns described in Chapter 5. Since one of the key questions was to find if the size distribution of the collectors catches was the same as the sampled one, interviews had to be made in this area. This was also an area with the highest number of collectors during the study, very few collectors were seen more than approximately 100 m away from this area.

Although invertebrate collectors are seen throughout the year in Maputo Bay (Scarlet, 2005), according to the findings of the arrangement meeting with CCP, collection of *E. paupercula* starts in September. From this month, it is possible to see several collectors on the sandy beaches. Collecting ends between March and April, with few collectors on the beaches. Collectors were usually concentrated in areas with high clams density, and all the interviewees were approached within the transect area.

The interviews were performed during the collection time, that is, during low spring tides. Each month, the number of people involved in invertebrate harvest was estimated by direct counting in the field, during five days of each low spring tide, resulting in ten survey days per month.

The interviews were conducted during two days in each month, in Changana, Rhonga and Portuguese, depending on the interviewee. One interview during February was carried out in N'dau, a local language from the centre of Mozambique, with an interpreter from the harvesters.

Each monthly spring tide, 20 different harvesters were randomly asked to become the interviewees during their activity. The site was primarily used for *E. paupercula* collection, but some harvesters, mainly those collecting for personal consumption, were also collecting some gastropods and other clam species, such as *Meretrix meretrix* in very low abundance.

Structured interviews with fixed response questions (see Appendix) were done with collectors during four months (October – November 2013; January – February 2014) in one spring tide. Counting of collectors was carried out during two spring tides in a month. During December, the interviews were not performed, due the presence of few harvesters caused by the festive season and by heavy rain days. This was advised by the CCP and later confirmed by personal observation. The objective was to avoid repetition of an interviewee, as only those harvesters that rely highly on clam collection for their livelihood would be on the clam grounds and probably would have been already interviewed.

For Question 7, which is about the collection zone on the shore, a schematic diagram showing shore divisions was shown to interviewees in order to explain to them where each zone was. The shore was divided into five parts namely, too upper, upper, middle, lower and too lower.

The price of a kilogram of fresh *E. paupercula*, with shell, in Question 14, is presented in United States Dollars (USD) instead of Mozambican Metical (MZN). The exchange rate used was USD 1 = MZN 30 (average rate during the study period, according to *Banco de Moçambique*).

Before starting the interview, a short explanation was given to each collector about the aim of the study. At the end of the session, each interviewee was asked to provide 30 random clams from their collection, which were taken to the laboratory for length measurements. During this process, some samples were bought from the interviewees, most of those collectors who were collecting to sell. In other cases, the harvesters offered the sample as this was an insignificant amount of a kilogram, and they were pleased to help. Each interview took approximately 12 minutes.

Biological field sampling

Every other month, sampling for length-frequency distribution (LFD) of clams was undertaken, as described in Chapter 2. Data for the period between October – November 2013 and January – February 2014 were used to compare the LFD from collectors samples and those from biological sampling.

Catch per unit effort (CPUE)

During clam harvesting at Costa do Sol, collectors usually leave the beach at different times and also through different places along the beach. Besides this collection pattern, during the study it was observed that collectors sell part of their catch while still collecting. They sold mainly to consumers recreating on the beach, but also to some clam resellers that go to the beaches to buy clams from them. Thus, the effort was calculated considering these factors and the number of individuals collecting between T1 and T6 area (see Chapter 2) and the daily amount declared in Question 11 by each interviewee. An average amount was taken per weight-class option given, and in the cases that an interviewee selected the final class amount (> 13 kg), he or she was asked to give the estimated amount, or the most common amount, he or she was used to collecting during the sampling month. Also, when giving the number of hours spent on the collection of that amount per day (Question 13) if the interviewee selected the last option (> 4 h), a follow-up question was made to the collector asking the approximate hours or an average she or he used to spend collecting each day in that month.

A preliminary test was made to assess the accuracy of catch weights as estimated by collectors, using five collectors per month, who stated that had not sold the clams yet. By weighing their total catch, it was found that the actual amount was indeed comparable to the estimate given by the interviewee. Out of the 20 tests over the study period, four were between 2-5 kg more and three were between 2-5 kg less than the estimated weight; 12 were 1-2 kg more/less than the estimated weight. One collector had removed 7 kg more than the estimated amount. CPUE was calculated by dividing the total catch weight reported by a collector by the time spent in hours. CPUE was expressed in kilograms collected per collector per hour (kg wet weight/col/h) for each sampling month for 20 collectors.

Data analysis

The monthly differences in the number of collectors were tested using a one-way ANOVA followed by Tukey post hoc test. Prior to test, data were tested for homogeneity of variances using Levene test.

Univariate analysis was used to analyse the effects of various socio-economic aspects of *E. paupercula* collection that were found more relevant to describe the collectors profile and collection activity. Also, univariate analysis was used to compare CPUE between months, and to compare LFD from collectors and sampled populations. The analysis was performed on SPSS 22.0 statistical package with a significance level at 0.05.

The extrapolation of catches was made based on the fact that the collector age had a significant effect on the numbers of days of collection of *E. paupercula* at Costa Do Sol Beach, and also on the fact that the number of collectors varied significantly during the sampling period. Thus, the mean numbers of collectors per day, proportion of collectors of each age class in that number, the average amount collected per day and total harvest days per month in each age class were used to estimate the total monthly amount (in kilograms) collected by each age class. This was done by multiplying the total number of days spent in collection per month by the mean amount (Kg) collected per day and then by the number of collectors in each age class.

RESULTS

The mean number of collectors in the study area decreased from October 2013 to February 2014, with the highest number of 133 collectors observed in October 2013 and the lowest, of 50 collectors, in February 2014. The differences in the mean numbers of collectors were statistically significant ($F = 10.67$; $df = 3$ $P = 0.000037$). The number of collectors did not follow any logical pattern within an individual set of spring tides. This means that a number of collectors did not decrease or increase with time within five days of sampling for both low spring tides (Figure 4.2).

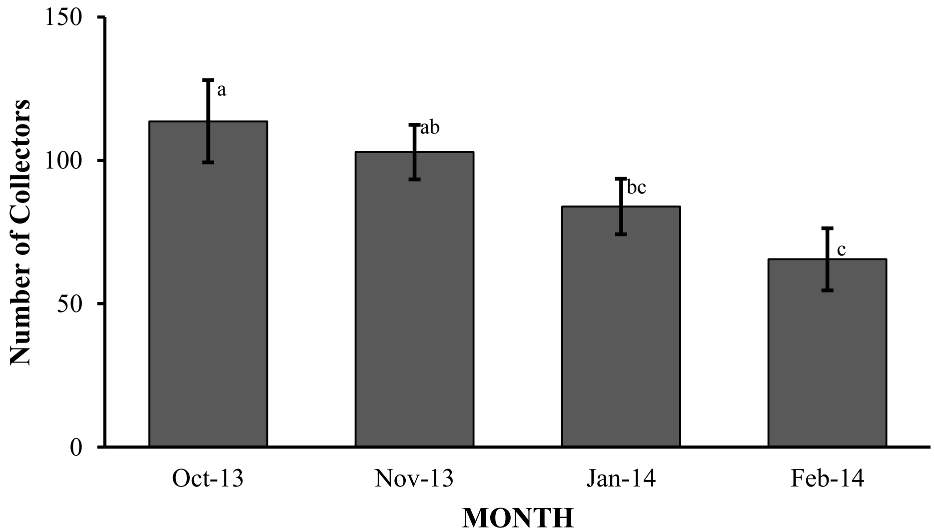


Figure 4.2: Monthly variations in the mean number (±SD) of *E. paupercula* collectors per day at Costa do Sol Beach. Different letters indicate significant differences between mean numbers of collectors among the months (P < 0.05).

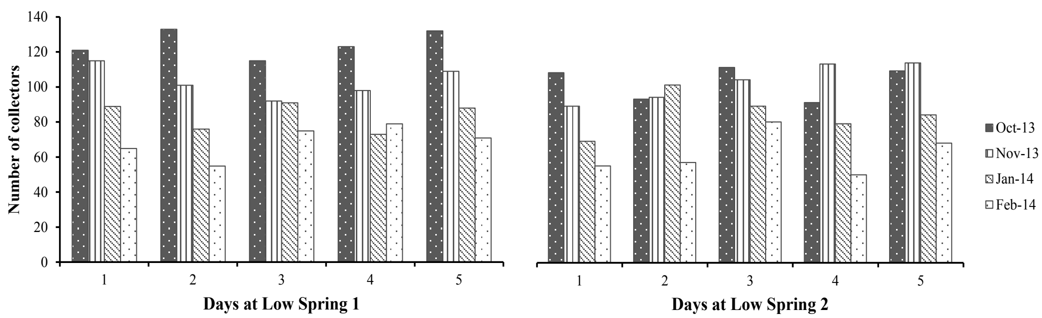


Figure 4.3: Daily variations in the mean number of *E. paupercula* collectors at Costa do Sol Beach. Spring 1 is the first spring tide of the month, and spring 2 is the second spring tide of the month

Demographic profiles of collectors

Of the total of 80 collectors interviewed at Costa do Sol Beach, 82.25% were women, and 17.75% were men. The age distribution among the interviewees is represented in Figure 4.4A, and included all the age classes defined in the questionnaire. Overall collectors comprised 15% of children, of which two were less than ten years old, and 85% of adults. The majority of collectors were 21-30 years old (30%), followed by those who were 31-40 (25%) and 11-20 (15%) respectively. The age-classes of oldest and youngest collectors represented the lowest percentages, with 3.75% and 2% respectively. The collectors 41-50 and 51-60 years old represented 10% and 13.75% of total interviewees respectively.

In terms of occupation, most women were housewives (48.75%), but 14% were saleswoman, a few of them were farmers (3.75%), and 12.5% were students (Figure 4.4 B). During this study, it was observed that the clam collection starts early in girls, at around 4-8 years of age; these prospective collectors often followed their mothers, or other family relatives, to learn how to collect.

Most interviewees had been collecting clams for more than five years (32.25%), but many of them (30%) were only beginning this activity, with less than six months experience in clam collection. Many of the collectors above 60 years old had been collecting invertebrates for more than 20 years.

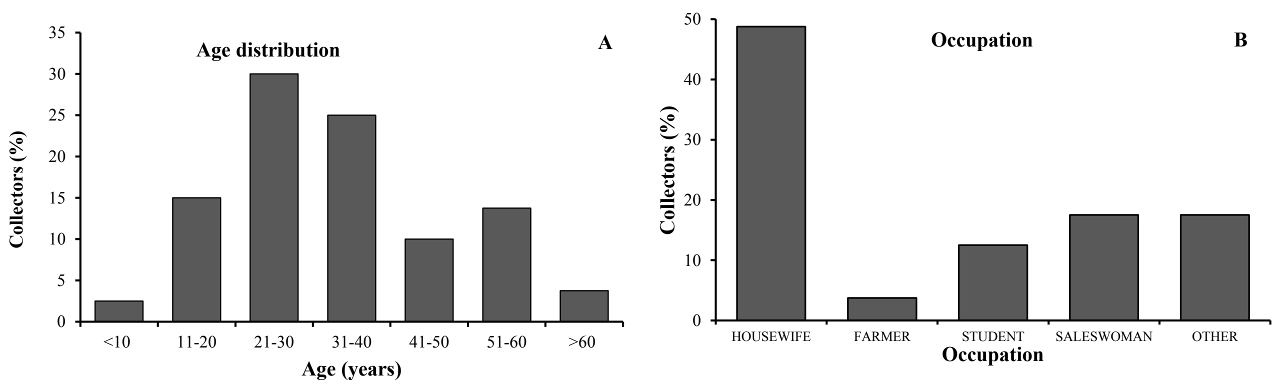


Figure 4.4: Age distribution (A) and occupation (B) of *E. paupercula* collectors.

Collection activities

All collectors were harvesting during daylight hours only, and most of them (58.75%) stayed on the beach collecting clams until the flooding tide starts (more than five hours). Only 4.25% collected for less than an hour. The highest number of collectors (38.75%) stated that they collect clams for 2-6 days per month. Those were followed by collectors collecting from 7-11 days (27.75%) and 12-14 days (21.25%) per month, respectively. Harvesters that were collecting only for a single day of the month, and also those who collected for more than 14 days per month, represented 6.25% each.

The *E. paupercula* collection is carried out almost exclusively in the sandy substrate (98.75% of collectors), and there is no clam collection in mangroves or rocky zones. One collector said that she used to collect in the seagrass beds. The activity is carried out on tidal flats mainly in the middle (48.75%) and upper (41.25%) shores and few collectors were going into lower (8.75%)

and too lower (1.25%) shores. No one was collecting in the too upper shore during the survey period.

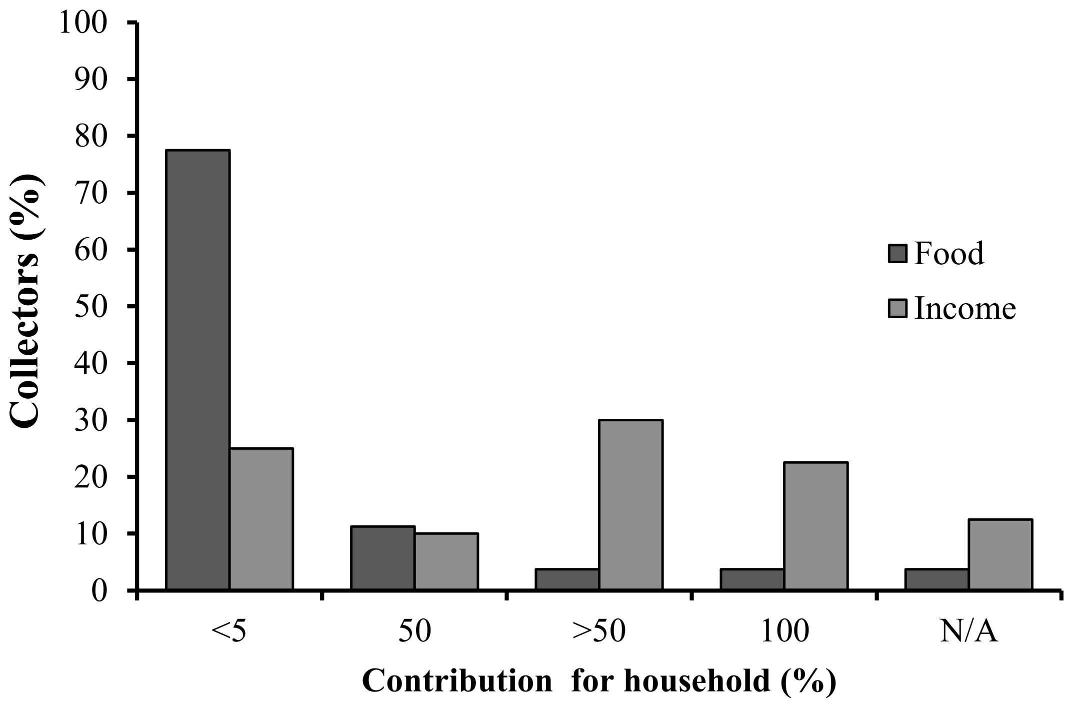
When asked about the group of invertebrates they were collecting, 98.75% of the collectors declared that clams were the main group they were looking for, while 1.25% were also looking for gastropods. Furthermore, if there are other species they were looking for besides clams, 61.25% of collectors stated that they only collect clams, but 30% also look for gastropods as a secondary group and a few (7.5%) also target other species, such as crabs and oysters.

Most of the collectors (86.25%) were using a tool adapted from a coal holder or a spoon for digging out clams and 13.25% were using direct hand grubbing to collect clams. No other techniques were used for clam collection. During the interviews, it was observed that many of those were using direct hand grubbing to collect, were collecting in shallow water channels, due to ease of removing the clams from the sediment. Figure 4.5 shows some collection and commercialization features of *E. paupercula* in Maputo.

Figure 4.5: *Eumarcia paupercula* collection underway at Costa do Sol (A and B), landings ready to sell to resellers (C) and commercial dealer selling to the final consumer at a fish market in Maputo City (D).

Importance of clam collection to the coastal communities

Most of the collectors (77.5%) stated that they did not have clams as their primary animal protein source, and only 3.75% affirmed that rely on clams as their main animal protein source. Also, 3.75% declared that they never eat the clams they collect (Figure 4.6). When it came to using the catch as an income source, 22.5% of the interviewees stated that they depend only on clam collection for their income and 12.5% declared that they never sell the clams they collect.



Figu
their collection only as an income source, and others only for personal consumption (N/A = not applicable).

Price and web market

Relevant information was taken from the preliminary meeting at the Costa do Sol CCP with clam collectors and CCP members, which was later confirmed during a conversation with collectors and is presented below.

The simple organization system existing in the area is that when the clams are not sold from the clam dealers, they are taken back to the beach to places locally known as "*viveiros*". "*Viveiros*" are small spots, located in small channels or tidal pools of the intertidal zone. Curiously, there are no visible marks like stones or poles bounding the spots, but the area is divided for common use for the clam traders. The "*viveiros*" are holding sites for live clams where everyone respects the space of each other and during the study I did not observe any discordance or stealing of clams, although some traders reported that this had happened previously. Due to traditional beliefs, no one goes to other person spot unless he or she wants to have bad experiences, particularly if the stock belongs to the oldest clam traders or an old woman, since there are beliefs that the oldest clam traders work with their ancestors to keep their places safe.

Clam dealers, often, are women that carry on their business on the beach, in a small fish market with less than 20 fish sellers. They buy clams from collectors, commonly at the lowest market price and in large amounts and resell mainly to people who sell it at the fish and central markets, but also to restaurants. They may eventually sell to final consumers. The clam dealer is, at most times, the one who determines the price of the product. There is also another group that only sells to the final consumer in markets, at home or door-to-door, and are considered clam resellers. The reseller, usually, gets the product from clam dealers, but can also get directly from collectors, and this happens particularly when both have already established a certain level of business.

For those harvesters selling to clam dealers, usually they do not get the money on the same day, and the market price is low (USD 0.22/kg). Nevertheless, during their communication they were satisfied because, as they ensured, they never had to throw their product away, as do some of those who sell directly to the final consumer. Those collectors who were selling to the final consumers, generally do not use the *viveiros* system and sell far from the beach along Maputo and Matola Cities markets, or in front of their houses. There are some collectors that take the clam meat out of the shell to freeze it, but most of them do not have freezing facilities, and the clams get spoiled if they are not sold fresh. Furthermore, as they used to leave the beach after collection at around 2 – 3 pm, they do not have enough time to sell the entire product, especially if the amount is substantial.

According to the questionnaire answers, the most preferred price for *E. paupercula* in the Maputo Bay neighbourhood, by collectors, is USD 0.44/kg with a total of 41.25% collectors selling at this price. The following price was USD 0.22 (30%), 1.25% sell below USD 0.22/kg and also another 1.25% sell above USD 0.88/kg, while 5% and 2.5% of collectors sell at USD

0.66/kg and USD 0.88/kg respectively (Figure 4.7). Most of the collectors (31.25%) would prefer to supply to the clam dealers and 27.5% of collectors choose to sell to the final consumers. Some collectors have no preferences to which they sell their collection (22.5%), whether to clams resellers or the final consumer.

The most common lowest price of USD 0.22/kg used by collectors can go up by up to seven times when the clams are sold to the final consumer, as noticed at the fish market. In the fish market, a kilogram of *E. paupercula* was sold at USD 1.50/kg and at the municipality market where the price is USD 1.40/kg. By contrast, the clam dealers sell at USD 0.45 – 0.60 a kilogram, depending on the size.

A possible web market or value chain for *Euamarcia paupercula* commercialization can be inferred from these findings, and the probable scenario is presented in Figure 4.8.

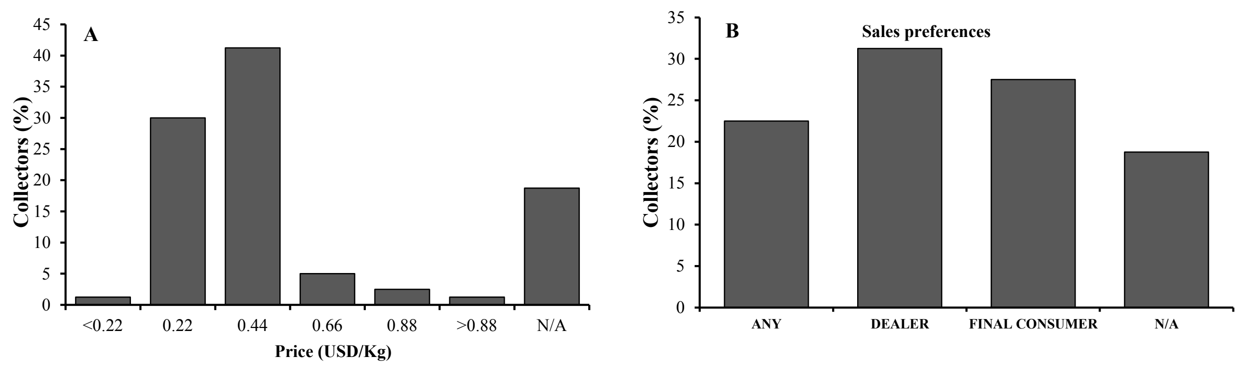


Figure 4.7: Variation in *Eumarcia paupercula* prices (A) and main groups to whom collectors were selling the catch in Maputo Bay neighbourhood (B) during the survey period. Other collectors indicated that were collecting only for consumption (N/A=not applicable).

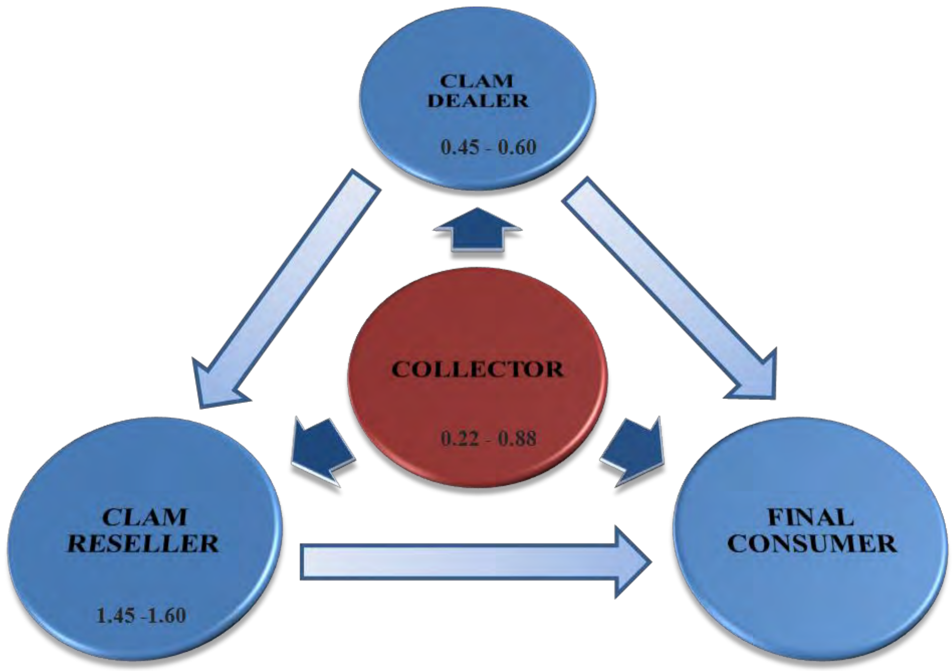


Figure 4.8: Schematic showing flow of *E. paupercula* between various participants in the clam market in Maputo. The numbers refer to price in USD per kilogram in each group.

Sustainability of clam collection

When collectors were asked if they thought that the amount they were collecting was harmful to the clam stock sustainability, 61.25% thought that was no harm and 38.75% that their collections caused little harm. No one said that the amount collected was damaging to the stock. When asked if the used tools used have negative impact on the environment, 68.75% thought it caused no harm, 2.5% little harm and no one thought that was very harmful.

When it came to changes of *E. paupercula* stocks during their collection experience, most of the collectors (46.25%) said that catches have been decreasing, but not very fast. The next largest group (21.25%) thought that catches have been increasing in the last few years, and 20% of collectors stated that the clam stock is the same over their experience time, while 8.75% were not able to answer.

