# Western Indian Ocean JOURNAL OF Marine Science

Volume 16 | Issue 2 | Jul – Dec 2017 | ISSN: 0856-860X

Chief Editor José Paula

Western Indian Ocean
JOURNAL OF
Marine Science

Chief Editor **José Paula** | Faculty of Sciences of University of Lisbon, Portugal

Copy Editor **Timothy Andrew**

## Published biannually

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**ISSN 0856-860X**

Cover image: Woman collecting ascideans at Ponta Mazondue, Inhaca Island, Mozambique (© José Paula, 2005)

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Volume 16 | Issue 2 | Jul – Dec 2017

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**Instructions for Authors**

# Effect of acidified seawater and high temperature on the survival and behaviour of supralittoral and sublittoral amphipods (Crustacea)

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## Abstract

Amphipods are one of the most diverse groups of marine crustaceans. The impacts of changing environmental parameters on such organisms are unclear. The study aimed to determine the effect of low pH and high temperatures on the survival and behaviour of two amphipods from contrasting environments; namely *Platorchestia cf platensis* (supralittoral) and *Cymadusa filosa* (sublittoral). Amphipods were collected from the field, exposed to artificially acidified seawater (pH 7.0, 6.0, 5.0), and to temperatures of 30 - 39°C. *C. filosa* could not build tubes, and *P. platensis* did not display its normal jumping behaviour but remained burrowed in the sediment at low pH and high temperatures. *P. platensis* was tolerant to 33°C but not to 36°C and 39°C. High temperatures (30°C, 33°C, 36°C) are lethal to *C. filosa* (100% mortality recorded within 10 days). *P. platensis* was able to tolerate pH variations with at least 50% survival at the end of 4 weeks. *C. filosa* do not survive more than 20 days at the lowest pH treatment (7.0). There was no significant difference between survival rates of the males, females and juveniles of both species ($p>0.05$) at the various temperatures and pH. Size and gender had little effect on the tolerance of the individual amphipod species. *P. platensis* was found to be more tolerant to changes compared to *C. filosa*. The current study provides insights into the species-specific nature of responses, survival and behaviour of organisms due to climate change related environmental parameters.

**Keywords:** Amphipods, survival, behaviour, low pH, high temperature

## Introduction

When climatic conditions change, organisms respond primarily by displaying physiological and behavioural adaptations (Somero, 2012; Guerra *et al.*, 2014). Over the last decade, the global average surface temperature has increased by approximately 0.6° C and is projected to increase at a rapid rate (Houghton *et al.*, 2001). Increasing temperature is thought to have an adverse stimulatory effect on metabolism until lethal levels are reached (Byrne, 2011). Richard *et al.* (2015) report that when an organism is exposed to high temperature, there are two particular processes that influence their survival potential; firstly tolerance, and secondly plasticity. Plasticity ensures long term survival as it dictates counter measures for the normal functioning of biological processes to achieve acclimation. However, tolerance only helps in short term survival. Studies on the impacts of temperature on amphipods include that of Tsoi *et al.* (2005), Bedulina *et al.* (2010), Guerra *et al.* (2014), Shyamasundari (1973), Moore and Francis (1986), Timofeyev *et al.* (2009), Madeira *et al.* (2015), Foucreau *et al.* (2014), and Magozzi and Colosi (2015).

Oceanic absorption of carbon dioxide changes the seawater chemistry causing a decrease in pH. If the use of fossil fuels and–greenhouse gases emissions continue at the current rate, the pH is expected to decrease by 0.3–0.4 units per year untill the end of this century, and by 0.67 units by 2300 (Caldeira and Wickett, 2003). The detrimental effects of elevated pH on crustaceans have been described by Fabry *et al.* (2008), Hernroth *et al.* (2012), Long *et al.* (2013), Hauton *et al.* (2009), and Egilsdottir *et al.* (2009). Two adverse consequences on marine biota are expected; namely changes in the internal acid/base balance of marine organisms, and a reduction in calcification rate by calcifying organisms (Hauton *et al.*, 2009; Logan, 2010).

In this paper, we aimed to describe the effects of high temperature and acidic pH on the survival of two amphipods from contrasting environments namely; *Cymadusa filosa* (sublittoral) and *Platorchestia cf platensis* (supralittoral). The objectives were to observe the survival and behaviour of the amphipods at different temperatures ranging from 30 °C to 39 °C and at different pH ranging from 5.0 to 7.0.

## Materials and methods

### Stock collection and maintenance

The species *P. platensis* and *C. filosa* were chosen because they are easily collected and sorted. *P. platensis* were collected from Vieux Grand Port (20°22'37.5''S; 57°43'08.3"E) during the months of September and October 2014. They were quickly transported to the laboratory in plastic bags and kept at room temperature together with a stock of algae (*Sargassum* sp.). *C. filosa* were collected from Pointe aux Sables (20°9'56''S 57°27'3"E) during the months of October and November 2014 from a depth of approximately 50 cm. They were kept in two continuously aerated aquaria stocked with *Ulva* sp. placed in a well-lit area. The aquaria were cleaned weekly by changing approximately 25 % of the water and removing excess detritus from the bottom. Males of both species are characterised by having enlarged gnathopod 2. Males of *C. filosa* have dense plumose setae whereas females have slender setae on their antennae. These characteristics were used to distinguish males from females using either a magnifying glass or a stereomicroscope. Amphipods approximately less than 5 mm and which were not displaying any adult characteristics were classified as juveniles. Organisms were allowed to acclimatize for one week before any experiment was conducted. The physical parameters during the acclimation period were room temperature and a pH of 7.8 ± 0.3 for both species. A salinity of 29 psu for *P. platensis* and 33 - 36 psu for *C. filosa* was recorded during this period. No mortality was observed during the acclimation period.

### Experimental set up

*P. platensis* were kept in beakers (1000 ml) filled with moist sediment and small pieces of algae. Seawater was added to the beakers every week, or as and when needed to maintain humidity, and algae (*Sargassum* sp.) were added when required. *C. filosa* species were kept in small triple vented Petri dishes (to allow free passage of air) containing 14 $cm^3$ of seawater collected from Pointe-aux-Sables. A single individual amphipod was kept in each Petri dish. A small piece of thallus (*Ulva* sp.) was added as food together with some detritus found at the base of the stock aquarium. Approximately 50 % of seawater was changed every 2 - 3 days. The algae in the Petri dishes were replaced every day, or as required. All Petri dishes were kept in a well-lit area in the laboratory.

### Effects of increased temperature

10 males, 10 females and 10 juveniles of each species with the experimental setup described above were left at room temperature as a control. Experimental trials were performed in incubators. The physical parameters used for the thermal treatments for *P. platensis* were 33± 0.5 °C, 36 ± 0.5 °C and 39 ± 0.5 °C. Salinity was maintained at 29 psu and pH at 7.8. The physical parameters for *C. filosa* consisted of temperatures of 30 ± 0.5 °C, 33 ± 0.5 °C and 36 ± 0.5 °C. Salinity varied from 33 - 36 psu and pH was maintained at 7.8 ± 0.3. For each set of temperatures, 10 males, 10 females and 10 juveniles of each species were used. The amphipods were placed in preheated Petri dished or beakers for each specific temperature used.

### Effects of acidic pH

10 males, 10 females and 10 juveniles of each species with the same experimental setup were left at room temperature as a control. pH of seawater was adjusted by bubbling carbon dioxide up to a pH of 5.0 (Long *et al.*, 2013). The resulting seawater was then added to seawater from the site to obtain the desired pH. For both species, pH of 5.0, 6.0 and 7.0 were used and maintained at room temperature. In the case of *P. platensis*, the salinity was maintained at 29 psu and pH at 7.8. Salinity varied from 33 - 36 psu and pH varied from 7.5 - 8.1 for the *C. filosa*. For each set of pH treatments, 10 males, 10 females and 10 juveniles of each species were used.

Length of the amphipods were measured upon the completion of the experiments.

### Statistical analyses

All statistical analysis were done using IBM SPSS statistics version 21. Normality and equal variance of the data were tested by the Shapiro-Wilk test and Levene's test respectively (Zhang *et al.*, 2015). Statistical significance was tested at $p$-value <0.05. Non-parametric Kruskal-Wallis ANOVA (assumptions for normality

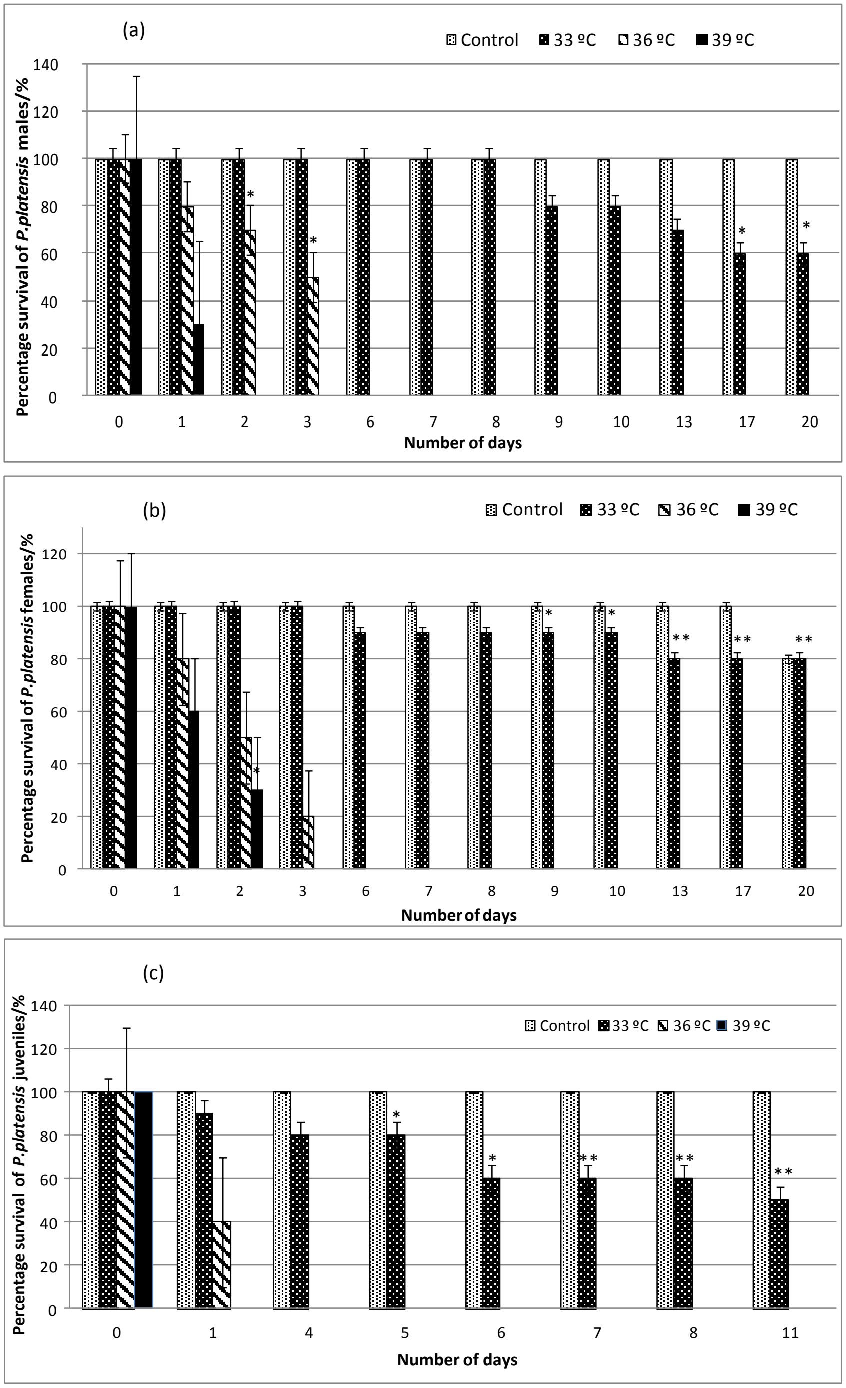

**Figure 1.** Percentage survival (± S.E) of *Platorchestia cf platensis* (a) males, (b) females and (c) juveniles at different temperatures (n=10 at each temperature and n=5 at control). * and ** indicate significant difference at $p < 0.05$ and $p < 0.01$ respectively, between the control and the heat shock treatments at each time point.

or homocedasticity of data were not met) was performed to find out if the differences between the mean survival rate of the control and that of the treatments are statistically different (Madeira *et al*., 2015). Moreover, Kruskal-Wallis tests were performed to determine if there was any significant differences between the mean survival rate of males, females and juveniles of both *P. platensis* and *C. filosa*. A regression analysis was done to investigate the relationship between *C. filosa* body length (measured after the experiment) and the respective tube length built by the latter in the control, and the different treatments. The Pearson correlation was used to determine the significance of that relationship (Appadoo and Myers, 2003).

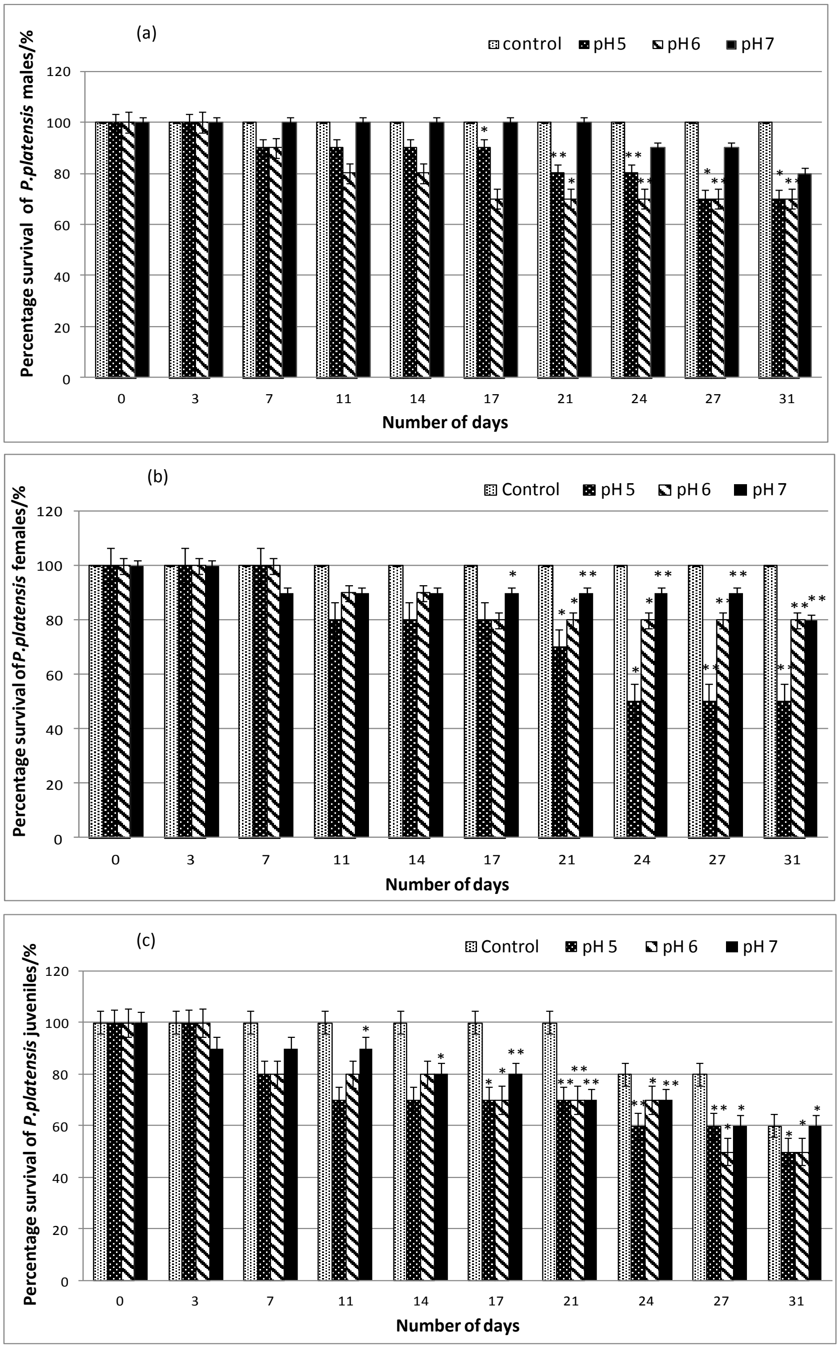

**Figure 2.** Percentage survival (± S.E) of *Platorchestia cf platensis* (i) males, (ii) females and (iii) juveniles at different temperatures (n=10 at each pH and n=5 at control). * and ** illustrate significant difference at p< 0.05 and p < 0.01 respectively between control and the pH treatments at each time point.

# Results

## Survival of *Platorchestia cf platensis* at different temperatures

At 36 °C and 39 °C, the amphipods (males, females and juveniles) did not survive more than 3 days (Fig. 1). At 33 °C, 60 % of males, 80 % of females and 50 % of the juveniles were alive at the end of the experiment. The mean survival rate at 33°C, 36°C and 39°C was significantly different compared to the control ($p<0.05$). Moreover, there was no difference between mean survival rates of the male, female and juvenile *P. platensis* (33 °C: df=2, n=32, p=0.057; 36 °C: df=2, n=13, p=0.893; 39 °C: df=2, n=9, p=0.990)

## Survival of *Platorchestia cf platensis* at different pH

It was observed that there was a high survival rate in all 3 treatments (at least 50 % of the males, females and juveniles of this species were alive at the end of

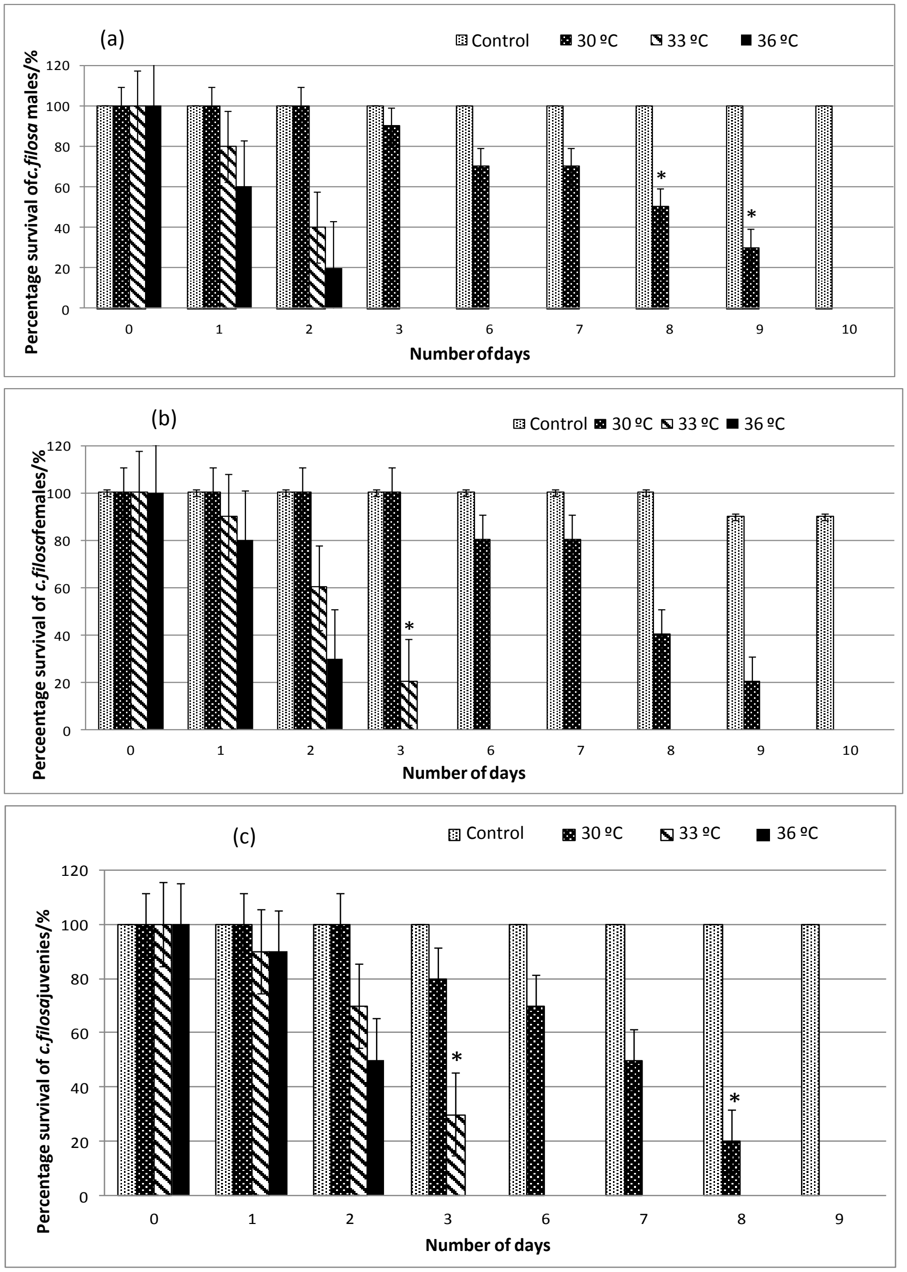

**Figure 3.** Percentage survival (± S.E) of *Cymadusa filosa* (a) males, (b) females and (c) juveniles at different temperatures (n=10 at each temperature and control). *p < 0.05 indicate significant difference between the control and the treatment groups at each time point.

4 weeks (Fig. 2). Mean survival rate (of males, females and juveniles)–was significantly different at all pH treatments ($p<0.05$) compared to the control, but no difference was found between the treatments ($p>0.05$). No difference was observed between the survival of the males, females and juveniles of *P. platensis* (pH 7.0: df=2, n=30, p=0.060; pH 6.0: df=2, n=30, p=0.087; pH 5.0: df=2, n=30, p=0.193).

### Survival of *Cymadusa filosa* at different temperatures

At temperatures of 33 °C and 36 °C, high mortality rates were observed within 6 days (Fig. 3) for males, females and juveniles. At a temperature of 30 °C, they survived for approximately 8 to 9 days. The mean survival rates recorded for the three treatments are significantly different from the control for males and juveniles ($p<0.05$). There was no difference between the survival rates of *C. filosa* males, females and juveniles (30 °C: df=2, n=26, p=0.945; 33 °C: df=2, n=14, p=0.988; 36 °C: df=2, n=12, p=0.924).

### Survival of *Cymadusa filosa* at different pH

The males and females survived for approximately 3 weeks at pH 7 and pH 6, respectively, and for 2 weeks at

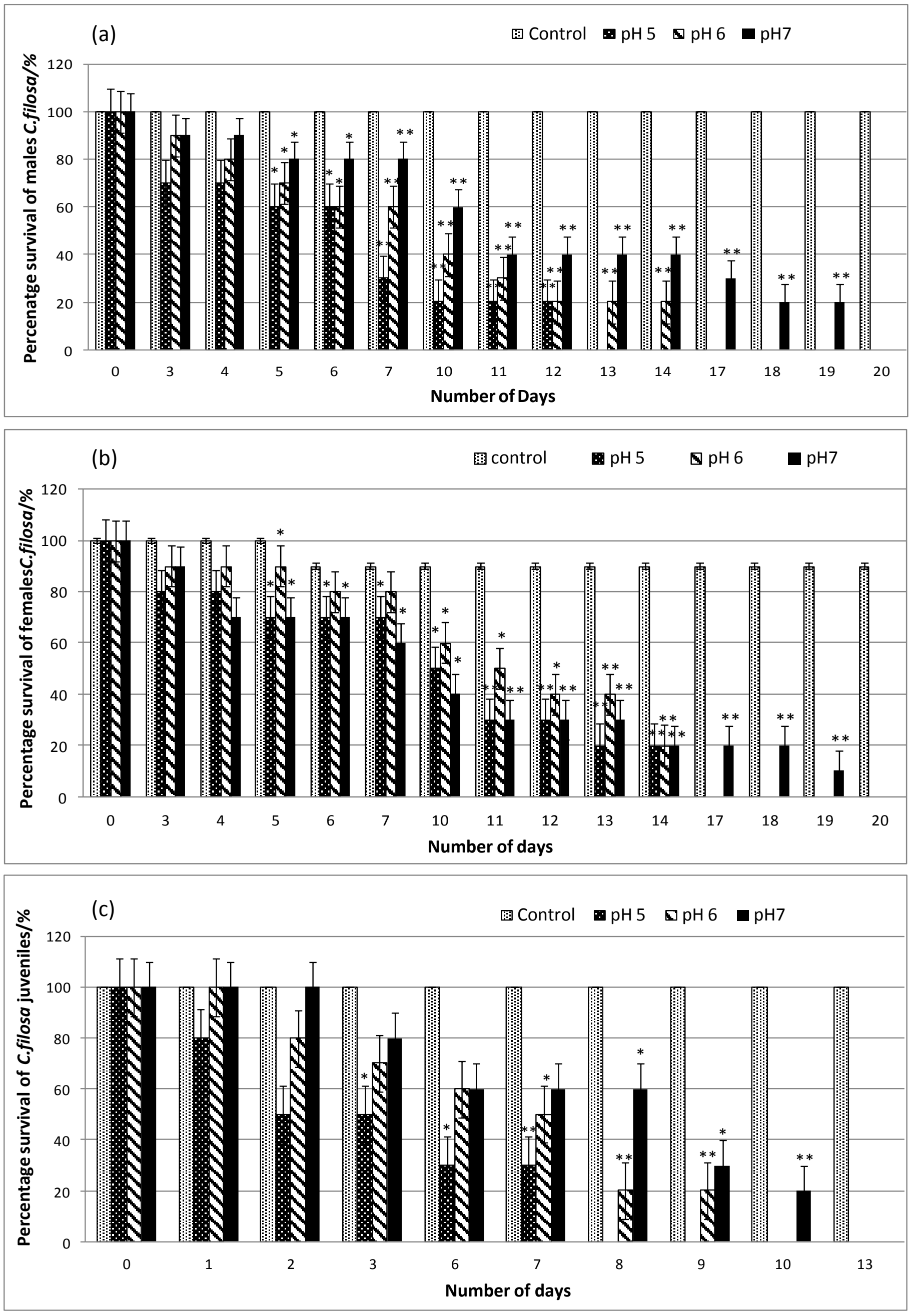

**Figure 4.** Percentage survival (± S.E) of *Cymadusa filosa* (a) males, (b) females and (c) juveniles at different pH (n=10 at each pH and n=5 at control). *p < 0.05 and **p < 0.01 indicate significant difference respectively between the control and the acidification groups at each time point.

pH 5 (Fig. 4). High mortality rates were observed for the juveniles. Statistically, there was no difference between the survival rates of the males, females and juveniles of this species (pH 7.0: df=2, n=40, p=0.393; pH 6.0: df=2, n=33, p=0.645; pH 5.0: df=2, n=29, p=0.798).