The reasons mentioned for the perceived decrease or increase in the stocks were diverse. For those collectors who said that the stock was increasing, significant numbers affirmed that environmental conditions (47.61%) and “God will” (28.57%) were causing the increase. Twenty-four percent said that other factors, such as abandonment of the activity by some collectors, caused this increase. On the other side, for those who said that the *E. paupercula* stock was decreasing, the largest number gave the cause of changes in environmental conditions (42.42%) and increase in collectors (36.36%). Also, "God will" (18.18%) and overexploitation (3.03%) were given as causes of the decrease. Other reasons given for declining stocks were poverty and increase of tourists leading to high consumption of seafood, while reasons for perceived increases in stock included low market price, contributing to neglect of the activity by collectors and thus increase of clam stock.

All the interviewees voiced that they had never had a contact with any person from a governmental institution, namely Ministry of Fisheries or its institutes, an NGO, any research institution or group regarding clams collection. One of the oldest collectors, who was around 75 years old, affirmed that during the colonial period there were military sea officers controlling the size of clams and crabs in the landing zones. When the size was not the ideal, the collector had to take the animals back to the sea; however, documents regarding the referred size were not found.

When it came to possibilities of setting a daily bag limit, or establishing a closed season for *E. paupercula* collection, 58.75% and 56.25% of collectors would agree to these measures, respectively. On the other hand, 11.25% and 3.75% disagreed and strongly disagreed in setting a daily bag, respectively. Also, 16.25% and 7.50% disagreed and strongly disagreed, respectively, about establishing a closed season for a certain period of the year. Twenty percent of collectors were not sure about their position in setting a daily bag and 12.5% were also not sure about creating a closed season, but 6.25% and 7.50% strongly agreed on setting a daily bag and establishing a closed season for the beaked clam collection in Maputo Bay, respectively (Figure 4.9).

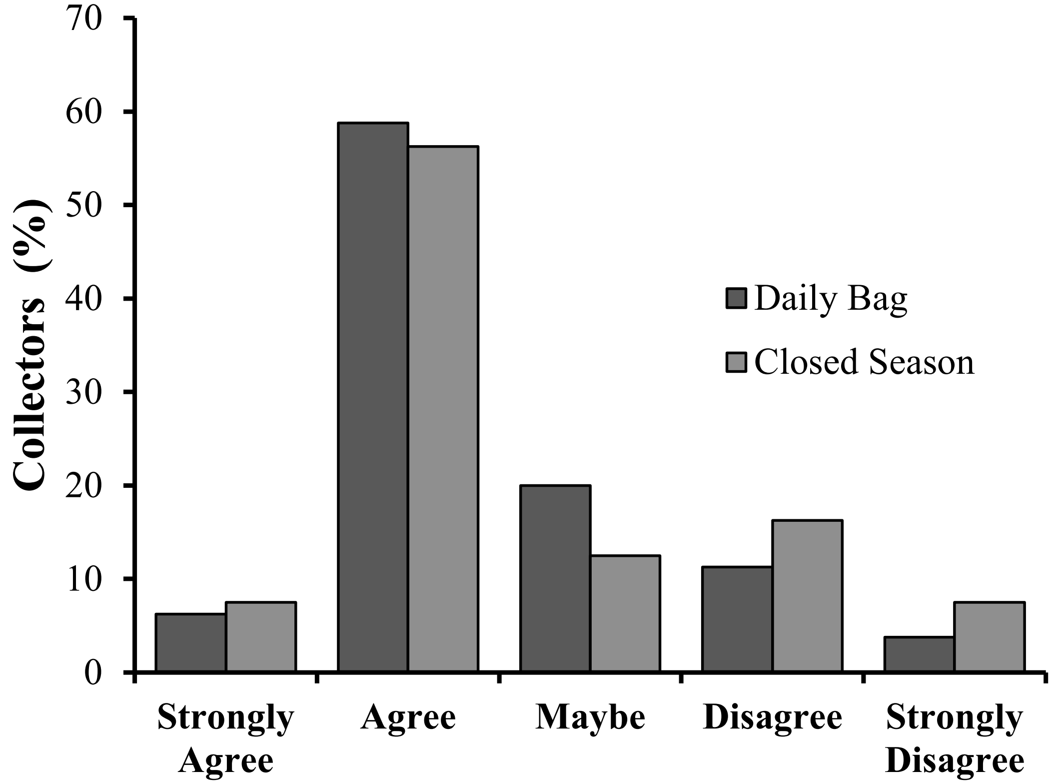


Figure 4.9: Different interviewee opinions about setting a daily bag or establishing a closed season for *E. paupercula* collection at Costa do Sol Beach.

Relationships between variables, that is, answers to questions formulated to collectors are presented in Table 4.1. Collectors with collecting experience between 13 – 24 months and those with experience of more than 60 months harvested more clams than those with less than six months of clam collection experience ($P < 0.05$). Collectors harvesting for a day and those who were harvesting from 2 – 6 days per month were collecting significantly lower amount per day than all the other groups. The remaining groups were harvesting similar amounts per day ($P > 0.05$). The days spent per month by collectors between 50-60 years in harvesting were significantly greater than those spent by 10-20 years old collectors ($P < 0.05$).

The experience in the clams collection (collection time) had significant effects on how collectors thought the clam stock had changes over their harvesting period. Answers of respondents with less than six months of the collection were different from those with 7-12 months collecting clams, as well as for those collectors with more than 60 months of collecting experience. These collectors with lowest experience in the activity (< 6 months) said that the stock was decreasing, while those collectors with 7-12 months thought that the clam stock was increasing. Collectors with more than 60 months of collection experience affirmed that the amount was the same over their experience time.

Table 4.1. One-way ANOVA relationships between some essential features of socio-economic aspects of *E. paupercula* collection at Costa do Sol Beach. F values and degrees of freedom (df) at P = 0.05.

Relationship		**P - value**	**F - value**	**df**
Gender	Collected amount	0.191	1.757	1
Age		0.096	1.915	6
Harvest days		0.010*	5.780	4
Occupation		0.447	0.967	5
Collection time		0.000016*	8.147	4
Occupation	Harvest days/month	0.070	2.269	4
Age		0.019**	2.486	6
Collection time	Opinion about set of daily bag limit	0.359	1.109	4
	Opinion about establishment of a closed season	0.407	1.012	4
	Idea about variation of clam Stock	0.002***	4.828	4

*Collection time and harvest days per month had a significant effect on the daily harvested amount;

** Age effect on the days harvested per month;

***Collection time had a significant effect on point of view about the variation of stocks with a time.

Landings during survey months

The total amount of the beaked clam collected at Costa do Sol Beach was extrapolated to 73 777 kg during the sampling period. The highest amount was collected in October 2013 and the lowest of in February 2014; collectors between 21-30 years hold collected the highest amount and children less than 10 years old collected the lowest amount (Table 4.2).

Table 4.2. Monthly amounts of *E. paupercula* collected at Costa do Sol Beach by collector age-class

Age (years)	**Months**				**Total (kg)**
	Oct-13	Nov-13	Jan-14	Feb-14	
<10	715.7	648.0	0.0	0.0	1363.7
11-20	2776.0	1256.8	2050.2	400.1	6483.1
21-30	10142.0	7142.5	1664.5	4548.2	23497.3
31-40	2126.4	4813.3	7067.0	2452.1	16458.7
41-50	1704.7	1543.5	3777.1	2948.7	9974.1
51-60	3021.8	4104.1	2231.7	3484.6	12842.2
>60	1272.3	1152.0	0.0	733.6	3158.0
Total	21758.9	20660.3	16790.6	14567.4	73777.1

Comparisons of monthly CPUE for *E. paupercula* in the study site showed no significant differences (F = 2.586; df = 3; P = 0.059) over the months although there were small declines in each successive month. The highest mean of CPUE was found in October (3.03 kg/col./hour), followed by that for November (2.47 kg/col./hour). In January and February were recorded the lowest CPUE of 2.32 kg/col./hour and 2.31 kg/col./hour, respectively (Figure 4.10).

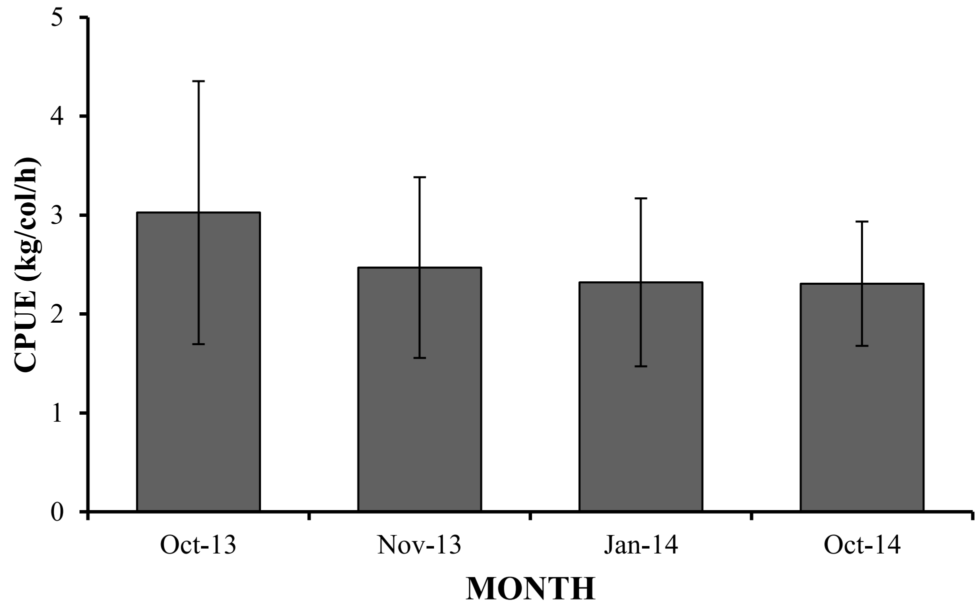


Figure 4.10: Monthly CPUE for *E. paupercula* collection at Costa do Sol Beach.

Relationship between collectors age and sizes of clams collected

Analysis of the effect of age of collector on the size of collected clams is presented in Figure 4.11. Collectors between 11-20 and between 21-30 years old were collecting smaller clams that those collectors less than ten years old, while collectors in the 31 - 40 age-class were collecting bigger clams than collectors less than 10 years old (P < 0.05). The mean length of clams harvested by collectors of 11-20 years old and 21-30 years old was significantly smaller than the mean length of all other age classes. Also, between both of these age-classes, the mean length did not vary significantly. Clams harvested by collectors in the 31-40 years old class were significantly bigger than those harvested by collectors less than ten years old and those in 51-60 years old class.

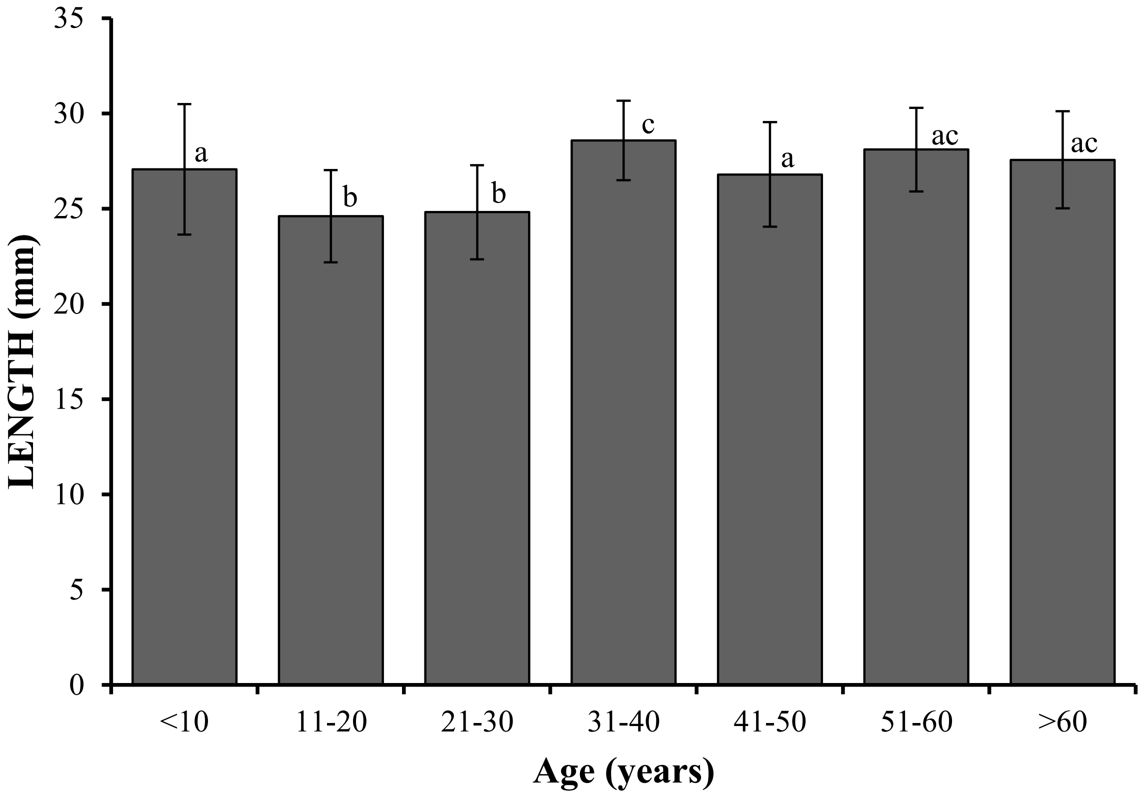


Figure 4.11: Effect of collector age on *E. paupercula* mean length (±SD) collected at Costa do Sol Beach. Different letters indicate statistically significant differences between age classes ($P < 0.05$).

Impact of *Eumarcia paupercula* *collection on the standing stocks*

Figure 4.12 shows the estimates of catches and fishable stock biomasses. The catches declined over the survey, including from October to November 2013 despite the increase on the fishable biomass between these months. The analysis of the percentages the clam catches comprised of the fishable stock biomass over the four-month sampling period showed a decline from 77% in October 2013 to 64% in January 2014. Then, the percentage of removed clams in January 2014 increased to 90%, which resulted in an increase in the average of clams removed over the fishing season to 75% per month.

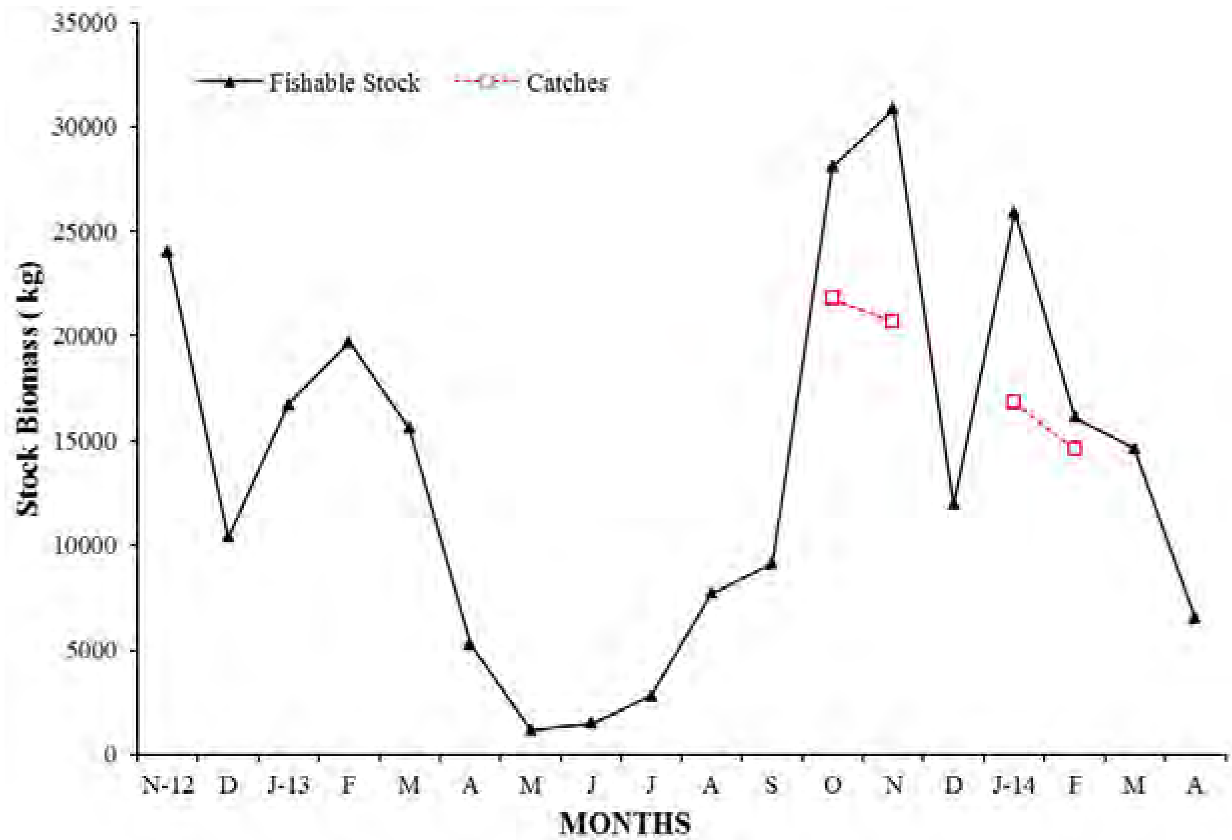


Figure 4.12: Estimates of *E. paupercula* monthly exploitations rates in relations to the fishable stock (≥ 22mm clams) biomass during October-November 2013 and January-February 2014.

DISCUSSION

Collectors profile and collection

Women constituted the majority of *Eumarcia paupercula* collectors. Similar to the present study, Nordlund *et al*. (2010) and Kyle *et al*. (1997) found that shellfish collection in Tanzania and South Africa, respectively is carried out mainly by women. Shellfish collection in Transkei, South Africa is also dominated by women and children (Hockey *et al*., 1988). Also, previously in Maputo Bay (de Boer & Longamane, 1996; de Boer & Prins, 2002; Vicente & Bandeira, 2014) and along the Inhambane Coast (Day, 1974; Filipe, 2006) in Mozambique, women constituted the predominant group of shellfish harvesters.

Although it has been discussed in several studies (Pomeroy *et al*., 2001; Kronen & Vunisea, 2007) why women dominate in shellfish collection, there is no overall explanation for this. Motivations range from the facility to reach the catches without financial investments to the lightness of the activity. The study area is located in an urban area, where alternative employment opportunities for men are available both in artisanal (shrimp and fish, using boats) and semi-industrial (shallow water shrimp) fisheries. Also, other occupations in the city, such as commercial activity, may constitute an easier alternative for men. Also, gender influences the impact of fishing income on overall household income, since, according to Kronen and Vunisea (2007), the income received via shellfish collection by a woman is more likely to be properly used for household keeping, whereas men use their income as they please.

The relatively high percentage of children (16%) would be expected to also lead to a higher percentage of students, because there are of school age, but this is not what the collectors occupation survey showed. This result suggests that there are children of school age that do not study, but are rather helping their mothers or relatives with clam collection, or they are heads of families. According to CNCS (2007), this might be caused by the Human Immunodeficiency Virus (HIV) that is increasing the numbers of orphans, but also by poverty, which is resulting in many children that are heads of family. The findings that a high percentage of collectors were housewives and the fact that 61.25% of collectors were only looking for clams suggest that the collection of *E. paupercula* is an important source of income or food for communities around Maputo Bay. Given the importance of clams as a source of income, it might appear surprising that many participants collected clams only for 2-6 days per month, that is, they use only one of the two spring tides per month. This last fact may be caused by the current density of the beaked clam at Costa do Sol, which is high, and hence collectors keep fulfilling their necessities with the catches made on these days, or they may not find market for additional product. The 6.25% of those who collect for more than 14 days shows that there is some collection during neap tides as well.

Although the pattern of variation in numbers of collectors was similar to that obtained by Scarlet (2005) in terms of decline in the numbers of collectors in the sampled months, the total numbers of collectors from the present study were higher than those found at Bairro dos Pescadores (4-5 km north from the present study area). The relative higher number of *E. paupercula* collectors found here, may be also related to fewer options of sources of animal protein, comparing with the rural areas. According to Hockey *et al*. (1988), in cases of a low occurrence of pastoral activities, shellfish collection may become an important activity for source of protein.

Usually, invertebrate collectors harvest where there is a high density of targeted species, where effort is reduced. It was found that almost 100% of collectors fish the sand substrate to collect the beaked clam. Also, the collection effort in the seagrasses may be greater than in sandy substrates. Only one collector affirmed also using seagrasses for clam collection. Probably this collector had targeted multi-species on her activity, as *E. paupercula* form low percentages of 0 – 10% of macroinvertebrates inhabiting seagrasses (Vicente & Bandeira, 2014).

The experience of clam collection, reflected by the time each collector had been in the activity, constituted an advantage in the amount collected and this is also related to the destination of the clams. In fact, 32.5% of the collectors are those with more than 60 months collecting clams and the preferred destination of their product is for sale (81.25%). This result shows that people collecting clams for such a long time, do so for income purposes, as noticed while the interviews were carried out. Some collectors were proud to say that they raised their children with income from clam collecting.

CPUE and collected amount

The decline in the number of collectors over the study period, and also a decrease in the amount of catches and CPUE are directly proportional to the amount of clams with catchable sizes (≥ 22 mm) in the sampled population, which decreased over the sampling period. The lower CPUE recorded in February 2014 (2.31 kg/h), when fewer collectors were found (65.5%), suggests that the collection of *E. paupercula* at Costa do Sol is having an impact on the stocks.

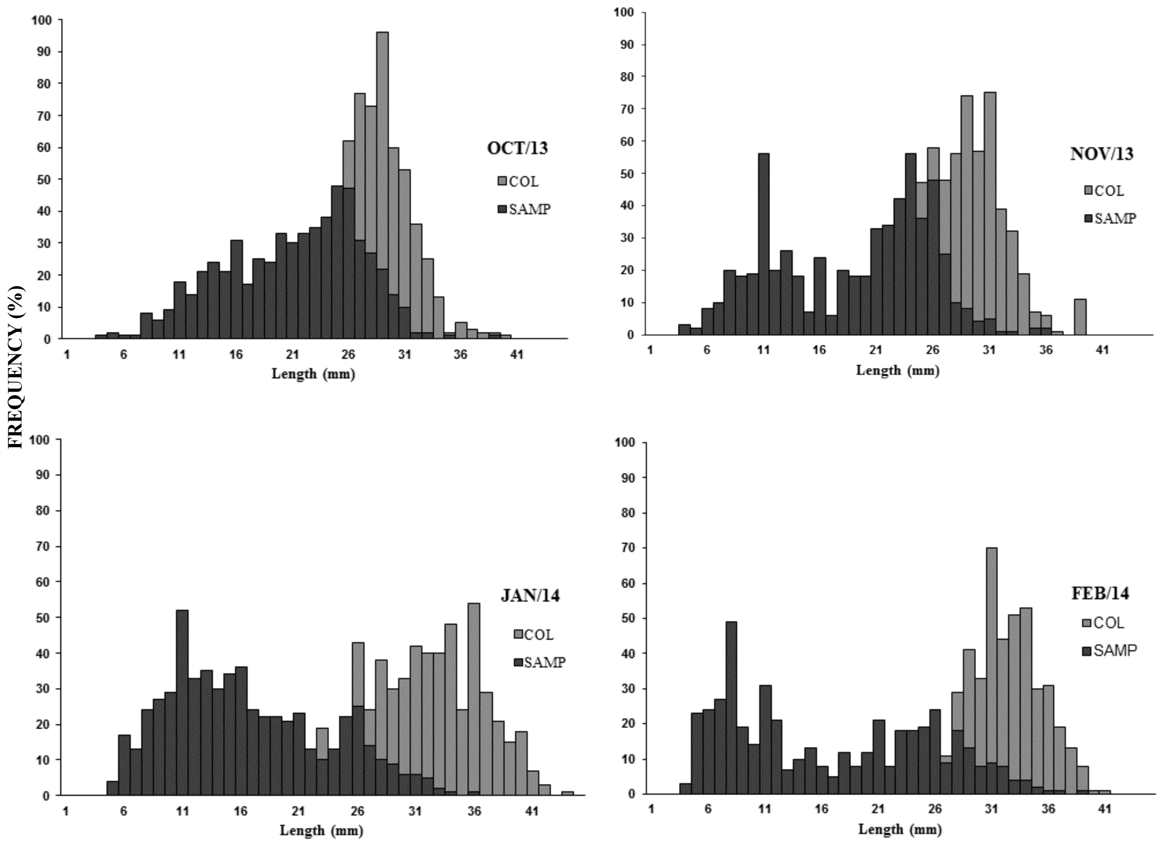
Variations in CPUE show different trends for some studied bivalves collection. In collection of *Tapes decussatus* in Azores, Portugal, CPUE increased with higher availability of the resource over time (Ferraz & Goncalves, 2001). On the contrary, Kyle *et al*. (1997) found that CPUE did not vary with time for collection of shellfish (mussels *Perna perna*, oysters *Striostrea margaritacea* and *Saccostrea cucullata*, and limpets *Patella* and *Fissurella* spp.), and red bait *Pyura stolonifera*, in the Maputaland marine reserve (South Africa), even with a decrease in density of the species. Number of collectors probably declined during their study period. According to King (2007), CPUE can also increase even with a decline in resource availability. When CPUE in a particular area declines, mobile harvesters usually move effort to other grounds, maintaining high CPUE levels, which may mask a real decline in stock abundance

(Kyle *et al*., 1997). This pattern is more likely to happen on Costa Do Sol, where clam grounds are available in other tidal flats close to the study area, although in lower densities during the study period.