## Behaviour of *Platorchestia cf platensis*

Under normal conditions, *Platorchestia cf platensis* were all well burrowed in the sediment. When the beaker was disturbed (moved or shaken) during the observations, the latter would actively jump for some minutes before burrowing back into the sediment. They were very "jumpy and energetic" (Simpson, 2011).

Generally, *P. platensis* (males, females and juveniles) were all well burrowed in the sediment during the observations in both acidic and thermal treatments. *P. platensis* were lethargic (less energetic and jumpy) at temperatures 36°C and 39°C compared to those at temperature 33°C, and the control. The same behaviour was displayed in the hypercapnic treatments.

### Behaviour of *Cymadusa filosa*

Tubes were made with detritus and amphipod silk, while in some cases, the algae were used as part of the construction materials for the tubes. These materials were glued together with amphipod silk. In some cases, multiple tubes were built (an average of the tube lengths were used for statistical purposes). A high positive linear relationship between tube length and body length of *C. filosa* (males n=9, r=0.825, $r^2$=0.861, p=0.006; females n=8, r=0.956, $r^2$=0.978, *p*=0.000; and juveniles n=9, r=0.941, $r^2$=0.885, *p*= 0.010) was obtained in the control (Table 1).

The amphipods did not build tubes at pH 5. In the hypercapnic treatments, there was no relation between the body length and the tube length of *C. filosa* (Table 1) males (pH 7.0: n=5, r=0.485, $r^2$=0.235, p=0.408; pH 6.0: n=5, r=0.179, $r^2$=0.032, p=0.773), and females (pH 7.0: n=4, r=0.169, $r^2$=0.028, p=0.831; pH 6.0: n=5, r=0.539, $r^2$=0.290, p=0.349). No tubes were built at pH 5 and pH 6 by the juveniles. Only 1 juvenile was seen to build tubes at pH 7. The tube appeared at day 6. At day 8, 2 tubes were built by the same amphipod.

In the treatments, tubes were observed only at 30°C and the percentage of individuals that built tubes at this temperature was very low compared to the control. There was no relationship between the body length and tube length (Table 1) for males (n=5, r=0.253, $r^2$=0.064, *p*=0.681), females (n=4, p=0.910), and juveniles (n=3, r=0.777, $r^2$=0.603, *p*=0.433). It was observed that those individuals that did not build tubes died prior to those that built tubes.

## Discussion

### Survival of amphipods at different temperatures

It is well known that rising temperature is one of the abiotic factors that affects survival of amphipods (Moore and Francis, 1986). The survival rate of the amphipods decreased with increasing temperatures. In this study there were no significant differences between the mean survival rates of males, females and juveniles of the same species. Similar observations have been reported in many studies (Shyamasundari, 1973; Edwards and Irving, 1943; Foucreau *et al.*, 2014). Shyamasundari (1973) observed that size and sex of amphipods *Corophium triaenonyx* did not have an effect on the tolerance of the amphipod to different temperatures. Male and females crab (*Emerita talpoida*) have the same response to increased temperature (Edwards and Irving, 1943). Hence, it can be inferred that the physiological responses in these organisms do not differ between genders, or between juveniles and adults.

*C. filosa* do not tolerate high temperatures. It was observed that most of the *C. filosa* individuals that did not built tubes died prior to those that built tubes. A similar result was obtained in the study by Shyamasundari (1973) where the amphipod *Corophium triaenonyx* that were within their tubes were found to be more tolerant to changes in physical parameters.

*P. platensis*, on the other hand, showed tolerance to a temperature of 33°C. However, survival rate decreases significantly with higher temperatures. A study by

**Table 1.** Relationship between body length and tube length of *Cymadusa filosa*.

| Category | Regression Model | n | F | *P* |
|---|---|---|---|---|
| Males (Control) | y= 0.961 + 0.709x | 9 | 14.972 | 0.006 |
| Females (Control) | y= 0.889 + 0.739x | 8 | 261.94 | 0.000 |
| Juveniles (Control) | y= -2.372 + 0.923x | 9 | 46.05 | 0.010 |
| Males (pH 7.0) | y= 11.334 + 0.419x | 5 | 0.922 | 0.408 |
| Males (pH 6.0) | y= 6.112 + 0.319x | 5 | 0.1 | 0.773 |
| Females (pH 7.0) | y= 0.173 + 0.834x | 4 | 0.59 | 0.831 |
| Females (pH 6.0) | y= -3.246 + 0.947x | 5 | 1.227 | 0.349 |
| Males (30 °C) | y= 25.944 - 0.885x | 5 | 0.205 | 0.681 |
| Females (30 °C) | y= 0.934 + 0.05x | 4 | 0.910 | 0.016 |
| Juveniles (30 °C) | y= -3.504 + 1.138x | 3 | 1.525 | 0.433 |

Moore and Francis (1986) with the amphipod *Orchestia gammarellus* (also family Talitridae) shows similar results. It is believed that this tolerance to thermal stress is due to the evolutionary adaptability of talitrid amphipods to non-marine conditions (Moore and Francis, 1986). The peroxidase enzyme is crucial for the resistance to oxidative stress caused by high temperatures (Timofeyev *et al*., 2009). These authors also concluded that in the freshwater amphipod *E. cyaneus*, this enzyme showed a ''clear tendency to reduced activities with exposure time'' which explains its early death compared to *G. lacustris* which expressed peroxidase activity for a longer period. Thermotolerance in amphipod species is also regulated by heat shock proteins which provide a certain degree of protection to the functioning of cells against fluctuations in temperature (Shatilina *et al*., 2011).

### Survival of *Cymadusa filosa* v/s *Platorchestia cf platensis*

In the present investigation, it was observed that *C. filosa* was more sensitive and has higher mortality rates compared to *P. platensis*. A similar result was obtained in the study by Bedulina *et al*. (2010) which found that *Gammarus oceanicus* (a sublittoral species) is less resistant to higher temperatures than the supralittoral species *Orchestia gammarellus*. It was argued that these differences may be due to the adaptations of these species to the various thermal conditions arising from their different natural habitats. Nevertheless, effects of "phylogenetic history, body size and other species-specific traits" also play a key role (Bedulina *et al*., 2010). Madeira *et al*. (2015) reports that organisms living in the higher intertidal zone had higher basal levels of HSP70. Consequently, higher basal biomarker levels can be attributed to effective buffering of thermal stress effects. Moreover, Magozzi and Calosi (2015) showed that shrimps (such as *P. elegans*) residing in variable environments have higher upper thermal limits which make them more tolerant to increasing temperatures at the cost of higher metabolism, as opposed to shrimps thriving in stable environments (such as *P. serratus*). They also attribute these differences to species evolutionary ecology, and not phylogenetic relations.

### Survival of amphipods at different pH

The current investigation demonstrated that *C. filosa* is lethally affected when exposed to acidified seawater. Multiple studies on crustaceans show similar results (Long *et al*., 2013; Zhang *et al*., 2015; Miles *et al*., 2007). A recent study by Long *et al*. (2013) reports that mortality rate of the crabs *Paralithodes camtschaticus* and *Chionoecetes bairdi* decreases with decreasing pH. The sea urchin *P. miliaris* also has low survival rates (Miles *et al*., 2007) at a pH of 6.16. This can be explained by the disruption of the acid-base balance responsible for sustaining protein conformation and ultimately enzymatic activity and metabolism, or a reduction in calcification rate caused by increase in hydrogen ions in seawater (Hauton *et al*., 2009). Furthermore, reduction in survival rate in calcareous marine organisms can be explained by "physiological compensation of maintaining normal processes such as growth, shell formation and metamorphosis in low pH marine environment" (Wood *et al*., 2008; Zheng *et al*., 2010).

On the other hand, *P. platensis* had low mortality rates when exposed to low pH values. Comparable results were obtained when such studies were undertaken with other crustaceans. Hendriks *et al*. (2015) stated that some calcifying organisms can biologically control their internal environment of carbonate deposition. They do so by producing sharp pH gradients in their diffusive boundary layer which controls the pH in extracellular fluid, or by controlling the deposition in a regulated, intracellular environment.

### Survival of *Cymadusa filosa* v/s *Platorchestia cf platensis*

Different species have different responses to fluctuations in environmental parameters even within the same taxon (Zheng *et al*., 2015). The majority of crustaceans are water-breathers (including *C. filosa*) and therefore in close contact with their exterior environment via their gills (Taylor and Taylor, 1992, cited in Whiteley, 2011). Environmentally induced acidosis disrupts normal excretion of carbon dioxide through the gills which causes the concentration of the latter to increase in haemolymph. This in turn disrupts the acid-base equilibria of body fluids required for protein function (Whiteley, 2011). pH disbalance in the haemolymph is important to maintain oxygen supply. Hypercapnia therefore can decrease the oxygen affinity of the respiratory pigment and hence reduce oxygen delivery to the tissues (Taylor and Whiteley, 1989, cited Whiteley, 2011). Such disruptions can therefore severely impact survival of crustaceans in hypercapnic conditions.

*P. platensis*, on the contrary, had high survival rates at the different pH used. Being a supratidal species, *P. platensis* lives in beach wracks. They are not fully in contact with seawater, as opposed to *C. filosa*. Moreover, they are also air-breathers (Griffiths *et al*., 2011). It can therefore be inferred that elevated seawater pH does not have the same negative effects as described by Whiteley *et al*. (2011) on water-breathing crustaceans. In addition, impacts on the survivorship may take a longer time than the experimental duration.

### Behaviour of *Platorchestia cf platensis*

Impacts of environmental parameters on the visible behaviour of talitrid amphipods is not well documented. The organisms were all in burrows during the observations which is thought to help them combat heat stress and desiccation (Karlbrink, 1969). Moreover, it is known that *P. platensis* can actually tolerate up to 30 % water loss (Poulin and Latham, 2002). It is known that high temperatures induce physiological responses such as production of antioxidant enzymes and heat shock proteins (Timofeyev *et al*., 2009). Energy resources of *P. platensis* could have been utilised for this purpose rather than displaying the active jumping behaviour.

The observed change in behaviour at different pH may be attributed to the acid - base disequilibrium induced by low pH. Energy resources might have been dedicated to essential reactions to maintain life (Whiteley, 2011). However, this effect might be limited given the high survival rate of *P. platensis* in all the pH treatments.

### Behaviour of *Cymadusa filosa*

Observations on the tube building behaviour and the relationship with body length (control experiment) concur with observations made in other studies such as on *Cymadusa filosa* (Appadoo and Myers, 2003), *Ampithoe laxipodus* (Appadoo and Volbert, 2011), *Lembos websteri* and *Corophium bonnellii* (Shillaker and Moore, 1978).

No relationship between body length and tube length was observed at temperatures of 30°C, as the survival rate was very low at this temperature. The organisms may have died before completing their tubes. Moreover, vital energy might have been diverted to the production of enzymes and proteins to counter the negative effects of elevated temperature (Timofeyev *et al*., 2009). In a previous study, Whiteley (2011) puts forward that exposure to hypercapnia has adverse effects on the growth and reproduction of crustaceans by diverting their vital energy towards the continuation of essential compensatory responses. The inability to build tubes makes these tube-building amphipods vulnerable to predators and also to the fluctuating environmental parameters.

One of the limitations of this study was that salinity used is that closest to the stock culture, and varies for each species. Salinity amplitude for *C. filosa* during the experiments may have been high and may have confounded the results.

## Conclusion

Chronic exposure to acidified seawater and elevated temperatures are detrimental to the studied amphipod species. This study demonstrated that *P. platensis* (a supralittoral species) is resistant to extreme pH values and to small increases in temperature. On the other hand, *C. filosa* (sublittoral species) cannot tolerate increases in temperature. Moreover, *C. filosa* is very sensitive to low pH. Survival rates of males, females and juveniles of the studied species do not significantly differ from each other. It can thus be inferred that gender and size does not affect the fitness of the organisms. The data from the experiments confirm the hypothesis that supralittoral species are robust (mainly because of the high variability in their natural environment and hence better adaptation mechanisms) and will survive better in the predicted climate change scenarios, as opposed to the sublittoral species which thrives in an environment where variations are minimal (compared to supralittoral environment). Behaviour was affected in all of the organisms when they were subjected to changes in temperature and pH. *P. platensis* could not display its normal active jumping behaviour but remained burrowed in the sediment when subjected to changes in physical parameters. *C. filosa* could not build tubes at high temperatures and low pH. The current study provides insights on the species-specific nature of impacts of climate change-related environmental parameters on marine organisms. It shows that it is not only survival but individual behaviours that are also affected. Such sublethal effects will definitely have consequences on the fitness of these individuals and needs further attention and research.

## Acknowledgements

We are thankful to the University of Mauritius for logistic facilities. We are also grateful to the Ministry of Fisheries for permission granted to work at the sites and to collect marine organisms during the study period.

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# Long-term changes in seagrass coverage and potential links to climate-related factors: the case of Inhambane Bay, southern Mozambique

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## Abstract

Changes in seagrass coverage in Inhambane Bay (southern Mozambique) from 1992 to 2013 were assessed using SPOT 5 and Landsat imagery mapping methods with support of extensive groundtruthing. Over a 21-year period, the total seagrass area was reduced from 12,076 ha to 6,199 ha (51% of the original area). 2001 was the year when seagrass occupied the smallest area in Inhambane Bay with 5,641 ha, apparently related to the impacts of tropical Cyclone Eline with winds of around 200 km/h, and lasting for 29 days with widespread damage on human and natural infrastructure, However, a steady seagrass recovery was observed between 2001 and 2004, where 958 ha of seagrass was restored naturally. Eight seagrass species occur in Inhambane Bay forming six seagrass community types. The three largest communities were *Thalassia hemprichii/Halodule uninervis* with 2,305.5 ha, followed by *Thalassodendron ciliatum/Cymodocea serrulata* with 2,280.3 ha, and *Halodule uninervis* with 1,393.9 ha. The loss of seagrass occurred mainly in the *T. hemprichii/H. uninervis* and H. *uninervis* communities. A specific study on *T. hemprichii* conducted at Barra Peninsula and Ilha dos Porcos showed that the total seagrass biomass varied between 947.08 ± 31.09 g DWm-2 and 1636.82 ± 80.52 g DWm$^{-2}$, respectively, being low at Barra Peninsula, where seagrass meadows have lower shoot density and appear to be more exposed to climate-related events such as cyclones compared to Ilha dos Porcos. This monitoring method creates a basis for better management and conservation, and a continuation of these types of evaluation actions to predict trends and impacts on marine habitats are recommended.

**Keywords:** Seagrass mapping, Satellite imagery, SPOT 5, Cyclone, Seagrass structure, Eastern Africa

## Introduction

Soft-bottom marine ecosystems, such as seagrass meadows and mangroves, play an important role as nursery and feeding grounds for marine animals (Bell *et al*., 1992; Hyndes *et al*., 2003; Cocheret De La Morinière *et al*., 2004; Whitfield, 2017). As a result, species richness in these systems is relatively high (Ferwerda *et al*., 2007). Seagrasses are shallow-water coastal marine plants that supply food to mega-herbivores such as dugongs, sea turtles and sea urchins (Lyimo, 2016) and are significant contributors to the primary production of the global ocean (Smith 1981; Silva, 2009; Felisberto *et al.,* 2015). They are also known to provide ecosystem services such as carbon sequestration (Fourqurean *et al*., 2012; Lyimo, 2016) and wave attenuation (Bradley and Houser, 2009; Maza *et al.,* 2016).

While seagrasses play a major role in the functioning of shallow-waters ecosystems, they comprise a small taxonomic group of marine angiosperms with a worldwide distribution (Short and Coles, 2001). In the Western Indian Ocean (WIO) region, 14 seagrass species occur comprising almost 25% of the total worldwide seagrass species diversity (Gullström *et al*., 2002; Duarte *et al*., 2012; Bandeira, 2011; Short and Coles, 2001). There is growing evidence that seagrasses are experiencing declines globally due to anthropogenic threats (Short and Wyllie-Echeverria, 1996; Hemminga and Duarte, 2000; Duarte, 2002; Bjork *et al.,* 2008) such as sedimentation (Ralph *et al.,* 2007; Wooldridge, 2017), aquaculture (Herbeck *et al*., 2014), dredging (Fraser, 2017) and boating (Bishop, 2008).

Climate change related events such as cyclones are also important contributors to seagrass growth and settlement patterns (Côté-Laurin, 2017), however, the detection of changes in seagrass distribution patterns may be complicated especially when seagrass sites are anthropogenicaly impacted (Bjork *et al.*, 2008). The Mozambique coastline forms the western border of one of the most active basins of tropical cyclones (the southwest Indian Ocean), and it is hence in the trajectory of tropical cyclones and storms (Mavume *et al.*, 2009; Roy and Kovordányi, 2012; Massuanganhe *et al.*, 2015). At least five climatic events affected Inhambane coastline from 1992 to 2013 (the cyclones Bonita in 1996, Eline and Gloria in 2000, Japhet in 2003, and Favio in 2007). Rainfall associated with Eline was the most destructive event since 1976 (Reason and Keibel, 2004) and caused massive floods in southern Africa (Massuanganhe *et al.*, 2015), including southern Mozambique and Inhambane Bay. Runoff from strong rainfall reduces salinity as well as increases the transfer of sediments and nutrients from catchment areas to seagrass beds (Bjork *et al.*, 2008). Seagrasses as well as other marine and coastal habitats require active monitoring and management (Orth *et al.*, 2006) to improve the understanding of their ecology at various spatial and temporal scales. Remote sensing data, especially the medium and high resolution satellite images, such as Landsat TM, ETM+, SPOT, IKONOS and Quick Bird, has made it possible to map and assess the distribution and health status of seagrass (Yang and Yang, 2009). In the WIO region, studies using satellite imagery have been conducted by Dahdouh-Guebas *et al.* (1999) on the Kenyan coast, Gullström *et al.* (2006), and Knudby and Nordlund (2011) in Tanzania, Ferreira *et al.* (2012) and Bandeira *et al.* (2014) in Mozambique. However, almost none of these studies were carried out using high resolution imagery. This study aims to assess seagrass coverage area variations during a 21-year period (from 1992 to 2013) in Inhambane Bay (Mozambique) by means of satellite image analysis using SPOT (2.5 m resolution) and Landsat images (30 m). The study also provides information on the structure of *Thalassia hemprichii*, the most common species within the Bay. The combination of SPOT 5 and Landsat TM imagery for assessment of seagrass vegetation changes was a means of capturing aerial and temporal details of seagrasses at different scales and coverage. The assumption is that changes in seagrass cover occur and may be driven by climate-induced events.

## Materials and methods

### Study Area

Inhambane Bay, with a size of about 25,000 ha, is situated on the southern Mozambican coast (Silva *et al.*, 1991; Halare, 2012) between 23° 40'S and 23° 53'S, and 35° 19'E and 35° 29' E (Fig. 1).

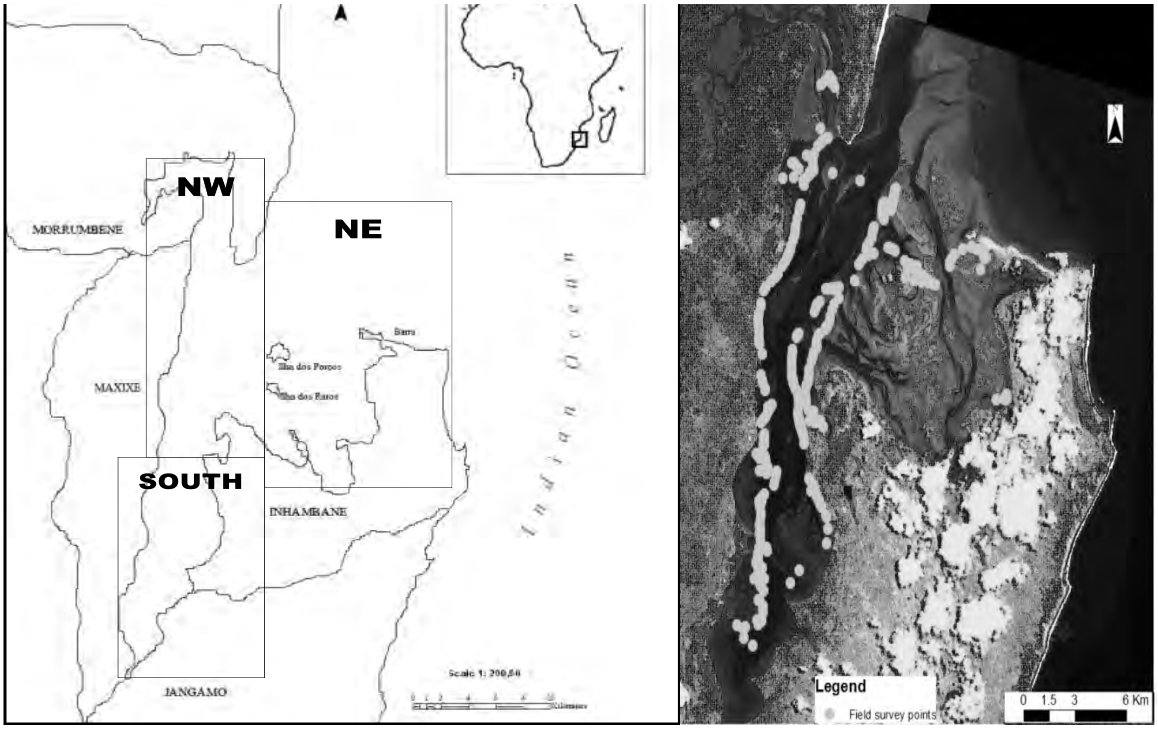

**Figure 1.** Map showing the location of the study area divided in three regions (NW, South, and NE) (left), and Spot 5 image of Inhambane Bay, Mozambique, captured in August 2013 showing field survey points in grey (right).

Administratively, the bay is composed of the four districts of Maxixe, Inhambane, Jangamo, and Morrumbene (Halare, 2012). In order to analyse seagrass cover changes, the bay was divided, based on physiographic aspects, into North West–NW (sandy dunes stretching from northern Maxixe to Morrumbene), Southern (sand flats of south Inhambane City, Jangamo and southern Maxixe), and North East-NE (sand flats of north Inhambane City, the islands of Porcos, Ratos and Barra Peninsula) bay regions (Fig. 1). Average depth varies between 5 and 10 m and the bottom sediment is composed of sand, mud and biogenic matter. The shores are relatively sheltered at Ilha dos Porcos (IP) and at the other sites in the bay, with the exception of Barra Peninsula (BP) and east of Morrumbene (Linga-linga), which are exposed to strong ocean currents. Tides are semi-diurnal and water temperature ranges from 21°C to 27°C (Halare, 2012). The average annual rainfall is 927 mm (Zacarias, 2013) and the mean salinity is 36 PSU (Gove, 2006). Sand flats are affected by channels, currents and freshwater coming from the Sambe and Mutamba rivers, which deposit terrestrial sediments during cyclone-related floods.

### Use of satellite images

Landsat TM (Thematic Mapper) images captured in August of 1992, 1998, 2001 and 2004 (Table 1) were obtained from the National Centre of Cartography and Remote Sensing (CENACARTA) in order to map historical seagrass distribution. The current cover of seagrass was obtained from a Spot 5 image of August 2013. Temporal resolution of imageries was selected in order to depict the impacts of cyclones (Eline, Gloria, Japhet and Favio). The 1992 imagery represents the year before a cyclone, and 2013 is the year after a cyclone. The spatial resolution of Landsat and Spot 5 imagery is 30 m x 30 m and 2.5 m x 2.5 m respectively, and the selected dates of images reflect spring low tides (Table 1).

Spot 5 images covered the overall study area (25,000 ha) while Landsat TM images covered an area of 24,145 ha of Inhambane Bay (96.6% of the total). Geometrical and spectral corrections of the images were performed at CENACARTA and useful spectral bands were selected in order to support the computation of a Normalized Difference Vegetation Index (NDVI). Spot 5 and Landsat TM had the same band set in the visible and infrared wavelengths. These bands were Band 1 (0.45-0.52 µm), Band 2 (0.52-0.59 µm), Band 3 (0.63-0.69 µm), and Band 4 (0.77-0.89 µm). Seagrass distribution was retrieved using the bands 1, 2, 3 and 4 combined in the form of the NDVI. NDVI, a tool used to compute seagrass chlorophyll, was first proposed for seagrass cover by using combination of red spectral band and near infrared by Tucker (1979), followed by authors such as Tucker *et al.* (1981), ESRI (1998) and Moreira (2001). This combination is utilized in the following equation:

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{R}}{\mathrm{NIR} + \mathrm{R}}$$

Where: NIR is the near infrared band, and R is the red band. The value of the "pixel" resulting from this estimation ranges from 0.1 to 1 (Tucker, 1979; Tucker *et al.*, 1981; Moreira, 2001). The highest values of the vegetation index correspond to denser seagrass cover, reducing with the reduction of digital values (ESRI, 1998).

In order to fully explore the useful spectral data, the red band reflectance of NDVI was replaced by the green and blue band reflectance.

The above equation was altered as follows:
Red NDVI RNDVI = (NIR-Red)/(NIR+Red)
Green NDVI GNDVI = (NIR-Green)/(NIR+Green)
Blue NDVI BNDVI = (NIR-Blue)/(NIR+Blue)

Three classes of seagrass distribution were classified and validated in the field. The main difficulty encountered in validating NDVI digital numbers (DN) was the fact that the substrate in Landsat TM and Spot 5 varied

**Table 1.** Date and time of capture of the Landsat and Spot 5 imagery (source: CENACARTA)

| Image | Year | Date | Time (h) | Tides (m) |
|---|---|---|---|---|
| Landsat | 1992 | 14 August | 11:45 | 0,57 - Spring |
| Landsat | 1998 | 11 August | 13:13 | 0,41 - Spring |
| Landsat | 2001 | 21 August | 12:35 | 0,57 -Spring |
| Landsat | 2004 | 03 August | 12:48 | 0,57 -Spring |
| Spot 5 | 2013 | 23 August | 12:22 | 0,29 Spring |

greatly. In order to make an accurate classification, typical ground objects, such as sand banks, dunes and sea cover were used to normalize the digital numbers of the whole images. Seagrass classification accuracy was calculated by comparing the pixels of satellite remote sensing data with *in situ* observations. For each location, a score of the match was assessed and the sum of the scores was normalized as the detection accuracy (ESRI, 1998; Jensen, 1996; Trisurat *et al.*, 2000; Mather, 2004).