The amount of clams collected is related to an area of clam grounds of approximately 0.14 km^2 (0.60 km x 0.24 km transect lines), harvested by an average of 113.6, 102.9, 83.9 and 65.5 collectors per day in October, November, January and February, respectively. Although the monthly pattern of variation in catches was similar to those found by Scarlet (2005), the amounts recorded in the present study are relatively higher. Her study took place mainly on seagrasses and communities of macroalgae (Balidy 2003; Scarlet 2005; Vicente & Bandeira 2014). The extension of the intertidal area on the beach is approximately 0.81 km^2.

Length-frequency distribution (LFD) of collectors samples and population

Analysis of LFD showed significant differences between the size distribution of clams from the catches of collectors and those from the field observations, with a bigger sizes of clam much more abundant for catches from the collectors. This shows a size preference by collectors, which is probably caused by two factors, namely the market size and destination of catches (sell or personal consumption). Those factors are directly affected by the market size and the sampling period. It was observed that the age of the collector had an effect on the size-distribution of catches, with the smallest sizes collected by collectors between 11-20 years. Figure 4.13 shows that the biological sampling failed to reveal a high density of the larger sizes. There are two possible reasons for this result, either sampling from collectors may come from other different grounds (although all affirmed to have collected within the study area) or sampling took place after a collection had already happened in the quadrat area. This shows that collectors are very selective, by collecting largest clams and probably searching for clams in a large area; however, continuous recruitment (Chapter 5) may also have affected this pattern.



Figu 'D from field observations (black) and collectors catches (grey) from October-November 2013 and January-February 2014. In all months, there were observed differences between LFD from collectors and LFD from field observation samples (P < 0.05).

Impact of <u>Eumarcia paupercula</u> collection on the standing stocks

The estimated catches declined over the four-month fishing period, when the exploited biomass increased and in there was a "collapse" during February 2014. The assessment of landings took place only during four months, as it was associated with the interviews, but probably if this time was extended, since the fishable biomass was undergoing a steep decline this would certainly result in a similarly large decline in catches. During February 2014 the estimated catches were approximately 90% of fishable biomass. This amount indicates a trend to a complete collection of the fishable population. The collection may be taking place in a bigger area than the sampled area, resulting in these high percentages, but the abandoning of collection after April shows that the fishable stock had been almost completely removed by this period, which supports the high removal rates of the fishable stock recorded. Annual landings estimates of *Cerastoderma edule* were larger than 100% of standing stock in some years, as a consequence of a biased estimation of the stock biomass (Dare *et al*., 2004). The data obtained in the present study can be considered as preliminary, as future or long-term exploitation rates estimation cannot be precisely obtained from this short survey period. The exploitation trend seems to have a large impact on the stocks of *E. paupercula*, which is probably tempered by the faster growth rates and reasonable recruitment rates in this species.

The mean percentages of removal of the fishable standing stock found in this study (74% per month) were greater than the 12% of monthly removal obtained by Scarlet (2005) in a sandflat area in Maputo Bay. The finding of Scarlet (2005) was related to a mix of *E. paupercula* and *M. meretrix* and was estimated at approximately 440 tons in an area of 19 km^2. Since in her study the mean clam densities were lower (maximum 12 clams/m^2), the ratio of area/biomass was greater for the present study, as the biomass is estimated at 25 500 kg (maximum 250 clams/m^2) in a clam bed of about 0.144 km^2. Also, the percentage of removal found by Scarlet (2005) was in relation to the total stock biomass, and not to the biomass of the clams suitable for collection, as calculated in the present study. Thus, that 12% would be greater if compared only to the larger targeted clams, which contribute more to the total stock biomass.

It should be noted that the following similarities in the amount of removed clams may not be accurate as the studies of Fahy and Gaffney (2001), Solidoro *et al*. (2003) Humphreys *et al*. (2007) and Kraeuter *et al*. (2008) used annual landing values while this study recorded monthly landings. Yet, the four-month period used to get the average of 74% fall in the period of high collection season, which is of 5-6 months per year, and the annual removal will be even greater than 74%. Unfortunately there is no statistics from the Fisheries Ministry on clam landings which would give a better base for comparisons with other studies.

Percentages of removed clams found in the present study are similar to the 75% removal found by Humphreys *et al*. (2007) for *Ruditapes philippinarum* in England. Also, these are similar to the 65% of removal in two years of the razor clam *Ensis siliqua* fishery in Ireland (Fahy & Gaffney, 2001). Nevertheless, the fishery for *R. philippinarum* and *Ensis siliqua* uses dredges, while the *E. paupercula* fishery uses artisanal methods (adapted metal or spoons), but the efficiency of removal seems to be good. According to Jennings and Kaiser (1998), in high-intensity fishing grounds (using trawls or dredges) the fishable population may be impacted in a short period of less than a year. Solidoro *et al*. (2003) simulated the effect of *Tapes philippinarum* collection and concluded that the population collapses with 100% of removal of the fishable stock (> 20mm), after the first spawning. An increase in the size at first collection of *T. philippinarum* to 30 mm and removal of 10% of the fishable stock was advised to maintain the population.

Kraeuter *et al*. (2008) simulated the effect of *Mercenaria mercenaria* fishing on the standing stocks and showed that the removal of 75% of the fishable clams can lead to a decline to less than 5% of the population size and biomass in 40 years, before the eminent collapse of the population in Great South Bay, USA. This scenario may occur in a shorter time for the *Eumarcia paupercula* population, as collectors move between the clam beds along the Bay once density declines in one bed and removed clams were over 70% of the fishable stock. Nevertheless, the models are based on local environmental conditions and population densities. Densities of *M. mercenaria* were of 4 clams/m^2, and the species has slow growth rate reaching about 80 mm in nine years (Harding, 2007).

Eumarcia paupercula management perspective

Nowadays, many management approaches have been discussed in commercial fisheries management. Some are traditional approaches and include restriction on periods of catches, imposition of total catch limits, where the objective, in both cases, is to control fishing mortality (Grafton *et al*., 2006). Others include the ecosystem approach to fisheries (EAF) and incentive approach with multiple stakeholders and collective action (Pitcher, 2001; Makino *et al*., 2009; Pomeroy *et al*., 2010; Parker, 2013).

According to the answers on whether there is any coordination of clam collection with other people or institutions, it would be nearly guaranteed that there is not any platform to impose clams regulation in the area. This is because 100% of the interviewees have not heard about regulation of clam collecting in Maputo Bay and never had any contact with other stakeholders that would be involved in clam management. Nevertheless, there is a CCP at Costa do Sol, Ministry of Fisheries or NGOs working with nature conservation in Maputo; thus, one of the most important factors to start a management plan may be the motivation of the collectors. This motivation was revealed by their thoughts in setting a daily bag limit or establishing a closed season for *E. paupercula* (58.75% and 56.25% respectively, say they would adhere to these management measures). Although in the present study high number of collectors would agree in setting a daily bag limit and in establishing a closed collection season, which can directly reduce the fishing effort, the success of this measure was not welcome in some islands of Southeast Asia (Salayo *et al*., 2008). Similarly, the daily bag limit was a good measure for clam collection at Cortes Island, a small island of British Columbia in Canada, probably due to the small population of around 1000 inhabitants in 2009.

The collectors who strongly disagreed with setting a daily bag limit argued that this would negatively influence their household income, and this would be an unfair decision from the government. Still, when the decision comes with some alternatives for their livelihood, they would follow easily, but some of those who agreed, commented that they could do nothing because it would be a decision from the government, and they must obey this.

Part of the success of any *E. paupercula* stock management in Maputo Bay would come from establishing a closed season. Collectors who agreed with a closed season establishment explained that there is a period of approximately five months that because of the lack of an acceptable size (larger than 20 mm) they do not collect clams. The period takes place from April to August. This may make them accept easily to stay away from clam collection during a certain period of the year. This low collection season was also confirmed during the almost two-year study period, when number of collectors reduced drastically. Nevertheless, this measure would not have an impact if the closed season takes place during the five-month period that there are no fishable clams in the stock. The closed season should be set to 7-8 months, beginning on March-April, as this would not only allow the adult population to spawned, but also the market price would be greater for the collectors, because they will start collection only when most clams are over 25 mm.

The few collectors found during the low collection season used to spend whole low spring tide to find 20% of the amount they usually get during the high collection season. This is in line with findings of Nordlund *et al*. (2010) in Zanzibar, who found that fishing effort increased during low collection season. In Maputo, during low collection season, harvesters dedicate their time for fish trading and small business, such as selling of fruit and vegetables in local markets. These remarks also corroborate with the findings of high frequency of smaller clams during the period of April to August (Chapter 5).

Hilborn (2007), on his hypothesis that managing fishing is also managing people, shows an overview that this sector is multidisciplinary and the key solution for this paradigm is to know how people involved in fisheries behave or mostly, how the fishermen think to reach the desired sustainability, profitability, and ecosystem balance. Other studies have agreed with this theory (Degnbol & Jarre, 2004; Grafton *et al*., 2006; Makino *et al*., 2009; Crawford *et al*., 2010), including the co-management approach suggested by the Ministry of Fisheries (de Sá, 2011). Furthermore, considering the study area as an ecosystem that provide humans with services such as fisheries, it would be seen as a socio-ecological system, where according to Hughes *et al*. (2005), another key element is the recognition of the linkages between the ecosystem services and people. A study for this recognition should be carried out, in the highest level, by the Ministry of Fisheries.

The use of MPAs is also an important tool, not only to protect endangered species, but to enhance resource sustainability (Roberts *et al*., 2001). For example, on Inhaca Island (an MPA), considerable number of invertebrates collectors showed a local ecological knowledge of the importance of ecosystems services (Vicente & Bandeira, 2014). In contrast, at Bairro Pescadores, an urban area in the vicinity of Costa do Sol, the collectors have little idea of the importance of the ecosystem or substrates that host marine invertebrates. Besides MPAs, there are the no-take zones that consist of identifying small areas that, in certain periods, shellfish will be not taken. The use of an ecological approach for bivalves management was introduced with some success for cockle collection by establishment of no-take zones in Tanzania (Crawford *et al*., 2010), but according to Grafton *et al*. (2006), the use of no-take zone is only positive in an ecologist point of view.

Although *E. paupercula* collection has an important value chain and contribution to the communities income, there is no available amount of its profits and yields that could be used to define the activity as commercial with high profits. What is suggested here is to consider the activity as commercial harvesting for subsistence.

There is no regulation for clam collection in Maputo Bay; however, as concluded in other seas by Salayo *et al*. (2008), all the stakeholders have their part to play in this complex field of study by complementing their actions. The stakeholders to be involved in Maputo Bay include the collectors, international and national organizations working in natural resources management and fisheries (e.g. FAO, WWF, IUCN), plus academic and research institutions. In addition, the ministerial institutions (Fisheries, Environmental affairs, Women and Social Action), private sector and investors and local level organizations (CCPs and Municipality government) would also play their role in *E. paupercula* management.

CONCLUSION

The present study showed that the collection of *E. paupercula* is carried out mainly by women with a wide age span, mainly housewives, but also children that start the collection assisting their mothers or relatives. Although the primary purpose of the catches is for sale for collectors household income, there is some collection for personal consumption. A web market for the beaked clam is composed of collectors, clam dealers, resellers, and the final consumer. The price of a kilogram throughout this web market increases from collectors to resellers.

The clams collected by harvesters had higher length-frequencies than those sampled in the experimental population-structure study. This indicates that collectors have a strong preference for larger sizes of collected clams, which is caused mainly by the market size. It was estimated that during four-month period of the collection season, approximately 74 tons of *E. paupercula* were removed from Costa do Sol. From this amount and decline of CPUE and fishable stock over the season (Chapter 5), it does seem that there is a marked depletion of the *E. paupercula* stock of interest to the fishery at Costa do Sol. The density of fishable stock could decrease to less than 5 clams/m^2 at the end of high collection season, compared to about 100 clams/m^2 at the beginning (Chapter 5). The exploitation rate of the beaked clam at Costa do Sol was estimated to be 75% of the fishable standing stock per month during the fishing season. A longer survey period on landings, that includes also the low fishing season and all months of high fishing season, may be necessary for a better estimation of the % of removal over the year.

An establishment of a closed season would likely be more effective than a setting of daily bag limit in case of Maputo Bay, as most of the collectors are used to leaving the harvest activity for a certain period during the year, usually during the winter. Conversely, the setting of minimum size limits does not seem to have an immediate relevance at Costa do Sol beach population. While it is obvious that there is no national or local directive for *E. paupercula* harvest, different stakeholders were identified during this study, and a setting of a community-based co-management plan for clams harvest would be adequate with everyone playing their part towards the success of the plan.

Appendix: Questionnaire on clams exploitation at Costa do Sol Beach

Date: ___ /___/201

1. Gender?

M	F

2. Age (Years)

<10	10-20	21-30	31-40	41-50	51-60	>60

3. Occupation

Housewife	Farmer	Student	Saleswomen	Other

4. What are the main invertebrates do you collect?

Clams	Oysters	Snails	Mussels	Sea cucumbers	Sea urchins	Other

5. What other invertebrates do you collect?

Clams	Oysters	Snails	Mussels	Sea cucumbers	Sea urchins	Other

6. For how long have you been collecting invertebrates (months)?

<6	7-12	13-24	25-36	37-48	49-60	>60

7. In which zones or shore levels do you, usually, collect?

Too Lower	Lower	Middle	Upper	Too upper

8. At which period of the day do you collect?

Day	Night

9. In which substrate do you collect clams?

Seagrasses	Sand	Mangroves	Rocky shore	Other

10. How do you collect?

Hand grubbing	Hand grub with tool	Sieve	Other

11. What amount do you usually collect per day, during this month (kilograms)?

<1	1-4	5-7	8-10	11-13	>13

12. How many days of the month do you collect clams?

1	2-6	7-11	12-14	>14

13. How many hours does it take to collect?

<1	1	2	3	4	>4

14. How much do you sell a kilogram (Metical)?

<5	5	10	15	20	>20	Not applicable

15. To whom are you selling?

Any	Dealer	Final consumer	Not applicable

16. What is the contribution of this collection for your monthly food?

<50%	50%	>50%	100%	Not applicable

17. What is the contribution of this collection for your monthly income?

<50%	50%	>50%	100%	Not applicable

18. What do you think about the amount collected for the sustainability of the resource?

Very good	Good	reasonable	Bad	Very bad

19. What do you think about the method of collection for the sustainability of the resource?

Too harm	Little harm	No harm

20. Would you agree about setting a daily bag limit?

Strong agree	Agree	Maybe	Disagree	Strong disagree

21. Would you agree about establishing a closed season for collection?

Strong agree	Agree	Maybe	Disagree	Strong disagree

22. How is the clam stock variation over your collection time?

Increasing Fast	Increasing	Same	Decreasing	Decreasing Fast

23. Why do think so?

Increase of collectors	Overexploitation	Environmental conditions	“God will”	other

24. Do you coordinate your collection with any institution, such as Ministry of Fisheries, any nature conservation NGO or CCP (Community Fisheries Council) regarding resource regulation or conservation?

Strong coordination	Good coordination	Reasonable coordination	Weak coordination	NO coordination

Chapter 5: Reproductive biology of *Eumarcia paupercula* from Maputo Bay

INTRODUCTION

While some bivalve species are hermaphroditic (Loosanoff, 1937; Sastry, 1979; Heller, 1993) and brood their eggs internally, the vast majority are dioecious broadcast spawners. This means that fertilization occurs externally and larval survival and recruitment are highly dependent on the external environment for their success (Walne, 1979; Newell et al., 1982; Griffiths & Griffiths, 1987; Thompson & Nichols, 1988; Honkoop et al., 1999; Ren et al., 2003; Calderon-Aguilera et al., 2014; Ruesink, Raay, et al., 2014). Sex in bivalves cannot be distinguished by their external morphology, rather, this is differentiated by microscopic observations, or by colour after opening the shells. In addition, bivalve populations tend to have equal sex ratios (Ansell, Lander, *et al*., 1964; Sastry, 1979; Spencer, 2002).

The stages and frequency of gonadal maturation in clams vary among species and are dependent on environmental conditions (Loosanoff, 1937; Ropes, 1968b; Seed, 1976; Peterson, 1983; Beninger & Lucas, 1984; Laruelle *et al*., 1994; Urrutia *et al*., 1999). Various studies on reproductive patterns have shown that clams mature at different length sizes (Paul & Feder, 1973; Hill, 1990; Ponurovsky & Yakolev, 1992; Herrmann, *et al*., 2009), and some exhibit long spawning periods over the year (Durve, 1964; Beninger & Lucas, 1984; Narasimham, 1988; McLachlan *et al*., 1996; Tirado & Salas, 1999). This is particularly evident in venerids, in which spawning typically peaks one to three times a year (Ansell *et al*., 1964; Ropes & Stickney, 1965; Laruelle *et al*., 1994; Jagadis & Rajagopal, 2007). Another example is *Anomalocardia brasiliana,* which has a continuous reproductive cycle, with gametes maturing throughout the year (Barreira & Araujo, 2005; Luz & Boehs, 2011).

For the majority of venerids, spawning occurs simultaneously in all individuals within a population – otherwise known as synchronous spawning (Ansell *et al*., 1964; Rodrıguez-Moscoso & Arnaiz, 1998; Morriconi *et al*., 2002; Gribben *et al*., 2004; Luz & Boehs, 2011). Asynchronous spawning is known to occur in only a few species (Tirado & Salas, 1999; Suja & Muthiah, 2007; Kandeel *et al*., 2013). Depending on the prevailing environmental factors, both synchronous and asynchronous reproductive stages can occur within the same reproductive season in a particular species (i.e. from development to spawning).

Depending on the species and location, males and females first mature at similar or distinctive length sizes. This is a result of endogenous and exogenous factors, as Sastry (1979) considered reproductive cycle as a genetically controlled process in response to the environment. Morriconi *et al*. (2002) found that males and females of the venerid *Eurhomalea exalbida* have their first maturation at different lengths. On the other hand, Jayabal and Kalyani (1987) and Jagadis and Rajagopal (2007) recorded first maturation in the same lengths in males and females of *Meretrix meretrix* and *Gafrarium tumidum*, respectively.

Temperature is often considered the primary environmental factor regulating spawning in bivalves (Nelson, 1928; Loosanoff, 1953; Honkoop *et al*., 1999; Spencer, 2002), where increases in temperature cause an onset of the event. Good quality and high concentrations of food availability are also important for spawning (Ansell, 1972; Thompson & Nichols, 1988; Kang *et al*., 2009; Newell *et al*., 2009; Baek *et al*., 2014). Most of the above-cited temperature related studies were confined to temperate waters; in tropical ecosystems, salinity is another factor that affects regulation of clam spawning (Narasimham *et al*., 1988). Durve (1964) found that high salinity had an adverse effect on the spawning of *Meretrix casta*; however, Jayabal and Kalyani (1987) found that low salinities prevented the spawning of *M. meretrix*.

Latitudinal changes also influence clam reproductive patterns, sometimes within the same species, specifically with respect to timing of gametogenesis and the number of spawning events (Laruelle *et al*., 1994; Drummond *et al*., 2006; Herrmann *et al*., 2009). Suja and Muthiah (2007) recorded different spawning seasons for *Marcia opima* in two geographically distinct areas in India, namely Ashtamudi and Tuticorin. Spawning of the Indian south west coast population occurred between March and May, while in the south-east, spawning occurred throughout May and July. In *Ruditapes philippinarum* on the French coast, the number of spawning events and the speed of maturation from the Morbihan Gulf were greater than those from the Bay of Brest (Laruelle *et al*., 1994). This suggests that local environmental factors that result from latitudinal changes play an important role in timing and duration of reproductive events such as spawning.

Giese (1959) presents a detailed comparison of differences in reproductive patterns of bivalves from polar, temperate and tropical regions. While there are some exceptions, the review generally showed that most temperate species have one to two short spawning events per year. On the other hand, tropical species undergo continuous spawning throughout the year, with various peaks, while polar species have one spawning event during periods of temperature increase.

Although there has been a relatively recent review of invertebrate reproduction patterns from Southern African inshore and estuarine areas (Hodgson, 2010), the review did not include any members of the Veneridae, despite the fact that about 32 such species occur in the region (Kilburn & Rippey, 1982). There is little known about venerids in the Southern Africa region; however, there have been numerous studies detailing the reproduction and changes in body conditions of Veneridae clams across the world, especially for *Ruditapes* (*Tapes*) spp. (Shafee & Daoudi, 1991; Laruelle *et al*., 1994; Rodrıguez-Moscoso & Arnaiz, 1998; Urrutia *et al*., 1999; Drummond *et al*., 2006), *Meretrix meretrix* (Jayabal & Kalyani, 1987) and *Mercenaria mercenaria* (Weiss *et al*., 2002; Marroquin-Mora & Rice, 2008).

The beaked clam *Eumarcia paupercula* is one of the most important commercial clam species in Maputo Bay, Mozambique, (Scarlet, 2005; Rosendo, 2008; Vicente & Bandeira, 2014); thus, in order to ensure the sustainability of this fishery, a comprehensive management plan needs to be implemented by fisheries stakeholders. Effective regulation of this fishery requires understanding of the annual reproductive cycle of *E. paupercula*, particularly its spawning time. This is because most of the management measures applied in fisheries are related to the capacity of a species to reproduce and recruit to cope with its removal by fishing. As such, this study represents the first attempt to describe the reproductive activity of clams inhabiting Maputo Bay, and of *E. paupercula* in particular.

This chapter aims to characterize the annual reproductive cycles of *Eumarcia paupercula* in Maputo Bay. In addition, it will determine the most important environmental factors affecting these reproductive cycles. To this end, seasonal fluctuations in the condition index (CI) of the beaked clam population were monitored and analysis of fresh gonad smears used to confirm that these changes were in fact due to gonadal conditions.

METHODS

Environmental variables

Sampling methods of environmental parameters, namely temperature, salinity, and rainfall were described in Chapter 2.

Description of reproductive cycles

Most studies on clam reproduction have applied histological techniques, macroscopic gonad observation (Ropes & Stickney, 1965; Ropes, 1968; Jayabal & Kalyani, 1987; Laruelle *et al*., 1994; Morriconi *et al*., 2002; Laudien *et al*., 2003; Gribben *et al*., 2004), or monitored fluctuations in the total body weight of standard-sized individuals (Ansell *et al*., 1964; Marsden & Pilkington, 1995; Delgado & Camacho, 2005) as an indicator of body condition and, by extension, reproductive condition. In this study, to describe the reproductive patterns of *E. paupercula*, a combination of body condition fluctuations and macroscopic observations were used. Sixty clams measuring ≥ 20 mm in length were collected each month between November 2012 and April 2014 during low spring tides by hand grabbing with a spoon-like tool. Samples were collected within a transect area (Chapter 2), usually in the middle shore zone. These were then taken to the Laboratory of Aquatic and Coastal Biology at Eduardo Mondlane University in a cooler box for analysis; the facility is roughly 8km away from the collection site. Thirty of these clams were used for the gonad smear observations and macroscopic gonad analysis. The remaining 30 were used for measuring the CI. Laboratory analyses were usually done on the same day for both methods. Occasionally, there was a one- or two-day delay between body condition analyses and fresh gonad smear observations; this happened roughly 15% of the time.