### Field survey

Groundtruthing was performed during 2012-2014 between July and August based on stratified random sampling to validate NDVI imagery digital numbers (Jensen, 1996; Trisurat *et al.*, 2000; Mather, 2004). Based on pre-classified shape files, the Inhambane Bay was divided systematically into quadrates. Thereafter, 538 quadrates of 0.5 m x 0.5 m were randomly selected along transects running perpendicularly from the coastline to the low water tide level to be able to sample seagrass species (McKenzie *et al.*, 2001). Along each transect, 0.5 m x 0.5 m quadrates were surveyed in order to assess the zonation patterns, species composition, substrate type and percentage cover of seagrass. In subtidal areas, photographs were taken using snorkeling in shallow waters (< 2 m depth), whereas in waters deeper than 2 m, SCUBA diving was performed, especially where the seagrass was not visible from the surface. The area occupied by each seagrass community was determined using a *calculate geometry* tool in ArcGIS 10.1. The communities were then characterized by one or two highly frequent species (Bandeira, 2002; Massingue and Bandeira, 2005) and seagrass composition was classified using a nominal scale of frequency of species occurrence (Bandeira, 2002; Sidik *et al.,* 2001; Massingue and Bandeira, 2005). The percentage cover was estimated using density classes (Tomasco *et al.*, 1993; Massingue and Bandeira, 2005).

The structure of seagrass was obtained by measuring seagrass biomass, shoot density and leaf length in two intertidal meadows dominated by *T. hemprichii* at Ilha dos Porcos (IP) and Barra Peninsula (BP). Twenty quadrats (0.25 m x 0.25 m) were sampled, 10 at each site on 12 and 13 August 2014, respectively. Samples were collected randomly within seagrass beds, then washed in freshwater and divided into above-ground and below-ground components (Duarte and Kirkman, 2001). The samples were dried for approximately 48h at 80°C to obtain the dry weight (DW) and processed in a muffle oven at 425°C for 2h to obtain the AFDW (ash-free dry weight). Leaf length was determined by the average of 10 leaf lengths measured per quadrat at each site, and shoot density by counting the total number of shoots per $m^2$.

Water temperature, depth, and light penetration were measured *in situ.* Water temperature and water depth were measured with a console instrument (ScubaPro). Light penetration was measured with a Secchi disk.

### Data analysis

Results from seagrass community distribution and extent were used to assess the changes in seagrass cover over larger areas. The data met the assumptions for normality and homoscedasticity, and therefore, one-way analysis of variance (ANOVA) and T-test were used to test if there were any significant differences between the means of the different parameters measured (seagrass biomass, shoot density and leaf length) between the Ilha dos Porcos and Barra Peninsula.

## Results

### Seagrass diversity and distribution mapping

Eight seagrass species were identified in Inhambane Bay in 2013: *Thalassia hemprichii* (Ehrenberg) Ascherson, *Halodule uninervis* (Forskål) Ascherson, *Thalassodendron ciliatum* (Forskål) den Hartog, *Cymodocea serrulata* (R.Br.) Ascherson & Magnus, *Cymodocea rotundata* Ehrenberg & Hempr. Ex Ascherson, *Halophila ovalis* (R Br.) Hook.f., *Syringodium isoetifolium* (Ascherson) Dandy, and *Enhalus acoroides* (Linnaeus f.) Royle. The most common species were *T. hemprichii,* followed by *T. ciliatum* and *H. uninervis*. In contrast *H. ovalis* and *S. isoetifolium* were scanty and found mostly in permanent subtidal areas (around 1.5 m at low spring tide). *E. acoroides* was only found in a localized area near Morrumbene shore. These seagrass species form six main community types: *T. hemprichii/H. uninervis*, *T. ciliatum/C. serrulata*, *H. uninervis*, *C. serrulata/H. uninervis*, *E. acoroides* and *H. ovalis/H. uninervis*. The *T. ciliatum/C. serrulata* community occurred in shallow channels from north to south and also on flats at the NE and NW Inhambane Bay regions. The *T. hemprichii/H. uninervis* community formed dense meadows on sand flats and biogenic platforms of the NW and NE bay regions. The *C. serrulata/H. uninervis* community occurred in the NW and in the lagoon at the NE. *H. uninervis* and *E. acoroides* communities occurred in intertidal areas where they were dominant on muddy substrates, while *H. uninervis* also occurred in subtidal areas. *T. hemprichii/H. uninervis* followed by *T. ciliatum/C. serrulata* were the most species-rich communities with seven and six species represented, respectively (Fig. 2; Table 2).

**Figure 2.** Map of Inhambane Bay showing the distribution of seagrass communities in 2013 produced from a combination of field – and SPOT 5 imagery data.

*T. hemprichii/H. uninervis* and *T. ciliatum/C. serrulata* communities, together with the monospecific *H. uninervis* community, form the three largest community types covering 96.4% of the total seagrass cover of Inhambane Bay (Table 3).

In 2013, seagrasses occupied an area of 6,199 ha, which was around 25% of the total bay area (25,000 ha) (Table 4). The NW bay beds covered the largest area of seagrass with 2,602 ha followed by the southern bay beds with 1,908 ha. The NE bay is widely dominated by dispersed patches in an area of 1,689 ha.

## Assessment of seagrass dynamics

In 1992, seagrass covered 12,076 ha of Inhambane Bay (Fig. 3; Table 5). Between 1992 and 1998, large areas of seagrass (5,714 ha, 47.3%) were lost (Fig. 3). Furthermore, 712 ha of seagrass disappeared between 1998 and 2001. Although 26 ha of seagrass disappeared in the southern bay between 2001 and 2004, a total of 958 ha of seagrass recovered naturally in the entire bay for the same period. The NE bay registered an increase of 76% of seagrass and in the western bay there was a slight increase of 1% (Table 5). In the 12-year span (i.e. from 1992 to 2004), the NW bay had

**Table 2.** Species composition in each seagrass community.

| Community type | Species | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Th | Tc | Hu | Cs | Cr | Ea | Si | Ho |
| Th/Hu | *** | * | *** | ** | * | | * | * |
| Tc/Cs | * | *** | * | *** | * | | ** | |
| Hu | | | *** | | | | | |
| Ea | ** | | ** | | * | *** | | |
| CS/Hu | | | *** | *** | * | | | |
| Ho/Hu | * | | *** | | * | | | *** |

*** -highly frequent,**-frequent, *-present. Th-*Thalassia hemprichii,* Hu-*Halodule uninervis,*Tc-*Thalassodendrom ciliatum,* Cs-*Cymodocea serrulata,* Cr-*Cymodocea rotundata,* Ea-*Enhalus acoroides,* Si-*Siringodium isoetifolium,* Ho-*Halophila ovalis*

**Table 3.** Seagrass communities' coverage in 2013.

| Seagrass Community | Area (ha) | Percentage of total |
|---|---|---|
| *Thalassia hemprichii/Halodule uninervis* | 2305.5 | 37.18 |
| *Thalassodendrom ciliatum/Cymodocea serrulata* | 2280.3 | 36.78 |
| *Halodule uninervis* | 1393.9 | 22.48 |
| *Enhalus acoroides* | 136.0 | 2.20 |
| *Cymodocea serrulata/Halodule uninervis* | 43.0 | 0.70 |
| *Halophila ovalis/Halodule uninervis* | 40.7 | 0.66 |

the highest losses of seagrass among the three areas studied (3,024 ha or 56.4%) followed by the southern zones of the bay (1,352 ha or 40%). Although the NE bay region showed the lowest loss of seagrass (1,101 ha, 33% of its total 1992 area), it seems to be more dramatic as the remnant seagrass occupied only 18.6% of the NE bay region.

### Structural complexity of *Thalassia hemprichii*

The total biomass of *T. hemprichii* differed significantly between Ilha dos Porcos or Porcos Island (IP) and Barra Peninsula (BP) in 2014. The area of IP had high total biomass (Table 6). The aboveground/belowground ratio was lower at IP compared to BP (Table 6). Shoot density was also significantly higher at IP than at BP (Table 7). Leaf length did not significantly differ between the two sites, although a tendency could be discerned that IP appeared having a higher leaf length than BP (Table 7). The seagrass cover at IP ranged from 75 to 100 % and was clearly higher ($p<0.01$) than the seagrass cover at BP, which had a range between 25% and 60%.

Biomass (Mean ± SE) of *Thalassia hemprichii*. N = 10, DW = dry weight, AFDW = Ash free dry weight. Asterisks denote values which are significantly different from one another determined by one-way ANOVA. *significant at 5%; ** significant at 1%.

**Table 4.** Seagrass areas in 2013 apportioned per bay zone (southern, NW and NE Bay).

| Region | Mapping area (ha) | Seagrass ( ha) |
|---|---|---|
| Southern Bay | 6,592 | 1,908 |
| NW Bay | 6,408 | 2,602 |
| NE Bay | 12,000 | 1,689 |
| Total | 25,000 | 6,199 |

**Table 5.** Change in seagrass coverage in Inhambane Bay over the years 1992, 1998, 2001 and 2004.

| Zone | Mapping area | 1992 | | 1998 | | 2001 | | 2004 | |
|---|---|---|---|---|---|---|---|---|---|
| | Ha | Ha | % | Ha | % | Ha | % | Ha | % |
| Southern | 6,592 | 3,380 | 51.0 | 2,504 | 37.9 | 2,054 | 31.2 | 2,028 | 30.8 |
| NW | 5,553 | 5,365 | 96.6 | 2,506 | 45.1 | 2,321 | 41.8 | 2,341 | 42.1 |
| NE | 12,000 | 3,331 | 27.8 | 1,352 | 11.3 | 1,266 | 10.6 | 2,230 | 18.6 |
| Total | 24,145 | 12,076 | 50.0 | 6,362 | 26.3 | 5,641 | 23.3 | 6,599 | 27.3 |

Asterisks denote values which are significantly different from one another determined by T-test. ** significant at 1%; NS: not significant.

### Environmental variables

There were no statistical differences ($p > 0.05$) in water temperature, light penetration and water depth between the two sites (Table 8), although BP tended to have slightly higher visibility and depth compared to IP.

Asterisks denote values which are significantly different from one another determined by T-test. NS: not significant.

## Discussion and conclusion

### Seagrass diversity and distribution

Inhambane Bay, with eight seagrass species (comprising around 13% of world seagrass biodiversity) within only 25 000 ha can be considered an area unusually

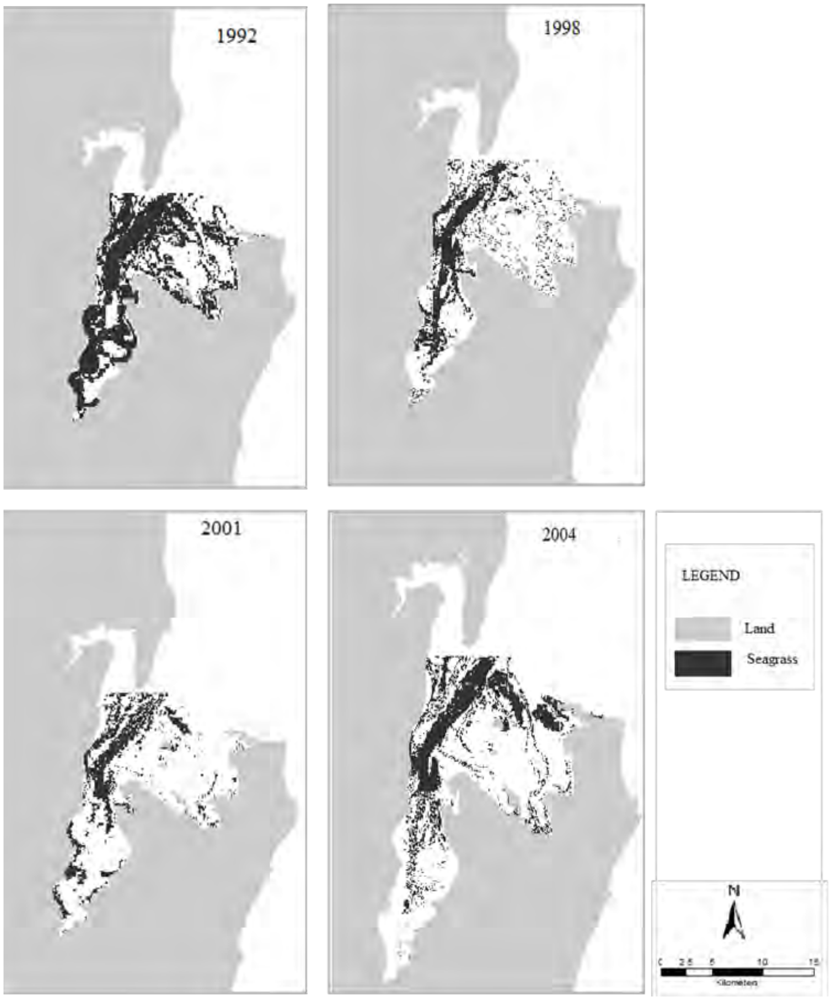

**Figure 3.** Distribution of seagrass cover in Inhambane Bay in 1992, 1998, 2001 and 2004.

**Table 6.** Comparison of Thalassia hemprichii biomass (gm-2) at two sites in Inhambane Bay, Mozambique.

| Structure | | IP | BP | Df | F-value | P-value |
|---|---|---|---|---|---|---|
| Above ground | DW | 564.93±38.06 | 425.08±35.26 | 1 | 7.264 | 0.015* |
| | AFDW | 249.30±25.42 | 123.67±22.42 | 1 | 13.729 | 0.002** |
| Below ground | DW | 1071.89±107.92 | 522.00±48.12 | 1 | 21.654 | 0** |
| | AFDW | 365.48 ±30.81 | 272.17 ± 26.68 | 1 | 5.239 | 0.034* |
| Above/Below ratio | DW | 0.57±0.07 | 0.83±0.60 | 1 | 7.646 | 0.013* |
| | AFDW | 0.71±0.09 | 0.43±0.05 | 1 | 7.215 | 0.015* |
| **Total Biomass** | DW | 1636.82±80.52 | 947.08±31.09 | 1 | 15.964 | 0** |
| | AFDW | 614.78±23.57 | 395.85±24.04 | 1 | 10.571 | 0.002** |

**Table 7.** Comparison of leaf length and shoot density between Ilha dos Porcos (IP) and Barra Peninsula (BP) of Inhambane Bay, Mozambique.

| Structure | IP | BP | Df | F-value | P-value |
|---|---|---|---|---|---|
| Leaf length (cm) | 9.8± 0.32 | 7.7± 0.47 | 1 | 0.577 | NS |
| Density (shoots/$m^2$) | 1413±15.89 | 812±71.06 | 1 | 12.193 | 0.003** |

rich in this kind of habitat. (Short and Coles, 2001). This pattern may be repeated across Mozambique and eastern Africa tropical regions such as Bazaruto, Inhaca and Zanzibar (de la Torre-Castro, 2006; Lyimo *et al.*, 2008; Bandeira *et al.*, 2008; Bandeira *et al.*, 2014). Inhambane Bay has around 60% of the total number of seagrass species occurring in WIO region (Bandeira, 2011; Gullström *et al.*, 2002). *Zostera capensis* Setchell and *Thalassodendron leptocaule* Maria C. Duarte, Bandeira and Romeiras, was not found within Inhambane Bay although documented elsewhere in eastern Africa (Bandeira and Gell, 2003). *T. leptocaule*, the only eastern African seagrass occurring in rocky habitats, was documented nearby only at Tofo village (with rough waters facing the Indian Ocean, outside Inhambane Bay) (Duarte *et al.,* 2012). Inhambane is the southern limit of *E. acoroides* across Africa. The occurrence of 8 species in such a small bay almost equals the seagrass diversity of the entire Caribbean (Creed *et al.* 2003). *T. hemprichii* co-occurred with *H. uninervis* and was the most species-rich community type within Inhambane Bay. This community has also been reported from northern Mozambique and Tanzania (Bandeira and António, 1996), Inhaca Island (Martins and Bandeira, 2001; Bandeira *et al.*, 2014) and other parts of the region (Gullström *et al.,* 2002).

### Assessment of seagrass dynamics

This study indicates a dramatic change in seagrass cover over a 21-year period (1992 to 2013). It was found that from 1992 to 1998 5,714 ha (nearly half of original area of seagrass coverage) was lost, primarily within *T. hemprichii/H. uninervis* and *H. uninervis* communities, similar to the findings of Côté-Laurin *et al.* (2017) who recently documented a short-term impact of Cyclone Haruna (150 km/h winds) within the *T. hemprichii* communities in Madagascar. It appears that the above mentioned change within Inhambane Bay could have been an impact caused by Cyclone Bonita (winds of around 180 mm/h), that struck the

**Table 8.** Comparison of environment conditions between two sites in Inhambane Bay.

| Environment conditions | IP | BP | Df | F-value | P-value |
|---|---|---|---|---|---|
| Water temperature (˚C) | 22.9±0.35 | 22.2±0.29 | 1 | 2.384 | NS |
| Light penetration (m) | 2.4±0.16 | 2.9±0.18 | 1 | 4.245 | NS |
| Water depth (m) | 1.1±0.06 | 1.4±0.14 | 1 | 4.151 | NS |

region in 1996. A global analysis of seagrass decline by Waycott *et al.* (2009) indicates various root causes, mostly anthropogenic, for seagrass decline, mostly in north America, Europe, and Australia, and includes some localized cases of seagrass increase as well, but with fewer examples of widespread seagrass decline from South America, Africa or NE and SE Asia (Waycott *et al*., 2009). Anthropogenic impacts in the Inhambane area still need to be tested, however it is surrounded by a relatively small rural population of up to 200,000 inhabitants with limited activities such as motor boating, point sewage discharges, and earth moving operations that are likely to have major impacts on seagrasses. It was further noted in this study that 721 ha had been lost between 1998 and 2001, coinciding with cyclone Eline that transited the region with winds of around 200 km/h in February 2000. In 2001 Inhambane Bay had the lowest seagrass cover (23% of its original area) in the period analysed. The cyclone Eline brought very strong winds associated with intense rainfall and created the worst natural disaster in a century (Mavume *et al*., 2014). It is suggested that the rainfall and flooding might have brought sediments into the bay impacting the seagrass meadows. Halare (2012) showed that 2001 was the year with the lowest annual catch of the sardine *Amblygaster sirm* in Inhambane Bay between the years 1999 and 2006. This pattern probably also represents an indicator of seagrass losses in Inhambane Bay during this period. *A. sirm* is a pelagic species, partly occurring in shallow waters and lagoons. It feeds on nauplii of crustaceans, bivalves and gastropods larvae (Halare, 2012) living in seagrass habitats. The 4% (958 ha) gain between 2001 and 2004 was the only large gain of seagrass cover. Between 2004 and 2013, 400 ha were lost, possibly from an anthropogenic impact, but it should be noted that the cyclone Favio (approx. 200 km/h winds) struck the region in 2007 as well. Related anthropogenic impacts on seagrass in WIO was documented in NW Maputo Bay where seagrass meadows are intensively dag for clam collection, a recurring activity mostly during spring tides; nonetheless also heavily impacted by an extreme climate event as documented during the 2000 floods (Bandeira and Gell, 2003; Bandeira *et al*., 2014)

### Structural complexity of *Thalassia hemprichii*

The environmental conditions at Inhambane Bay were in general similar to other southern Mozambique sites (Paula *et al*., 1998; Bandeira, 2000; da Silva and Rafael, 2014; Canhanga and Dias, 2014). The sediment at BP was composed of coarse sand, which reveals this site to be more exposed than IP. Exposure usually enables sedimentation of heavier sands and may also display greater variability of seagrass distribution, or in the structure of seagrass meadows. Such analysis may help in understanding the roles of seagrass species in protection of sandy and exposed shores (Paul, 2017). Van Rijn (2011) showed that the presence of coarse sand played a role in erosion control. In general, the total biomass of *T. hemprichii* obtained in this study seems to be similar to that obtained at Inhaca Island (southern Mozambique) for the same species (Martins and Bandeira, 2001), and is also corroborated in studies elsewhere (Chiu *et al.,* 2013). Within Inhambane Bay, IP had slightly higher above- and belowground seagrass biomass compared to BP, although environmental parameters in the two areas did not differ significantly. At IP, the aboveground biomass was about half of the belowground biomass, implying a greater allocation of resources belowground. This might indicate a survival strategy by seagrasses to minimize anthropogenic pressure from heavy collection of invertebrates, or exposure to desiccation at low tide, and to increase stability when exposed to high tides (Lyimo *et al*., 2008). SE Asia studies on biomass revealed a higher biomass for Inhambane Bay (Heijs, 1984) and similar shoot densities (Brouns, 1985). The higher shoot density was shown to coincide with lower canopy height (Eklöf e*t al*., 2005; Gullström *et al.,* 2006).

In conclusion, this study has demonstrated that the spectral and spatial resolution of Landsat TM and SPOT 5 imagery was appropriate for assessing seagrass dynamics creating a basis for better management of this habitat. Seagrasses in Inhambane Bay have decreased in their coverage between 1992 and 2013. The decrease was about 5,877 ha, which implies losses of 50% over these 21 years. It is postulated that some of this decrease may be related to recorded climate events. *T. hemprichii* seagrass biomass varied between 947.08 ± 31.09 g DWm-2 and 1636.82 ± 80.52 g DWm$^{-2}$, respectively, being low at BP, where seagrass meadows have lower shoot density and appear more exposed compared to IP. It is recommended that there is a continuation of these types of evaluations to predict trends in seagrasses.

## Acknowledgments

We kindly acknowledge the funding for this study provided by the Ministry of Science and Technology of Mozambique (scholarship to Manuela Amone Mabuto) that supported fieldwork and imagery data.

Eco Africa provided additional financial support for fieldwork. Our votes of thanks are extended to Bitonga Divers for field assistance during fieldwork and Mr. Marcos from CENACARTA who provided the additional imagery analyses. This paper was part of Manuela Amone Mabuto MSc thesis (UEM-Mozambique) and we take this opportunity to acknowledge Prof. Martin Gullström for valuable comments.

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# Factors influencing migrant fisher access to fishing grounds

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## Abstract

Fisher migration plays a critical role in artisanal fisheries in the Western Indian Ocean. The present study uses a multiple method approach to evaluate fishing behaviour of migrant fishers at four destinations in Kenya, and focuses on fishing grounds used by migrant fishers to illustrate spatial characteristics that attract or determine access and fishing behaviour. Migrant fisher knowledge of natural trends, cycles and oceanographic processes that influence the abundance of target resources largely determines access to fishing grounds. Calm winds and a fairly high Chl-*a* concentration make favourable conditions at fishing grounds on the north coast during the northeast monsoon. Fishing grounds on the south coast include sheltered areas that remain accessible during the southeast monsoon. Increased fisheries productivity is experienced during the rainy season due to sediment loading and increased supplies of particulate matter. The main catch landed on the north coast included octopus, grouper and tripletail that were found within the reefs and on the deep slopes, while on the south coast it included needlefish, tunas and mackerels, barracuda and sardine, among other highly migratory pelagic species. Besides natural conditions, local regulations at the destination, including gear and licence restrictions, were also found to be important determinants of access by migrant fishers.

**Keywords:** Environmental factors; Fisher knowledge; Migration destination; Space; Strategies

## Introduction

Artisanal fisheries support over 10,000 small-scale fishers in Kenya. These fishers use multiple gear and target multiple species (Fondo, 2004; Mangi *et al.*, 2007; Obura and Wanyonyi, 2001). Fisher migration is a common feature in coastal East African fisheries (Fulanda *et al.*, 2009; Glaesel, 2000). Unlike non-migrant fishers who are often limited in range to inshore shallow waters, within sheltered reefs and lagoons adjacent to their landing sites (Mangi and Roberts, 2007; Obura and Wanyonyi, 2001; Samoilys *et al.*, 2017), migrant fishers travel to distant fishing grounds (Crona and Rosendo, 2011; Fulanda *et al.*, 2009; Wanyonyi *et al.*, 2016b). They try to avoid competition and conflict with local fishers by choosing remote locations away from designated landing sites.

Migration expands the fishers' access beyond their place of origin to include fisheries resources at the destination locality. However, access is subject to conditions at the destination that influence availability of target species such as changes in natural cycles or the rules governing access and use of resources (Allison and Ellis, 2001). Fishing, like other natural resource-based livelihoods, reflects the seasonal and cyclical trends of resources (Allison and Ellis, 2001). Users embrace various adaptive strategies to be assured continued access. The expanded space at migration destinations is subject to the influence of governance

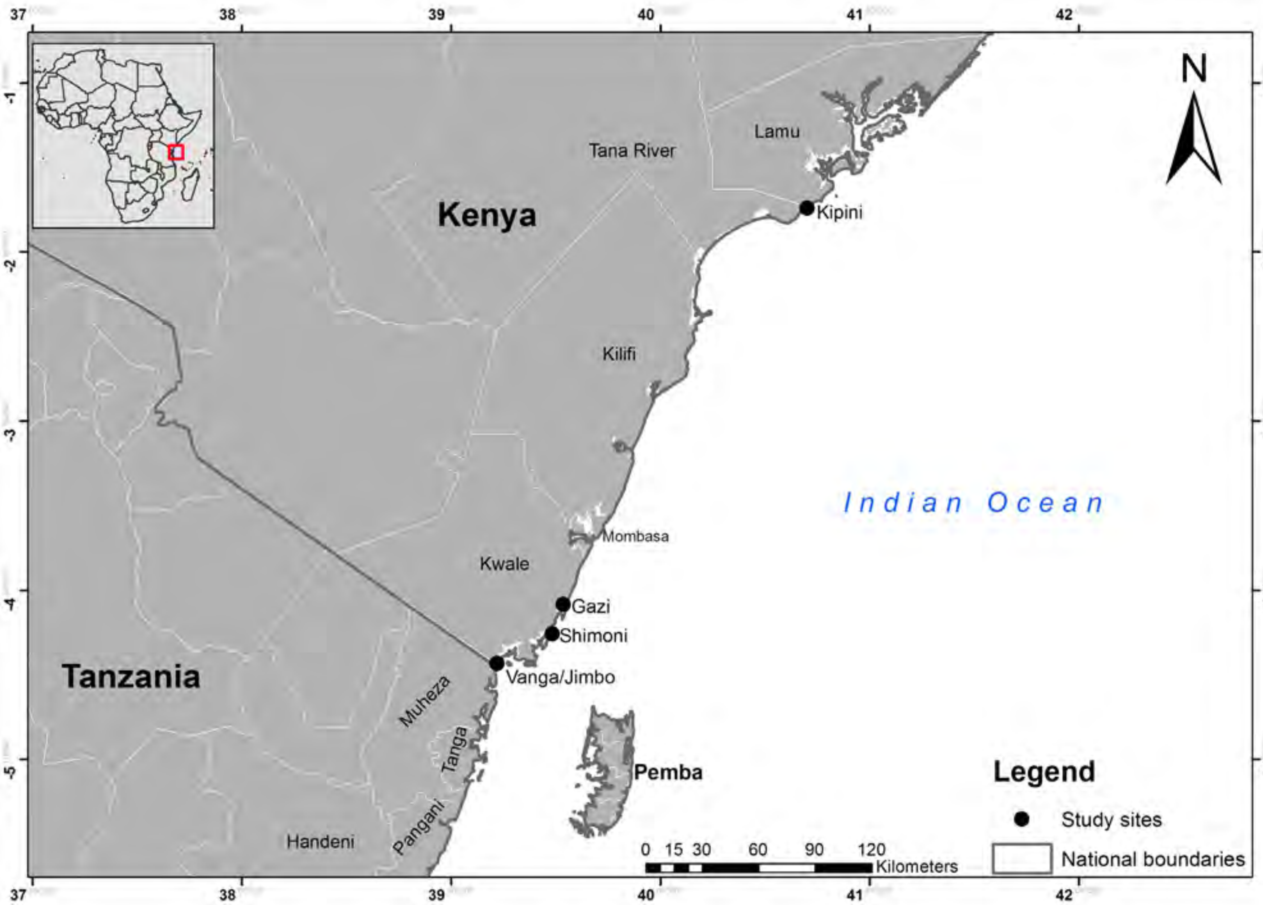

**Figure 1.** Map of study sites at four migrant fisher destinations in Kenya.

institutions that determine access to the fishing grounds. Among the common approaches used to regulate fisheries include limiting access through licensing, No Take Zones, and gear regulations (Mangi *et al.*, 2007). These factors, in addition to natural cycles and trends, influence access for migrant fishers.