<u>Condition index</u>

For the determination of a monthly body condition index, individual flesh dry weights (FDW) and shell dry weights (SDW) were recorded each month, with the CI calculated according to Mann and Glomb (1978) (Equation 5.1). On reaching the laboratory, clams were rinsed in cold water, and then dried on absorbent paper. Individual lengths were recorded to the nearest 0.1 mm using a Vernier calliper. Thereafter, adductor muscles were cut and the flesh (consisting of soft tissues) was separated from the shell, placed in an aluminium dish, dried in an oven at 60 ºC for

48 hrs and then weighed. The aluminium dish weight was then deducted from the total weight to obtain FDW. In addition, the CI was determined in relation to length. Dry meat and shell were then weighed to the nearest 0.01 g, using an OEM Wincom® electronic analytical balance, model FA2004B.

$$CI = \frac{FDW}{SDW} \times 1000 \quad (5.1)$$

The CI of a standard 30 mm individual was then calculated from a monthly length/condition regression, which was fitted to the power function (Equation 5.2); the monthly equations are presented in Table 5.1. This method has been widely applied for mussels (Bayne & Worrall, 1980; van Erkom Schurink & Griffiths, 1993) as well as clams (Ansell *et al*., 1964; Urrutia *et al*., 1999).

$$CI = aL^b \quad (5.2)$$

Table 5.1: Monthly regression equations of length-weight relationships. CI = condition index, L = length (mm), a = intercept and b = slope.

Month-Year	**Regression Equation** ($CI = aL^b$)
N – 12	$y = 645.2x^{-1.5}$
D – 12	$y = 409.9x^{-1.1}$
J – 13	$y = 416.5x^{-1.5}$
F – 13	$y = 164.5x^{-0.4}$
M – 13	$y = 133.4x$
A – 13	$y = 328.6x^{-1.1}$
M – 13	$y = 220.3x^{-0.7}$
J – 13	$y = 207.8x^{-0.7}$
J – 14	$y = 134.2x^{-0.3}$
A – 13	$y = 91.15x^{-0.01}$
S – 13	$y = 321.1x^{-1.0}$
O – 13	$y = 428.3x^{-1.3}$
N – 13	$y = 184.5x^{-0.5}$
D – 13	$y = 155.7x^{-0.3}$
J – 14	$y = 149.3x^{-0.3}$
F – 14	$y = 226.8x^{-0.7}$
M – 14	$y = 354.2x^{-1.1}$
A – 14	$y = 199.3x^{-0.7}$

Gonad smear observations

Fresh gonad smears were analysed using a Leitz® Laborlux K (WZ 25 IC 280) binocular microscope to determine the sex. Clams were opened at the hinge by cutting adductor muscles. Reproductive materials were then taken from the gonads using a lancet and sex determined by performing a smear of the tissue on a microscopic slide and observing this at 400 X magnification. The presence of oocytes and spermatozoa in smears were considered indicators of female and male individuals, respectively. Male and female gonadal conditions were then visually assessed to estimate gamete stage. As little research has been done on *Eumarcia paupercula,* these methods are based on those used in other venerids, such as *Ruditapes decussatus* (Shafee & Daoudi, 1991), *Tapes philippinarum* (Kang *et al*., 2007; Matozzo & Marin, 2010) and *Marcia opima* (Suja & Muthiah, 2007).

In the studies by Shafee and Daoudi (1991) and Suja and Muthiah (2007), the authors also used histological analyses and showed comparable results on reproductive cycles to those obtained using CI. The use of macroscopic analysis to describe the reproductive cycle of clams, as used here, has also been used for other clam families, such as Solenidae and Donacidae (Darriba *et al*., 2004; Remacha-Trivino & Anadon, 2006; Deval, 2009), and pearl oysters (O'Connor & Lawler, 2004). Sexes of *E. paupercula* were not distinguished during description of macroscopic gonad maturation stages and gonad stages were described as follows:

Stage 1 – Inactive (INA): the gonad is barely discernible macroscopically and tissue is limited to a thin translucent and colourless layer. In most individuals, sex is indeterminate at this stage.

Stage 2 – Maturing (MAT): whitish gonad clearly observed. The space occupied by the gonad is small and the digestive diverticula (dark green to black) can be seen once a clam is opened.

Stage 3 – Ripe (RIP): gonad is cream coloured, has reached the maximum size and becomes turgid, covering a major part of the digestive diverticula and diffusing to the foot area. The release of reproductive material is rapid when the gonad is pricked with a needle.

Stage 4 – Partial Release (PR): gonad is cream coloured and has a loose consistency.

Stage 5 – Total Release (TR): colour of gonad becomes light cream to white shade. Sex remains identifiable when cutting the gonad tissue. At this stage, all mature gametes are released.

Female and male gonads have the same morphology and coloration for the same stages described above. Changes in colour intensity that were recorded related to changes in stage rather than being between sexes, as noted in other venerids. The above scale was developed based on a combination of scales developed in previous studies for venerids (Shafee & Daoudi, 1991; Baron, 1992; Jagadis & Rajagopal, 2007a).

After observing the gonadal stages, the relationship between fresh weight fluctuation and gamete release was investigated to understand whether weight changes are indeed related to the loss of reproductive mass. Thus, by using macroscopic gonad observation and CI fluctuation, combined with environmental data, it was possible to determine the seasonality of spawning peaks.

Statistical and numerical analyses of data

To determine if the sex ratio differed from 1:1, a Chi-square test (χ^2) was conducted on a monthly basis. Pearson correlation was used to compare relationships between environmental variables and CI. The null hypothesis tested was that the increase in temperature and rainfall will positively affect the condition of *Eumarcia paupercula*, and low salinity negatively affects the CI. Length and CI were log transformed for regression analysis. One-way analysis of variance (ANOVA) followed by a post hoc Tukey test, was used to test for significant differences in CIs between the 18 study months. Before ANOVA, normality and heteroscedasticity of the data were tested. Numerical analyses were done in Excel 2010 and statistical analyses in SPSS V. 22. Statistical significance was considered at $P < 0.05$ for both correlation and ANOVA tests.

RESULTS

Sex Ratio

No sexual differences in external appearance were observed macroscopically, as both male and female gonads showed the same whitish to cream coloration and morphology. The mean sex ratio (percentages) of males to females in the 18 monthly samples was 52: 48, and 12 individuals were of indeterminate sex (n = 540). The male:female ratio did not differ significantly from 1:1 ($x^2 = 0.60$, $df = 1$ $P = 0.44$).

Condition Index (CI)

Seasonal changes in the CI of a standard individual (30 mm shell length) are presented in Figure 5.1., with these ranging between 69.70 and 132.14. Condition increased rapidly from December 2012 and stabilised five months later, in May 2013. During this time, a peaked was noted in December 2012 (132.14) before a decline in January 2013. Immediate and significant drops in condition ($F = 35.75$, $P < 0.05$) were observed during January, March, August and December 2013, as well as April 2014, suggesting possible spawning peaks of *Eumarcia paupercula* in these months.

The monthly distributions of gonadal stages are illustrated in Figure 5.2. Ripe *Eumarcia paupercula* individuals were present during all sampling months. Only during four months (November and December 2012, and August and November 2013) did they occur in more than 50% of individuals in the sample. These periods preceded the months in which the highest percentages of individuals releasing gametes were recorded (individuals in PR and TR phases). Similarly, individuals in maturing stages (MAT) were present throughout the sampling period, comprising over 50% of the sample during the end of summer (February and March 2013) and the greater part of winter (April – July 2013). Over the course of the 18 sampling months, inactive or sex indeterminate individuals (INA) were only recorded in eight months. During these months, they always represented less than 10% of the sample, never reaching more than 6.7%, which they previously did in June 2013 and January 2014.

The spawning events were assumed to occur when there was a sudden decline in CI, of which the greatest declines were in January and March 2013, and April 2014. A smaller magnitude decline in CI was recorded in August 2013. Considering changes in both condition (Figure 5.1) and maturity stages (Figure 5.2), *E. paupercula* can be described as a continuous spawner. The most noteworthy spawning period occurs during the summer (December – March), and others in early winter (April - May). The minor peak in August was illustrated by a drop in CI combined with small percentage (20.0%) of individuals being PR and TR (Figure 5.2). The most significant spawning event was considered to be the period when most clams were in PR and TR stages. With the exception of November 2012 and July 2013, totally spent (TR) individuals were always present.

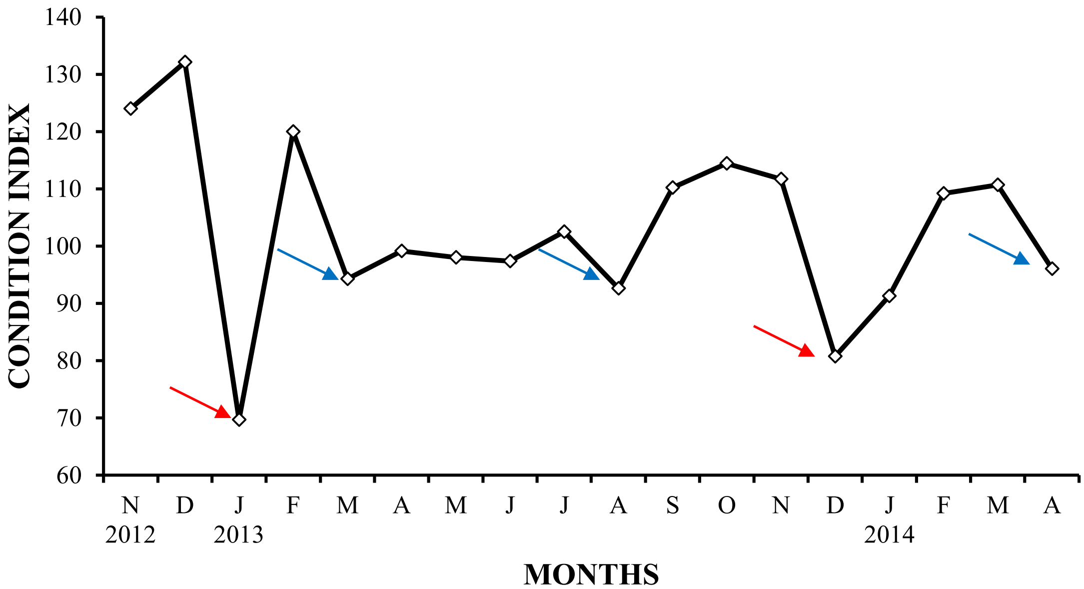


Figure 5.1: Monthly changes in condition (n = 30) of a standard sized individual (30 mm shell length) from November 2012 to April 2014. Red and blue arrows indicate major and minor spawning speaks, respectively.

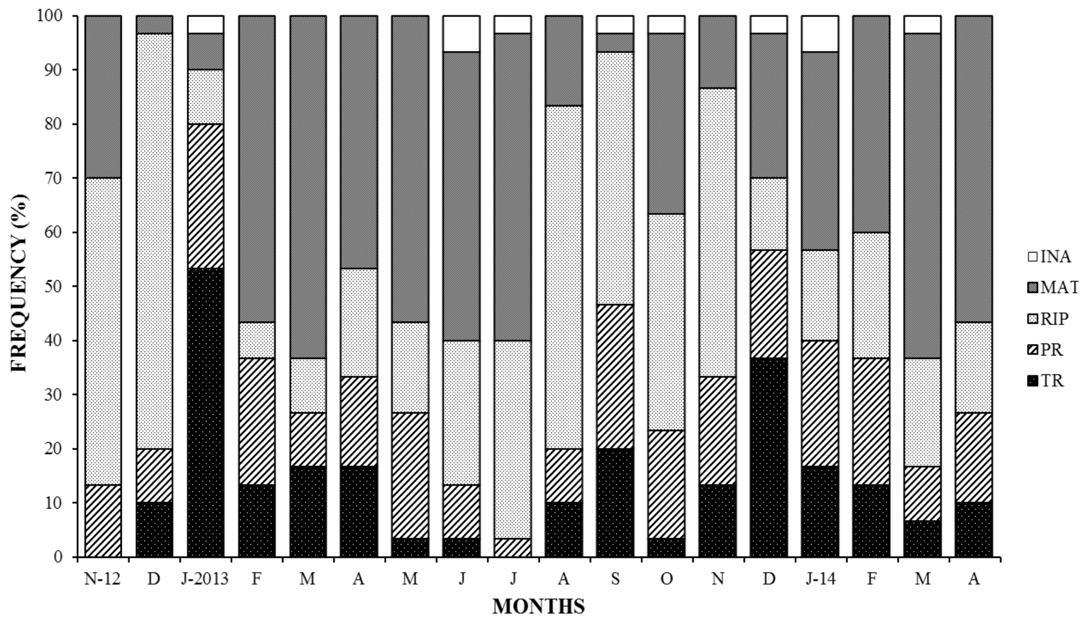


Figure 5.2: Percentages of mature *E. paupercula* at Maputo Bay showing various stages of gonadal maturation as derived from macroscopic observations of gonads. Abbreviations: INA, indeterminate; MAT, Maturing; RIP, Ripe; PR, Partial Release and TR, Total Release stages.

Correlation of the reproductive cycle with environmental parameters

The correlation between environmental factors and reproductive cycles was assessed using changes in CI as an indicator of spawning events. Figure 5.3 shows the variation of environmental parameters and CI throughout the study period. Pearson correlation analysis indicated non-significant correlations between CI of the standard individual of 30 mm and all of the environmental drivers analysed, namely temperature ($r = 0.022$, $P > 0.05$), rainfall ($r = -269$, $P > 0.05$), and salinity ($r = 0.036$, $P > 0.05$).

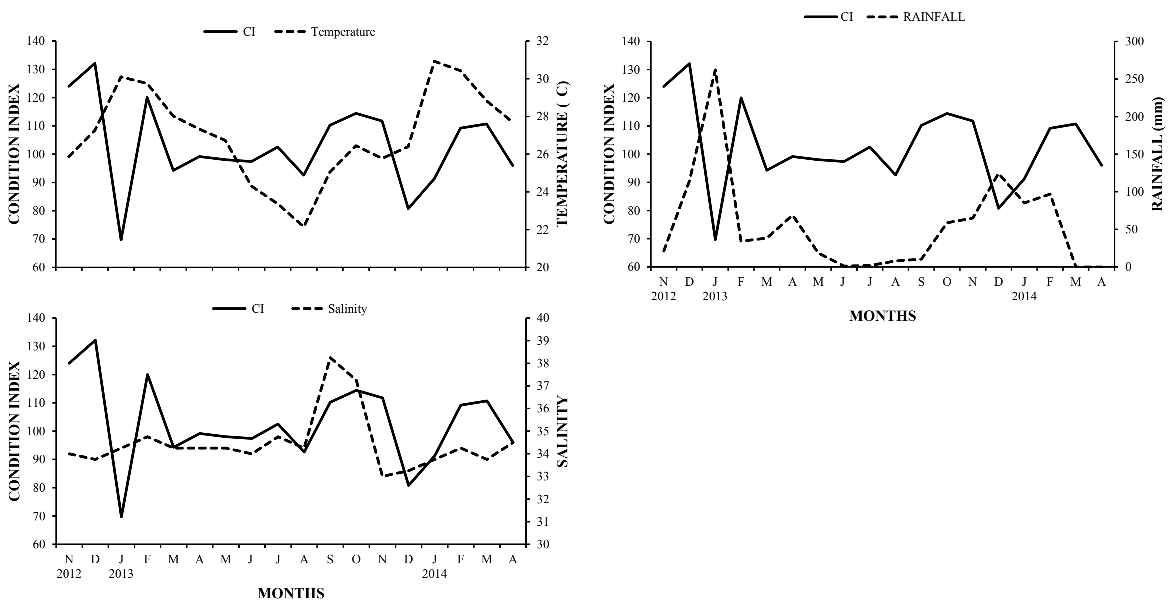


Figure 5.3: Monthly changes in CI (continuous line) of standard *Eumarcia paupercula* individual (30.00 mm shell length) and temperature, rainfall and salinity (dashed lines), over the period November 2012 to April 2014.

DISCUSSION

While literature discussing the beaked clam *Eumarcia paupercula* is limited, particularly with regards to the management of its stocks and understanding its reproductive cycle, in Maputo Bay this species is being heavily exploited for food; thus it is even more important to start considering the implementation of management practices based on the much-needed collection of the above information.

Sex ratio

There are no published accounts of sex ratios of *Eumarcia paupercula* generally; however, the sex ratio of this species in Maputo Bay is similar to those noted for the majority of Veneridae populations, this being 1:1. For example, Morriconi *et al*. (2002) recorded a sex ratio of 1:1 for *Eurhomalea exalbida* in Ushuaia Bay, Argentina. On the other hand, Drummond *et al*. (2006) revealed male:female ratios of 1:1.15 and 1:1 for two Manila clam populations in Ireland. Table 3.1 displays sex ratios for different species, with the overall trend being 1:1. When sex ratio analysis was performed on a monthly basis during this study, changes in the dominance of a particular sex were noted sporadically. For example, in November 2012 and July and November 2013, males were in dominance (63, 67 and 60%, respectively). In contrast, during October 2013, females were in dominance at a recorded rate of 60%. For the remaining sampling months ratios were found to be equal. While not being able to find the causes for the variations in dominance from the data collected in this study, unequal sex ration in not uncommon for protandrous bivalves. This have been recorded for *Mercenaria mercenaria* in Georgia, USA (Walker & Heffernan, 1995) and for *Arctica islandica* in Nova Scotia, Canada (Rowel *et al*., 1990), and is likely the result of age, since it is common in yearling individuals.

Description of the reproductive cycle of Eumarcia paupercula

Gonad maturation of *Eumarcia paupercula* occurred throughout the year and individuals with mature gonads (MAT) mostly composed over 40% of individuals each month. Ripe individuals, which were also present throughout the year, composed over 50% of individuals only for two/three months prior to spawning peaks. This may be an indication of a short period of maturation of *E. paupercula*. The combination of a drop in CI and macroscopic observations showed that spawning of *Eumarcia paupercula* occurred during summer in January and

December 2013. On the other hand, condition index alone showed a spawning peak in August 2013, while macroscopic gonad observations showed high percentages of partially (PR) and totally (TR) spawned individuals in September 2013. The small drop in CI during March 2013 was not accompanied by an increase in a higher percentage (close or over 50% combined) of PR or TR individuals.

During all the months in which samples were collected for this study, PR individuals were found. Since *E. paupercula* undergoes partial spawning – meaning that individuals only partially release mature gametes – it was considered that a spawning peak occurred when the sum of individuals in TR and PR stages was ≥ 50%. In addition, indeterminate individuals may be added to the group of animals considered spawned, as a complete spawning would have recently occurred. Consequently, September 2013 is also considered a spawning peak, and this is supported by the drop in condition of *E. paupercula* in the previous month, August 2013. Although TR and PR individuals were present throughout the sampling period, their highest percentage occurrences were in summer. Similarly, *Marcia opima* in Kayamkum, India, reaches its spawning peak during summer (Maqbool, 1993).

Peak spawning during summer months likely explains the accumulation of reserves during the winter, since these are transformed into reproductive material prior to gamete releases in the summer. In fact, some species spawn during winter, most likely due to an interaction of exogenous and endogenous factors. For example, the core pattern of *Donax serra* in South Africa is that it undergoes a partial release of gametes over an extended period, including in winter (de Villiers, 1975). Furthermore, most tropical and subtropical clams follow a similar spawning pattern (Table 5.2).

Table 5.2 also shows reproductive patterns for various clam species within a wide latitudinal range. While the latitudinal limits in the tropics are clearly defined, here, subtropics are defined as occurring between ±23°40’ and ±30°00’ latitude (Corlett, 2013). When venerids from tropical and subtropical areas are analysed, species found furthest from the tropics spawn two or three times a year for prolonged periods (Jayabal & Kalyani, 1987; Maqbool, 1993; Barreira & Araujo, 2005; Suja & Muthiah, 2007; Luz & Boehs, 2011), while others exhibit year-round spawning (Durve, 1964; Jagadis & Rajagopal, 2007a). Thus, the spawning pattern of *E. paupercula* in Maputo Bay does not differ from that of other clam species inhabiting tropical or subtropical systems. The limited number of species from tropical-subtropical areas referred to in this table reflects a deficiency of studies on venerids from these regions.

Studies on venerids from temperate areas are abundant. Generally, these populations are found to have short spawning periods (Loosanoff, 1937; Ansell & Lander, 1967; Bourne, 1982; Beninger, 1984; Beninger & Lucas, 1984; Ponurovsky & Yakolev, 1992; Laruelle *et al*., 1994; Marsden & Pilkington, 1995; Morriconi *et al*., 2007; Hamasaki *et al*., 2014). An exception, however, is a study by Drummond *et al*. (2006), which recorded a long spawning period for *Ruditapes philippinarum* in Ireland. Laruelle *et al*. (1994) also recorded multiple spawning events in an extended spawning period for *R. philippinarum*; the authors termed this spawning pattern as atypical for the species. Nevertheless, Laruelle *et al*. (1994) also found a short spawning for *R. decussatus* on the intertidal flats of Brittany. Strangely, two spawning peaks were recorded for the Antarctic clam *Laternula elliptica* (Kang *et al*., 2009), as the species inhabit cold areas.

Jagadis and Rajagopal (2007) suggest that most members of the Veneridae are continuous or prolonged spawners, exhibiting one to three spawning peaks a year. A similar result was obtained for *E. paupercula* in this study; however, unlike in this study – where spawning peaked during the wet season (summer), as evidenced by the decline in the FW and the presence of the highest percentages of TR and PR individuals during this period – Jagadis and Rajagopal (2007) show that none of the Veneridae clams spawned during the monsoon period. It should be noted though that the monsoon period in India is characterized by the lowest winter temperatures of the year, and this likely had an effect on the species.

Contrary to tropical and subtropical species, most temperate Veneridae species have a single, short spawning period, generally coinciding with peak annual temperatures (Nelson, 1928; Loosanoff, 1937) and phytoplankton blooms (Newell *et al*., 2009; Yan *et al*., 2010). Generally, for temperate bivalves, spawning patterns are based on the accumulation of nutrient reserves during the long period, when temperatures are low, followed by spawning, as temperatures begin to increase (Gabbott & Bayne, 1973). This pattern has also been described for other taxa, such as the Mactridae *Spisula solidissima* (Ropes, 1968b) and the Pharidae *Ensis arcuatus* (Darriba *et al*., 2004).

All in all, the reproductive season of *E. paupercula* in Maputo Bay is characterized by a long spawning season with three peaks. This is the general reproductive pattern for clams inhabiting tropical-subtropical regions – year-round spawning with more than one peak. In contrast, with some exceptions though, temperate species have a definite spawning season. Local environmental factors seem to be the major regulators of the reproductive cycles of clams, and this is discussed in the following section. The simultaneous use of both macroscopic gonad observations and assessments of fluctuations in CI gave equivalent results similar to the reproduction patterns of clams in other studies (Durve, 1964; Drummond *et al*., 2006; Gab-Alla *et al*., 2007; Jagadis & Rajagopal, 2007a; Suja & Muthiah, 2007; Marroquin-Mora & Rice, 2008; Kandeel *et al*., 2013).