The patterns of fisher migrations largely reflect the seasonality in the fish stocks (Fulanda *et al.*, 2009; Jiddawi and Ohman, 2002). Fisher migration is mainly seasonal, lasting 2-3 months during the northeast monsoon, but other patterns also exist and migrations can last between 1-7 months (Fulanda *et al.*, 2009; Wanyonyi *et al.*, 2016a). The behaviour of migrant fishers at destination fishing grounds is relatively unknown. This paper empirically attempts to fill that gap by evaluating ecological, oceanic and governance factors influencing migrant fisher access to, or choice of, fishing grounds.

## Methodology

### Study Location

The study was conducted at Vanga-Jimbo, Gazi, Shimoni and Kipini, which are well known migrant fisher destinations in Kenya. Kipini was the remotest of the locations while Vanga-Jimbo, lies within the Pemba Channel, and is closest to Pemba Island, which is the place of origin of most migrant fishers (Fig. 1).

The study used a mixed methods approach to collect data between October 2010 and March 2011. Migrant fishers were involved in mapping by tracking and locating their fishing grounds using a geographic positioning system (GPS). They recorded information about their fishing operations using fisher log books. Additional data was sourced from available literature, and long term reef monitoring and remote sensing data.

### Geographical, fishery, ecological and oceanographic aspects of relevance to migrant fisher's access to fishing grounds

Migrant fisher 'spaces' were assessed in terms of their geographical, fishery, ecological, and oceanographic attributes. To assess local geography, three fishing vessels representative of the main migrant fishing vessels and gear at each site were randomly selected to participate in tracking their fishing routes using a GPS. GPS track data was converted into a fishing ground

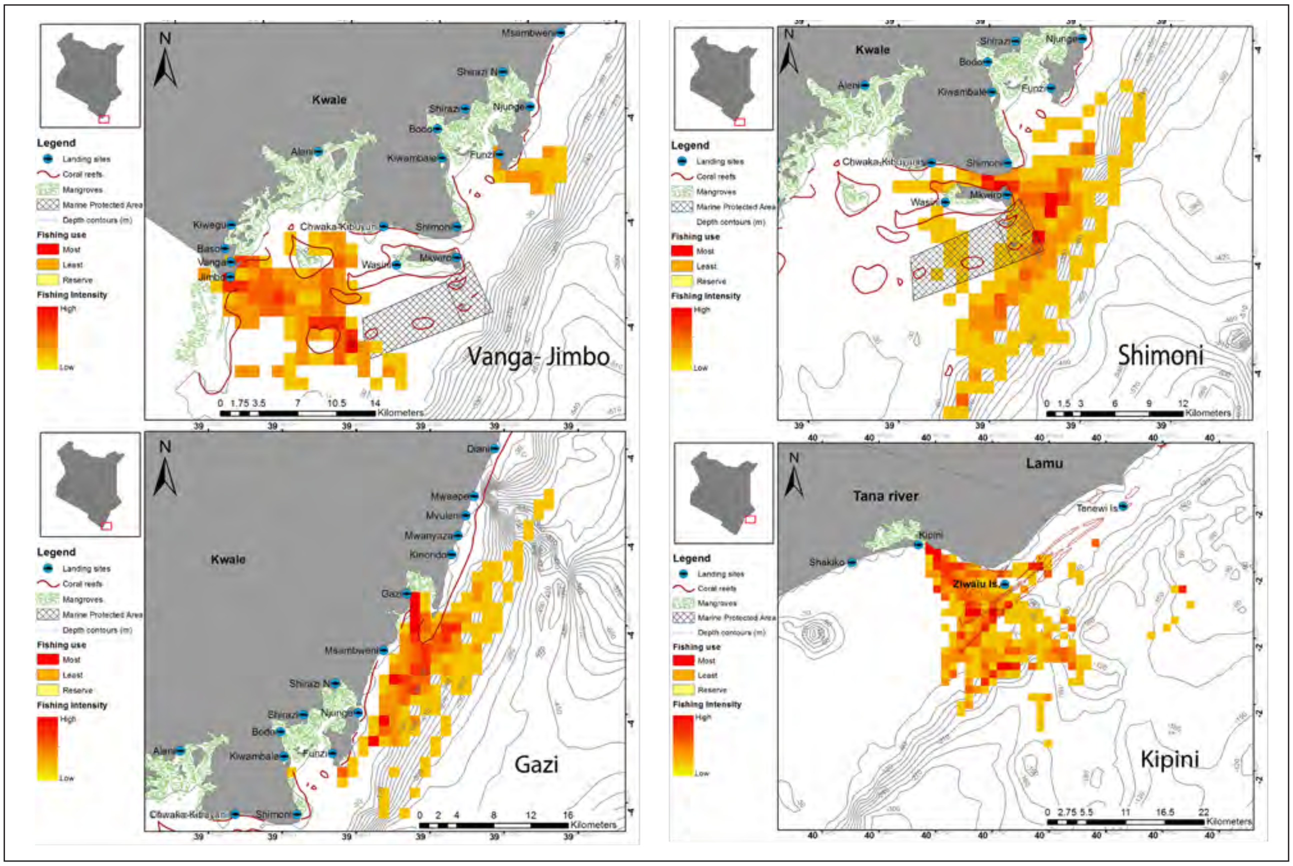

**Figure 2.** GPS map of principal fishing grounds used by migrant fishers combined by landing site.

intensity of utilisation map in ArcGIS software. Maps of vessels operating from one landing site were combined into a single intensity map per site (Fig. 2).

Fisheries at destination were assessed to determine the scale of resource use by migrant fishers. Each vessel recorded the number of fishers on board, type of gear, type of vessel, size and main composition of catch during each fishing trip on log sheets. Analysis of this data determined fish families targeted per vessel/gear type and landing site. Fishing duration and catch per unit effort (CPUE) by vessel/gear types at each destination was analysed using the Kruskall-Wallis test followed by the Mann-Whitney *post hoc* test after failing parametric assumptions of normality and homogeneity of variance. Generalised linear models (GLM) were used to study fishing intensity associations with crew size, fishing site depth, fishing site distance, and fishing vessel type, which allowed accounting for the non-independence of samples.

Data from Nighttime Moderate Resolution Imaging Spectroradiometer (MODIS) (NASA Goddard Space Flight Center-Ocean Ecology Laboratory-Ocean Biology Processing Group) covering the northern Tanzanian and Kenyan coast at 4 km spatial resolution was used to map sea surface temperature (SST), chlorophyll-*a* concentration (Chl-a), and detect thermal fronts. Thermal fronts are areas of sharp temperature gradient between adjacent water masses (Legeckis, 1978; Mooers *et al.*, 1978). They are indicators of many oceanographic processes apart from being sites of increased biological activity. Monthly level 3 data from 2003 to 2016 was downloaded from the NASA Jet Propulsion Laboratory (JPL) Physical Oceanography Distributed Active Archive Center (PO.DAAC) and processed using Matlab to create seasonal plots. Data is presented for December to February, the peak season for migrant fisher arrival in Kenya (Wanyonyi *et al.*, 2016a). The rest of the data is available as supplementary information. Detection of thermal fronts was achieved using the single image edge detection (SIED) algorithm as derived by Cayula and Cornillon (1992; 1995). Remote sensing data was chosen over direct measurement of the biological and physical parameters due to its reliability in providing a synoptic-scale window into the ecosystem in coastal areas, which are characterised by

**Table 1.** Migrant fisheries and fishing area characteristics at four landing sites.

| Landing site | Kipini | Gazi | Shimoni | Vanga-Jimbo |
|---|---|---|---|---|
| Gear | Hook and line, hook and stick, long line | Cast net, drift net, ring net, shark net | Gill net, hook and line, shark net | Basket trap, long line, ring net, shark net |
| Crew size | 5-20 | 2-30 | 2-5 | 3-28 |
| Fishing duration (hrs.) | 6-14 | 1-16 | 1-19.8 | 3-9.5 |
| Fishing area (km²) | 582.6 | 303.7 | 333.4 | 280.3 |
| Maximum depth | 180 | 400 | 510 | 260 |
| Maximum distance | 40 | 25 | 22 | 21 |

high variability of their physical and biogeochemical processes (Semba *et al*., 2016).

Ecological characteristics of the main fishing grounds were assessed from previous scientific assessments on marine biodiversity and habitat health studies (Coppejans *et al*., 1992; Gullström *et al*., 2002; Obura, 2001a; Samoilys, 1988).

### Local governance and migrant fisher access to fishing grounds.

Content analysis of thematic issues using key informant data was used to determine governance institutions with an influence on access to the fishing grounds. Key informants included fish traders, migrant fisher crew leaders, experienced local fishers, and leaders of local beach management units (BMUs) at each study site. Thematic issues discussed included local fisheries governance and the relationship between migrant fishers and local fisheries stakeholders.

## Results

### Fishery, geographical, ecological and oceanographic aspects of migrant fisher 'space'

According to GPS tracking, the overall resource area utilised by the migrant fishers at Kipini was largest (582.6 km²), and smallest at Vanga-Jimbo (280.3 km²) (Table 1). The fishing grounds at Kipini extended from the northern tip of Ungwana Bay northwards to Lamu, and seawards to about 25 km from the shore (Fig. 2). The highest intensity of use was concentrated within the seagrass beds and fringing reef near Ziwayuu Islands and isolated offshore areas south of the Tenewi Islands. Offshore fishing occurred from 60-120 m deep along the gradual slopes of the small islands and barrier reef. The main fishing areas at Gazi were the fringing reef in front of the Bay, along the reef to Msambweni, the back-reef and fore-reef to 20 m deep, the gradual fringing reef slope to the ocean floor at 60 and 120 m depths further south off Kinondo, and the shallow patch reef in Funzi Bay at about 20 m deep. Offshore areas greater than 400 m deep were not used intensively. The Shimoni fishing grounds included areas inside and on the peripheries of Mpunguti Marine Reserve (Fig. 2). Most of the fishing was concentrated along the fringing reef and slopes at 10-160 m deep. Intensive fishing areas at Vanga-Jimbo were in sheltered lagoons and patch reefs nearshore, and in isolated pools in the Funzi area.

The deepest fishing area in Shimoni was 510 m compared to 180 m in Kipini. The longest maximum distance to fishing grounds was 40 km at Kipini, which was twice that of Gazi and Shimoni, while the shortest was 21 km, at Vanga-Jimbo (Table 1). Fishing areas between Funzi and Moa had overlapping use by migrant fishers at Gazi, Shimoni and Vanga-Jimbo.

Fishing duration varied for different types of vessels and gear. Canoe (dugout or outrigger) fishers in Gazi and Shimoni spent the least time (minimum 1hr) while outrigger canoe and wooden plank boat fishers in Shimoni and Gazi spent the most time (maximum 19.8 and 16 hours respectively) (Fig. 3).

The 14 year MODIS SST plot (Fig. 4a) for December to February showed warm pools of water offshore, southeast of the domain between 40° to 43° E extending to 4° S. The SST range was 27 °C to 27.5 °C around the Pemba Channel. The region's general pattern of surface thermal fronts is illustrated by a dashed line overlay on the SST map (Fig. 4a). Several stable fronts were evident on the south coast of Kenya and marginal waters, in addition to a few open oceans fronts. There was considerable spatial variability in mean chlorophyll concentration (Fig. 4b); the lowest ranging from 0 – 0.1 mg/m$^3$ in the southeast, and elevated concentrations on the north coast of Kenya, with the highest being the shelf, and moderately high offshore.

A GLM analysis of factors influencing fishing intensity showed crew size, depth of fishing location and distance from the destination landing site were all significant at 5%, and type of vessel at 10% (Table 3).

In general migrant fishers mostly targeted pelagic fish (Fig. 5), although in Kipini octopus were targeted. The main target catch was Belonidae (needlefish), Scombridae (tunas and mackerels) and Sphyraenidae (barracuda) in Gazi, Lethrinidae (emperors) in Shimoni, and Clupeidae (sardine) in Vanga-Jimbo. Clupeidae and Sphyranidae were the common catch taken by ringnets in Vanga-Jimbo and Gazi respectively. Shark nets targeted Dasyatidae (rays) in Vanga-Jimbo, Xiphidae (swordfish) and Carcharhinidae (sharks), and Sphyraenidae and Istiophoridae (billfishes and sailfishes) in Gazi, and Xiphidae in Shimoni. Longlines mainly targeted Dasyatidae in Kipini, and Ophidiidae (cusk eels) in Vanga Jimbo. Hook and lines in Shimoni and Kipini targeted Lethrinidae, similar to the basket trap in Vanga-Jimbo. Hook and stick in Kipini targeted Octopodidae. Gill nets in Shimoni targeted Belonidae and Pomacentridae, while cast nets and drift nets in Gazi targeted Scombridae (Fig. 5).

CPUE for each landing site and vessel/gear type showed variability in catch rates (Fig. 6). Ring nets in Vanga-Jimbo recorded a higher CPUE of 4.8 ± 0.6 kg/fisher/hr compared to basket traps, longlines and shark nets (Fig. 6). Catch rates in Shimoni and Gazi were similar across all gears for the different vessel types, except shark nets in Gazi, which had a relatively higher CPUE of 1.2 ± 0.2 kg/fisher/hr.

The ring nets at Vanga-Jimbo had the highest CPUE, followed by long lines, and hook and line at Kipini (Fig. 6). CPUE of other gear types was < 2 kg/fisher/hr, and lowest for long lines in Vanga-Jimbo and Shimoni.

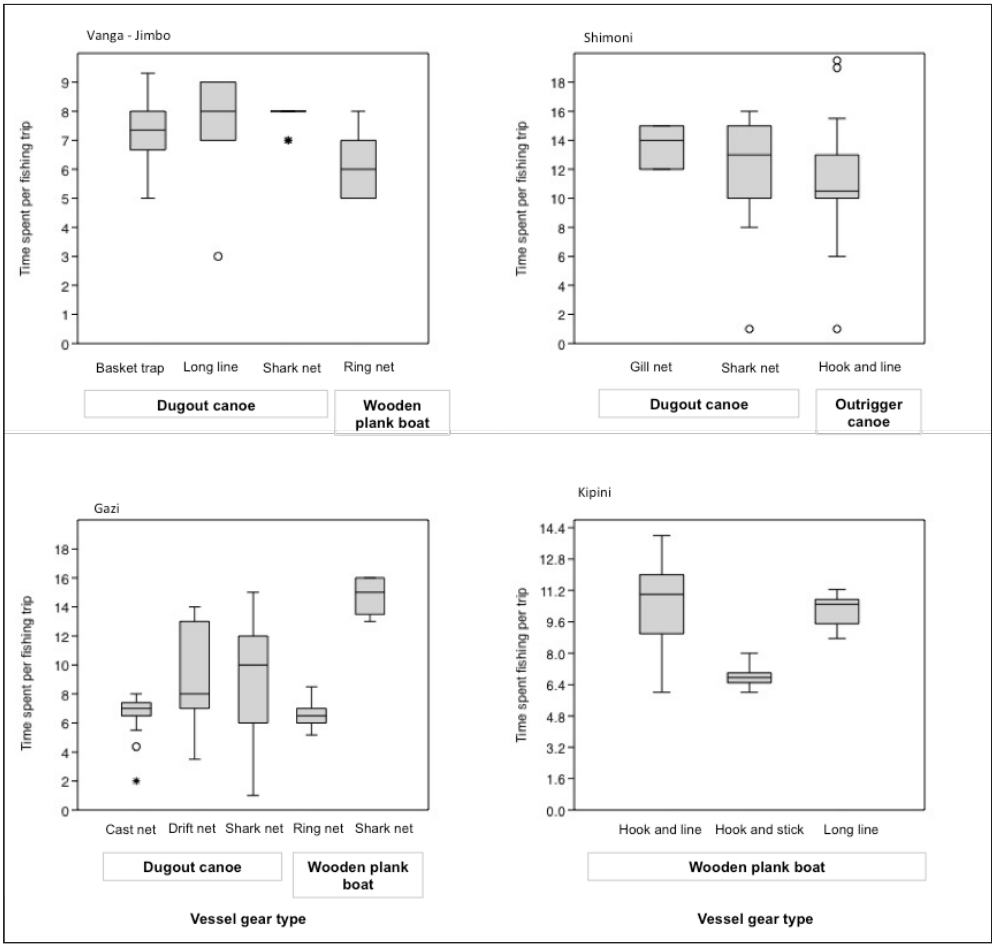

**Figure 3.** Fishing time (in hours) by different vessel/gear types.

**Table 3.** GLM of factors influencing fishing intensity

| Variable | Coefficient | Std. Error | z-Statistic | Prob. |
|---|---|---|---|---|
| C | -2.576 | 0.18 | -14.66 | 0.00 |
| Crew | 0.01 | 0.01 | 2.47 | 0.01 |
| Depth | -0.00 | 0.00 | -3.05 | 0.00 |
| Distance | -0.01 | 0.01 | -2.15 | 0.03 |
| Vessel | -0.02 | 0.02 | -1.76 | 0.08 |

The largest volume of total catch landed by migrant fishers comprised of squid and sardine landed in Vanga-Jimbo, followed by sharks and rays in Kipini, sardines in Gazi and mackerel in Vanga-Jimbo (Fig. 7). Species landed mainly at one landing site included triple tails and octopus in Kipini, and milkfish in Shimoni.

In terms of volume of catch per landing site, the highest was for reef fish followed by oceanic pelagic fish for Kipini, and coastal pelagic fish followed by reef fish for Vanga-Jimbo, whereas pelagic fish and oceanic pelagics were highest in Gazi and Shimoni, respectively, followed by demersals (Fig. 8).

The main gears used to catch the greatest volume of landings were ringnets in Vanga-Jimbo, and long lines, hook and line, and hook and sticks in Kipini (Fig. 9). In Gazi, various types of net were used (ie. ringnets, castnets, and sharknets), whereas in Shimoni, sharknets and gillnets landed the greatest volume of catch.

### Social and institutional aspects determining migrant fisher access to fishing grounds

Traders mainly decided the destination of migrant fishers from Pemba. Traders also facilitated fishing licenses and immigration clearance, and provided fishing equipment, freezers and transport to market. Migrant fishers landed fish at the local landing sites rather than transporting it back to their place of origin. The local BMUs received and approved the migrant fishers using acceptable fishing gear, as long as they had introductory letters from their home authorities and valid travel documents from the host country. The migrant fishers paid levies for all fish landed and boat anchorage fees to the BMU.

## Discussion

### Spatial aspects of migrant fisher 'spaces' at destination

The East African coast has a wide range of oceanographic environments, as influenced by the monsoon winds that blow from the southeast in boreal summer (South East monsoon (SEM) from June to August)

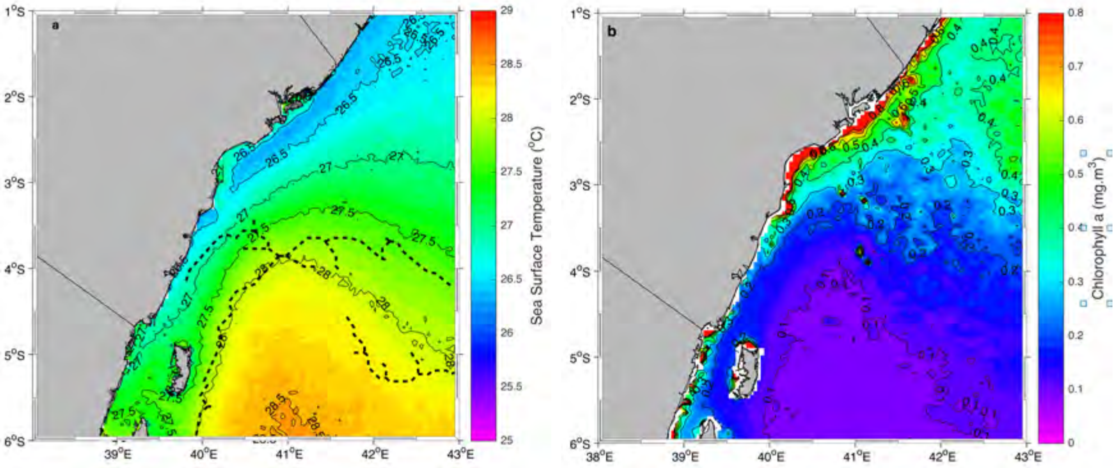

**Figure 4.** a) Detected thermal fronts overlaid (dashed line) on sea surface temperature plot with contours spaced at 0.5 °C; b) Favourable range of chlorophyll-a concentration with contours spaced at 0.1 mg/m3 from December to February.

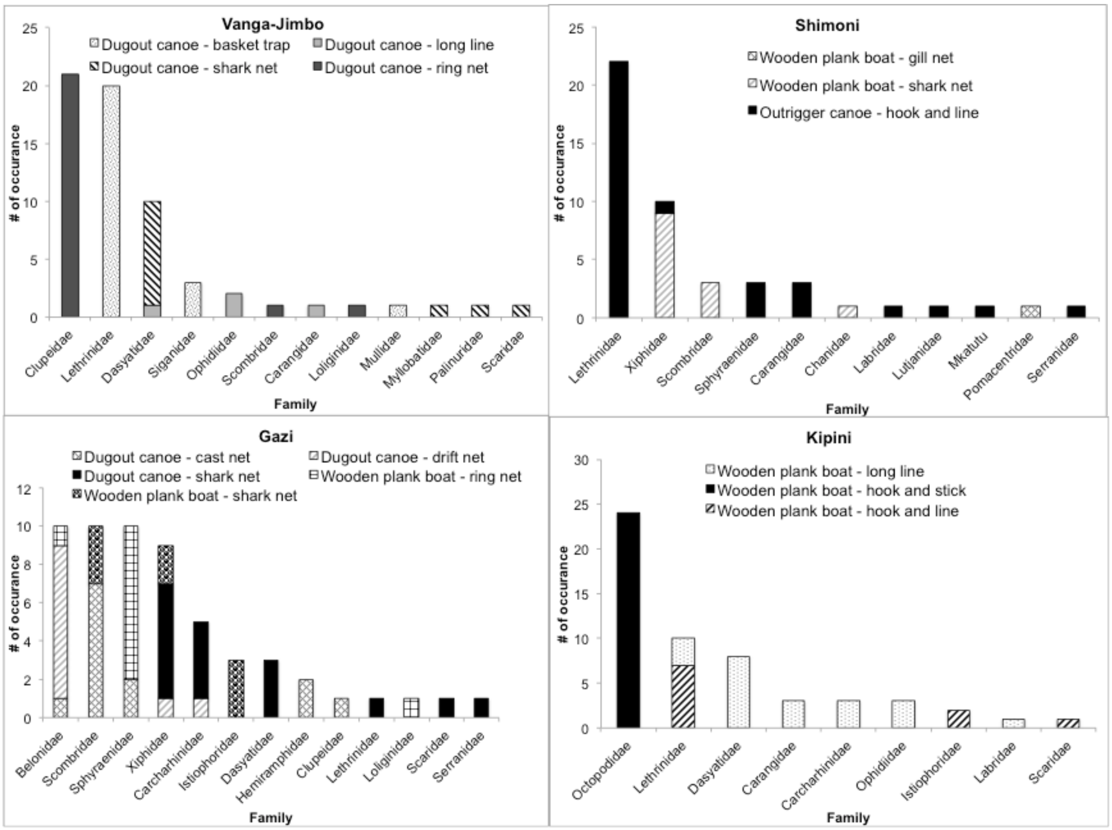

**Figure 5.** Occurrence of fish families in migrant fisher landings at four landing sites.

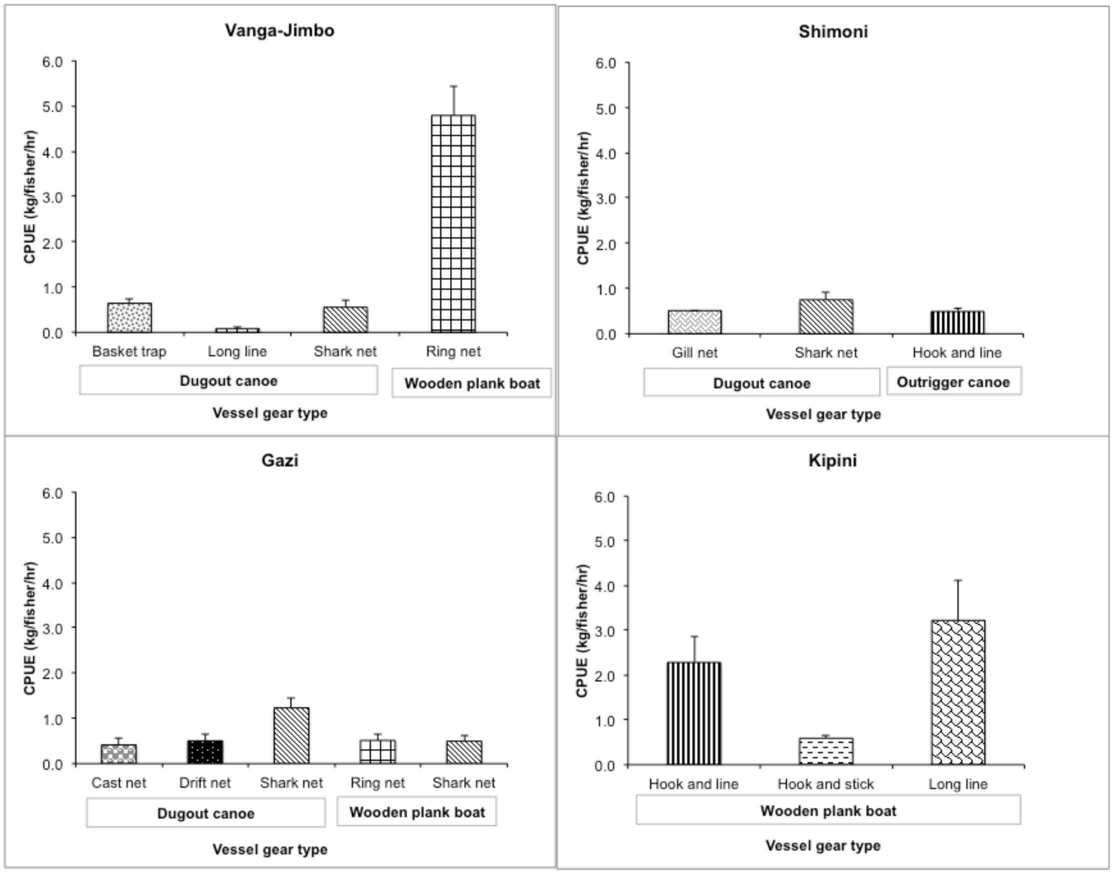

**Figure 6.** Catch per unit effort of migrant fishers using different vessel/gear types at four sites.

and the northeast in boreal winter (North East monsoon (NEM) from December to February) (Bruce, 1979). These wind patterns play a pivotal role in influencing access to fishing grounds and fish availability. Strong winds during the SEM also enhance wind induced evaporative cooling and vertical mixing of the water. This paper uses satellite data, which provides a synoptic view of ocean factors influencing migration to potential fishing grounds.

The stable fronts on the south of the Kenyan coast influence the distribution of pelagic fish due to nutrient rich water advected by the East African Coastal Current (EACC). Compared to other seasons the December to

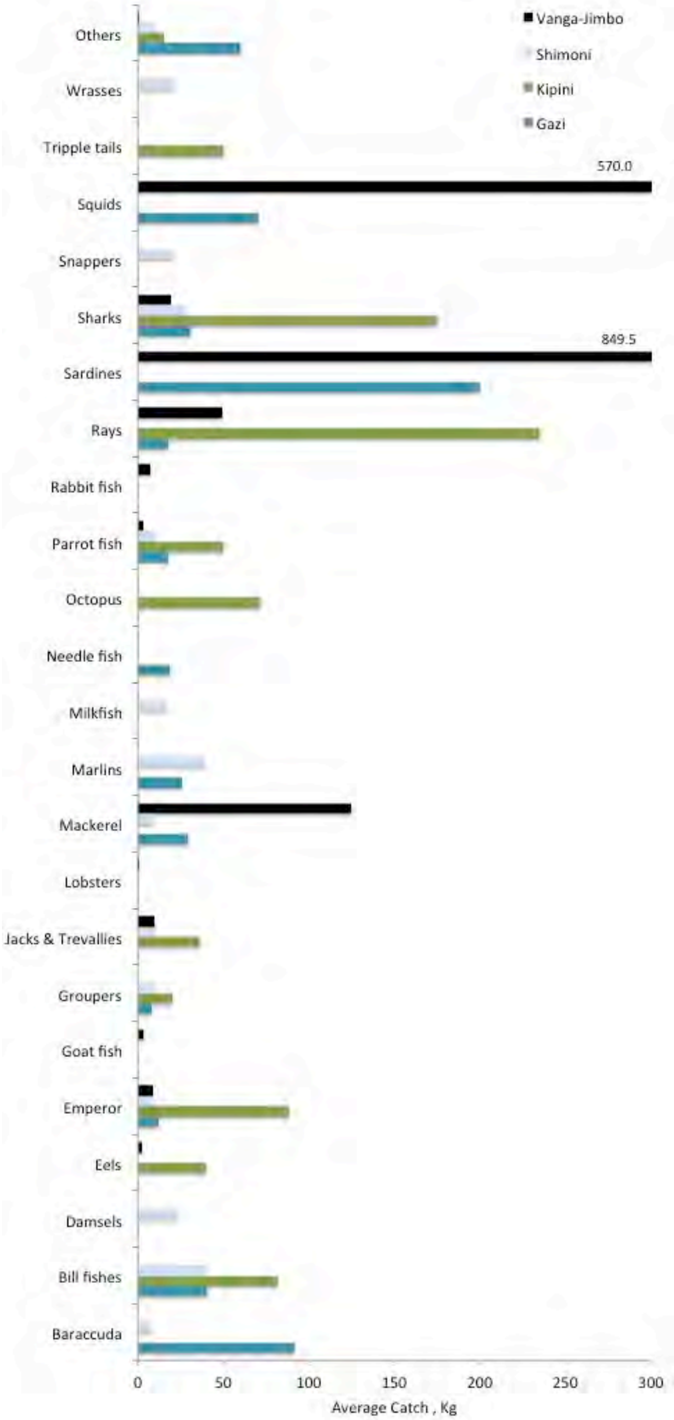

**Figure 7.** Average catch of target fish in migrant fisher landings.

February season has more thermal fronts, mainly due to the weak NEM, which results in the formation of fronts at the boundary between water masses of different temperature and density. It should be noted that many genuine fronts will not be clearly seen as a single colour palette across the wide range of SST values is insufficient for revealing thermal structures where differences are less than 0.5 °C.

The current study postulates that choice of fishing location on the north coast was associated with high productivity of marine ecosystems. Migrant fishers take advantage of the seasonal variability in the region occasioned by the monsoon patterns. This argument is confirmed by seasonal arrivals of migrant fishers in high numbers and their preference of fishing grounds in the north during the NEM (Wanyonyi *et al.*, 2016a). Calm winds and a fairly high Chl-*a* concentration in the north provide favourable conditions at fishing grounds during the NEM. The EACC, which flows northwards throughout the year, is the dominant current and is stronger during the SEM (June-August) on the north coast. Thus, offshore fishing grounds on the north coast are less accessible during the SEM, but migrant fishers continue fishing within sheltered fishing grounds adjacent to Vanga-Jimbo in the south.

The region experiences a bimodal rainfall pattern with the long rains in March/May, and the short rains in October/December (Yang *et al.*, 2015), which coincides with the transition periods from the NEM to SEM, and from SEM to the NEM, respectively (Okoola, 1999). Rains are associated with sediment and nutrient loading from rivers such as the Umba, Ramisi and Mwena, and increased turbidity levels in fishing grounds around Vanga-Jimbo and Shimoni (Opello *et al.*, 2006). Similar effects are seen in Kipini from the Tana River. Turbid conditions are conducive for basket trap and prawn fishing. The rivers and mangrove bays around the fishing areas of Gazi, Msambweni, Funzi and Vanga ensure a supply of particulate matter that replenishes the marine ecosystems, increasing fisheries productivity through the food chain (Munyao, 1998).

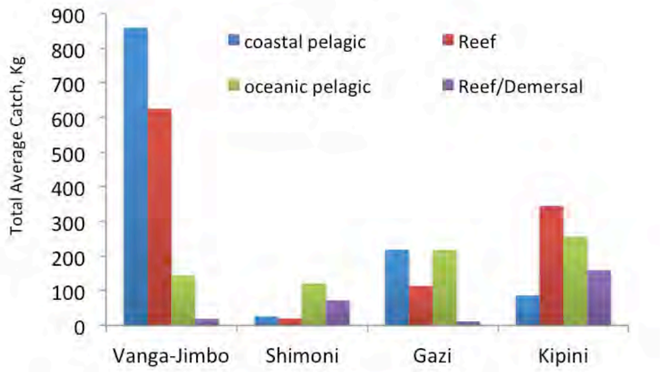

**Figure 8.** Average catch and type of fish landed by migrant fishers at four landing sites.

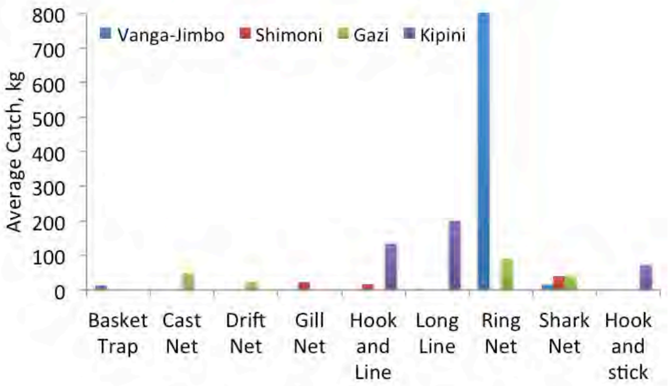

**Figure 9.** Average catch by different fishing gear used by migrant fishers at four landing sites.

Fishing patterns observed confirm important fishing areas for migrant fishers. In Kipini these are less than 200 m deep, but may be more than 20 km offshore due to the gradual depth change in this area. Gazi Bay appears to be a main access point to fishing grounds in Gazi, Kinondo, Funzi and Msambweni, due to the shorter distance to the main fishing grounds, which includes deep fishing areas. The fishing patterns on the south coast indicating that particular fishing spots are not targeted are consistent with fishers targeting schooling and highly migratory species, which are often caught in deep areas. Conversely, fishers targeting coral reef and seagrass associated species tend to concentrate at particular fishing grounds. These patterns of use have been confirmed by the catch composition on the north coast and south coast, respectively.

The concentration of migrant fishers at particular fishing grounds, as shown from GIS tracking maps, confirm suitability of these fishing areas to migrant fishers. The type of fishing vessels used relate to accessibility of fishing grounds in respective areas. This is reflected in the dominant use of wooden plank boats in the north, and outrigger and dugout canoes in the south. Fishing areas are accessed using specific vessels in combination with particular gear to target particular catch. Various net types were used to catch Belonidae, Scombridae and Sphyraenidae in Gazi, Xiphidae in Shimoni, and Clupeidae in Vanga-Jimbo, while hooks and stick were used for Octopidae in Kipini. These findings are in agreement with previous studies that catch composition largely depends on the gear used and fishing location (Bastardie *et al*., 2010). Artisanal fisher catch is dominated by *Siganus sutor* (African whitespotted rabbitfish) and *Leptoscarus vaigiensis* (seagrass parrotfish) for most gear in Kenya (Samoilys *et al*., 2017). This type of catch indicates a concentration of fishing activity in reef and lagoon areas, unlike what has been shown to be the case with migrant fishers in this study.

Fisher knowledge of their marine environment and geographic location of suitable fishing grounds is an important influence on their use patterns (St. Martin and Hall-Arber, 2008). The diverse ecosystems and habitat types in Kenya, include sheltered seagrass beds and coral reefs, and harbour diverse and economically important species ( Samoilys, 1988; Samoilys *et al*., 2011; UNEP, 1998). Migrant fishers target these diverse species, which explains their diverse utilisation patterns at fishing grounds spread out from Kipini in the north to Vanga-Jimbo in the south. Species dominating the migrant catch in Kipini such as crustaceans, octopus, grouper and tripletails are found within the reefs, rocky substrates, deep slopes, coastal waters and estuaries. Pelagic species on the other hand are important to migrant fishers in the south coast areas and include needlefish, tunas, mackerels, barracuda, and sardine, that are found in the open sea, around reefs and in coastal waters (Anam and Mostarda, 2012). The area between Gazi and Vanga-Jimbo has high biodiversity with complex ecosystems making it attractive to fishers (Gullström *et al.*, 2002).

The notable absence of migrant fishers from the fringing reef off Kinondo and Galu and their higher concentrations offshore reflect the attractiveness of the areas to migrant fishers. Local fishers are known to limit their fishing within lagoons and reef areas nearshore, leaving little room for entry of migrant fishers. At the same time, this particular area is over-exploited, with extensively degraded coral reef ecosystems (McClanahan *et al*., 1997; Obura, 2001b), making it unattractive to migrant fishers. The unsustainable resource utilization of coral reefs and continental shelf fisheries is a global challenge, and many are over-utilised (Allison and Ellis, 2001; ICLARM, 1995). Nonetheless, most offshore resources remain underutilized, explaining why they are highly attractive fishing grounds to migrant fishers. In Kipini, however, the state of the offshore fish populations in areas used by migrant fishers is poorly understood and fishing pressure may be relatively high ( Samoilys, 1988; Samoilys *et al*., 2017).

On the south coast, spawning grounds for commercially important fish species, including rabbit fish (*Siganus sutor*) and groupers, have been confirmed near Msambweni (Samoilys *et al*., 2013). The high concentrations of migrant fishers, and the sale of most fish landed in Gazi locally, suggest a demand for fish that outstrips supply. This is unlike in the more remote areas of Kipini and Vanga-Jimbo, which depend on distant markets and sale of dried fish due to low demand.

The type of vessel and gear influence access to fishing grounds and fishing time. Wooden plank boats using ring nets in Gazi showed the greatest significant difference compared to other vessel/gear combinations. Fishing duration is also influenced by distance from shore, and fishers at Vanga-Jimbo took the least time to access fishing grounds. This explains the area's attractiveness to migrant fishers during the SEM.

Studies have shown that large vessels are more efficient, accessing distant or deep fishing grounds, usually avoided by small dugout canoes (Wanyonyi *et al.*, 2016a). Wooden plank boats using ringnets in Vanga-Jimbo had the highest CPUE. This is attributed to the catch composition, largely made up of clupeids, the vessel type, the catchability coefficient of gears, and location of fishing grounds. In general, migrant fishers CPUE exceeds the artisanal fisheries average in Kenya, which steadily declined before stabilising at 3.2 ± 0.1 kg/fisher/trip in the 1990s (Samoilys *et al.*, 2017). This suggests that migrant fisher's operations are more efficient and successful than local fishers.

### Social and institutional aspects influencing migrant fisher access to fishing grounds

Migrant fishers selected fishing grounds and destinations where they were likely to catch more high value fish. They used their skills and knowledge about rich fishing grounds, and relationship with traders, who also provided them with gear and vessels, to access these fishing grounds.

BMUs are responsible for local fisheries at the landing site (McClanahan *et al.*, 1997; Obura, 2001a). They grant migrant fishers permission to fish and land their catch in the area (Evans *et al.*, 2011). Access to landing sites grants the migrant fishers access to local fishing grounds. BMUs and fisheries agencies can also reject migrant fishers as happened in Malindi, Mwaepe, Mvuleni and Msambweni (Fulanda *et al.*, 2009; Glaesel, 2000; Wanyonyi *et al.*, 2016a) where migrant fishers were associated with using unsustainable practices such as beach seines, spear guns, ring nets, cast nets, monofilament nets and scuba, or using scuba diving equipment during fishing for octopus, lobsters, sea urchins, and ring net fishing.

## Conclusion

Migrant fisher resource exploitation patterns are influenced by the drivers for migration, which are best described in spatial terms. Access to fishing grounds reflects opportunities such as availability and abundance of target taxa at the destination fishing grounds, and existing fishing regulations that determine this access. It also depends on migrant fisher knowledge of the environment. Migrant fishers chose productive fishing grounds, and fishing gear and vessels to take advantage of the natural trends in resource availability, and the changes in cycles that redistribute or influence availability of target species. These changes include seasonality of wind and current patterns.

## Acknowledgements

This work was funded by the Linnaeus University through the Coastal and Marine Research in the Indian Ocean (COMARIO) Programme, and WIOMSA/MASMA/CR/2008/02. We are grateful to the research team members involved at various stages of this work. The Government of Kenya granted research permit no. MOST 13/001/38C 76.

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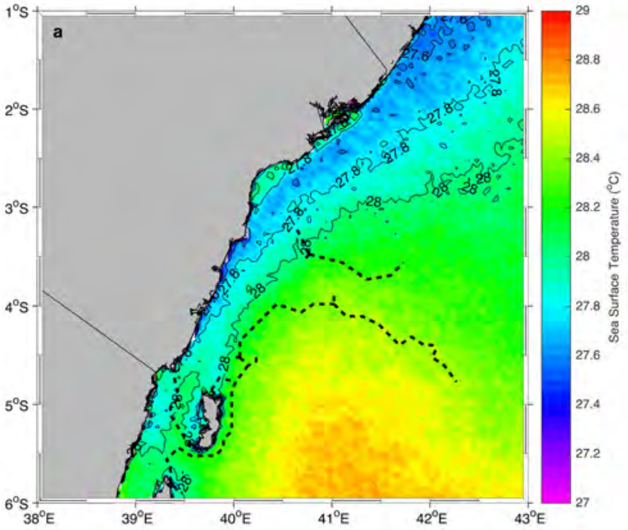
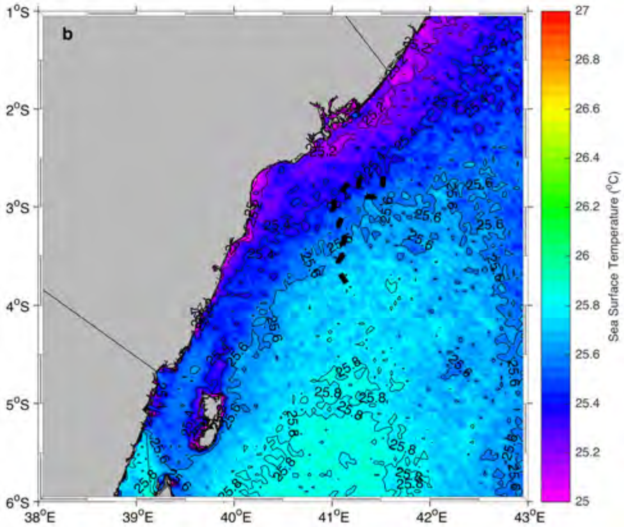
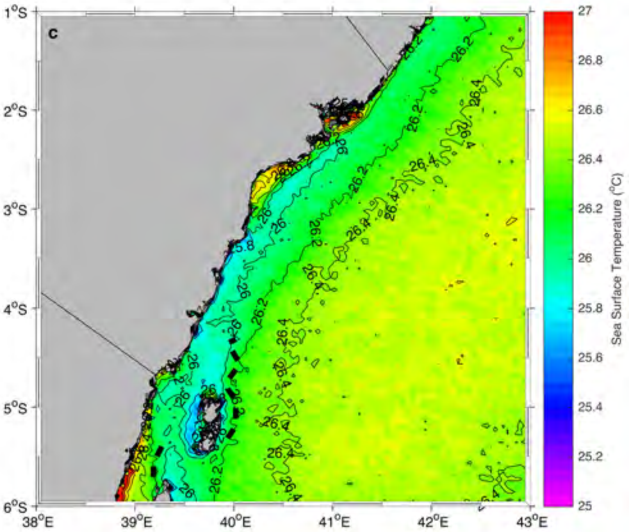
## Supplementary information



**Supplementary Material -Figure 1.** Sea surface temperature plot with contours spaced at 0.5 °C during March to May.



**Supplementary Material-Figure 2.** Sea surface temperature plot with contours spaced at 0.5 °C during June to August.



**Supplementary Material-Figure 3.** Sea surface temperature plot with contours spaced at 0.5 °C during Septemeber to November.

# Phenology of mangroves and its implication on forest management: a case study of Mida Creek, Kenya

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## Abstract

Mangrove forest decline has continued despite establishment of protected areas, restoration and other conservation efforts. This is due to anthropogenic pressure, and phenological traits that together with adverse environmental factors derail natural and artificial regeneration. An understanding of phenological traits can inform planning and management of mangrove forests with benefits to restoration and increased mangrove area cover. Phenological traits of *Rhizophora mucronata, Ceriops tagal, Bruguiera gymnorrhiza* and *Sonneratia alba,* were studied in Mida Creek. Litter fall data was collected monthly on 10 m × 10 m plots from July 2010 to July 2012, oven dried, sorted into leaves, stipules, flowers and propagules, and weighed. Results obtained showed that leaf production occurred throughout the study period for all the species. Propagule fall occurred in the dry season for *Ceriops tagal* and *Bruguiera gymnorrhiza*, and during the wet season for *Rhizophora mucronata* and *Sonneratia alba.* Immature propagules accounted for 99 %, 86 % and 67 % of the cumulated propagules for *R. mucronata, B. gymnorrhiza* and *C. tagal* respectively. The longest propagule for *R. mucronata* was 40.5 cm. This indicates the need for nursery propagation of propagules of these species for seed availability. The findings of this study are discussed in relation to mangrove forest management,

**Keywords:** Leaf production, Leaf fall, Mida Creek, Phenology, Propagule abscission

## Introduction

Mangrove forests provide a wide range of goods and services to coastal communities and are important in carbon sequestration (Alongi, 2012), and have the potential for climate change mitigation (Murdiyarso *et al*., 2015). However, world mangrove ecosystems are continually being threatened by anthropogenic factors and climate change, leading to 20% loss of mangroves since 2005 (FAO, 2007). Climate change has been projected as a serious threat to mangroves through sea level rise, temperature increase and changes in rainfall patterns (Field, 1995; Ellison, 2000; Elizabeth and Rodney, 2006; Hoegh-Guldberg and Bruno, 2010; McKee, 2012). This may lead to localized extinction of species that will not be able to cope with sea level rise due to differences in growth characteristics and environmental preferences for different mangrove species (Ellison, 2000; Di Nitto *et al*., 2014). In order to effectively address the continued mangrove forest loss, there is a dire need for forest managers involved in restoration of degraded mangrove forests to understand phenological traits of mangrove species and to integrate this information for successful restoration of mangrove forests.

A link between vegetative and reproductive phenologies of mangroves has been reported widely (Duke, 1990; Coupland *et al*., 2005) and is attributed to resource partitioning by plants. Phenological studies enhance the understanding of growth and development characteristics of mangrove species. This helps with understanding of how mangroves are likely to be affected by changing climatic factors. Longer leaf growth periods could affect benthic fauna and other food webs that are dependent on mangrove leaf litter for their survival. Mangrove benthic fauna are ecosystem engineers, hence important for healthy mangrove ecosystems (Kristensen, 2008; Nagelkerken *et al*., 2008). Changes in plant phenological traits have already been documented in terrestrial forests (Chung *et al*., 2013). Increased temperatures have been observed to result in longer leaf growing seasons characterized by earlier emergence and late senescence of leaves in terrestrial forests, in addition to other impacts on biotic and abiotic factors (Chung *et al*., 2013).

Availability of mangrove propagules for planting is affected by continued loss of mangrove forests, lack of planting material (seedlings) and propagule predation, prior to and after abscission, which in turn negatively affects restoration projects. Natural and reforested mangroves forests experience high floral and propagule abortion rates (Coupland *et al*., 2006; Ewe, 2007) and this affects the availability of seedlings for natural regeneration or artificial planting. Ewe (2007), in his study on *Rhizophora mangle*, observed that not all abscised propagules are viable and viability is size dependent, and that seedling survival can be predicted from propagule size. Propagule size has also been reported to have an effect on early seedling growth of mangrove species (Sousa *et al*., 2003).

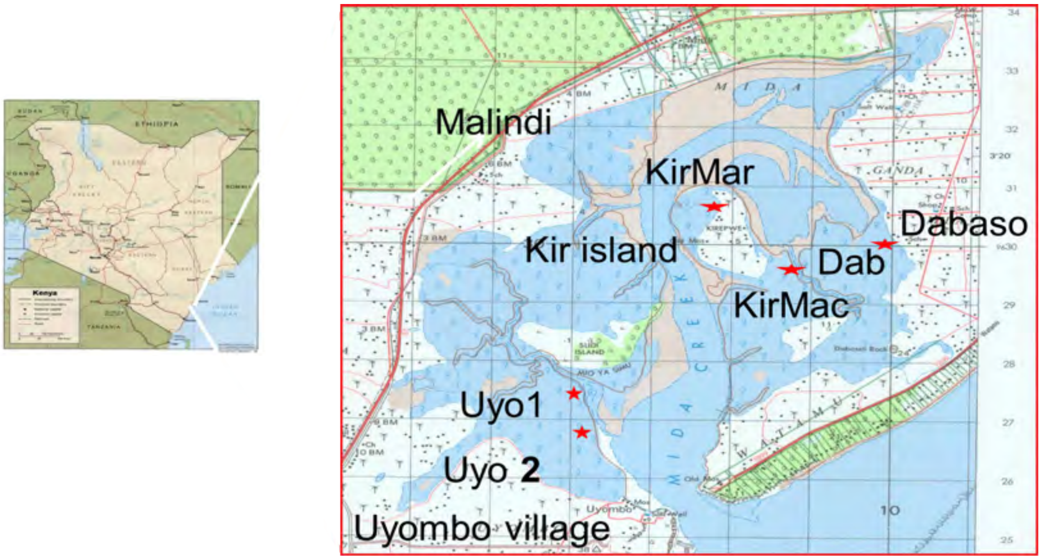

**Figure 1.** Map of Kenya (left) and Mida creek (right) indicating the study stations. Dab - Dabaso; Kir - Kirepwe; KirMac- Kirepwe Mach; KirMar - Kirepwe Mark; Uyo - Uyombo.

Propagules are predated on and damaged by insects and crabs while still growing on the mother tree, after abscission, during dispersal and early planting stages, leading to their death (Dahdouh-Guebas *et al*., 1998; Clarke *et al*, 2002; Sousa *et al*., 2003; Langston *et al*., 2017). This causes a decline in the establishment, viability and overall success rate of mangrove seedlings during artificial planting and natural regeneration.