Table 5.2. Some reproductive characteristics of venerids globally. The latitude of each study site is presented in the column "Location". Species have been named according to references, and synonyms were treated separately. Cells with a dash (-) denote an absence of data from the source

Species	Location	Temperature (°C)	Sex Ratio (M:F)	Spawning events: Peaks	Reference
Anomalocardia brasiliana	Brazil	-	1:1.2	Two: Feb – Apr; Jul - Oct	Barreira and Araujo, 2005
A. brasiliana	Brazil	20 – 35	1:1.2	Two: Jan – May; Sep - Nov	Luz and Boehs, 2011
Cyclina sinensis	China (37°84' N)	2.0 – 30.0	-	One: Aug	Yan *et al*., 2010
Eumarcia paupercula	**Mozambique (25 5 4' S)**	**22.2 – 30.9**	**1:1**	**Year-round: Apr-May; Sep; Nov – Feb**	**This study**
Gafrarium tumidum	India (08°35' - 09°25' N)	-	1:1.3	Year-round: Nov; Apr	Jagadis and Rajagopal, 2007
Marcia opima	India (09°02' N)	27.0 – 30.0	1:1	Two: Nov – Jan; May - Jun	Maqbool, 1993
M. opima	India (08°45' N)	26.0 – 32.3	1:1	Two: May – Jul; Sep – Dec	Suja and Muthiah, 2007
M. opima	India (09°28' N)	24.0 – 34.0	1:0.7	Two: Mar – May; Sep – Dec	Suja and Muthiah, 2007
Mercenaria mercenaria	USA (41°11' N)	5.0 – 19.0	-	One: Jul – Sep	Loosanoff, 1937
M. mercenaria	USA (41°67' N)	17.5 – 25.5	-	One: June	Rice and Goncalo, 1994
M. mercenaria	USA (38°.77' - 39°06' N)	-	-	One: Jul - Sep	Marroquin-Mora and Rice, 2008
M. mercenaria	USA (41°67' N)	2.0 – 28	-	One: May – Oct	Keck *et al*., 1975
M. mercenaria	USA (40°55' - 41°01' N)	-	-	One: May Sep	Doall *et al*., 2008
Meretrix casta	India (09°28' N)	27.0 – 33.0	Variable[1]	Year-round: break in few months	Durve, 1964
M. meretrix	India (11°17' N)	-	1:1	One long: Feb – Sep	Jayabal and Kalyani, 1987
Ruditapes decussatus	UK (47°40' N)	-	-	One: Jul – Oct	Laruelle *et al*., 1994
R. decussatus	UK (47°51' N)	-	-	One: Spring	Beninger and Lucas, 1984
R. decussatus	France (43°23' N)	-	-	Two: Jun – Aug	Borsa and Millet, 1992
R. philippinarum	Ireland (54°33' N)	7.1 – 18.5	1:1.2	One: Jun – Sep	Drummond *et al*., 2006
R. philippinarum	UK (47°30' - 48.20 N)	-	-	Three: May, Jul-Aug	Laruelle *et al*., 1994
R. philippinarum	UK (47°52' N)	-	-	One: Spring	Beninger and Lucas, 1984
R. philippinarum	France (44°68' N)	4 – 28	-	One: Sep-Oct	Robert *et al*., 1993
R. philippinarum	Spain (42°68'N)	-11 – 22	-	Two: Apr – Aug; Aug – Nov[2]	Rodrıguez-Moscoso *et al*., 1992
Tapes philippinarum	Russia (42°30' - 43°53' N)	-1.0 – 25.0	1:1	One: Jul – Aug	Ponurovsky and Yakolev, 1992
T. philippinarum	Canada (50°10' - 55°00'N)	≥ 15	-	One: Jul – Sep	Bourne, 1982
Tawera gayi	Argentina (54°50'S)	3.4 – 8.2	1:1.1	One: Oct	Morriconi *et al*., 2007
Venerupis japonica	USA (47°63' N)	13 - 26	-	One: Jul – Oct	Holland and Chew, 1974
Venux nux	Spain (36°56' N)	12.0 – 16.0	1:1	Year-round: Jun – Jul	Tirado *et al*., 2011
V. nux	Spain (36°34' N)	13.0 – 21.8	1:1	Year-round: Apr – May	Tirado *et al*., 2011

[1]Parasite infection affected sex ratio analysis over sampling

Reproductive cycle in relation to environmental parameters

The Pearson correlation analysis indicated a non-significant correlation between CI and salinity ($P > 0.05$). The effect of salinity on reproduction of bivalves is not well understood; however, it has been shown that when clams are exposed to low saline conditions (13-18), their feeding rate is lowered and inactivity may occur (Robert *et al*., 1993; Marsden & Pilkington, 1995). The ability of intertidal bivalves to acclimate with changes in a salinity content may mean that saline conditions are not entirely an environmental stressor, especially if exposure to particular saline conditions is limited in duration (McLeod & Wing, 2008).

For most of the study period, salinity was >32 and remained stable at levels considered normal for marine salinity. Despite high salinity levels being recorded (38.3 and 37.3 during September and October 2013, respectively), the effect on the release of gametes by *Eumarcia paupercula* was limited. This finding may be comparable to reproductive patterns in other bivalves; Sphigel (1989) found that high salinity (up to 41) did not affect gametogenesis of the European flat oyster *Ostrea edulis*. Long exposure to low salinity suppressed spawning of *Meretrix meretrix,* which ceased when salinity was lower than 10 (Narasimham *et al*., 1988). Some studies on venerids showed opposite results, and seem to be dependent on the habitat or species under consideration. For instance, higher salinity levels (≥13) negatively affected the reproduction of the estuarine *Austrovenus stutchburyi* (Marsden, 2004); and unlike in the present study, Barreira and Araujo (2005) considered low salinity to be a major factor in regulating the spawning of *Anomalocardia brasiliana* in Ceara, Brazil. Similar to the present study, Loosanoff (1953) found no effect of salinity in spawning activity of *Cyprina islandica*.

The correlation between CI and water temperature was found to be non-significant ($P > 0.05$) by the present study. There seemed to be a drop in condition following a rise of temperature, as recorded in January 2013, or when high temperatures were recorded, as in December 2013; this also occurred when there was a decline in temperature (August and September 2013). In tropical tidal flat environments, the effect of temperature on the spawning of clams seems to be non-linear. For instance, Clemente and Ingole (2011) found that both rises and declines of temperatures can stimulate spawning of the mud clam *Polymesoda erosa*. Nevertheless, this pattern have also been recorded in temperate sandy beaches by Ropes (1968) in *Mercenaria mercenaria*. In June 2013, the PR and TR stages accounted only for 13.3% of the individuals and INA for 6.67%, which means that 20% could not lead to a drop of CI. An absence of relationship between temperature and reproductive cycles was also recorded for the year-round spawning venerid *Marcia opima* by Suja and Muthiah (2007). Generally, in tropical ecosystems, where fluctuations of temperature are minimal, bivalves have continuous reproductive cycles

A possible environmental condition during August 2013, combined with a decline of temperatures in that month, could have prompted winter spawning, as reflected by the decline of CI and 20 – 40% of PR and TR individuals. Under stressful environmental conditions, fluctuations of energy reserves can cause declines in the condition of clams (Baek *et al*., 2014). The peak condition in length-standardized individuals happens when the accumulation of proteins and carbohydrates is high, while the opposite happens during spawning (Kang *et al*., 2007). In addition, energy reserves available for reproduction in clams are related to seasonal fluctuations of temperature (Mann, 1979), although temperature fluctuations seemed not to affect spawning activity in this study.

Rainfall is often indirectly considered a driving factor of reproductive cycles in clams inhabiting tidal flats, because of its ability to reduce salinity (Riascos V, 2006; Nakamura *et al*., 2010; Baek *et al*., 2014). The total monthly rainfall recorded for each month in the present study was considered insufficient to actually lower levels of salinity, which could have, for example, caused spawning to cease. In addition, total monthly rainfall was used for consideration as sampling days may have been before or after actual rainfall events, meaning that the short-term effects of rainfall would not have been detected.

Another useful method of confirming the reproductive patterns of *E. paupercula* found in this study would be to assess the seasonal biochemical composition of soft tissues. For example, it has been shown that high quantities of lipids tend to be present during maturation, whereas their amounts tend to lower in the spawning period (Ansell, 1972; Maqbool, 1993). Moreover, changes in the biochemical composition in venerids are often highly influenced by the gonadal cycle, rather than the availability of food within the environment (Jayabal & Kalyani, 1986).

The reproductive process in bivalves starts from germ differentiation to larval development, and between these stages there is gonadal development and maturation, followed by spawning. By using changes in the condition of *E. paupercula* and observing fresh gonad smears, it was possible to determine the spawning periods of the beaked clam in Maputo Bay. Nevertheless, it remains necessary to understand how intrinsic and extrinsic factors affect each stage of spawning and the reproductive processes in between. Newell *et al*. (1982) showed that the influence of environmental factors on the reproduction of *Mytilus edulis* may be complex, and a single factor analysis may lead to the conclusion of biased assumptions. The same study illustrated this when assessing the interaction between food availability and reproductive cycle in the same mussel. The availability of food depends on prevailing environmental conditions, including light and water temperature, both of which affect changes in the growth rates of phytoplankton.

CONCLUSION

Macroscopic gonad observations and changes in the body condition revealed that *E. paupercula* in Maputo Bay is a year-round breeder with three spawning peaks. Major spawning periods occurred during summer, with others also recorded in winter. Between these two periods, another event took place at the beginning of summer. The beaked clam in Maputo Bay undergoes a partial release of gametes. The presence of few individuals in indeterminate stages during sampling may be interpreted as a very short resting period before recuperation. Nevertheless, further research with other methods, such as histological techniques, is needed in order to provide greater insight into reproductive cycles. Peak body conditions of *E. paupercula* coincided with large numbers of individuals in maturing and ripe stages being present in the sample, confirming that both methods give a consistent estimate of the reproductive patterns of the beaked clam in Maputo Bay.

This study showed that spawning peaked during the summer, when the water temperature was higher. Thus, there could well be an interaction of environmental factors during the summer, namely increased food availability and elevated temperatures, which regulate spawning intensity. In addition, factors preceding the spawning season, such as nutrient reserve accumulation, particularly through maturation stages during winter, have to be considered. The low range changes of environmental factors, especially temperature in the study area, resulted in the spawning pattern of *E. paupercula* found in this study being similar to those of other clams inhabiting similar tropical ecosystems. It can be inferred that the loss of *E. paupercula* body condition in summer is the result of spawning.

Chapter 6: Growth estimations of *Eumarcia paupercula* in Maputo Bay

INTRODUCTION

As with other bivalves, temperature is the primary environmental influence reported as determining rates of clam growth (Paul & Feder, 1973; Jones *et al*., 2004; Henry & Cerrato, 2007). Other important factors that impact on growth include food supply (Grizzle & Morin, 1989; Watanabe & Katayama, 2010), tidal exposure and currents (Grizzle & Morin, 1989; Beal, 2006), and salinity (Marsden & Pilkington, 1995). Lesser, or less well studied, influences on growth are light (particularly in giant clams, due their symbiotic relationship with photosynthetic zooxanthellae), water circulation (Wall *et al*., 2013), pH (Ringwood & Keppler, 2002) and chemical pollution (Munari & Mistri, 2007). Also, light can indirectly affect growth by limiting primary production and hence food supply (Griffiths & Griffiths, 1987). Intraspecific growth patterns of the Manila clam *Ruditapes bruguieri* and Littleneck clam *Protothaca staminea* have been shown to vary considerably among different areas (Paul & Feder, 1973; Silina, 2014), demonstrating that clam growth rates is variable and depends upon prevailing environmental conditions (Paul & Feder, 1973; Mann, 1979; Robert *et al*., 1993).

The effects of changes in water temperature on the growth of clams have been tested in both controlled conditions (Mann, 1979; Laing *et al*., 1987) and *in situ* (Filippenko & Naumenko, 2014). In general, growth is greater in areas with stable temperatures (Laudien *et al*., 2003), but within the maximum tolerance level of the species in question (Laing *et al*., 1987). Laing *et al*. (1987) found that after a steady increase in the growth rates of *Mercenaria mercenaria* and *Tapes decussata* between 10 and 25 °C, growth decreased at temperatures above 25°C. A table (Table 6.2) reviewing the growth rates of various clam species in relation to temperature is presented in the discussion section, where comparison is made with findings of the present study.

Seasonal differences in growth rates are often recorded in areas with strong seasonal temperature variations (Mann, 1979; Herrmann *et al*., 2009). Indeed, annual growth rings are often formed during winter in such areas and are indicative of a low to zero growth rate in clams during this season (Paul & Feder, 1973; Cerrato *et al*., 1991; Laudien *et al*., 2003; Lizarralde & Cazzaniga, 2009; Filippenko & Naumenko, 2014).

In contrast, the growth rates in a population of a *Ruditapes decussatus* from Urdaibai Estuary in Spain were highest in spring, but slower during summer (Urrutia *et al*., 1999). This is an unusual pattern, particularly for temperate areas, since for most species growth rates are faster during warmer seasons. In their study, the low food availability was considered to be the main driving force of growth.

Some studies (Thompson & Nichols, 1988; Lima *et al*., 2000; Carmichael *et al*., 2004) rank food availability, rather than temperature, as the primary factor controlling growth in clams. Urrutia *et al*. (1999) suggested that it is the seasonal interaction between these two factors that governs growth of clams. Wall *et al*. (2013) found that the growth of *Mercenaria mercenaria* or the 'quahog' was positively correlated with food concentration. They compared the growth of different bivalves against an eutrophication gradient, and found that the maximum growth of *M. mercenaria* was attained within the areas with highest nutrient levels. Another food-related factor influencing quahog growth is the phytoplankton type. Elevated concentrations of nanoflagellates and diatoms resulted in quahog growth increases, while other types, such as micro and dinoflagellates, did not affect the growth, even when concentrations were increased (Wall *et al*., 2013). Laudien, Brey and Arntz (2003) concluded that the extraordinary, year-round primary production in upwelling regions may account for the high growth rates of donacids inhabiting these areas.

Physiological responses to food quantity and quality were also recorded for *Mya arenaria* by Macdonald *et al*. (1998). In their study, growth potential increased even with increased poor quality food concentration. Furthermore, recorded responses included maintenance of oxygen consumption and ammonia excretion rates, and changing absorption efficiency (which increased when the quality was good). Also, clams maintained high absorption efficiency by reducing clearance rates and producing pseudofaeces. The Manila clam *Ruditapes philippinarum* (Baek *et al*., 2014), the cockle *Cerastoderma edule* (Iglesias *et al*., 1994) and *M. mercenaria* (Carmichael *et al*., 2004), are among the species undergoing these responses to changes in food quality and quantity. This shows that both quality and quantity of food supplied are essential for healthy growth rates in clams.

Effects of salinity on growth have been rarely documented in clams. In general, low salinity decreases growth rates, as recorded for *Austrovenus stutchburyi* in the Avon-

Heathcote Estuary (Marsden & Pilkington, 1995) and *Mya arenaria*, were growth reduced by a third with a decline in the salinity gradient (Filippenko & Naumenko, 2014). Most clams have a high range of tolerance to salinity and physiological adaptations to cope with changes in salinity (Allen & Garrett, 1971; Marsden, 2004). For example, *Mya arenaria* increased ammonia excretion by up to 64.3 mg per day when exposed to low salinity levels (17.5 ‰) in the first four days of exposure (Allen & Garrett, 1971). After return of normal salinity levels, its excretion returned to normal concentrations of about 3 mg NH_3-N day^{-1}, without affecting growth rates. Also, the venerid *Chamelea gallina* undergoes immune response to cope with the negative effect of both low and high salinities (Matozzo *et al*., 2006). Nevertheless, according to these authors, the mechanism by which salinity variability affects the immune response is unclear and the most probable mechanism is that a stress syndrome affects the functional response of haemocytes.

Across-shore differences in growth rates of intertidal clams are mostly due to tidal regime, since clams higher on the shore experience shorter feeding times (Grizzle & Morin, 1989; Cerrato *et al*., 1991; Beal, 2006). For example, *Mya arenaria* inhabiting a study site located on the upper shores of Passamaquoddy Bay in Maine took 25% longer to reach commercial size than individuals from the middle and lower shores (Beal, 2006). Also, changes in water depth influence growth rates in clams. Schweers *et al*. (2006) found growth rates (represented by mean length) of the venerid *Megapitaria squalida* increased with depth at Magdalena Bay. They concluded that these changes of growth rates were caused by active migration of adults from upper intertidal to subtidal areas.

Environmental factors are not the sole influence on clam growth; fishing effect (Defeo, 1998) and biotic factors (Lima *et al*., 2000; Beal, 2006) also have an impact. Population density may also indirectly affect clam growth through its negative influence on food supply (Griffiths & Griffiths, 1987). Since the present study largely assesses bivalve growth based on shell size increments, the focus here is on comparable studies, and not on somatic growth.

Growth rate variability, however, may also vary among cohorts within a population (Zeichen *et al*., 2002), and studies must allow for specific cohort sensitivities to environmental change to avoid bias. These conditions include external factors, such as temperature and other intrinsic factors, like clam maturation stage (Mann, 1979; Zeichen *et al*., 2002).

Intrinsic factors that affect growth of bivalves include not only their sexual maturity (Griffiths, 1981), but also age (Hawkins & Bayne, 1992; Beal & Kraus, 2002). Griffiths (1981) found that when sexual maturity is attained in the mussel *Choromytilus meridionalis*, the growth slows, as more energy is diverted to reproduction in mature animals. This pattern is similar for some clams, although not discussed in relation to the reproductive condition; thus smaller (8.50 mm) *Mya arenaria* grew faster than larger ones (11.80 mm) (Beal & Kraus, 2002). Differences in growth rates with age are somewhat related to changes in the metabolic rates (von Bertalanffy, 1957; Lewis & Cerrato, 1997; Ahn & Shim, 1998; Urrutia *et al*., 1999).

Few previous studies have addressed growth in clam species in Mozambique. A study by Scarlet (2005) listed size distributions from a population of *E. paupercula* in Maputo Bay (5 km from the site of the present study). A recent study by Scarlet *et al*. (2015) assessed the scope for growth and condition of *Meretrix meretrix* as an indicator of pollution in the Espirito Santo Estuary (Maputo Bay). This study is the first to assess growth patterns of the species in the region.

Growth parameters are required before the production and reproductive capacity of bivalve populations can be estimated (Bayne & Worrall, 1980; Herrmann *et al*., 2009; Dang *et al*., 2010). Hence, this study is a pre-requisite to drafting any management plans for this resource. This study aims to characterise the growth pattern of the beaked clam in its natural habitat at Maputo Bay. The objective of this study was also to ascertain if intertidal zonation affects growth. Furthermore, the life span and seasonal growth rates of the species were determined.

METHODS

Environmental parameters

Collection and analysis of environmental parameters are described in Chapter 2. Those results were used to discuss the growth of *Eumarcia paupercula* in relation to environmental parameters, namely temperature, salinity, and rainfall.

Growth data collection and analysis

Two methods were used to study growth patterns of *Eumarcia paupercula*. The first method was based on using size-frequency data obtained from the 18-month study of population structure (Chapter 5). The second method was based on length increment data obtained from mark-recapture measurements taken during a growth transplant experiment *in situ*. The mark-recapture experiment lasted for 12 months, from April 2013 – March 2014.

Length-frequency analysis

Samples of *E. paupercula* were collected from the same area where the clams were released for the mark-recapture experiment (see Chapter 2 for details on sampling). To collect data for the size-frequency analysis, eight random stations, 10 m apart, were located along a transect perpendicular to the shoreline and were sampled at each shore level. Anterior-posterior lengths of 30 clams per quadrat were measured to obtain monthly length-frequency distributions. Length-frequency analysis (LFA) was used to determine the effect of aerial exposure on the growth of the beaked clam.

Mark-recapture experiment

One hundred beaked clams were tagged with colour-coded geometric forms cut from various discarded plastic containers (Figure 6.1). These tags were between 0.5 and 1 mm thick, depending on the container used. The shell was first scratched to allow better attachment of the tags, which were then attached using super glue (Pattex®, gel). Another 100 clams were numbered on both valves (two groups each numbered from 1 - 50) with a waterproof permanent marker (Pentel®), giving a total of 200 marked clams. These clams were also gently scratched to allow the ink to permeate and last longer. This procedure was necessary, since the shells of *E. paupercula* are smooth, especially among smaller individuals. After the second recapture, re-writing was necessary for most marked individuals, as the ink was fading.

Each marked clam was measured in the anterior-posterior dimension (length mm) with Vernier callipers with an accuracy of 0.1 mm (time 0). The initial sizes ranged from 15 - 30 mm in length.

Figure 6.1: Colour-coded marked and numbered clams used for the mark-recapture experiment (left). Five colours: pink, red, white, yellow and blue and ten forms/letters (triangle, rectangle, square, lozenge, pentagon, hexagon, trapezium, V, W, and N) were used. Clams were numbered from 1-50 (right).

Marked clams were buried directly in the sediment at a depth of 3-4 cm, without any fencing protection. The across-shore division is described in Chapter 2 (study area description and general methods). Marked clams were released at a density of 50 individuals per m^2 in both experiment stations (ST1 and ST2). ST1 and ST2 were located in the middle shore, 100 m from high water mark, and separated by 100 m along-shore. Fifty colour-coded clams were combined with 50 numbered ones, resulting in 100 marked clams in each station. The experiments at ST1 and ST2 were set in March 2013 and April 2013 respectively. Figure 6.2 shows a schematic diagram of the growth experiment.

The growth mark-recapture experiment was set up in the intertidal area, in the site that had also been used as a clam collection area. All the *E. paupercula* individuals in the sediments, especially the adult ones, were removed from the 2 m^2 area prior to the release. The final clam density of $50/m^2$ was less than the density found in the middle shore during the month of experiment set-up (mean density 96 clams/m^2, see Chapter 5). This density was set assuming that not all clams may have been located and removed by hand from the area, especially smaller individuals, and also because recruitment may occur.

To stop clams from being removed, warning signs were placed in the experimental areas, not only to warn potential harvesters not to collect clams, but also to help re-identify the sites. Geographical coordinates of the site were also taken, and stones and poles were used as signs to help localize the area for recapture efforts. Furthermore, an awareness meeting was held to inform the collectors about the planned work prior to establishing the experiment.

Individual shell length (mm) increments were recorded monthly, and clams returned to the station after an hour interval. The mark-recapture experiment lasted for 12 months with recovery of the marked clams every 30 days. The marked clams found dead were counted every month and the differences in number of clams between months recorded.

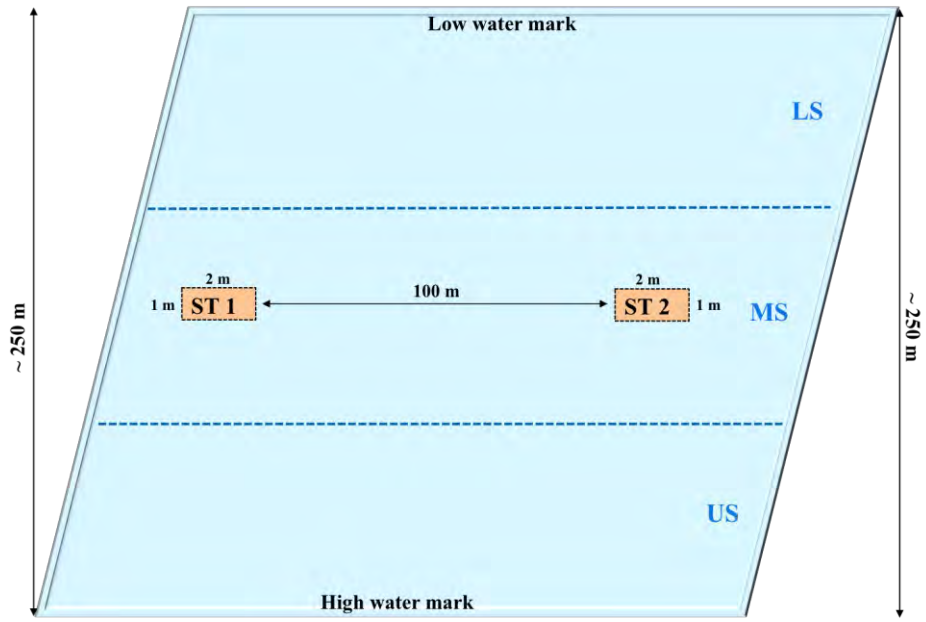


Figure 6.2: Schematic illustration of the mark-recapture experimental set up, showing the distance between the stations of clams release (ST1 and ST2). The shore was divided into upper (US), middle (MD*)* and lower shore (LS) zones.