Substantial studies have documented the phenology of mangrove species worldwide; however, there is paucity in the application of the findings in mangrove forest management. Creation of protected areas in the form of natural reserves and national parks is a positive step towards mangrove conservation (Field, 1998). Mida Creek which is located within Watamu National Reserve in Kenya is one such site, having been declared a national reserve in 1968. However, mangrove destruction has continued in the recent past (Dahdouh-Guebas *et al*., 2000; Warui, 2011; Alemayehu *et al*., 2014) indicating that mangrove conservation is still ineffective. In Mida Creak the abundant mangrove species are *Ceriops tagal* (Perr.) C.B. Robinson, and *Rhizophora mucronata* Lamk.; also the most preferred by the local community for wood, fuel and other uses, hence they are likely to be most affected by cutting and destruction.

Restoration, planning and management of mangrove forests requires an understanding and documentation of phenological traits of mangrove species geared towards informing management practices by foresters. This includes information such as: (1) leaf litter productivity that will inform the choice of species combination during planting, to ensure provision of mangrove litter throughout the year for mangrove benthic fauna and continued organic matter supply that will ensure heathy mangrove ecosystems; (2) propagule size at the time of abscission will guide the timing for collection for nursery propagation of the immature propagules to mitigate scarcity during lean seasons; (3) knowledge on seasonal availability and quantity of mature propagules for planting will inform planning of restoration projects and planting activities.

This purpose of this study was to: (a) investigate the vegetative phenology of *Rhizophora mucronata Ceriops tagal*, *Bruguiera gymnorrhiza* and *Sonneratia alba* Sm, in mono and mixed species stands in Mida Creek; (b) quantify propagule productivity of the Rhizophoraceae species; and (c) determine the size of abscised propagules of the Rhizophoraceae species and link the findings to mangrove management.

## Materials and methods

### Description of the study area

The study was conducted in three stations (Dabaso, Kirepwe and Uyombo) in Mida Creek within Watamu Marine National Reserve (Fig. 1). Study site co-ordinates, and inundation classes are shown in Table 1. The reserve was declared a protected area and established as a reserve in 1968. It was gazetted under the Wildlife Conservation Management Act in 1976. Seven out of the nine mangrove species in Kenya are found in Mida Creek, of which the dominant species are *Rhizophora. mucronata* Lamk. *Ceriops tagal* (Perr.) C.B. Robinson, and *Avicennia marina* (Forsk.) Vierh. (Kairo *et al*., 2002). A mangrove forest cover of 1 746 ha for Mida Creek has been reported (Kairo *et al*., 2002) and 1 655.7 ha in 2010 (Alemayehu *et al*., 2014). The community in Mida Creek utilizes the mangrove species for wood (house and boat construction, fuel, and medicinal purposes (Dahdouh-Guebas *et al*., 2000).

### Determination of phenological trends

Ten randomly selected 10 m × 10 m plots were established in the study sites from which phenological trends were extrapolated through monthly

**Table 1.** Site co-ordinates, elevation and inundation classes for the study sites.

| Station/Site/Species | Elevation | South | East | Inundation class |
|---|---|---|---|---|
| **Dabaso**<br>Site 1and 2:<br>*R. mucronata* | 26 feet | S 03° 20.748 | E 039° 59.349 | II |
| **Kirepwe Macho**<br>Site 1:(*S. alba*)<br>Site 2: (*R. mucronata)* | 22 feet | S 03°21.107 | E 039° 58.740 | I/II |
| **Kirepwe Mark**<br>Site 1: *R. mucronata*;<br>*C. tagal*<br>Site 2: *R. mucronata, C. tagal,*<br>*A. marina, B. gymnorrhiza* | 18 feet | S 03 ° 20.616 | E 039° 58.005 | II |
| **Uyombo 1**<br>Site 1: *R. mucronata, C. tagal,*<br>marina, B. gymnorrhiza<br>Site 2: : *R. mucronata, C. tagal,*<br>B. gymnorrhiza | 29 feet | S 03° 22.991 | E 039° 57.541 | III |
| **Uyombo 2**<br>Site 1: *R. mucronata, C. tagal,*<br>marina, B. gymnorrhiza<br>*Site 2: R. mucronata, C. tagal,*<br>*B. gymnorrhiza* | 19 feet | S 03° 23.107 | E 039° 57.654 | III |

**Table 2.** Stand structure of the study sites (±S.E).

| Site | n | Height (m) | DBH (cm) | Density (trees/ha) |
|---|---|---|---|---|
| **Monospecific stands** | | | | |
| Dab site 1; *Rhizophora mucronata* | 12 | 14.6 ± 0.7 | 85.5 ± 4.3 | 1,200 |
| Dab site 2; *Rhizophora mucronata* | 17 | 17.5 ± 3.2 | 87.2 ± 3.5 | 1,700 |
| Kir mc site 1; *Sonneratia alba* | 31 | 6.5 ± 0.2 | 29.6 ± 2.4 | 3,100 |
| Kir mc site 2; *Rhizophora mucronata* | 47 | 7.4 ± 0.9 | 29.7 ± 4.1 | 4,700 |
| **Multispecific stands/abundant species** | | | | |
| Kir mk site 1; *Rhizophora mucronata* | 27 | 7.9 ± 0.7 | 35.9 ± 3.8 | 2,700 |
| Kir mk site 2; *Rhizophora mucronata* | 47 | 6.0 ± 0.5 | 37.5 ± 4.2 | 4,700 |
| Uyo 1 site 1; *Bruguiera gymnorrhiza* | 26 | 10.7± 1.1 | 42.2 ± 6.5 | 2,600 |
| Uyo 1 site 2; *Rhizophora mucronata* | 54 | 4.6 ± 0.5 | 29.5 ± 4.4 | 5,400 |
| Uyo 2 site 1; *Ceriops tagal* | 37 | 9.7 ± 0.7 | 33.1 ± 4.2 | 3,700 |
| Uyo 2 site 2 ; *Ceriops tagal* | 51 | 4.4 ± 0.4 | 26.6 ± 3.5 | 5,100 |

**Key:** *n*= number of trees in 10x10m study site; **Dab**-Dabaso; **Kir mc**- Kirepwe Macho; **Kir mk**- Kirepwe mark; **Uyo**- Uyombo

mangrove litter collection by use of 10 litter traps per plot. Dabaso had 2 study sites (Dabaso 1 and Dabaso 2); Kirepwe had 4 study sites (Kirepwe Macho site 1 and 2, and Kirepwe Mark site 1 and 2), and Uyombo also had 4 study sites (Uyombo 1 (site 1 and 2), and Uyombo 2 (site 1 and 2). Litter traps with a trap mouth of 0.25m$^2$ were randomly suspended below the crown canopy but above the highest tide mark to avoid litter submergence during high tide. Litter collected in the traps (hereafter referred to as litter fall) was collected monthly from July 2010 to July 2012 from the stands. For comparative purposes, a second site was established adjacent to each study plot and data collected from November 2010 to July 2012 (referred to as site 2 in each study station). Collected litter was processed according to the procedure of Pool *et al.* (1975), whereby litter was dried at 70° C for 72 h to a constant dry weight and sorted into leaves, reproductive parts (buds and flowers), propagules/fruits (hereafter referred to as propagules) and small branches (twigs), and weighed. Length of propagules at time of fall was also measured. The stand structure for the mangrove stands was determined using trees with a $D_{130}$ of ≥25 cm.

### Statistical Analysis

Data on vegetative and reproductive phenology of seasonal production of leaves, stipules, reproductive parts and twigs was not different within a single species, therefore the phenological time series data for each of the four species is represented from a representative study site where the species was dominant. Propagule size data for each Rhizophoraceae species has been pooled (cumulative) from all the study sites due to the low number of propagules produced over the entire study period.

Data sets were tested for normality and homogeneity of variance for analysis of productivity of the various phenophases. However, the data were analyzed by non-parametric methods since it did not meet these requirements even after log transformation. Kruskal–Wallis ANOVA and pairwise comparison of mean ranks was used to determine significant differences in the weight of litter components. For presentation purposes of the phenograms, data presented is from representative sites.

## Results

### Stand structure

*Rhizophora mucronata* was the most abundant species and was present in all the study sites except in Kirepwe Macho site 1, which comprised a single species stand of *S. alba* (Table 2). This was followed by *C. tagal* and *B. gymnorrhiza* respectively. Though not included in this study, *A. marina* was the least abundant species in the study sites. *Rhizophora mucronata* sites in Dabaso had a stand density of 1 200 trees/ha, $D_{130}$ of 87.2 ± 3.5 cm, and mean tree height of 17.5 ± 3.2 m, whereas Uyombo 1 site 2, where *R. mucronata* was the most abundant species, had a stand density of 5 400 trees/ha.

## Vegetative and reproductive phenology

### *Rhizophora mucronata*

Data presented for this species is from Dabaso site 1 and site 2, and Kirepwe Macho site 2 for comparative purposes. In the three study sites leaf fall in *R. mucronata* occurred throughout the year without distinct peaks (Fig. 2). Dabaso site 1 recorded a leaf fall at 3.55 g $m^{-2}$ $day^{-1}$ in November 2011. Dabaso site 2 and Kirepwe Macho site 2 showed leaf fall peaks of 6.03 g $m^{-2}$ $day^{-1}$ in November 2010. There was no significant difference in leaf fall between sites $H_{(2,\ N=67)} = 2.805$, p=0.2386). New leaf production as demonstrated by stipule production was continuous with no distinct peaks, but highest production was in September 2011. There was no significant differences in leaf growth,

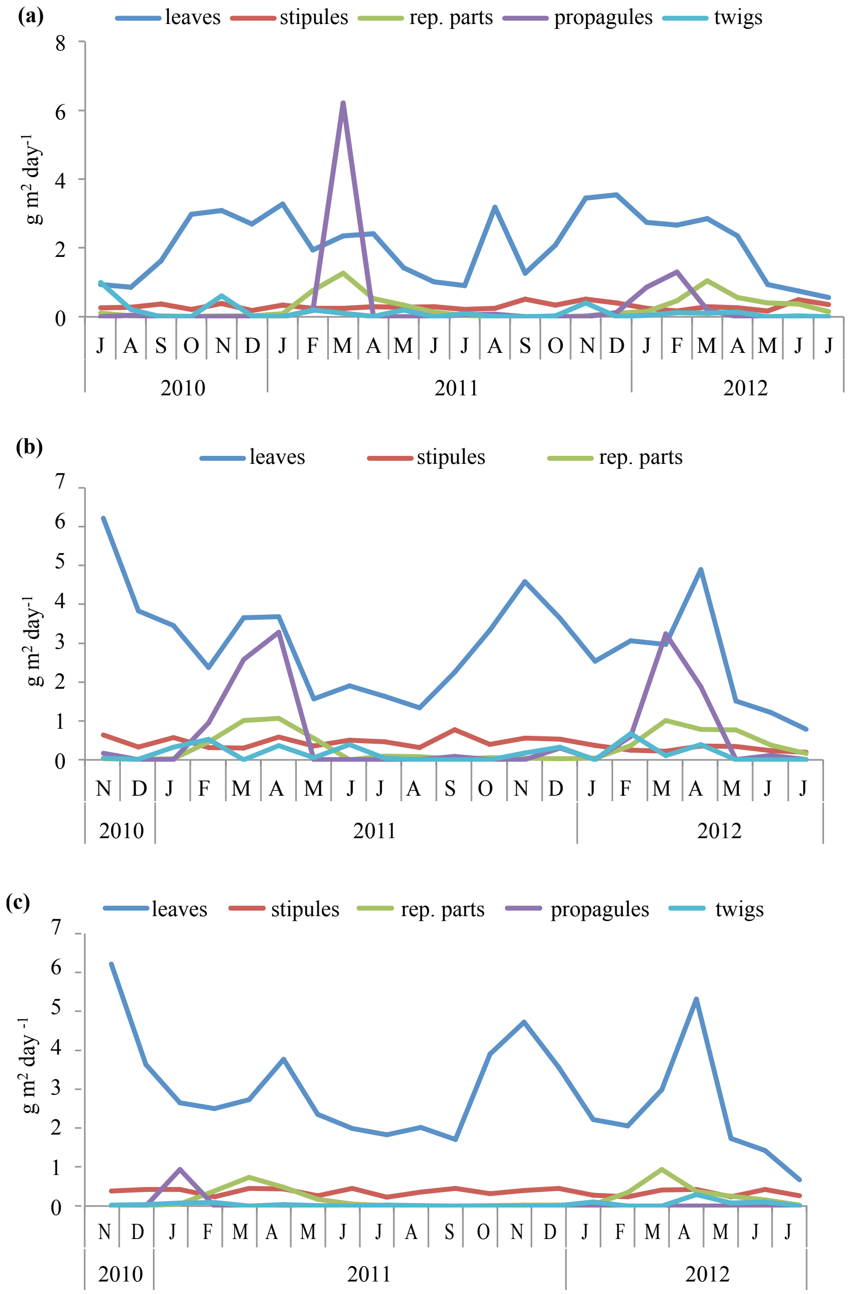

**Figure 2.** Monthly production of phenological components *of Rhizophora mucronata* in (a) Dabaso site 1, (b) Dabaso site 2, and (c) Kirepwe Macho site 2.

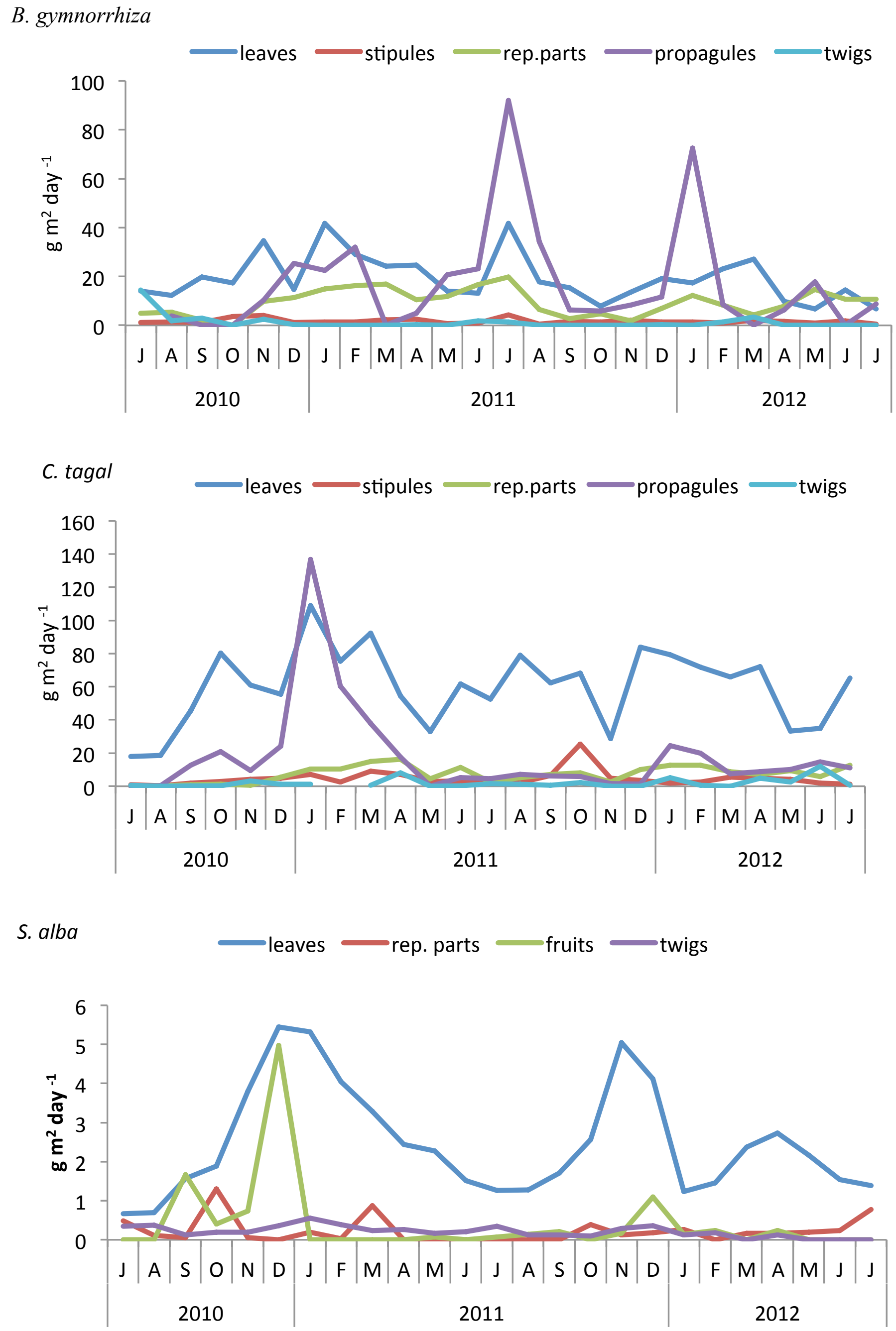

**Figure 3.** Monthly production of phenological components of *Bruguiera gymnorrhiza*, *Ceriops tagal* and *Sonneratia alba*.

$H_{(2,\ N=67)} = 5.0769$, p=0.0790) between sites. Production of twigs was minimal in comparison with the other litter components, with some months recording no fall. Reproductive parts of *R. mucronata* peaked in March in the three study sites with Dabaso site 1 showing a peak of 1.27 g $m^{-2}$ $day^{-1}$ in March 2011, but this was not significantly different from the other sites ($H_{(2,\ N=67)}=1.934$, p=0.3801). Propagule fall was significantly different between sites ($H_{(2,\ N=67)} = 9.781$, p = 0.0075). Dabaso site 1 had a peak production in March 2011, and January and February 2012. Dabaso site 2 had a longer and consistent propagule production period from February to April in 2011 and 2012. Kirepwe Macho site 2 showed the least propagule production which occurred only in January 2011. The highest peak of 6.21 g $m^{-2}$ $day^{-1}$ was recorded for Dabaso site 1. The total number of propagules recorded for Dabaso site 1, 2 and Kirepwe Macho site 2 throughout the study period was 14, 33 and 1 respectively. This translated to 700, 1 650, and 50 propagules ha-1 $yr^{-1}$, respectively.

### *Bruguiera gymnorrhiza*

Leaf growth and stipule production occurred throughout the year with no consistent peaks (Fig. 3). Highest leaf fall was observed in January and July of 2011 and 2012 measuring 41.8 g $m^2$ $day^{-1}$. Stipule production which signifies new leaf production occurred throughout the year with peaks in November 2011 and July 2012 (4.1 and 4.2 g $m^2$ $day^{-1)}$ respectively. Fall of twigs was minimal in comparison to other components and was totally absent in most of the months during the study period. Production of buds and flowers was observed throughout the study period with increased production from November 2010 to July 2011. Propagule fall was observed in most months with peaks in July 2011 and January 2012 (92.1 and 72.6 g $m^2$ $day^{-1}$ respectively), which coincided with the dry season.

### *Ceriops tagal*

Leaf fall in *C. tagal* occurred throughout the study period with the highest peak recorded in January 2011 at 109.1 g $m^2$ $day^{-1}$. Leaf growth was also continuous, peaking in October 2011 at 25.5 g $m^2$ $day^{-1}$. Fall of twigs was minimal as observed in all the studied species with the highest peak in June 2012 at 12.1 g $m^2$ $day^{-1}$. Reproductive parts were observed in all the months except in July 2010. Peak months were March to April and January to February of 2011 and 2012, respectively. The highest production was recorded in April 2011 at 16.3 g $m^2$ $day^{-1}$. Fall of propagules in *C. tagal* was observed in most months from September 2010 to April 2011, with a smaller peak in 2012. However, peak propagule production was observed in the dry months of January and February in both years, with the highest peak in January at 136 g $m^2$ $day^{-1}$.

### *Sonneratia alba*

Leaf fall, as in the other species, was continuous, but peaks were observed from November to January 2010 and November to December 2011. The highest peak in leaf fall was in December 2010 at 5.45 g $m^{-2}$ $day^{-1}$. Twig production in *S. alba* was the lowest among the species studied and occurred in most of the months, peaking in January 2011 at 0.56 g $m^{-2}$ $day^{-1}$. Reproductive parts were produced in most of the months. However, peaks were inconsistent in the studied years at 1.3 and 0.87 g $m^{-2}$ $day^{-1}$ in October and March of 2010 and 2011, respectively. Fruits in *S. alba* were observed in 13 out of the 25 months of the study. There were consistent peaks in December at 4.98 and 1.1 g $m^{-2}$ $day^{-1}$ in 2010 and 2011, respectively.

### Propagule length at abscission

Due to the low number of propagules collected in the litter traps at different study sites, data has been pooled from all the plots for each species. The number and length of abscised propagules varied with the species (Fig. 4). *Rhizophora mucronata* had the highest cumulative number of propagules followed by *C. tagal* and *B. gymnorrhiza* at 293, 104 and 74, respectively. The longest abscised propagule was 40.5 cm, 30 cm and 28 cm in length for *R. mucronata*, *B. gymnorrhiza* and *C. tagal*, respectively. The size class with the highest number of abscised propagules for *R. mucronata* was 10.1 -15 cm (60 propagules), and 5.1 – 10 cm for both *C. tagal* and *B. gymnorrhiza* at 26 and 30 propagules respectively. Immature abscised propagules were recorded at 99 %, 86 % and 67 % for the three species. The recommended mature propagule size for *R. mucronata, B. gymnorrhiza* and *C. taga*l is >40 cm, >15 cm and >20 cm, respectively (Kairo, 2010). The number of abscised propagules decreased with an increase in size class.

## Discussion

Mangrove species display very different growth and reproductive characteristics as outlined by Tomlinson (1986). Three species were studied (*R. mucronata*, *C. tagal*, *B. gymnorrhiza*) belonging to the family Rhizophoraceae, all of which exhibit the adaptation of being viviparous, and one fruit bearing species, *S. alba*. Despite the varying characteristics, it is important to make a comparison and document the phenological characteristics of the species in order to derive information that can be used for forest management and conservation. Various studies have discussed their findings in light of their application to mangrove forest conservation (Nagarajan *et al.*, 2008) (Raju & Karyamsetty, 2008). The findings from this study are discussed with the aim of providing information with application in planning, management, restoration and conservation of mangrove forests locally, and in other geographical regions.

Leaf production and fall characteristics of the four species indicate a continuous growth throughout the study period, characterized by multimodal peaks. This has also been reported for mangroves locally (Gwada and Kairo, 2001; Wang'ondu *et al.*, 2013), elsewhere in the Western Indian Ocean region (Shunula and Whittick, 1999), and globally (Wium-Andersen and Christensen, 1978; Wium-Andersen, 1981). Kamruzzaman *et al.* (2016) reported high and low litter fall in summer and winter respectively for *B. gymnorrhiza*. Peak leaf fall for *R. mucronata* and *S. alba* was in the wet season, whereas that for C. *tagal* and *B. gymnorrhiza* was in the dry season. Mangrove stands composed of these Rhizophoraceae species can therefore be recommended, where possible, to ensure continued detrital input into the mangrove ecosystem all year round.

In this study the highest leaf production and fall was observed in *C. tagal* and *B. gymnorrhiza* in the mixed species stands. These sites also had the highest organic matter content in the sediments, in comparison with the single species stands. Sources of organic matter content in mangrove ecosystems are many and diverse, and mangrove litter input is important (Bouillon *et al.*, 2003). The high and continuous input of leaf litter all year round could be a contributing factor as this ensures availability of detrital material for benthic fauna that are responsible for processing and degrading this litter into organic matter. This is an indication that, where possible, mixed stands of these species should be prioritized in conservation, due to this high leaf litter productivity.

The four mangrove species demonstrated varying characteristics in production of reproductive inflorescence with regard to their seasonality and number of

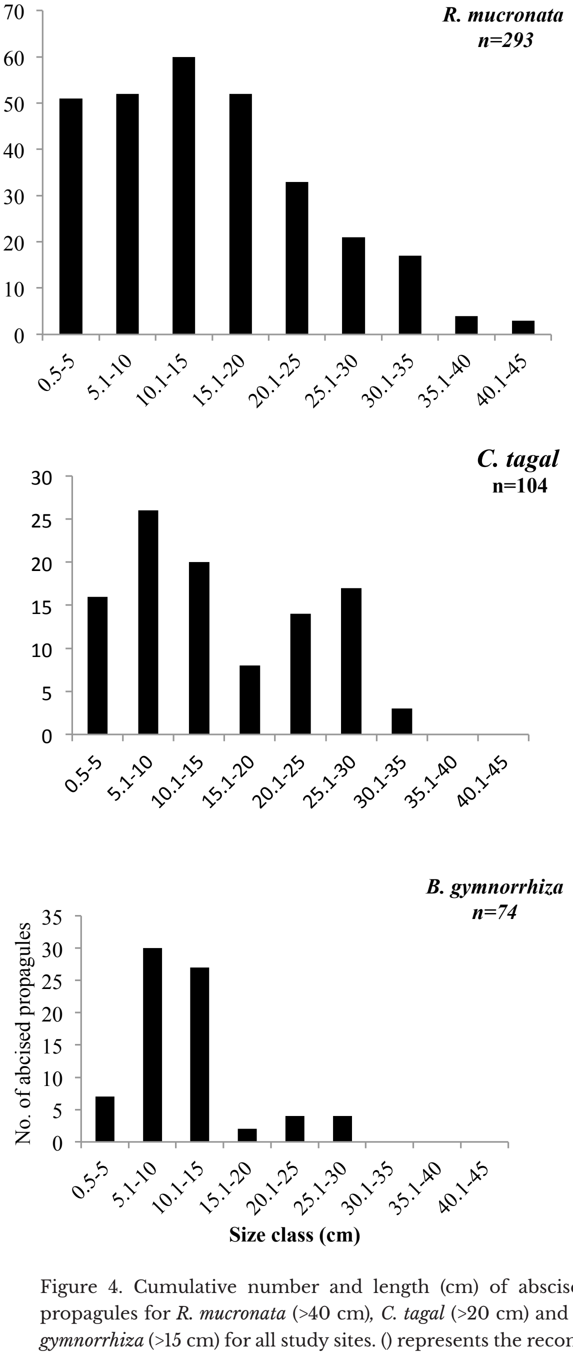

Figure 4. Cumulative number and length (cm) of abscised propagules for *R. mucronata* (>40 cm), *C. tagal* (>20 cm) and *B. gymnorrhiza* (>15 cm) for all study sites. () represents the recommended abscission size for a mature propagules.

production months. *R. mucronata* has been reported to have a prolonged development period from initiation of floral buds to maturation of propagules, ranging between 16-20 months (Wang'ondu *et al.*, 2013), while this can last up to 3 years for *R. apiculata* (Christensen and Wium-Andersen, 1977). Documentation of peak propagule production months is important to ensure that proper planning of planting activities occur in restoration projects.

Abortion of reproductive structures has also been reported widely with a few mature propagules apparent at the end of the reproductive season (Christensen and Wium-Andersen, 1977; Wium-Andersen, 1981; Coupland *et al.*, 2006; Sharma and Kamruzzaman, 2012). Prolonged propagule development coupled with high abortion rates (abscission of immature propagules), and propagule predation prior to and after abscission, are some factors that may lead to a scarcity of propagules either for natural or artificial regeneration. This study also observed that a high propagule production season in one year was followed by a lower propagule production in the following year. This is important information for forest managers as they can plan for propagule harvesting during peak production for nursery propagation, to ensure availability of seedlings in the following year when productivity is low. This is especially so for *C. tagal* which was observed to have peak propagule fall during the dry months. A study by Robert *et al.* (2015) reported that *C. tagal* propagules are more prone to dehydration upon abscission than those of *R. mucronata*, and this is likely to aggravate the situation for *C. tagal*. This further emphasizes the need for nursery propagation of mangrove propagules of these species.

In this study *R. mucronata* stands showed different reproductive potential (Dabaso site 2 >Dabaso site 1 > Kirepwe Macho site 2, in decreasing order) even for sites at close proximity to each other. This indicates that mangrove forest productivity is site specific, and that there is a likelihood of no propagule production in some stands. This necessitates the identification of the highly productive mangrove stands for conservation as live seed banks. In this study, the mixed species stands in Uyombo were more productive compared to the other single species stands, and should be earmarked as no take areas within Mida Creek National Reserve to ensure seed availability for either natural regeneration through seed dispersal, direct planting, or nursery propagation. Highly productive single species stands should also be identified and those found to be productive should be used for conservation purposes.

*Rhizophora mucronata*, *C. tagal* and *B. gymnorrhiza* are the preferred species for the supply of wood for construction and fuel which top the list of uses of mangroves in Mida Creek (Dahdouh-Guebas *et al.*, 2000; Kairo *et al.*, 2002). The three Rhizophoraceae species showed varying propagule abscission sizes, however, it was clear that most of the propagules (50%) abscised before attaining the recommended maturity size. According to Kairo (2010), the recommended size at maturity for nursery rearing is >15cm, >20cm and >40 cm for *B. gymnorrhiza, C. tagal* and *R. mucronata*, respectively. Propagule size, pre- and post- dispersal damage by insects and crabs before and after abscission, are important aspects, and to some extent, determines dispersal, recruitment and establishment (De Ryck *et al.*, 2012; Sousa *et al.*, 2003). Even though, *R. mucronata* recorded the highest propagule abortion rates, more than 50% of propagules of the other two species were immature. In addition, *C. tagal* has been reported to have lower establishment rates due to its small propagule size, sensitivity to dessication, and slower root growth (De Ryck *et al.*, 2012; Robert *et al.*, 2015). Sousa *et al.* (2003) also noted that irrespective of the species, propagule size contributes significantly to initial seedling establishment and early growth. *Sonneratia alba* is also on the IUCN red list of threatened mangrove species (Kathiresan *et al.*, 2010). This study therefore indicates that there is need for nursery propagation of propagules of these species for continued availability of seedlings for artificial regeneration.

This study provides important information to forest managers, suggesting that the four mangrove species included in the study should be at the top of the conservation list. It also emphasizes the need for species-guided conservation strategies with the needs of the dependent human communities for sustainable utilization and provision of goods and services taken into account. This is coupled to the fact that mangrove forests are on the decline locally, experiencing losses of between 2.7-5.1%, rates higher than the global mean, due to anthropogenic pressure (Bosire *et al.*, 2014).

The unique characteristics of the studied mangrove species cannot be overemphasized, but it is important to note that management and conservation of mangrove forests should not be generalized. Characteristics of each species should be considered if effective conservation and management strategies are to be achieved. Planning, management and conservation practices for mangrove forests should be guided by the phenological traits of species as well as the needs of the local community. This study further recommends nursery propagation studies to establish which of the aborted propagule sizes are viable in the nursery to guide collection of abscised immature propagules for nursery propagation in the future.

## Acknowledgements

We are grateful to Mr. Jackson Mwamure for field assistance, and the University of Nairobi for grant administration, time and laboratory space to carry out the research. This work was funded by a research grant from VLIR-UOS under the RIP project. The Western Indian Ocean Marine Science Association (WIOMSA) is thanked for a travel grant to present these findings at the 8th WIOMSA conference in Durban, South Africa in October 2015.

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# Diet dynamics and feeding strategies of *Hilsa kelee* (Cuvier, 1829) and *Valamugil buchanani* (Bleeker, 1853) in the Pangani Estuary, Tanzania: Insights from stomach contents and fatty acid biomarkers

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## Abstract

Stomach contents and fatty acid (FA) biomarkers were used to investigate the diet and feeding strategies of the marine fish species *Hilsa kelee* and *Valamugil buchanani*, across three Pangani estuarine zones (about 7 km apart). The three zones depict heterogeneous distribution of trophic resources along the longitudinal estuary gradient. Despite ecological index and FA trophic niche widths indicating high overlap of trophic resources, the permutational multivariate analysis of variance revealed significant interspecific variations in diet and FA compositions. This highlights the importance of using statistically supported tools when drawing inferences on the diet dynamics of estuarine fish. The dominant diatom and detritus diets reflected the high herbivory C22:6(n-3):C20:5(n-3) and omnivory C18:1(n-9):C18:1(n-7) FA trophic indices of *V. buchanani*. The diatoms and copepods dominating the diet of *H. kelee* concurred with the species' higher carnivory C22:6(n-3):C20:5(n-3) and lower omnivory C18:1(n-9):C18:1(n-7) FA biomarkers. The diet niche breadth index, the Amundsen feeding strategy diagrams, and the FA trophic niche suggest that *V. buchanani* exhibits a generalist feeding strategy, and *H. kelee* a mixed feeding strategy that is intermediate between a specialist and a generalist. Due to these differences, it is suggested that *V. buchanani* demonstrates a higher degree of resilience to anthropogenic disturbances than *H. kelee* in the Pangani estuary.

**Keywords:** Fish, diet, fatty acid profiles.

## Introduction

Estuaries are characterized by variations in primary food sources due to temporal fluctuations of river discharge and tidal seawater flow. The myriad of primary food sources derived from autochthonous and allochthonous sources contribute to high estuarine productivity (McLusky and Elliott, 2004; Antonio *et al.*, 2012). Such frequent fluctuations in food sources and physico-chemical parameters allow fish assemblages in estuaries to demonstrate different feeding strategies for satisfying their nutritional requirements (Elliott *et al.*, 2002). Specifically, the mangrove-fringed estuaries, apart from demonstrating diverse and abundant food resources, provide refuge areas to juvenile marine fish species (Igulu *et al.,* 2014). Due to this, many marine fish species live in estuaries at different stages of their life cycles (Mbande *et al.,* 2005). The ecological status of many estuaries has been modified by anthropological activities and the food webs that link estuarine and coastal ecosystem boundaries have been impaired (Pasquaud *et al.*, 2010; Selleslagh *et al.,* 2012). There is a compelling need to understand the functions and ecological roles of individual estuarine systems in relation to the species with estuarine-ocean connectivity for maintaining healthy coastal ecosystems. An essential step towards achieving this is to study the dietary niches and the feeding strategy of marine fish in estuaries. This helps to enhance knowledge on how different fish species with related trophic requirements co-exist and contribute to the resilience of estuarine food webs.

Numerous studies have reported that most estuarine fishes demonstrate omnivorous and opportunistic feeding strategies at all sizes; a characteristic which enables them to consume the variable food resources in a dynamic environment (Cabral, 2000; Lobry *et al.,* 2008). However, there is limited knowledge on the diet and feeding strategies of marine fish at various life history stages in Tanzania estuarine systems. Studies on the diet and feeding strategies of marine fish species in estuaries are essential, especially when methods are used reveal their long term feeding history. Lança *et al.* (2013) was able to better explain the long term feeding strategy of sea lampreys on the Iberian coast of the Atlantic Ocean by using fatty acid (FA) biomarkers. Studying the diet and feeding strategy of fish by solely relying on stomach content analysis not only represents the static situation, but also neglects temporal and spatial estuarine diet dynamics (Antonio *et al.,* 2012). Fatty acid trophic markers are frequently used in studying the feeding ecology of fish because they tend to accumulate in adipose tissues over a long period through dietary intake (Maranto *et al*., 2011). These FA biomarkers produced by the primary producers are usually transferred unchanged higher up the food chain (Dalsgaard *et al.,* 2003; Parrish, 2013). In the fresh water environment, where the fish species cannot readily accumulate some FA biomarkers such as C20:5(n-3) and C22:6(n-3), they biosynthesize them by modifying other dietary FAs, mainly C18:2(n-6) and C18:3(n-3). Similarly, the FA biomarkers are used to infer habitat boundary connectivity since some FA are produced by habitat-specific primary producers. Among others, these include terrestrial plant FA biomarkers, mainly C18:2(n-6) and C18:3(n-3) (Meziane *et al.,* 2007), and marine micro-algae derived FA biomarkers such as C20:5(n-3) and C22:6(n-3) (Dalsgaard *et al.,* 2003). These attributes justify the role of FA trophic markers in understanding the quality of each diet item and the mechanisms employed by the species to acquire such food sources.

The filter feeder *Hilsa kelee* (clupeidae) and phytodetritivorous *Valamugil buchanani* (mugilidae) are among the most abundant marine fish caught for the local market and consumption by the local fishing community in the Pangani estuary. These two marine fish species use estuaries as nursery and feeding grounds during the juvenile stages. The abundance of *H. kelee* in estuaries increases during spawning periods (September-February and June) (Gjosaeter and Sousa, 1983). *Valamugil buchanani* spends most of its life in estuaries and inshore waters, and migrate to marine waters at sexual maturity for spawning (Rajesh *et al*., 2014). The trophic resources of both species include micro-algae, small fauna and other organic particles (Reintjes, 1974; Wijeyaratne and Costa, 1990). The two species are likely to share basal trophic resources, in particular in shallow and macro-tidal estuaries like the Pangani, where the mixing of trophic resources within the water column is common (Sotthewes, 2008; Pamba *et al*., 2016). There is a need to further explore how and to what extent the two species partition the trophic resource base, and their level of opportunism in the utilization of estuarine trophic resources.

The present paper reports on the diet, dietary niche overlap, and feeding strategies of *H. kelee* and *V. buchanani* from the Pangani estuary, studied by using stomach content analysis and FA biomarkers. Specifically, the objectives of this study were to: (a) describe the diets and feeding niches of *H. kelee* and *V. buchanani* in the Pangani estuary; and (b) analyze fish feeding strategies by using their dietary and FA compositions. It was hypothesized that the dietary and FA biomarkers between the two species, and during different ontogenic stages were significantly different across the longitudinal gradient of the estuary. Due to the differences in foraging mode of these species, it was expected that *V. buchanani* would exhibit higher opportunistic omnivory indices and feeding niche areas than *H. kelee* in the Pangani estuary. The findings of the present study provide baseline information that will be useful for improving the management strategies for the rapidly changing Pangani estuarine system.

## Materials and methods

### Study area

The present study was carried out in the funnel-shaped and permanently open Pangani estuary (38° 50˝E, 5° 20˝S and 39°E, 5° 26˝S) in the northern part of the Tanzanian coast (Mwanukuzi, 1993). It is a macro-tidal estuary of semi-diurnal type with a mean amplitude of about 3.5 m at spring tides and 3.0 during neap tides (Pamba *et al*., 2016). Average depth is about 5 m (Sotthewes, 2008). The present study was conducted within 16 km of the Pangani estuary mouth.

The estuary is fringed with mangrove forest stretching to about 11 km from the river mouth (PWBO/IUCN, 2008). Sampling was based within three predetermined zones designated as upper, middle and lower estuarine zones (Fig. 1), located in the longitudinal salinity gradient. The lower estuarine zone was located 3 km inland from the estuary mouth (salinity range 20-35 ppt), the middle zone was located 10 km from the estuary mouth (salinity range 7 – 16 ppt), and the upper portion of the estuary was situated at about 16 km from the estuary mouth (salinity range 1 - 6 ppt).

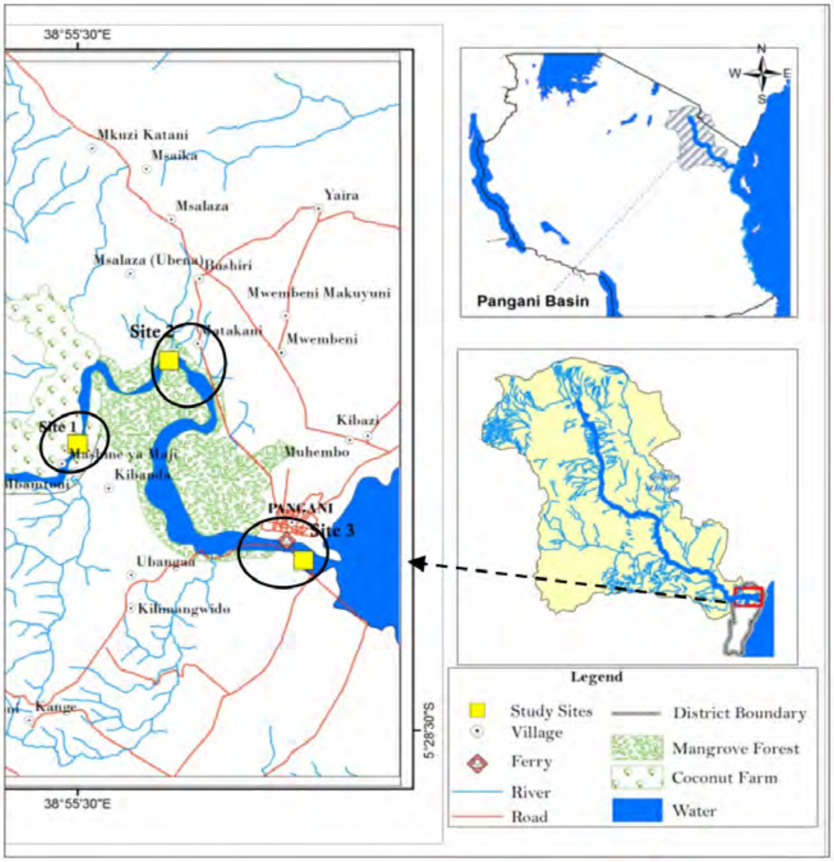

**Figure 1.** Map of the Pangani estuary indicating upper (site 1), middle (site 2) and lower (site 3) sampling zones (in oval shapes) along the longitudinal salinity gradient.

### Collection of fish samples and analysis of diet composition

The fish species *H. kelee* and *V. buchanani* were sampled in October, 2014, and January, March, May and July, 2015 in the estuary. For each sampling period, fish were collected in daylight using seine nets with the dimension of 15m length, 1.5m width and mesh size of 0.5mm. After retrieval of the nets, all the species of interest were selected and thereafter stored in a cool box with dry ice. Later on during the evening, wet weight (nearest 0.1g) and total length (nearest 0.1cm) were recorded, and fish stomachs were removed and frozen at -20°C. At the end of each sampling period, frozen samples were transported to the laboratory at the University of Dar es Salaam, College of Agricultural Sciences and Fisheries Technology. In the laboratory, the stomach contents were examined at 200x and 400x magnification using an Olympus inverted microscope. Benthic and planktonic organic food particles were identified using available keys (Crosby and Wood, 1958; Utermohl, 1958; Mwaluma *et al*., 2014). The frequency of occurrence (%F) and percentage volumetric contributions of food item to the total stomach volume (%V) were then determined by using the point method described by Hyslop (1980). This point semiquantitative method was selected due to the nature of food items found in the stomachs of both species. The scale points representing the volume occupied by each dietary category used included 1, 2, 4, 8 and 16, with 1 representing the minimum amount and 16 representing the maximum amount. All food items in the stomachs were identified to the lowest taxon possible and then grouped into broader taxonomic categories for further data analysis. Non-food items like sand, gill epithelia and unidentified materials were excluded in further steps of data analysis.

### Feeding strategy and estimation of dietary indices

The feeding strategy at individual and population levels for each species was evaluated by adopting the graphical method described by Amundsen *et al.* (1996). This two-dimensional graph is defined by the percentage frequency of occurrence (%F) of diet categories on the x-axis, and the percentage of prey-specific abundance, biomass, or volume of prey i (%$P_i$), on the y-axis. The %F was obtained using the formula Ni/N x 100 where: Ni = number of stomachs containing food item $i$, and N = total number of stomachs with food. The percentage of prey (any food item found in the stomach) specific volume (%$P_i$) was expressed as:

$$\%\mathrm{P}i = \left(\frac{\sum \mathrm{B}i}{\sum \mathrm{B}ti}\right) \mathrm{x}\ 100$$

Where %P$i$ is the percentage of prey-specific volume of prey $i$, ∑B$i$ is the volume of food item $i$ in all stomachs of the species, and B$ti$ is the total volume of all food items only in stomachs with food item $i$. As described by Amundsen *et al.* (1996), the prey importance, feeding strategy, and niche width were obtained by examining the distribution of data points of food items along the diagonals and the axes of the graph.

The Levin's standardized equation for food niche as described by Krebs (1999) was used to estimate the dietary niche breadth of each species in each estuarine zone. The dietary volume data were used to calculate the trophic niche breadth of each species. The Levin's standardized equation is expressed as:

$$B_A = \frac{(\sum_j P_{ij}^2)^{-1} - 1)}{(n-1)^{-1}}$$

Where: $B_A$ is the standardized trophic niche breadth, $P_{ij}$ is the proportion of food category $j$ in the diet of the species $i$ and, $n$ = total number of food items in the diet of species i. The $B_A$ values range between 0 and +1. Values closer to 0 indicate a narrow food niche (specialist), while values closer to +1 imply a broad diet niche (generalist).

Species dietary overlap ($O$) for the two species in each estuarine zone was calculated by using Pianka's index of niche overlap (Pianka, 1973). It was assumed that the different dietary resources were equally accessible to both species. The following dietary overlap formula used was:

$$O = \frac{\sum P_{ij}\, P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$

Where $P_{ij}$ and $P_{ik}$ are the proportions of diet category $i$ comprised in the diets of $j$ (*H. kelee*) and $k$ (*V. buchanani*), respectively. According to Sá-oliveira *et al.* (2014), the diet overlap between species value is low when the value falls within the 0 - 0.39 range, intermediate when it is within the 0.4- 0.6, and high when its range is in between 0.61 - 1.

### Lipid sample preparation, extraction, and fatty acid analysis

Fish samples for lipid extraction and FA analysis were limited to the upper and lower sampling zones, as well as to two sampling periods conducted in March and July 2015. This took into consideration the longitudinal movement of the species, the efficiency of the method which reveals long-term dietary dynamics, and also the budget. Fish FA data for the two sampling periods were pooled together due to less pronounced freshwater flow occurring in March and July in the estuary (Selemani *et al.*, 2017). These samples were selected after their weights and lengths had been recorded and stomachs removed for stomach content analysis. Seventy fish samples of both species (34 samples from upper zone and 36 samples from lower zone) were subjected to FA analysis. The flesh from the dorsal white muscle of the individual fish was cut, skin removed, washed with distilled water, freeze-dried and kept in dry glass vials in desiccators until FA analysis. The samples were later transported to the State Key Laboratory of Estuarine and Coastal Research (SKLEC) of the East China Normal University (ECNU) in China, for FA analysis.

Lipid extraction was performed following the reduced-solvent method described by Folch *et al.* (1957). 100 mg of each freeze-dried sample was mixed with 2 µg of C21:0 FA (Fluka) as the recovery of internal standard. This was followed by the addition of 15 ml of a mixed solution of dichloromethane and methanol (v:v = 2:1), and the antioxidant BHT (butylhydroxytoluene; 0.01%). The mixture was then extracted in the CEM – Mars microwave (USA), cooled and centrifuged at 3000 rpm at 4 °C for 10 minutes. The upper phase was collected in clean glass tubes and the residue re-extracted twice. All extracts were pooled together and evaporated to 0.5 ml before drying under a stream of nitrogen to obtain the total lipid.

The FA methyl esters (FAMEs) were prepared from total lipid extracts. The total lipid was treated with 2 ml n-hexane and 4 ml methanol (containing 5% HCl) in 20 ml glass tubes, and heated at 50°C for 12 hours. After cooling in water, 1 ml Milli-Q water was added and the resulting FA methyl esters (FAMEs) were extracted three times by using 4 ml of n-hexane. The total FAME extracted were analyzed and quantified by using a gas chromatograph system equipped with a flame ionization detector and an autosampler (Agilent 6890A series GC-FID), and a silica capillary column (30 m length, 0.32 mm inner diameter, 0.25 µm film thickness; Supelco). Helium was used as the carrier gas. The programmable temperature vaporizer injector was applied for the standards (FAME Mix, Supelco, USA) and for the sample injection exercise. For each sample, the different FAMEs composition were identified by comparing their specific retention times with those from standards of known composition. The retention times and the peak area were recorded and used to quantify the relative percentage of each FA to the total fatty acids (FAs) identified in a sample. All FAs were expressed as a percentage of total FAs. The FA biomarkers and feeding strategy indices applied were referred from Graeve *et al.* (1997), Dalsgaard *et al.* (2003), Gatune *et al.* (2012), Kelly and Scheibling (2012), Lança *et al.* (2013), and Parrish (2013).

### Statistical analysis of diet and fatty acid composition data

Non-parametric multivariate and parametric univariate analyses were used to examine the level of similarity and to test for intra- and inter-specific variations in dietary and FA composition among estuarine zones. The multivariate analyses of dietary and FA data were performed by using PRIMER6 (Clarke and Gorley, 2006) and its PERMANOVA+ software packages (Anderson *et al.,* 2008). By using a two factorial design (fish species and estuarine zone factors) permutational multivariate analysis of variance (PERMANOVA), the study revealed the degree of variations in dietary and FA composition for the fish species. Square roots of estimated variance components obtained when running PERMANOVA were used to assess the contribution of each factor to overall variations in the tests. The non-metric multidimensional scaling ordinations (nMDS) were used to visually assess the feeding patterns of the species as well as the variations in FA composition of each species between the estuarine zones.

The pair-wise PERMANOVA tests were run in order to assess the variations in diet and FA profiles of individual species across the three estuarine zones. In addition to that, one-way PERMANOVA was performed to evaluate the level of variation in diet and FA composition by the size of each fish species in each sampling zone of the estuary. Different length groups with the size-class interval of 4 cm total length were used to determine diet differences by fish size, depending on the availability of enough samples for stomach content analyses. Due to the limited FA data in all length groups, two size classes (12 -15 cm and 20-23 cm total length for *V. buchanani*; and 12-15 cm and 16-19 cm total length for *H. kelee*) were used to explore the pattern of FA compositions by fish sizes. All PERMANOVA tests and nMDS were run based on the Bray-Curtis similarity matrices of square root transformed dietary, and untransformed FA composition data. Similarity percentage (SIMPER) was run based on the dietary and FA composition data in order to identify the main food items and FAs responsible for differences detected by PERMANONA.

Stable Isotope Bayesian Ellipses in R (SIBER) package was applied to assess the feeding niches by using FAs. That is, the FA profiles of each fish species were used in the SIBER package to examine the species trophic niches in space, as a proxy of isotopic niche space. The x and y coordinates of the nMDS analysis of untransformed FA data for each fish species were used. The data points identified as outliers in the FA profile of each species were put aside when developing the nMDS plot. The nMDS analysis in each zone was done using the vegan package under the function “monoMDS” in the R statistical working environment. Then, according to the concept of the SIBER package (Jackson *et al*., 2011; Layman *et al*., 2011), FA niche widths were presented by the standard ellipse areas comprising the maximum percentage of possible datasets along the convex hulls. Thereafter, the differences in areas of the ellipses (FA niche width) between the species were tested using one-way ANOVA.

## Results

### Diet compositions

In total, 185 stomachs of *H. kelee* and 196 stomachs of *V. buchanani* were found to contain food, while 49 *H. kelee* and 37 *V. buchanani* stomachs were empty. Among stomachs containing food, 25.4% for *H. kelee* and 13.8% for *V. buchanani* comprised unidentifiable food items (Table 1). The size of *H. kelee* analyzed ranged from 8 to 21 cm (total length) whereas that of *V. buchanani* ranged from 8.5 to 35.2 cm (total length). The diet of *H. kelee* was largely dominated by diatoms

**Table 1.** Percentage frequency of occurrence (% F) and mean percentage volumetric contribution (% V) of diet categories found in stomachs of *Hilsa kelee* and *Valamugil buchanani* from Pangani estuary.

| Major dietary categories | Upper estuary | | | | Middle Estuary | | | | Lower Estuary | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *H. kelee* | | *V. buchanani* | | *H. kelee* | | *V. buchanani* | | *H. kelee* | | *V. buchanani* | |
| | %F | %V | %F | %V | %F | %V | %F | %V | %F | %V | %F | %V |
| Diatoms | 96.77 | 42.43 | 97.37 | 27.30 | 96.91 | 42.51 | 97.01 | 26.89 | 96.49 | 46.64 | 98.90 | 30.47 |
| Dinoflagellates | 22.58 | 1.92 | 18.42 | 0.66 | 16.49 | 1.28 | 17.91 | 0.76 | 14.04 | 1.83 | 18.68 | 0.82 |
| Filamentous and other green algae | 35.48 | 5.05 | 15.79 | 0.76 | 22.68 | 2.07 | 16.42 | 1.01 | 8.77 | 1 | 41.76 | 3.83 |
| Cyanobacteria | 11.18 | 0.48 | 10.53 | 0.72 | 10.31 | 0.91 | 25.37 | 2.31 | 3.51 | 0.27 | 62.64 | 3.36 |
| Copepods | 61.29 | 13.24 | 10.53 | 0.82 | 37.11 | 4.96 | 10.45 | 0.94 | 35.09 | 5.75 | 4.40 | 0.18 |
| Fish larvae | 3.23 | 0.97 | - | - | 5.15 | 1.24 | - | - | 8.77 | 1.67 | - | - |
| Nauplii copepod larvae | 12.90 | 1.5 | 10.53 | 0.84 | 14.43 | 1.44 | 7.46 | 0.39 | 14.04 | 1.57 | - | - |
| Other crustacean larvae | 22.58 | 4.18 | 15.79 | 1.53 | 12.37 | 2.45 | 2.99 | 0.22 | 7.02 | 0.93 | 1.10 | 0.06 |
| Fish eggs and other unidentified eggs | 16.13 | 1.55 | - | - | 15.46 | 1.63 | - | - | 14.04 | 1.7 | - | - |
| Plant vascular tissues | - | - | 34.21 | 7.24 | - | - | 31.34 | 6.63 | - | - | 60.44 | 7.40 |
| Detritus | 48.39 | 12.27 | 86.84 | 31.82 | 82.47 | 26.18 | 83.58 | 30.97 | 77.19 | 28.07 | 91.21 | 28.81 |
| Gill epithelia | - | - | 21.05 | 1.34 | - | - | 13.43 | 1.36 | - | - | 35.16 | 4.03 |
| Sand/sediment | 51.61 | 15.29 | 94.74 | 26.97 | 42.27 | 12.23 | 94.03 | 27.96 | 29.82 | 6.54 | 73.63 | 19.21 |
| Unidentified materials | 9.68 | 1.13 | 0 | 0 | 24.74 | 3.09 | 5.97 | 0.55 | 29.82 | 4.03 | 25.27 | 1.63 |
| Total - empty stomach (%) | 6 (16.22) | | 5 (11.63) | | 9 (8.49) | | 21 (23.86) | | 34 (37.36) | | 11 (10.78) | |
| Total - stomach with food (%) | 31 (83.78) | | 38 (88.37) | | 97 (91.51) | | 67 (76.14) | | 57 (62.64) | | 91 (89.22) | |

(percentage volume (%V) 42.4 - 46.6 %V), detritus (12.3 – 28.1%V) and copepods (5.0 to 13.2 %V) in all three estuarine zones (Table 1). The dominant food items in the diet of *V. buchanani* were detritus (28.8 – 31.8%V), diatoms (26.8 - 30.5 %V) and decaying vascular plant tissue (6.6 - 7.4 %V) in all estuarine zones (Table 1).