During mark-recapture pilot experiments, there was a loss of clams placed at the upper shore after the first reading (probably due to harvesting by collectors). Also, clams released on the lower shore were not relocated, perhaps because they were removed by collectors, or displaced by waves. During interviews recorded in Chapter 4, two collectors confirmed that had found a few marked clams in their catches, and that they had not been returned to where they had been found. Thus, only the experiment from the middle shore was used to analyse the growth increments. Possible reasons of the loss of marked clams on upper and lower shores are discussed later in this chapter.

Data analysis

As bivalve growth rates decrease as their age increases, growth curves are commonly used to represent changes in mean size or weight against age (Pauly, 1984; Dugan & McLachlan, 1999; Laudien *et al.*, 2003; Schweers *et al.*, 2006; Dang *et al.*, 2010). The most commonly applied growth models are von Bertalanffy (Equation 6.1) and Gompertz (Equation. 6.2) growth curves, which according to McLachlan *et al.* (1996) produced similar results for *Donax serra*. These equations assume that a maximum attainable size exists for any given population (Sainsbury, 1980) and age-class data are fitted in the models (Bayne & Worrall, 1980).

$$l_t = L_\infty\left[1 - e^{-k(t-t_0)}\right] \quad (6.1)$$

$$\log_{10} l_t = \log_{10} L_\infty\left[1 - e^{-k^1(t-t_1)}\right] \quad (6.2)$$

Where:

l_t = length at time t
L_∞ = asymptotic or maximum length,
k = growth constant
t_0 = constant representing time when $l_t = 0$
k^1 = rate constant
t_1 = constant representing time when $l_t = 1$.

Although some studies (Monti *et al.*, 1991; Rawson & Hilbish, 1991) have applied the Gompertz model to study clam growth within populations, this is mostly used to describe growth in other bivalves, such as mussels (Griffiths & King, 1979; Bayne & Worrall, 1980) and scallops (Pedersen, 1994). Since the von Bertalanffy growth function (VBGF) is the most commonly used technique to describe clam growth rates (Narasimham *et al.*, 1988; Laudien *et al.*, 2003; Herrmann *et al.*, 2009; Dang *et al.*, 2010), it was used in this study to allow comparisons with other previous studies.

Length-frequency analysis

Monthly over the study period (November 2012 – April 2014), clam length-frequency distributions were counted per 1 mm size-class for growth estimation. These data were fitted to a VBGF curve, applying the non-parametric Electronic Length–Frequency Analysis (ELEFAN I) routine of the FAO-ICLARM Stock Assessment

Tools II (FiSAT II) computer program package (version 1.2.2) (Gayanilo *et al.*, 2005). The subroutine Response Surface in ELEFAN I evaluates the best K/L_∞ pair, by calculating the goodness of fit index (R_n) defined by Equation 6.3. In this program, data are reconstructed to generate "peaks" and "troughs".

$$R_n = \frac{10^{ESP/ASP}}{10} \tag{6.3}$$

Where ESP is the Explained Sum of Peaks and ASP (computed by summing all the peaks and troughs) is the Available Sum of Peaks (calculated by adding the "best" values of the peaks). A higher R_n value reveals the best fit between the components and the growth curve (Gayanilo *et al.*, 2005).

The growth performance index (Φ') (Pauly & Munro, 1984) was applied to compare the growth performances across-shore (Equation 6.4) from the average growth parameter estimates for each shore level. This index was chosen because it assumes that there are no changes in the shell shape of *E. paupercula* across-shore, and the negative correlation between VBGF parameters undermines direct comparisons between individual parameters.

$$\Phi' = \log K + 2\log L_\infty \tag{6.4}$$

Where:

K = growth constant
L_∞ = asymptotic length

In addition, the monthly growth rate (ΔL per month) was assessed following one cohort, by analysing a curve fitted by eye for this cohort in each shore level. The cohort chosen was one well defined at all shore levels, to allow comparisons among the shore levels. The post hoc Tukey test was used to compare the growth performance index between the three shore levels. Hotelling multivariate T^2 test was used to compare the von Bertalanffy growth curves from the three shore levels, with the assumption being that each shore level comprised a separate population. Tests were performed in SPSS (version 22.0) with a significance level of 0.05.

Length frequency data for the entire population were directly fitted to a VBGF curve by applying the non-parametric Shepherd method of the FiSAT II (Gayanilo *et al.*, 2005). The Shepherd method evaluates the best K/L_∞ pair, by calculating the goodness of fit score (S) defined by Equation 4.5.

$$S = (S_A^2 + S_B^2)^{1/2} \tag{4.5}$$

Where S_A and S_B are the goodness-of-fit scores (Equation 6.6) obtained with the origin of the VBGF set to 0 and 0.25 respectively. The best score results from the best combination of L_∞ and K, in an 11 by 11 matrix of S values output. Thus, the equivalent VBGF parameters were selected based on the best score in the matrix.

$$S_{tz} = \sum T_i \cdot \sqrt{N_i} \tag{6.6}$$

Where:

N_i = frequency for group i
$T_i = D \cdot \cos 2\pi\ (t - ti)$
$D = [\sin\pi\ (\Delta t)/\pi(\Delta t)]$
$t = \Delta t/2$
$\Delta t = t_{max} - t_{min}$
$t_i = t_z - (1/K) \cdot \ln[1 - (Li/L_\infty)]$
$t_z = (1/2\pi) \cdot \tan^{-1} (s_A/s_B)$

After constructing length-frequency histograms for the entire population, an inverse of the von Bertalanffy equation was then used to estimate the life span of *E. paupercula*. The theoretical life span (t_{max}) was estimated according to Equation 6.7, which considered the maximum shell length as being 95% of the L_∞ (Taylor, 1958).

$$t_{max} = \frac{[\ln L_{95\%} - \ln(L_\infty - L_{95\%})]}{K} \tag{6.7}$$

Where:

K = growth constant
L_∞ = asymptotic length
$L_{95\%}$ = 95% of the maximum shell length recorded from the LFA used to fit the von Bertalanffy growth curve.

Mark-recapture

The same growth function (VBGF) was used to describe clam growth, using the data from the mark-recapture experiment. The Munro method (Munro, 1982) in FiSAT II was applied to determine the K-value of VBGF represented in Equation 6.8.

$$K = \frac{ln(L_\infty - L_m) \times ln(L_\infty - L_r)}{(t_r - t_m)} \qquad (6.8)$$

Where:

K = growth constant
L_∞ = asymptotic length
L_m = length at marking
L_r = length at recapture
$t_r - t_m$ = time interval (in days) between marking and recapture

In the Munro plot, an individual K-value is generated using a constant input value for L_∞, which minimizes the variance of the mean K-values (Gayanilo *et al.*, 2005). The constant L_∞-value that produces the lowest coefficient of variation of K-values (CVK, Equation 6.9), was selected by trial and error (Pauly, 1984).

$$CVK = \frac{\sigma K}{\bar{K}} \qquad (6.9)$$

The relative growth index (Equation 6.10) was used to analyse the differences in growth rates with size. Three class sizes were defined, namely 20-24, 25-29 and 30-34 mm. Because of the few observations, 3 and 6 respectively, the 15-19 and 35-40 mm class sizes were not included in the analyses.

$$RGI = \frac{GR - GM}{GM} \times 100\% \qquad (6.10)$$

Where:

GR = length at recapture
GM = length at marking

One-way ANOVA was performed to compare the residuals of estimated lengths from the mark-recapture experiment and from the length frequency analysis of the whole population (SPSS, version 22.0). Similarly, the monthly growth rates of the entire population were used in a Pearson correlation analysis between the growth of *E. paupercula* and environmental parameters. A t-test of residuals, automatically computed in the Gulland and Holt method of FiSAT II, was used to assess seasonality in the growth of marked clams. Means of Φ' were compared for the three shore levels to test differences in growth across-shore, using One-way ANOVA. All statistical tests were considered significant when P-value was less than or equal to 0.05.

RESULTS

Across-shore growth rates from length-frequency analysis

Figure 6.3 shows the length-frequency distributions of *E. paupercula* from the monthly samples collected between November 2012 and April 2014. By analysing the histograms of the population as a whole, it was possible to identify three cohorts of *E. paupercula* during the study period. These cohorts, defined according to when they were first sampled, are termed cohort I (November 2012), II (April 2013) and III (March 2014), all of which showed different growth patterns across-shore. Cohorts II exhibited higher recruitment rates than cohorts I or III, and consequently was designated as the major cohort used to estimate growth rates.

For the sake of clarity, the growth curves across the shore were assessed for the major cohort – cohort II (recruitment of April 2013), which was followed from April 2013 to February 2014. Cohort II was chosen because it was clearly represented across all shore levels, and could be tracked for a longer period than any other cohort. Figure 6.4 shows the growth pattern of cohort II across the shore. The period of highest growth rate (ΔL/month) for cohort II was between August and September on the upper (5.94 mm) and middle (4.47 mm) shores. On the lower shore, it was between September and October 2013 (4.78 mm). Lowest growth rates in the upper (0.09 mm) and middle shores (0.12 mm) both occurred between June and July 2013. On the lower shore, clams grew slowest (0.21 mm) between October and November 2013. Mean monthly growth rates were 2.56, 2.35 and 2.69 mm for upper, middle and lower shores respectively, and analysis of growth rates showed no significant difference across-shore ($F = 0.103$; $P = 0.902$).

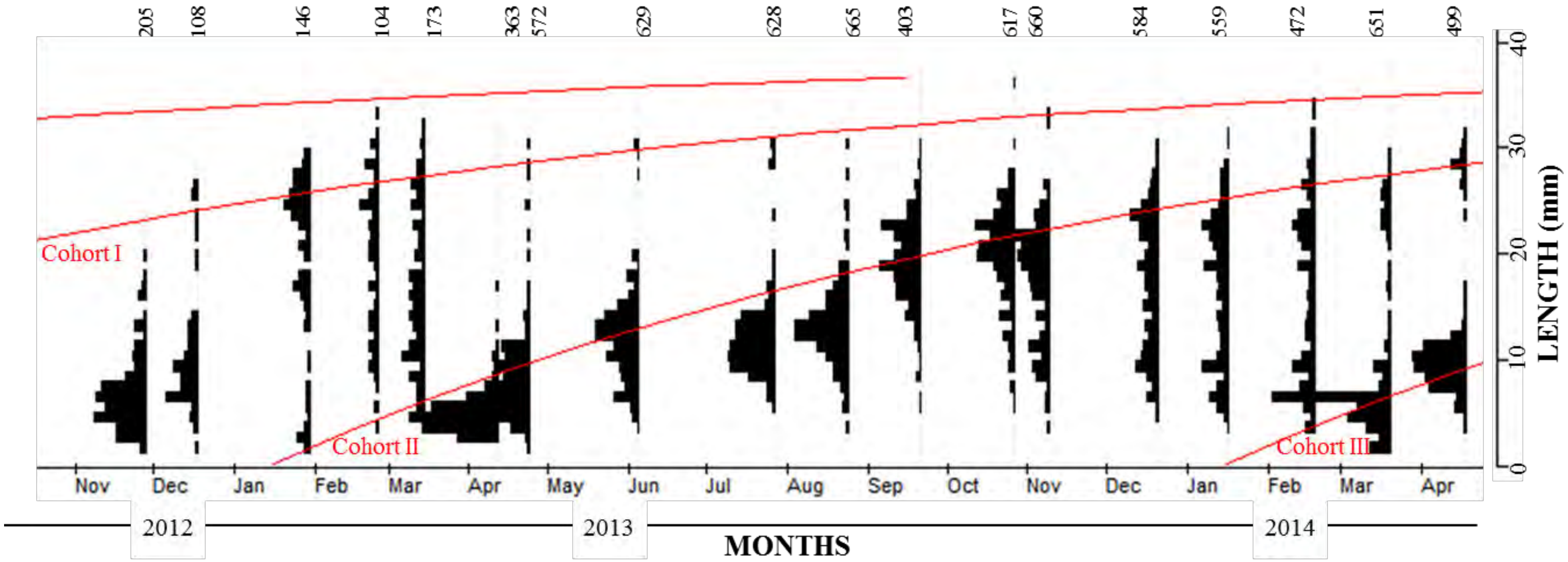


Figure 6.3: VBGF growth curves (red lines) of the whole population of *E. paupercula* at Costa do Sol estimated from the Shepherd method. The VBGF parameters were used to fit the curve were $L_\infty = 41$ and $K = 1.01$. A new major cohort (cohort II) appeared in April 2013. Numbers above histograms are the *n* used for the monthly length frequency distribution.

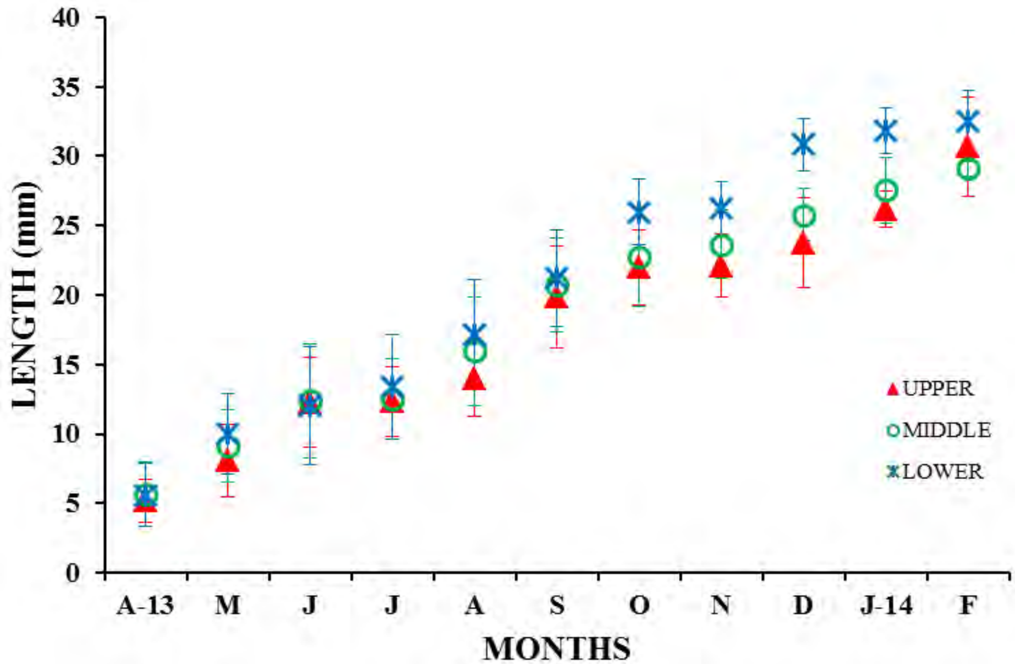


Figure 6.4: Changes in shell size (mean ± SD) of cohort II between April 2013 and February 2014 at each of three tidal levels. Determination of the mean monthly length of cohort II started when it was first identified in the population (April 2013) and terminated when it was no longer detectable (February 2014).

The best pairs of VBGF parameters (L_∞ and K) for the growth curves on the three shore levels are presented in Table 6.1. Fixed intervals of L_∞ (35 – 45) and K (0.2 – 1.5) were used to generate these pairs in the response surface analysis subroutine. A Hotelling T^2 test of the von Bertalanffy growth curves of *E. paupercula* indicated that it grew faster on the lower shore than in the middle or upper shores ($P < 0.05$) (Figure 6.5). The growth performance index (Φ') did not vary across-shore (Tukey test: $P > 0.05$).

Table 6.1. Across-shore variation of *E. paupercula* VBGF parameters: L_∞ is the asymptotic length and K is the growth constant. R_n is the goodness-of-fit, which originated the best VBGF pair of K and L_∞ in ELEFAN I, and Φ' is the growth performance index.

Parameter	**Shore level**		
	Upper	Middle	Lower
L_∞ (mm)	40.00	39.50	41.55
K (yr^{-1})	1.10	1.20	1.51
R_n	0.16	0.16	0.13
Φ'	3.25	3.27	3.42

The pair of the VBGF parameters estimated by the Shepherd method for the growth analysis of the entire population, using LFA, were $L_\infty = 41.0$ and $K = 1.01$ ($S = 0.955$). The life span (t_{max}) calculated for *E. paupercula* was 1.97 years.

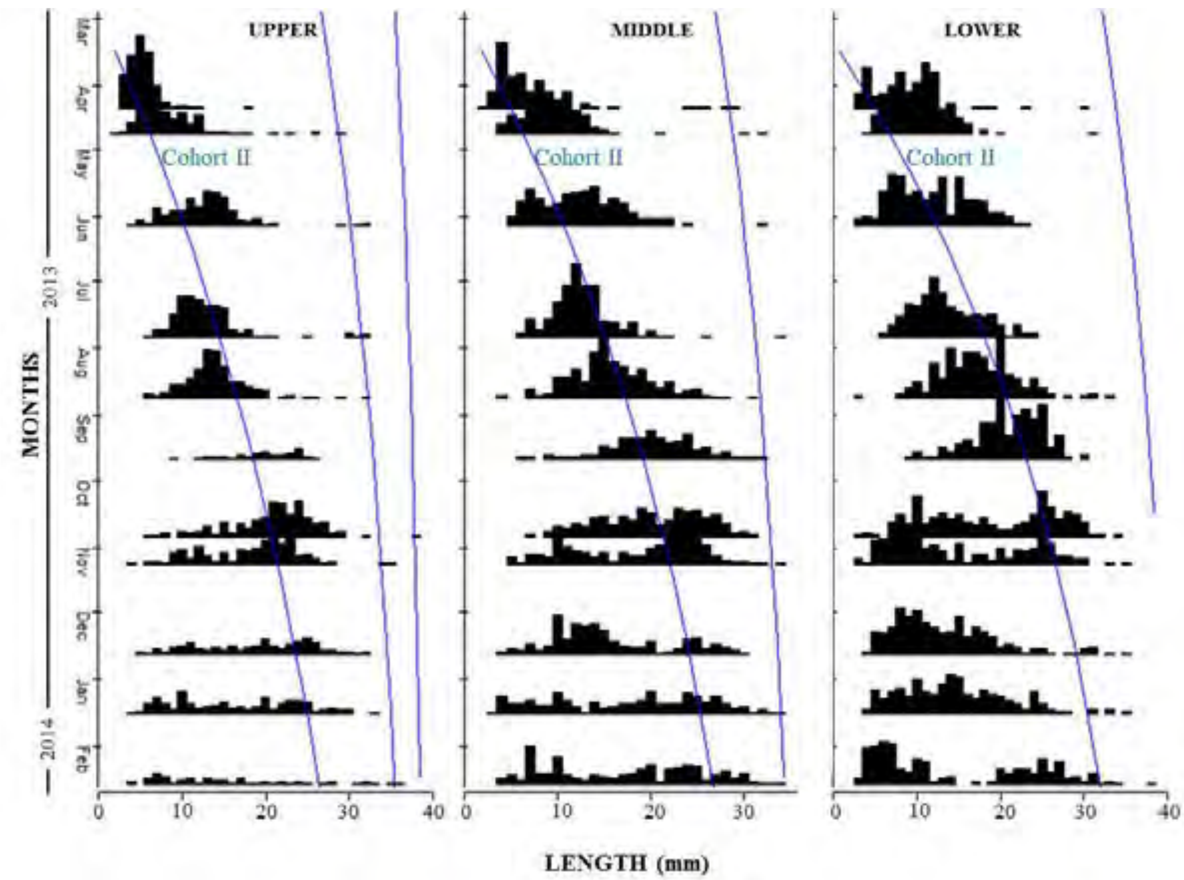


Figure 6.5. Growth curves of *Eumarcia paupercula* estimated from length-frequency analysis during the period when cohort II was clearly discernible from the upper to the lower shores, which was between April 2013 and February 2014. Blue lines represent the growth curves.

Growth in terms of mark-recapture increment data

Out of 200 marked clams, 126 were recaptured (63%) in at least one pair of successive monthly samples, allowing a growth rate to be estimated over that month, but there was some variation in numbers of days elapsed between samples monthly. These recaptures resulted in 527 growth increment data pairs computed on FiSAT II for growth analysis by the Munro method. Of the 527 observations, only 352 were computed by the model to generate the VBGF parameters, as the remaining 175 observations resulted in recapture lengths that were equal to the marked lengths (no growth observed).

Due to the slight variations in numbers of days elapsed between samples the growth rates (ΔL/Δt) of marked clams were calculated and depicted as growth per day (Fig. 6.6). Daily growth varied between 0.008-0.21 mm per day, equivalent to approximately 0.24-6.30 mm/month. These growth rates were related to the initial lengths and sizes. When separated into three size classes, namely 20-24, 25-29 and 30-34 mm, there were significant differences in relative growth index (RGI), which decreased with increase of class size. The former class grew faster with an average of 19.13% of length increment per month, while the latter only increase at 1.96% of the marking size. The RGI of the 26-29 mm size class was 5.56% per month. The highest mean growth rates were recorded in individuals of 25.50 mm, whereas the lowest were recorded in individuals of 28.50 mm (Figure 6.6).

The mark-recapture experiment indicated significant and strong seasonal growth oscillations (C < 0.80), suggesting the month of July as the winter point (lowest growth rates), and January as the month of high growth rates.

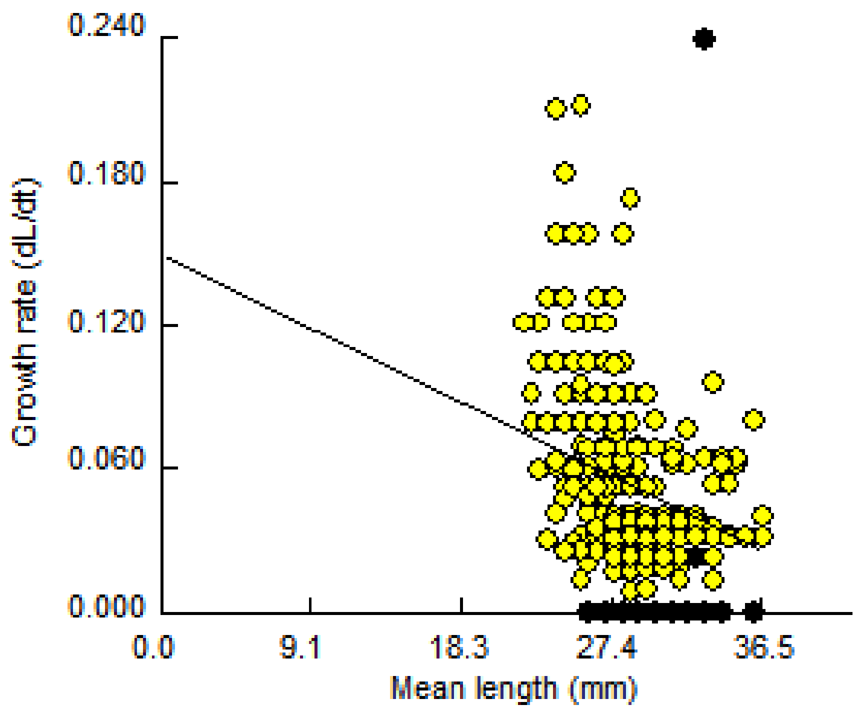


Figure 6.6: Monthly growth rates (mm/day) of *E. paupercula* from the mark-recapture experiment. Black filled circles denote unused observations by the Munro method when no growth was observed between mark-recapture individuals.

The VBGF parameters estimated by the Munro method were L_∞ = 40.50 and K = 1.65. The growth performance index estimated from these parameters was Φ' = 3.43. According to the growth curve (Figure 6.7) obtained from the Munro plot of $\Delta L/\Delta t$, the monthly K-value was estimated at 0.14. By using the Munro computed L_∞ (40.50), it was possible to estimate the origin of the growth curve (t_0). The empirically estimated t_0 was calculated using individuals measuring 20 mm. This length corresponds to the length class of the smallest marked individuals, and by reading off the equivalent t = 0.38 year on the growth curve. By applying the von Bertalanffy growth equation, t_0 is estimated at -0.03 year. Thus, the von Bertalanffy growth equation for *E. paupercula* in Maputo Bay obtained from mark-recapture experiment is presented in Equation 6.11.

$$l_t = 40.5[1 - e^{-1.65(t-0.03)}] \qquad (6.11)$$

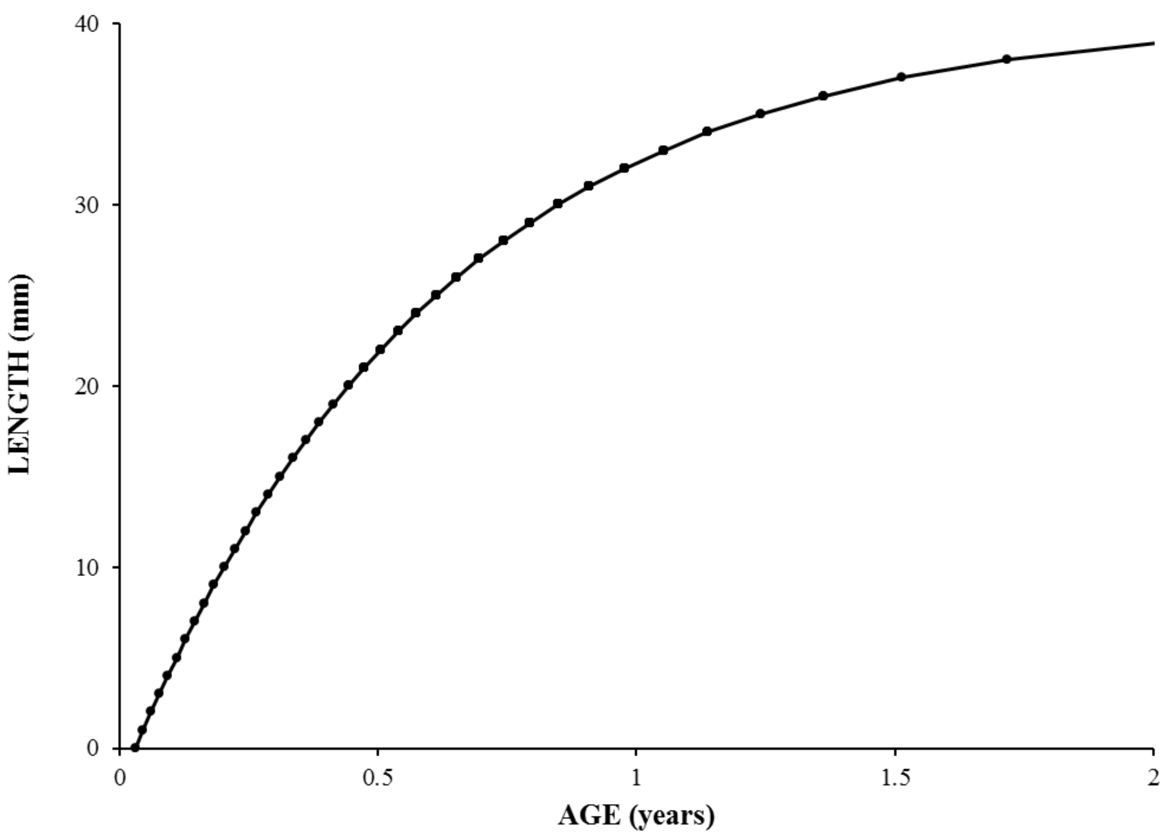


Figure 6.7: Growth curve for *E. paupercula* from Maputo Bay, obtained from the mark-recapture experiment and drawn according to equation 4.11.

Growth pattern from LFA versus mark-recapture experiment

Figure 6.8 shows the plot of residuals against the estimated lengths from the LFA and mark-recapture experiment. Analysis of variance showed no significant differences ($P > 0.05$) between the residuals of estimated lengths from LFA and the mark-recapture experiment. The strong fit obtained ($R^2 = 0.97$) between residuals of estimated lengths from both methods supported this finding.

Low growth rates ($\Delta L/\Delta t$) of *E. paupercula* in Maputo Bay were recorded during the winter – June and July, from LFA. Similarly, the Gulland and Holt equivalent plot from mark-recapture experiment determined that the lowest growth rates occurred in July ($C < 0.80$).

Clam age was estimated using the von Bertalanffy growth equation for *E. paupercula* (Equation 4.7) based on their being no significant differences ($P > 0.05$) between the residuals of the estimated clam lengths derived from the LFA and the mark-recapture methods. The estimated ages for the largest clam recorded (38 mm) using the biological sampling method for this length frequency distribution was 1.30 years.

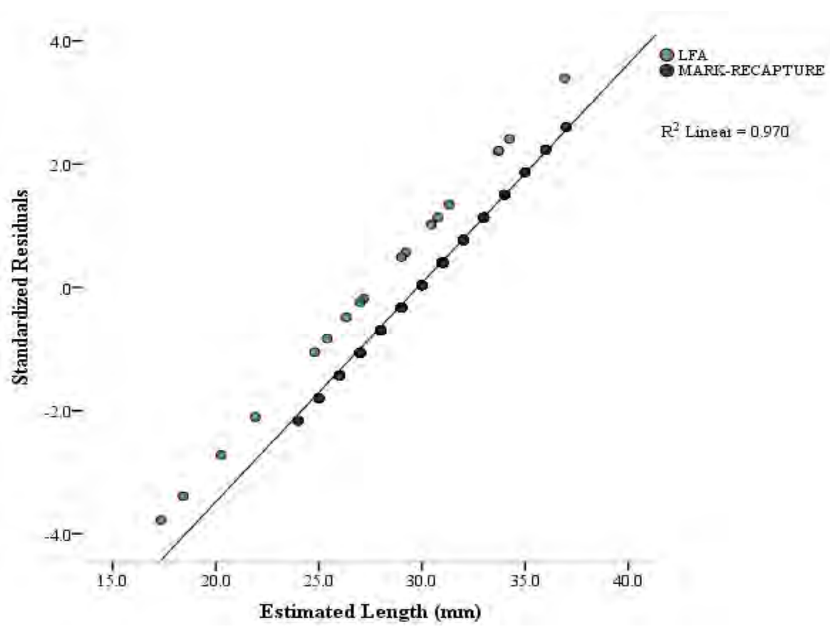


Figure 6.8: Residuals of the estimated lengths of *E. paupercula* from mark-recapture experiment (blue fill) and length frequency analysis (green fill). A One-way ANOVA showed no significant differences between residuals of the two groups ($P > 0.05$).

DISCUSSION

Various methods were used to assess growth patterns and parameters of *Eumarcia paupercula* in Maputo Bay. These methods included the analysis of length-frequency distributions using two different routines in FiSAT II, one for the across-shore assessment of growth, and the other for the population as a whole. Another approach used was Munro method for growth increment data, also performed on FiSAT II. This was necessary because this study covers an unsteady-state population, as it is being impacted by the fishery.

Growth rates from length frequency analysis

Analysis of growth rates of cohort II showed that highest shell growth occurred in April and September, with some variability across-shore. Highest growth rates in upper and middle shore were in September at 5.94 and 4.79 mm/month, respectively. Although the growth rate in lower shore was also high (4.02 mm) during September, the highest value was recorded during May (4.42 mm).

The final mean shell length was significantly larger on the lower shore than on the middle and upper shores. Thus, the Hotelling analysis of the growth curves showed significantly faster growth on the lower shore area. In contrast, although a trend was visible, the overall growth rates did not vary significantly across-shore. Some studies on clams (e.g. Beal, 2006) have shown that while growth is often faster on the lower shore, the growth rate is not necessarily proportional to the greater submerged time in this area. Therefore, biotic factors such as competition (intra and interspecific) and predation have to be considered. These factors were not directly tested in this study, but differences in densities along-shore probably did not result in effects of competition within this population. For instance, mean density on the lower shore during the period when cohort II was discernible was approximately one-third higher than it was on the upper shore and similar to that of the middle shore. Likewise, other infaunal bivalves (*Meretrix meretrix*; *Dosinia hepatica*) and gastropods (*Polinices mammilla*) were found in low densities in the study area. Thus, competition, either for space or food, from other macroinfauna was unlikely to hamper growth of *E. paupercula*.

Although evidence of predation was present (drilled shells in marked individuals), association of predation with growth patterns of *Eumarcia paupercula* across-shore was not tested. In the presence of predators, decreases in the growth rates of clams are usually reported (Beal, 2006). Some clam species may change their burrowing behaviour by burrowing deeper to evade foraging crabs (Blundon & Kennedy, 1982; Beal & Kraus, 2002). Such behavioural change may lead to reduced growth, as feeding in the deeper sediment layers is restricted. The faster growth rates at the beginning of cohort II appearance in the lower shore (May) in this study might be related to the presence of Portunidae crabs. These crabs are major predators of clams (Hunt *et al*., 2003; Polyakov *et al*., 2007) and are frequent in the study area (de Boer *et al*., 2002; Balidy, 2003; Vicente & Bandeira, 2014), and usually prey upon smaller individuals (Arnold, 1984), which may lead to apparent faster growth rates using LFA. Nevertheless, a narrow length range (15 – 30 mm) was used for the mark-recapture experiment.

Bird predation on the tidal flats of Maputo has been considered as one of the major factors contributing to removal of intertidal organisms after fishing mortality. De Boer and Longamane (1996) estimated that sacred ibises (*Threskionis aethiopicusi*) and green herons (*Ardea Cinerea*) feed entirely on benthos. Gribben and Wright (2014) and Scarlet (2005) found, among other birds, herons (*Egretta novaehollandiae*) and little egrets (*Egretta garzettae*) foraging during their surveys and concluded that these birds were the main predators of the venerids *Katelysia scalarina* and *Eumarcia paupercula*, respectively.

Table 6.2. A comparison between growth performance indices calculated for various clam species, from VBGF parameters obtained from mark-recapture experiments. Letters in brackets refer to family: C = Carditidae; D = Donacidae; M = Myidae; Ma = Mactridae; Me = Mesodesmatidae; P = Psammobiidae; T = Tellinidae and V = Veneridae. Different Φ' for the same species and reference are the result of seasonal sampling.

Species	Latitude	Φ'	Reference
Donax incarnatus (D)	12°27'N	2.19	Thippeswamy and Joseph, 1991
Cardita affinis (C)	03°55'N	2.31	Riascos *et al*., 2008
C. affinis (C)	03°55'N	2.55	Riascos *et al*., 2008
Donax dentifer (D)	04°05' N	2.70	Riascos and Urban, 2002
D. hanleyanus (D)	23°03'S	2.75	Cardoso and Veloso, 2003
D. faba (D)	12°57' N	2.80	Singh *et al*., 2011
D. hanleyanus (D)	23°03'S	2.86	Cardoso and Veloso, 2003
D. hanleyanus (D)	37°19'S	2.90	Herrmann *et al*., 2009
Gafrarium tumidum (V)	08° 35' – 09°25'N	2.93	Jagadis and Rajagopal, 2007
Tellina petitiana (T)	42º 46' S	2.97	Lizarralde and Cazzaniga, 2009
Ruditapes philippinarum (V)	44°40'N	2.99	Dang *et al*., 2010
Donax trunculus (D)	36°56'N	3.08	Deval, 2009
Mya arenaria (M)	53°20'N	3.09	Schäffer and Zettler, 2007
D. trunculus (D)	40°55'N	3.11	Gaspar *et al*., 1999
Mercenaria mercenaria (V)	37°15'N	3.17	Harding, 2007
Tivela mactroides (V)	23°40'S	3.22	Turra *et al*., 2014
Mercenaria mercenaria (V)	41°33'N	3.26	Carmichael *et al*., 2004
D. serra (D)	22°59'S – 22°47'S	3.27	Laudien *et al*., 2003
Mactra discors (Ma)	36°46'S	3.28	Cranfield *et al*., 1996
Mya arenaria (M)	41°33'N	3.32	Carmichael *et al*., 2004
Paphies donacina (Me)	36°46'S	3.43	Cranfield *et al*., 1996
***Eumarcia paupercula* (V)**	**25 5 4'S**	**3.43**	**This study**
Meretrix meretrix (V)	8°45'N	3.50	Narasimham *et al*., 1988
Spisula aequilatera (Ma)	36°46'S	3.57	Cranfield *et al*., 1996
Gari solida (P)	14°15'S	3.61	Urban, 1998
Mactra murchisoni (Ma)	36°46'S	3.65	Cranfield *et al*., 1996

The lowest growth rates were recorded in July for the upper (0.09 mm/month) and middle (1.13 mm/month) shores, but for the lower shore, lowest growth occurred during November (0.21 mm/month). Other low growth rates of 1.57 and 0.67 mm/month were recorded in the middle and lower shores respectively during February 2014. February 2014 corresponded to the period when cohort II was no longer discernible in the population; most individuals were in the adult stage, when growth rates decreased. Furthermore, this period corresponded to the main harvesting season of *E. paupercula* in the area, and harvesters select the larger individuals (Chapter 4), which may result in a reduction in the apparent growth rate.

Growth patterns of *Eumarcia paupercula* from this study are similar to those found by Brazeiro and Defeo (1999) for the yellow clam *Mesodesma mactroides*, where the lowest growth rates recorded coincided with peak fishing effort and vice versa. Low growth rates recorded in the lower shore during November are probably related to spawning events during this period (Chapter 5), because most of the energy may be diverted into reproduction (Urrutia *et al*., 1999). When taking into account that cohort II was considered, individuals were sexually mature, thus the majority of the population would have been spawning in November. Similarly, Brousseau (1979) found low growth rates in *Mya arenaria* during spawning.

As growth in clams is primarily a function of environmental parameters (Mann, 1979; Laing *et al*., 1987; Thompson & Nichols, 1988; Robert *et al*., 1993; Marsden, 2004; Baek *et al*., 2014; Hernández-Otero *et al*., 2014), tidal exposure should be a major factor regulating growth across-shore. Low growth rates recorded during February (summer) in middle and lower shores are probably not related to stress from aerial exposure and consequential high temperatures during the low spring tides, as rates of energy loss due to aerial exposure would be expected to be minor for lower shore bivalves relative to upper shore ones (Griffiths, 1981b). To meet their metabolic requirements, bivalves from upper shores reduce their oxygen consumption to compensate for the effects of aerial exposure (Griffiths & Griffiths, 1987).

Surprisingly, aerial exposure and related energy loss do not explain why the overall growth rates were similar across-shore in this study. These observations of energy loss across-shore were made for mussels, which may experience the impacts of aerial exposure more strongly than clams, as the latter live buried within the sediment, where they remain cool and wet. A possible tolerance to life-threatening temperatures and desiccation may become limiting before the growth potential declines to extreme (van Erkom Schurink & Griffiths, 1993). Also, the significantly lower densities on upper shore (Chapter 3) may have contributed to the similar growth rates across-shore, as this was composed of larger individuals that have lower growth rates.

Although the regular presence of cohort II allowed growth modelling 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). This means that larger numbers of individuals of the same age are required to predict an equivalent length of the individual in that age and vice versa, which is not always possible to find within a population. For instance, out of 3401 individuals used to fit the population growth curve here, only 451 were between 25 – 38 mm. Thus, a fixed L_∞ corresponding to the length of the largest individual recorded in a sampled population has been used by many authors to estimate growth in exploited populations (Laudien *et al*., 2003; Carmichael *et al.*, 2004; Herrmann *et al*., 2009). Because cohort II was often detectable, this approach was not applied in this study.

Growth rates from mark-recapture experiment

The growth curve showed that smaller individuals have a faster growth rate than larger individuals approaching their terminal adult size. Frequently, no growth increment in the last months of the experiment was recorded. Analysis of growth increment data allows a better estimation of continuing patterns in the growth of bivalves (Carroll *et al*., 2011). It was difficult to design the mark-recapture experiment at the three shore levels, to allow proper comparisons of the effect of tidal exposure on the growth of the beaked clam. Specifically, trials from the lower shore resulted in the loss of marked individuals – recapture was less than 10% after 30 days, and 0% after 60 days. Artisanal fishing boats moor on the lower shore area, so probably the removal of clams was caused by the boats, the predation by birds and/or fish can also be considered. It is difficult to explain of loss of the marked experiment on upper shore, but as this zone is the most used by diverse beach users, it is most likely that they were collected as food soon after the experiment was established, as after 30 days no marked clam was found in the planted area.

Also, as in general the upper shore in the area shelter lower densities of *E. paupercula* (Chapter 5), it is possible that clams failed to colonize when buried and waves may have moved them to other areas.

This is the first growth study of this species. The growth rates reported here are compared with those of other species from the literature in Table 6.2. These studies also applied various mark-recapture methods to estimate the VBGF parameters, thereby allowing the calculation of Φ' for comparative purposes. This index can also be used for interspecific growth comparisons (Pauly & Munro, 1984). Table 6.2 indicates a species and habitat-specific related variability in the growth performance index. Local characteristics, rather than simple latitudinal differences, would better explain the differences of Φ'. For instance, in different latitudes (36°56'N and 40°55'N), the same growth performance index (3.1) was recorded for the donacid *Donax trunculus* (Gaspar *et al*., 1999; Deval, 2009). When venerids only are considered, *E. paupercula* has the highest growth performance index after *Meretrix meretrix* from the study of Narasimham *et al*. (1988).

Figure 6.9 shows a comparison of overall growth performance (OGP) among several venerids with latitude proposed by Pauly (1979) for both inter- and intra-specific comparisons. The index *P* (Equation 4.11) assumes that slope of the growth curve has one maximum value of mass growth rate, and therefore *P* is proportional to the mass increase at the inflexion point of the VBGF. Although there is not a distinct limit of *P* between subtropical/tropical and temperate among the selected species, it appears that the growth performance of venerids increases with latitude (Figure 6.9). The OGP for *Eumarcia paupercula* is similar to that found for other venerids from subtropical/tropical regions, such as *Paphia cor* (Niamaimandi, 2013) and *Tivela mactroides* (Arrieche & Prieto, 2006; Turra *et al*., 2014).

$$P = \log (K [L_\infty]^3) \qquad (4.11)$$

Contrary to the scattered trend in OGP among venerids, Laudien *et al*. (2003) found and showed a definite trend, where a growth performance decreased from upwelling to temperate, and subtropical-tropical donacids. Unlike most studies from temperate waters, Peterson *et al*. (1983) found fast growth rates for *Mercenaria mercenaria* (latitude 34'N), which are similar to those found in the present study, although inhabiting different environments (4°C minimum temperature and subtidal shallow water). In their study, *M. mercenaria* reached approximately 45 mm (commercial size) in 1.5 years.

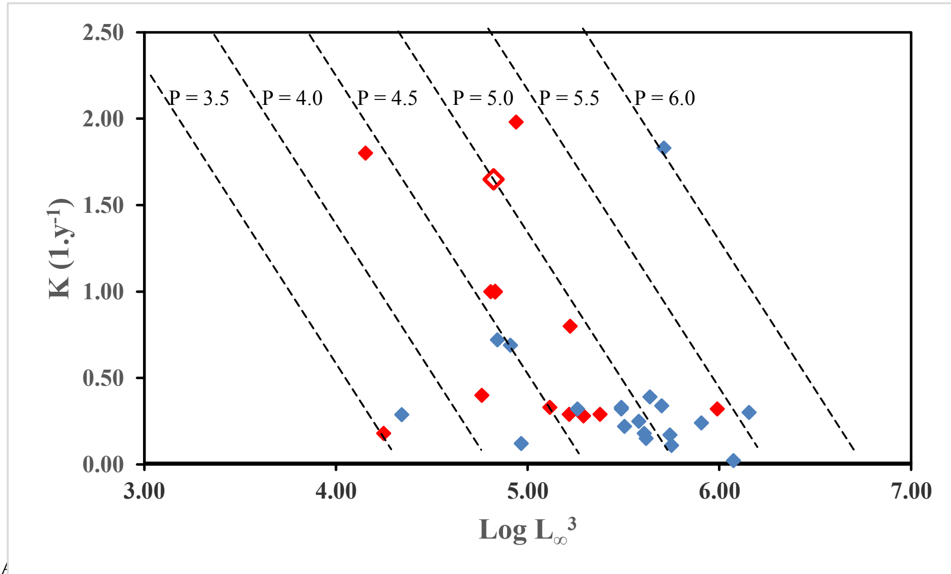


Figure 6.9 A [illegible] (P) of several venerids from subtropical/tropical (◆) and temperate (◆) regions with *Eumarcia paupercula* (◇). Diagonal lines indicate equal values of P. Auximetric grid obtained with data from present study and: *Amiantis umbonela* (Saeedi *et al*., 2010); *Amiantis purpuratus* (Morsan & (Lobo) Orensanz, 2004); *Callista chione* (Forster, 1981; Metaxatos, 2004; Ezgeta-Balić *et al*., 2011); *Circenila callipyga* (Bagher *et al*., 2007); *Eurhomalea exalbida* (Lomovasky *et al*., 2002); *Gafrarium tumidum* (Jagadis & Rajagopal, 2007); *Meretrix casta* (Laxmilatha, 2013); *Meretrix meretrix* (Narasimham *et al*., 1988); *Paphia cor* (Niamaimandi, 2013); *Ruditapes philippinarum* (Chung *et al*., 1994; Humphreys *et al*., 2007; Ponurovskii, 2008; Dang *et al*., 2010; Colakoglu & Palaz, 2014) *Tivela mactroides* (Arrieche & Prieto, 2006; Turra *et al*., 2014); *Venus antiqua* (Clasing *et al*., 1994).

Growth in relation to environmental parameters

The growth performance index of *E. paupercula* (Φ') showed no significant correlation with any of the environmental parameters tested ($P > 0.05$). While for temperature and rainfall the relationship was weakly positive, for salinity it was weakly negative (Figure 6.10). Growth of *E. paupercula* in relation to these parameters has not been studied before. Thus, it is possible that the parameters were within the ordinary range for growth of this species, although some relationship was expected at least with temperature. In addition, Grizzle *et al*. (2001) noted that other venerids have high tolerance to many environmental factors, including those recorded in this study. The small temperature variation in the tropical ecosystems has little effect on the growth patterns of clams, in comparison with those from temperate regions, which are subject to much larger seasonal temperature variations (Broom, 1982).

The seasonality in the growth of *E. paupercula* seems not to be directly related to either changes in temperature or variation in any other environmental parameter. This finding is similar to that of Cardoso and Veloso (2003) for *Donax hanleyanus* in a similar latitudinal range (23°03'S). Low growth rates recorded during June – July from both methods might be related to energy being diverted to the reproductive cycle (Griffiths, 1981a). This is a period of high gamete production for the late winter-early summer spawning (Chapter 3). Similarly, growth rates of *Ruditapes bruguieri* in South Korea were lower during winter (Silina, 2014); however, this conclusion was based on the formation of annual rings, as no direct correlation was found with the recorded temperature.

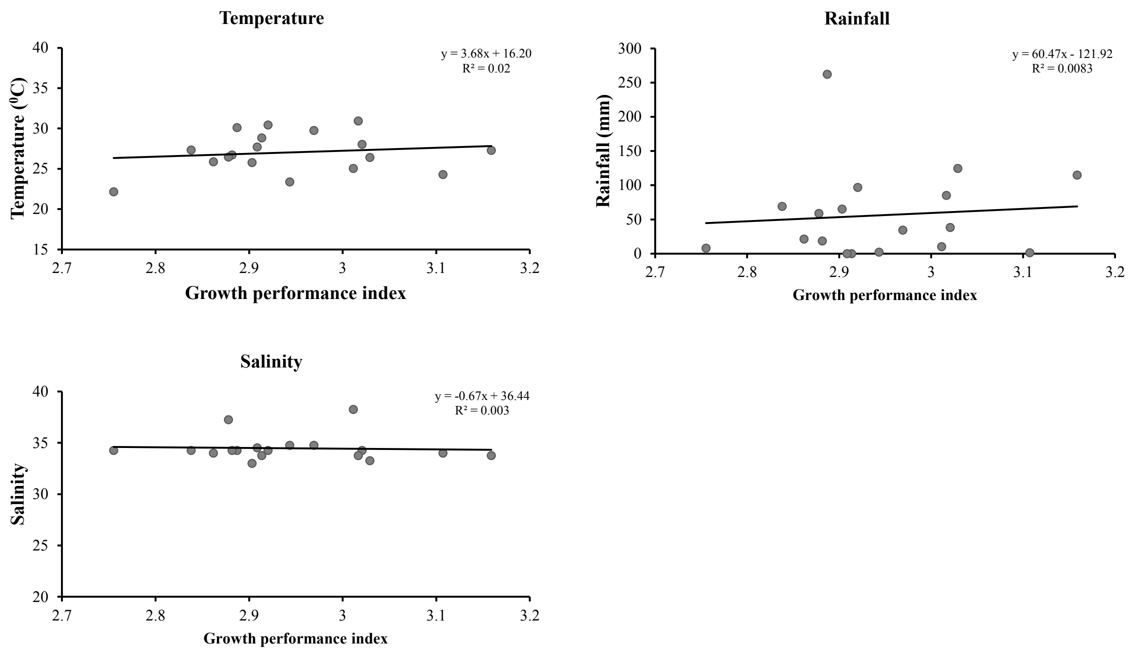


Figure 6.10: Relationships between the growth performance index (Φ') of *E. paupercula* and environmental parameters at Costa do Sol. Pearson correlation analysis indicated no significant relationships between the growth performance index and environmental parameters ($P > 0.05$).

Growth pattern from LFA versus mark-recapture experiment

This study showed that the utilization of the two distinct methods to estimate growth of *Eumarcia paupercula* resulted in similar growth parameters and rates. Residuals analysis of estimated length rates from both length-frequency analysis and mark-recapture methods gave similar distribution patterns, with ANOVA results showing no significant differences between the two. The high R^2 coefficient suggests that both methods are appropriate for determination of growth rates of *E. paupercula*.

The LFA method appeared to be sensitive to the collection season and recruitment. The small frequency of large size classes during and after collection season may have led to a small estimated L_∞. The relatively fast growth rates and the year-round spawning pattern of *Eumarcia paupercula* (Chapter 5) created overlapping cohorts, which may have led to a biased estimation of growth parameters using computed LFA (see Sparre & Venema, 1998). Other sources of bias in growth estimation using LFA are across and along shore movements (Laudien *et al*., 2003). These movements were documented for *Donax* spp. (Schoeman & Richardson, 2002; Laudien *et al*., 2003; Herrmann *et al*., 2009), *Ruditapes philippinarum* (Nakamura *et al*., 2002) and for the hard clams *Meretrix lusoria* (Hashiguchi *et al*., 2014). Then, such bias may be more common in growth analysis of clams. The relatively high recapture rate (63% for live clams) within approximately 6 m^2 of the experiment area, suggest that shore movements by *E. paupercula* are limited, as no size stratification across shore was recorded.

The *in situ* experiment was also affected by loss of marked specimens, whether by natural mortality, predation (marked clams found with holes), or through harvesting by tourists or collectors. It was still possible, however, to get growth increments pairs that allowed analysis on FiSAT II. The relatively long mark-recapture experiment in this study allowed for comparisons of seasonality in growth rates from both methods.

Dalgiç *et al*. (2009) reported greater growth performance of *Chamelea gallina* from non-fished, compared to fished, populations. This can be a biased conclusion, as the clam collectors will most probably selectively collect the larger individuals, which would then lead to an apparent slower growth. Also, the addition of smaller individuals by recruitment to a population may affect growth rates analysis, as concluded by Bonsdorff and Nelson (1992) for *Donax variabilis*. It is difficult to determine the effect of fishing on the populations for *E. paupercula* in Maputo Bay due to the absence of comparable non-fished populations; however, unpublished data from a less exploited area (40 km north) in Maputo Bay shows that collected clams have a larger average size than those from this study site.

The use of LFA to fit the von Bertalanffy growth curves may also have led to our relatively smaller values of L_∞ (41.00 mm). This length is smaller than the largest individual (42 mm) recorded for the species (Branch *et al*., 2010). The maximum size was probably collected in a different site, as in the present study three individuals measuring 43 mm were recorded from collectors sampling (Chapter 6). This means Maputo Bay has the largest *E. paupercula* ever recorded. The small value of L_∞ was probably affected by temporal changes in size frequencies, with certain months having low densities of bigger clams (> 20 mm) because of fishing. These months correspond to the period between major recruitment and pre-collection season (March – August); however, VBGF parameters obtained from the mark-recapture experiment were similar to those from LFA that shows some negative effect of fishing.

Also, a difference of approximately 1 mm/month in maximum growth was observed between the two methods, with the highest rates obtained from the mark-recapture experiment. This difference is in concordance with the theory of Sparre and Venema (1998) that LFA may underestimate growth estimations. A growth rate of 5.94 mm/month was observed on the upper shore from LFA, which is close to the maximum rate of 6.30 mm/month obtained from mark-recapture; however, the experiment was set on the middle shore, where the highest growth rate from LFA was 4.47 mm/month. Also, the mean growth rate of 2.53 mm/month (mean of growth rates across-shore from LFA) is similar to the 2.13 mm/month (mean of RGI in marked clams) from mark-recapture. Note also that for the mark-recapture experiment only individuals greater than 20 mm were used (due to the difficulty of tagging smaller individuals), and these would already be showing slowed rates of growth as they approached adult size (Figure 6.7). Although the mark-recapture experiment used a narrow range of length, the RGI between the three classes (20-24, 25-29 and 30-34) decreased with monthly shell increments falling from 19 % in the smaller size class to only 2 % of the marked size in the largest size class. Moreover, the low growth rates from mark-recapture (through RGI) was also obtained from LFA for the largest clams at the end of cohort II (November-February), when clams were larger.

In addition, the growth performance index (3.43) calculated for the mark-recapture experiment was not significantly different and is comparable with that obtained from LFA (3.31, average from the three shores). Although LFA was found unsuitable for growth analysis of bivalves in tropical-subtropical regions (Sparre & Venema, 1998), in the present study the method led to equivalent findings with the mark-recapture analysis. Since larger individuals are seasonally removed by the fishery and smaller ones are continuously added by recruitment, the growth estimation by analysis of cohort II might be expected to show a decline with beginning of collection season (as larger individuals are selectively removed at that time). This decline is reflected by lower apparent growth rates, which agrees with Sparre and Venema (1998). While the low growth rate from the mark-recapture experiment was about 0.24 mm/month, similarly low growth rates from LFA were obtained during November 2013 (0.21 mm/month) and February 2014 (1.57 mm/month).

Life span

Both overall mean growth rates estimated from cohort II and the computed growth performance index revealed no differences in growth rates across-shore. *Eumarcia paupercula* is a fast growing species (see also Table 6.2); taking into account that the maximum size recorded for the species in the literature is 42 mm (Branch *et al*., 2010). Theoretically, it would take 17 months for a clam to reach this size, regardless of changes in growth rates with age. This assumption is supported by the life span (1.3 years) estimated for the largest individual recorded in the sampling, and that of 1.97 years estimated for this species in Maputo Bay.

A review on the life span and growth rates for different species is presented in Table 6.3. As growth rates are determined using various indicators (K, Φ' and ΔL), this table only considered those that used ΔL. The life span for *Eumarcia paupercula* (1.97 yrs.) for the L_{max} recorded of 38 mm is shorter than that estimated for the venerid *Ruditapes bruguieri* (6.6 yrs.) when the L_{max} (36 mm) was smaller than that of this study. This suggests a latitudinal variability in the growth parameters and life spans within the Veneridae, when the local environmental conditions are favourable to growth. In fact, Urrutia *et al*. (1999) found that the growth of *Ruditapes decussatus* was slower than in other previous studies from similar latitudinal ranges, due the low food concentration in their study site. Thus, size (McLachlan *et al*., 1996) is not the only factor related to the life span, but also the latitude and local environmental conditions. Similarly, life span of *Mesodesma mactroides* increases with latitude within South America (Fiori & Defeo, 2006). Another contrasting finding of size and life span obtained from the review in Table 6.3 is that by

Turra *et al*. (2014) in *Tivela mactroides* – smaller maximum size produced longer life span than the larger maximum size in the same area three years later.

Life span in clams can vary from one to hundreds of years (Cardoso & Veloso, 2003; Brix, 2013). The oldest clam ever recorded is the ocean quahog *Arctica islandica* in Iceland, estimated at 507 years (Brix, 2013). Within the short-lived species (< 5 years), there are intraspecific differences in the life span between geographical regions. For example, the life span of *D. hanleyanus* from Brazil (1.44 years) is shorter (Cardoso & Veloso, 2003) than the 4.96 years estimated from Argentina (Herrmann *et al*., 2009). Also, even within an identical geographical area, life span can differ between different populations (Riascos *et al*., 2008; Turra *et al*., 2014). Regardless of the method used for age determination, this may mean that many other factors are contributing to the intraspecific variability in the life spans.

Genetic factors also contribute to the variability of the life span in clams (Abele *et al*., 2009). In fact, the large infaunal clams with thick shells have a longer life span, partly because they experience lower predation pressures than those with lighter shells. According to Abele *et al*. (2009), the species with long life span may have enhanced their genomic life story by increasing the reproductive output at old ages. The mechanism for adjustment of the reproductive output include low spawning frequency (Abele *et al*., 2009), reproductive capacity regardless of age and lack of a post reproductive stage (Bauer, 1987), features which characterize most species with long life spans.

The life span of *Eumarcia paupercula* can be considered short, based on the largest individual (38 mm) having a lifespan of just 1.30 years. Since cohort II was followed for ten months and a mean length of 32.50 mm (lower shore) was recorded from an initial mean of 5.59 mm, this estimation is considered consistent for the species. The shorter life span of clams recorded from tropical regions (Alagarswami, 1966), makes *E. paupercula* fit in with the tropics group, when compared to the temperate group, which live longer, such as reported for *Mya arenaria* (15 years) in the Baltic Sea (Filippenko & Naumenko 2014). Nevertheless, life span can change among different cohorts in the same beach, or among different populations from the same geographical area (McLachlan *et al*., 1996). The relatively high growth rates and the short life span of *E. paupercula* in Maputo Bay constitute good characteristics for an exploited population, since they facilitate rapid recovery of the population.

Table 6.3. A comparison between growth parameters for various clam species. Letters in brackets within species' column mean family: C = Carditiciae; Co = Corbiculidae; D = Donacidae; M = Myidae Ma = Mactridae Me = Mesodesmatidae; P = Psammobiidae and V = Veneridae.

Species	Location (latitude)	Temperature (°C)	L_{max} (mm)	Life span (years)	Growth rates (mm/month)	Reference
Donax incarnatus (D)	India - 12°27'N	35[iii]	26.10	>1.25	0.30 – 3.22	Thippeswamy and Joseph, 1991
D. hanleyanus (D)	Brazil, 23°03'S	-	22.38	1.47	-	Cardoso and Veloso, 2003
***Eumarcia paupercula* (V)**	**Mozambique – 25 5 4'S**	**22.2 – 30.9**	**38.00**	**1.97**	**0.24 – 6.30[iv]** **0.14 – 4.96[v]**	**This study**
Tivela mactroides (V)	Brazil – 25°54'S	-	32.47	2.4	-	Turra *et al*., 2014
Gafrarium tumidum (V)	India – 08°35' -09°25'N 35'	-	37.70	3	0.38 – 2.24	Jagadis and Rajagopal, 2007
T. mactroides (V)	Brazil – 25°54'S	-	26.04	3.3	-	Turra *et al*., 2014
Donax trunculus (D)	Italy – 41°55'N	-	37.00	4	-	Zeichen *et al*., 2002
D. hanleyanus (D)	Argentina – 37°19'S	9.1 – 24.8	44.00	4.96	-	Herrmann *et al*., 2009
D. trunculus (D)	Turkey – 40°55'N	8.3 – 27.6	44.8	6	-	Deval, 2009
Mya arenaria (M)	Germany – 54°40' – 54°60'N	-	50.10	6	0.12 – 0.84	Filippenko and Naumenko, 2014
Ruditapes bruguieri (V)	Korea – 33°12' - 33°30'N	13.0 – 29.0	36.00	6.5	-	Silina, 2014
Meretrix meretrix (V)	India – 8°45'N	25.0 – 31.0	91.00	7.8	0.15 – 2.20	Narasimham *et al*., 1988
Mercenaria mercenaria (V)	USA – 37°15'N	4.0 – 27.0	84.00	9	-	Harding, 2007
Cardita affinis (C)	Colombia – 03°55'N	-1.2 – 0.5	39.00	9.21	0.6 – 9.8	Riascos *et al*., 2008
Cardita affinis (C)	Colombia – 03°55'N	-1.4 – 1.5	40.00	17.25	-	Riascos *et al*., 2008

[iii] Highest sediment temperature
[iv] Estimated from Mark-recapture
[v] Estimated from LFA

CONCLUSION

Both the mark-recapture experiment and LFA detected seasonal differences in growth of *E. paupercula*, with lowest growth rates recorded during winter; however, there was not enough variation in any of the physical factors to cause major changes in growth rates of *E. paupercula* in Maputo Bay. This is not a negative result; in fact it is typical for tropical versus temperate sites, the later being very seasonal. An establishment of an *in situ* mark-recapture experiment in other areas with known differences in environmental parameters with Costa do Sol might help in discerning the effects of these factors on the growth of *E. paupercula*.

In general, *E. paupercula* can be considered a fast growing species (2.53±1.65 mm/month) with a life span of only 1.97 years. Although the final length of *E. paupercula* did not differ across the shore, this study showed growth pattern differences between the lower shore and the other tidal areas. While the growth on the lower shore was faster for clams of smaller size classes, in the middle and upper shores, the mid-range size classes grew faster. Nonetheless, it is unclear as to what the forcing mechanism/mechanisms for these differences and similarities are. Biotic factors, such as predation have to be assessed to further explain growth patterns in *E. paupercula.*

Both the mark-recapture experiment and LFA produced similar growth patterns; hence both are considered suitable analytical methods of growth patterns in this species. The annual growth rates obtained from length-frequency analysis appeared to be considerably influenced by the high collection season. The use of other approaches, such as analysis of growth rings, may improve the understanding of the seasonality of the growth in this species. The formation of growth ring occurs when growth rates are decreased (Urrutia *et al*., 1999). This phenomenon usually takes place in winter.

Chapter 7: Synthesis and management recommendations

The hitherto neglected biological features of *Eumarcia paupercula* were investigated by the current study, including aspects pertaining to growth and reproductive cycles. In addition, an assessment of the ecological features of the population structure was determined for the population of *E. paupercula* in Maputo Bay. The overall objective of the present study was to investigate the population structure and biological aspects of *E. paupercula*, as well as its status of exploitation and importance to the local community. A study on growth and reproductive patterns of *E. paupercula* was essential to connect the temporal and spatial distribution aspects of the species with the exploitation parameters in Maputo. Research instruments included *in-situ* experiments, interviews, and laboratory work.

Biology and population structure of Eumarcia paupercula in Maputo Bay

The population structure of *E. paupercula* is outlined in Chapter 5. During this study, the largest *E. paupercula* individual recorded measured 43 mm from the collectors catches and 38 from the sampling. The study showed variability in size distribution across-shore, with larger individuals concentrated on the middle shore. The study demonstrated strong month-by-month changes in *E. paupercula* sizes and density compositions; therefore, analysing the species in a seasonal level may lead to biased conclusions, due the dynamic of the population. It is important to note that this structure may change among various clam grounds throughout the Bay, as differences in sediments, substrates and beach slope change. For example, Luis Cabral is an estuarine area with a dominance of muddy sediments; *E. paupercula* also occurs there, albeit in lower densities and smaller sizes (Scarlet, 2005). Likewise, at Pescadores and Inhaca Island, *E. paupercula* is associated with sea grasses and its distribution is sparse. The present study was carried out on a population collected from a flat sandy beach. As factors influencing distribution patterns may vary, this study highlights the collection and reproductive patterns as regulating the temporal size and density variability.

With the use of VBGF, the present study showed that *E. paupercula* is a fast-growing species, with strong estimated seasonality growth rates ($C > 0.8$). The best growth rates occur during the summer, and the estimated age span of 1.97 years is considered typical for fast-growing species. It was concluded that the use of length-frequency distributions and growth-increment analysis are both suitable to study the growth of *E. paupercula*, as both methods led to comparable growth rates. The effects of collection and recruitment have yet to be analysed and discussed; this will assist to understand better the influence of removing larger and adding smaller individuals in the growth estimations using length-frequency distribution. The unimodal histograms of only small sizes during the winter months (see Chapter 5) indicate a possible effect of the recruitment in a biased estimation of growth rates.

Although spawning of *E. paupercula* occurs throughout the year, two to three peaks during the year take place for the studied population. Recruitment follows spawning peaks, which occur mainly when an interaction of environmental conditions are conducive for the process. Yet, a single environmental parameter, except rainfall, did not indicate an effect on the reproductive cycle of this species. Consequently, recruits were also observed throughout the year, although a high density was recorded in the winter. When assuming that the recorded recruits originated from the adult stock of the same population, it can be inferred that an initial settlement occurs between 20-40 days after fertilization. The fluctuations in dry meat showed that the percentage of dry meat in relation to the total fresh weight can vary from 3.15-13.04%. This means that the meat yield is affected by seasonality of spawning of *Eumarcia paupercula*;

Management recommendations for Eumarcia paupercula exploitation in Maputo Bay

This study has highlighted the importance of shellfish collection for women in coastal areas. As found in previous studies, and confirmed in this study, the involvement of women in artisanal fisheries has a significant impact on household income. The collection of *Eumarcia paupercula* is primarily done for income generation. The suggestions made in this section to better explore the beaked clam in Maputo Bay are based on the findings of interviews conducted, population structure analysis, the known platform as well as the level of organization of the fishery sector and fishing communities.

The establishment of a closed season and a set of a daily bag limits are the most significant management approaches that could be considered in a short to medium-term. It was found that if a size preference of larger clams for collection (≥ 22 mm) (Chapter 6) and significant recruitment takes place (Chapter 5), then a minimum legal size may not be needed for immediate consideration; however, if an increase in the collected sizes takes place, a higher sale price can be applied. Although the introduction of a daily bag limit was not well supported by most collectors, such a measure would have major ecological implications on this population. The implementation of a daily bag may allow extension of the collection season and ensure that the spawning stock breed before being collected. The rapid decline of collectors and amounts of clam collected over the collection season revealed that the daily amounts collected per person were high; this was expected, as the main destination of catches is to sale. Regarding the establishment of a closed season, a woman in Costa do Sol beach affirmed during October 2013 interviews:

> *I would postpone the commencement of my collection to October or November, instead of September, because the clams I am collecting now are small and I can only sell them to the dealers, who pay less. Nevertheless, if I do that, my catches in the next month would be obviously less because my fellow collectors are already in the grounds, despite the fact that I could sell a kilogram in a bit higher price. We have been waiting long for this season, and this makes us come to beaches earlier to collect clams. At the same time, the clam dealers may keep the clams I sell to them in the "viveiros" for a month or more to sell them when are bigger.*

The opinion of the collector reveals that if a closed season is established, this should be somewhere between April and October. More deeply, her declaration shows that profound work has to be carried out with collectors, since they may not agree on this timing, depending on which stakeholders of the *E. paupercula* web market they sell to. In the artisanal fisheries of Mozambique, it is has been shown that if stakeholders work together and build social support networks which include the government, fishers will generate secondary benefits (Menezes et al., 2009); these include the building of social infrastructures, which are important in fighting poverty within fishing communities.

From the community-based perspective, small associations of clam collectors may emerge to enhance the profitability of their activity. They can keep the small collected clams in *viveiros* or other culture facilities on the area until they grow and fetch a better market price. In addition, the collectors would be involved in creation of brood stock sanctuaries (which are the *viveiros*) in the future if repopulation is necessary. Besides, processing facilities would add a value to the product, and the promotion of their use should be led by the IDPPE through sponsoring and outreach. For instance, with the growth of the urban area and the economic development in the past years, it can be found in the supermarkets of Maputo city frozen mussels with prices around $USD 35 per kilogram, while in the collection area the prices remain below $USD 2 fresh weight with shell. Nonetheless, in the near future culture of *E. paupercula* has to be considered.

Small no-take areas of less than 5 km^2 may be introduced in a rotational approach around Maputo Bay. The recovery time of the species after an intense collection has to be assessed in future studies, to decide better the timing between rotations of a no-take zone. Since a "natural" movement of collectors around clam grounds takes places in Maputo Bay, after depletion of fishable sizes in a certain area, it should be ensured that the area left is completely closed for collection. A year after the present study, a higher number of collectors was observed in Miramar Beach and five – seven years before, the most collection was at Pescadores (Scarlet, 2005). This indicates that some collectors still use the previous grounds, despite the greater effort required, which may lead to a high-density decline of *Eumarcia paupercula* on that ground. In the application of any management measure, an understanding of the factors regulating the collectors behaviour and interaction between these factors is crucial to comprehend the fishery system (Hauck et al., 2014). Thus, as a co-management initiative is already present in artisanal fisheries via the existing legislation, it has to be fully applied, with exhaustive involvement of all stakeholders, particularly identifying and protecting the interests of fishers, by promoting social justice. Nevertheless, the Ministry of Fisheries must consider introducing clams and other bivalves in their landings data collection routines, and, therefore, reflect on the better management of the resources.

Detailed studies regarding the reproductive patterns need to be carried out in future research on determination of age at first maturity and spawning effort for *Eumarcia paupercula*. While in this study there no histological analysis applied, with the current data less can be considered about management of the stock based on the reproductive pattern. Below are the pros and cons of an establishment of the suggested management measures in Maputo Bay, based on the data acquired in this study.

Daily bag limit: this measure should be applied when a control committee has been established on the ground to ensure most of harvesters adhere to the limit established. A limit of 6-8 kg per harvester would be enough to extend the collection season by two months, and hence increase the size of collected clams. If number of collectors remains similar to that found in this study over the collection season, this would lead to a removal of 45% of the standing stock per month. It should be noted that these estimations did not include other drivers, such as natural mortality and effects of environmental factors on the density of *Eumarcia paupercula*, but considered the number of collectors and amount collected during the study. As found in the study most collectors use clams as a source of income and the market price is low; these are the main reasons that would cause non-compliance of limits established.

Closed Season: Clam harvesting should be closed between April-September. Although size at first maturity was not determined, *Eumarcia paupercula* individuals spawn at their first year of life. Thus, with major spawning happening in December-January and with recorded growth rates, most individuals would be greater than 25 mm in October, which would allow better profit to harvesters. Also, clams would have spawned during the late winter spawning (August-September) and with the bag limit measure above, more individuals would reach the period of major spawning peak. Constraints for this measure are same as at bag limits, but this would be easily accepted, as collectors already break collection during certain period of the year.

No-take zones: in chapter 2, several localities of occurrence of *Eumarcia paupercula* in Maputo Bay were shown. Possible no-take zones should be rotated among these areas once a removal of over 75% of standing stock has been recorded in the population of Costa do Sol. This measure has more probability to be accepted by harvesters that others; this is because effort is high when less clams are available.

Further research directions

Information on clam stocks in this region is limited. The next step should be to continue collecting reliable data that includes other areas of the Bay, to have a large geographic span of data on collected amounts, which can also assist in the decision making for clam management. Moreover, surveys must include the low-collection season, to understand the socio-economic importance of clam collection for those collectors that continue collection year-round, regardless of the decline in amount of fishable sizes during winter.

In the future, studies should include laboratory experiments of the larval cycle of *E. paupercula,* to assist in the prediction of higher settlement and recruitment periods, and so better understand the stock-recruitment relationships. Further, it has been shown that in many venerids that use of gonad smears, body condition and histological techniques to assess reproductive cycles result in a similar pattern. Though, it would be necessary to include in future studies of the temporal histological analysis of gonads, since the present study marked the first attempt of determination of the reproductive pattern of *E. paupercula*. We also need to understand the dynamics of larval dispersal along Maputo Bay, so as to make better suggestions regarding the application of management approaches, such as no-take zones.

There is a lack of an inaccessible, unfished *Eumarcia paupercula* population in Maputo Bay. In consequence, a reference population for comparison purposes with the studied *E. paupercula* population was not included in the present study. When management approaches like establishments of no-take zones suggested in this study are applied, an inaccessible/less exploited site can arise and the hypothesis that remote sites have a higher animal abundance than the exploited sites can be tested in Maputo Bay populations. Still, a deeper assessment of social aspects of the collection of *E. paupercula* has to take place to guarantee a compliance of management measures, as a failure of several initiatives of clams collection has been documented.

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