The two way-PERMANOVA test revealed significant differences in dietary composition between species and estuarine zones (two factors, species and zones), and the interaction between the main factors (pseudo-$F \geq 4.15$; $p = 0.001$) (Table 2). However, the non-metric MDS ordination depicted the marginal differences in dietary compositions of the two fish species in all three estuarine zones (Fig. 2). This was indicated by the unclear pattern and overlaps of some dietary data points for both species in the ordination space. According to the similarity percentage (SIMPER) routine, the average dissimilarity in diet of the two species were about 50.3% in the upper zone, 39.9% in the middle zone, and 41.7% in lower zone of the estuary. Such dissimilarity mainly resulted from different amount of detritus, diatoms, copepods, and decomposing vascular tissue present in the stomachs of both *H. kelee* and *V. buchanani*. The PERMANOVA test also showed that the factor of fish species explained twice as much of the variations relative to the interactions between the species and estuarine zone factors. The estuarine zone factor contributed the lowest variability in diet when compared with other factors (Table 2).

**Table 2.** Two-ways PERMANOVA of dietary composition in *Hilsa kelee* and *Valamugil buchanani* in upper, middle and lower zones of Pangani estuary. Note: df = degrees of freedom, pseudo –F = pseudo-F ratios, p = significance level and CoV = square root component of variation.

| Source of variation | df | Mean square | Pseudo-F | *p* | CoV |
|---|---|---|---|---|---|
| Main factor | | | | | |
| Fish species | 1 | 43748.00 | 57.29 | 0.001 | 16.38 |
| Estuarine zone | 2 | 3167.80 | 4.15 | 0.001 | 4.55 |
| Two-way interactions | | | | | |
| Fish species Vs zone | 2 | 5303.30 | 6.95 | 0.001 | 8.84 |
| Residual | 375 | 763.65 | | | 27.63 |
| Total | 380 | | | | |

The pair-wise PERMANOVA tests and non-metric MDS ordination further confirmed estuarine zone to be a weak factor. Both analyses indicated that there were slight intra-specific differences in diet across the upper, middle and lower sampling zones (Table 3, Fig. 2). The non-metric MDS ordination indicated less intra-specific dissimilarity in diet of both species among the estuarine zones as the data points were close and only slightly distinguishable. The diets by size for *H. kelee* were slightly different in the upper (one-way PERMANOVA, pseudo-$F_{2,\,28}$ = 4.93, $p$ = 0.001) and lower (pseudo-$F_{2,\,54}$ = 6.44 $p$ = 0.001) estuarine zones only. With regard to the diet of different sizes of *V. buchanani,* the variations were marginally detected in the samples caught from the upper estuarine zone (pseudo-$F_{4,\,33}$ = 2.67, $p$ = 0.01).

The Pianka's index measure of diet niche overlap between *H. kelee* and *V. buchanani* were very high and agreed with the findings portrayed in the dietary non-metric MDS ordination. The diet overlap was extremely high in the lower portion of the estuary ($O$ = 0.95), followed by the middle zone ($O$ = 0.94), and lastly the upper estuarine zone ($O$ = 0.79). The overall dietary niche breadth of *H. kelee* was relatively low compared to that of *V. buchanani* in the three zones of the estuary. The dietary niche breadth of *H. kelee* was slightly higher in the upper estuary ($B_A$ = 0.40) and decreased gradually in the middle ($B_A$ = 0.33) and lower ($B_A$ = 0.26) estuarine zones. In contrast, the dietary niche breadth of *V. buchanani* progressively increased from the upper zone ($B_A$ = 0.56) via the middle zone ($B_A$ = 0.60), and eventually to the lower estuarine zone ($B_A$ = 0.63).

### Feeding strategies in relation to fish diet

The results of the study on feeding strategy of fish species indicated that diatoms had a food item-specific volume above 50% and the highest frequency of occurrence in the diet of *H. kelee* (Fig. 3a-c). Detritus

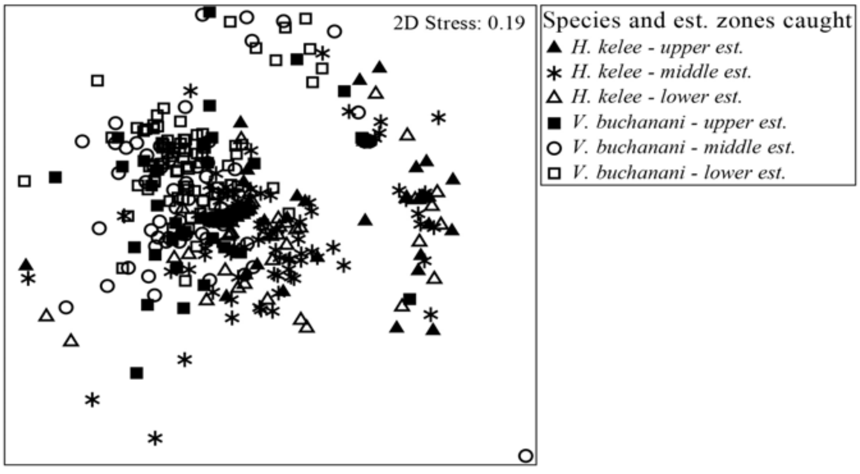

**Figure 2.** Non-metric multi dimension scaling ordination (nMDS) plot showing the dietary composition pattern of *H. kelee* and *V. buchanani* in upper, middle and lower zones of Pangani Estuary

**Table 3.** Pair-wise PERMANOVA tests comparing the feeding patterns of *H. kelee* and *V. buchanani* at estuarine zonal scale in Pangani estuary.

| | *H. kelee* | | | *V. buchanani* | | |
|---|---|---|---|---|---|---|
| **Estuarine zone comparisons** | **Den. df** | **t** | ***p*(perm)** | **Den. df** | **t** | ***p*(perm)** |
| Upper and middle zone | 126 | 2.99 | 0.001 | 103 | 0.61 | 0.772 |
| Upper and lower zone | 86 | 2.83 | 0.001 | 127 | 2.92 | 0.001 |
| Middle and lower zone | 152 | 1.09 | 0.33 | 156 | 2.77 | 0.001 |

Significance threshold at p (perm) = 0.05; Den. df = denominator degrees of freedom.

and copepod dietary categories of *H. kelee* indicated moderate to high frequency of occurrence, and below 50% food item-specific volume. This verified the generalist nature of the population with moderate diet niche width contributed by mostly generalist individuals (high within-phenotype component). *V. buchanani* showed an even more generalized feeding strategy and a broader diet niche width contributed to by most individuals in the population feeding on diatoms and detritus (higher within-phenotype component) (Fig. 3a-c). That is, the diet of *V. buchanani* comprised all dietary categories with food item-specific volume ≤ 50% and some, such as diatoms and detritus, with highest frequency of occurrence in all three estuarine zones. Furthermore, the population of *V. buchanani* displayed a generalist feeding strategy with about half of the individuals utilizing decaying vascular tissues, cyanobacteria and green algae in the lower estuarine zone.

## Fatty acid composition in *H. kelee* and *V. buchanani*

The total length of the fish specimens utilised in FA analysis ranged from 12-19 cm for *H. kelee*, and 12-23 cm for *V. buchanani*. Twenty eight FAs were detected in these two species from the upper and lower estuarine zones. The FA profile of *H. kelee* comprised about 48.2%, 49.4% saturated FAs (SFAs), 21.7%, 22.2% monounsaturated FAs (MUFAs), and 29.7%, 28.2% polyunsaturated FAs (PUFAs) in the upper and lower estuarine zones respectively. In contrast, *V. buchanani* showed lower levels of SFAs (45.0%, 45.5%), higher levels of MUFAs (24.7%, 25.8%) and PUFAs (30.2%, 28.6%) in the upper and lower portions of the estuary (Table 4). The PERMANOVA tests showed the differences in the FA present in the two species (pseudo- $F_{1,66}$ = 36.42; $p$ = 0.001) and between the sampling zones (pseudo-$F_{1,66}$ = 4.61, $p$ = 0.002). However, the same test suggested an absence of interaction between the factors, species and estuarine zones (pseudo- $F_{1,66}$ = 1.54; $p > 0.05$). The nMDS support the PERMANOVA results to some extent because the data points of FA for the two species were at least distinguishable in both sampling zones (Fig. 4). Similarly, this PERMANONA test showed that the FA profiles of the individual species were the main determinant of variation (square root component of variation = 8.53), followed by estuarine zone factor (2.72), and lastly the interaction between the species and estuarine zone (1.49). According to SIMPER, DHA, C16:0, EPA, C16:1, C18:1(n-9), ARA and C18:0 were the major FAs responsible for the distinction of the FA profile of *H. kelee* and that of *V. buchanani*.

The results of the FA biomarker analysis indicated that *V. buchanani* exhibited elevated levels of the diatom FA marker, EPA, in the upper (11.2%) and lower (12.2%) estuarine zones when compared to the level of EPA shown by *H. kelee* in the respective zones (9.3%, 9.1%) (Table 4). The proportion of dinoflagellate FA biomarker, DHA, in *H. kelee* (11.6%, 11.7%) was about twice as much as that found in *V. buchanani* (6.13%, 6.7 %) in the upper and lower zones respectively. Due to this, the DHA:EPA ratio was higher in *H. kelee* (1.3) than that in *V. buchanani* (0.6) in both sampling zones (Table 4). The terrestrial input FA biomarkers, linoleic acid (LIN) plus alpha linolenic acid (ALA) were more elevated in *V. buchanani* in comparison to that of *H. kelee* from both estuarine zones (Table 4). Also, the levels of LIN plus ALA were more elevated in *V. buchanani* caught from the upper portion of the estuary (3.8%) than those collected in the lower estuarine zones (1.7%) (Table 4). The n-3: n-6 PUFA ratio of *H. kelee* (6.8, 8.8) and *V. buchanani* (3.5, 6.2) in corresponding sampling zones were also different (Table 4). Similarly, the FA index markers of foraging mode, and thus feeding strategy, C18:1(n-9):C18:1(n-7), was relatively lower in *H. kelee* (4.50, 4.25) compared to that of *V. buchanani* (7.0, 5.2) from the upper and lower sampling zones, respectively. The levels of bacterial FA biomarkers between the two species were more or less similar (Table 4). Additionally, the copepod marker, C20:1(n-9), was relatively higher in *H. kelee* when compared to that of *V. buchanani*.

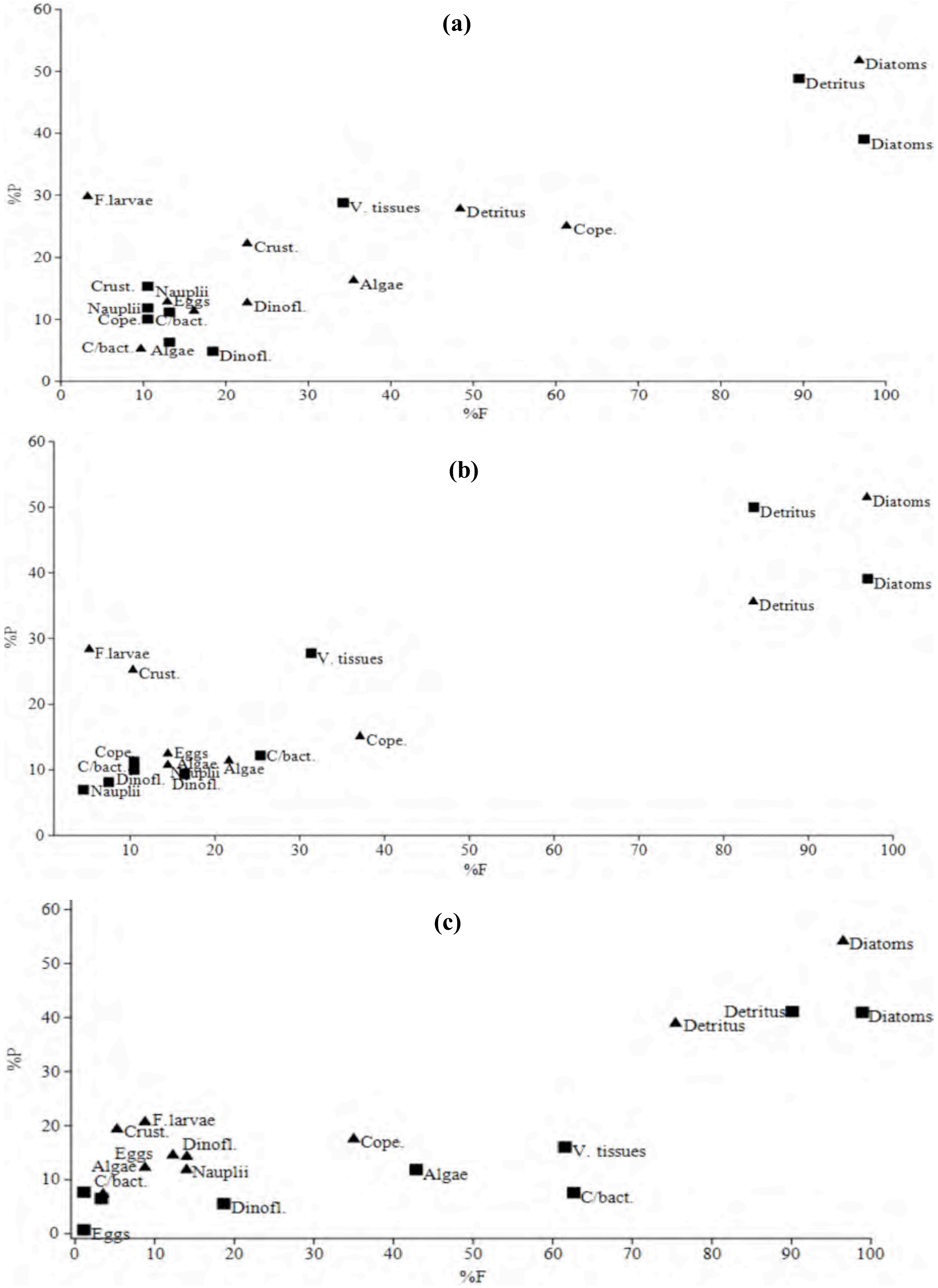

**Figure 3.** Feeding strategy diagrams for *H. kelee* (filled triangle data points) and *V. buchanani* (filled square data points) in (a) upper (b) middle and (c) lower zones of Pangani estuary. The percentage of food item-specific volume (%P) plotted against frequency of occurrence (%F) of dietary categories found in the stomachs of fish. Legend: Dinofl = dinoflagellates; Algae = green filamentous algae; c/bacteria = cyanobacteria and other bacteria; V. tissue = decaying vascular plant tissues; Cope. = copepod; F.larvae = fish larvae; Crust. = other crustacean larvae; Eggs = fish eggs and other unidentified eggs.

**Table 4.** The composition of fatty acids (mean % of total FAs ± standard deviation) in *Hilsa kelee* and *Valamugil buchanani* from Pangani estuary.

| **Fatty acid** | **Upper estuary** | | **Lower estuary** | |
|---|---|---|---|---|
| | ***H. kelee*** **(n = 17)** | ***V. buchanani*** **(n = 17)** | ***H. kelee*** **(n = 18)** | ***V. buchanani*** **(n = 18)** |
| C12:0 | 0.21 ± 0.13 | 0.18 ± 0.24 | 0.14 ± 0.09 | 0.08 ± 0.06 |
| C14:0 | 6.41 ± 0.99 | 6.55 ± 0.85 | 6.32 ± 1.53 | 6.77 ± 1.30 |
| C15:0[b] | 1.49 ± 0.79 | 1.40 ± 0.83 | 1.18 ± 0.40 | 1.86 ± 1.05 |
| C16:0 | 30.27 ± 2.28 | 27.0 ± 2.09 | 31.87 ± 2.63 | 27.38 ± 2.73 |
| C17:0[b] | 0.79 ± 0.20 | 0.96 ± 0.55 | 0.66 ± 0.15 | 0.95 ± 0.70 |
| C18:0 | 8.24 ± 1.35 | 8.17± 1.22 | 8.35 ± 1.51 | 7.63 ± 1.36 |
| C20:0 | 0.29 ± 0.17 | 0.32 ± 0.24 | 0.34 ± 0.14 | 0.23 ± 0.17 |
| C22:0 | 0.24 ± 0.10 | 0.34 ± 0.19 | 0.29 ± 0.09 | 0.34 ± 0.16 |
| C24:0 | 0.31 ± 0.15 | 0.13 ± 0.14 | 0.28 ± 0.14 | 0.23 ± 0.22 |
| C14:1 | 0.09 ± 0.15 | 0.09 ± 0.06 | 0.02 ± 0.03 | 0.10 ± 0.12 |
| C16:1 | 5.27 ± 0.86 | 7.78 ± 1.09 | 5.62 ± 1.90 | 7.87 ± 1.86 |
| C17:1 | 1.36 ± 0.68 | 2.03 ± 1.10 | 1.71 ± 0.86 | 2.27 ± 0.89 |
| C16:1(n-7) | 0.17 ± 0.12 | 1.10 ± 0.35 | 0.05 ± 0.19 | 0.03 ± 0.05 |
| C18:1(n-7) (VA)[b] | 2.46 ± 0.86 | 1.87 ± 0.95 | 2.90 ± 0.97 | 2.73 ± 1.03 |
| C18:1(n-9) (OA)[ci] | 9.55 ± 0.83 | 10.74 ± 1.36 | 9.38 ± 1.11 | 11.19± 2.39 |
| C20:1(n-9)[c] | 2.19 ± 1.09 | 0.41 ± 0.40 | 1.97 ± 0.98 | 0.88 ± 0.56 |
| C22:1(n-9) | 0.28 ± 0.21 | 0.33 ± 0.19 | 0.30 ± 0.11 | 0.36 ± 0.22 |
| C24:1(n-9) | 0.35 ± 0.23 | 0.30 ± 0.26 | 0.20 ± 0.10 | 0.35 ± 0.17 |
| C20:2 | 0.29 ± 0.17 | 0.30 ± 0.22 | 0.18 ± 0.15 | 0.27 ± 0.17 |
| C18:2(n-6) (LIN)[t] | 1.61 ± 0.77 | 2.02 ± 0.87 | 1.07 ± 0.55 | 0.76 ± 0.27 |
| C18:3(n-3) (ALA)[t] | 0.98 ± 0.53 | 1.74 ± 0.92 | 0.76 ± 0.60 | 0.90 ± 0.85 |
| C18:3(n-6) | 0.14 ± 0.16 | 0.55 ± 0.24 | 0.08 ± 0.01 | 0.18 ± 0.18 |
| C20:3(n-6) | 0.40 ± 0.22 | 0.57 ± 0.30 | 0.25 ± 0.16 | 0.23 ± 0.18 |
| C18:4(n-3) | 0.49 ± 0.30 | 0.76 ± 0.39 | 0.52 ± 0.26 | 1.74 ± 1.03 |
| C20:4(n-6) (ARA)[be] | 2.08 ± 1.02 | 3.77 ± 1.00 | 1.67 ± 0.89 | 2.29 ± 0.95 |
| C20:5(n-3) (EPA)[d] | 9.29 ± 1.47 | 11.18 ± 1.63 | 9.09 ± 1.61 | 12.19 ± 1.91 |
| C22:5(n-3) | 2.84 ± 1.06 | 3.18 ± 0.81 | 2.75 ± 1.34 | 2.83 ± 0.96 |
| C22:6(n-3) (DHA)[f] | 11.56 ± 1.48 | 6.13 ± 1.16 | 11.86 ± 1.83 | 6.56 ± 1.45 |
| ∑SFA | 48.18 ± 2.92 | 45.04 ± 3.06 | 49.44 ± 3.04 | 45.47 ± 3.68 |
| ∑MUFA | 21.72 ± 2.43 | 24.65 ± 1.96 | 22.15 ± 1.98 | 25.78 ± 1.76 |
| ∑PUFA | 29.68 ± 3.40 | 30.20 ± 3.08 | 28.22 ± 2.78 | 28.64 ± 3.69 |
| DHA:EPA[hi] | 1.28 ± 0.28 | 0.56 ± 0.13 | 1.33 ± 0.29 | 0.55 ± 0.15 |
| ALA+ LIN[t] | 2.59 ± 1.01 | 3.76 ± 1.33 | 1.82 ± 0.79 | 1.66 ± 0.8 |
| OA:VA[om] | 4.50 ± 1.96 | 7.00 ± 2.92 | 4.25 ± 4.25 | 5.19 ± 4.20 |
| BAFAs | 4.66 ± 1.02 | 4.22 ± 1.41 | 4.75 ± 0.87 | 5.54 ± 1.99 |
| n-3PUFA/n-6PUFA | 6.75 ± 2.46 | 3.54 ± 1.02 | 8.77 ± 2.93 | 6.18 ± 1.61 |

The lowercase superscripts indicate FA biomarkers: b = bacteria; c = copepods; d = diatoms; f = dinoflagellates; t = terrestrial vascular plant; be = benthic feeding mode and macro-algae indicator; ci = carnivory index; hi = herbivory index ratio; and om = omnivory index ratio. n-3PUFA and n-6PUFA = sum of the levels of all PUFA of which the first double bound counted from the terminal methyl group occurs at the third and sixth positions respectively. DHA = docosahexaenoic acid; EPA = eicosapentaenoic acid; ALA = alpha linolenic acid; LIN = linoleic acid; OA = oleic acid; VA = vaccenic acid; BAFAs = total bacterial fatty acids; SFA = saturated FAs; MUFA = monounsaturated FAs; PUFA = polyunsaturated FAs.

Spatially, the FA profiles of *V. buchanani* from the two estuarine zones were significant different (pair-wise PERMANOVA, $t_{33}$ = 2.03, $p$(perm) = 0.002). This correlated with the nMDS which indicated spatial dissimilarity for the FA profiles of *V. buchanani* from the upper and lower estuarine zones (Fig. 4). The SIMPER highlighted that such spatial dissimilarities in the FA profile were mostly related to C16:0, C18:1(n-9), C20:5(n-3), C16:1, C18:0, C22:6(n-3), C18:1(n-7) and C18:2(n-6). In contrast, the FA profiles of *H. kelee* from both upper and lower parts of the estuary were relatively similar (pair-wise PERMANOVA, $t_{33}$ = 1.32, $p$ (perm) > 0.05; Fig. 4). Furthermore, the one-way PERMANOVA indicated low levels of variation in FA profiles for the larger size classes of *V. buchanani* collected from the lower part of the estuary (Pseudo-$F_{1,16}$ = 3.21, $p$ = 0.01). The FA compositions by size for *V. buchanani* from the upper estuarine zone were very similar (Pseudo- $F_{1,15}$ = 1.46, $p$ > 0.05). The FA composition in *H. kelee* changed significantly with increasing fish length in both the upper and lower estuarine zones (Pseudo-$F_{1,15} \geq 3.5$, $p < 0.05$). The SIMPER highlighted that the differences in size-classes of both species were largely contributed to by C16:0, DHA, EPA, C18:0, and C14:0.

### Fatty acid trophic niche width

The FA niche areas (niche width) between fish species overlapped to a greater extent in the upper estuarine zone as compared to the lower portion of the estuary. The FA niche widths measured by standard ellipse area (SEAc) and total area of the convex hulls (TA) between *H. kelee* and *V. buchanani* were marginally different (Fig. 5a, b). The SEAc and TA of *H. kelee* were wider in the lower estuarine zone than that of *V. buchanani* (Fig. 5b), and the opposite situation was found in the upper estuarine zones (Fig. 5a) (ANOVA, $F$ = 0.55, $p$ > 0.05 in upper zone, ANOVA, $F$ = 7.39, $p$ = 0.02 in lower zone). These results highlighted that the two species had different trophic niches comprising different proportions of dietary FA across the estuary salinity gradient.

## Discussion

### Diet composition and feeding strategies

As previously predicted, substantial differences in diet and feeding strategy were found that together, contributed to dietary resource partitioning of *H. kelee* and *V. buchanani* in the Pangani estuary. The ecological index revealed strong dietary overlap for the two species, but the multivariate analyses revealed significant differences in the dietary and FA compositions of the two species. This is presumably explained by the weakness of overlap ecological index, and the power of statistical multivariate analyses for dietary and FA related data. The observed variations in dietary data for *H. kelee* and *V. buchanani* is most likely due to spatial segregation in foraging area within the water column, as well as differences in foraging mode. It is known that *H. kelee* is a filter feeder in the pelagic habitat (Blaber, 1979; Debasis *et al.,* 2013) and *V. buchanani* is a benthic feeder (Wijeyaratne and Costa, 1990; Rao and Babu, 2013). Thus, *H. kelee* and *V. buchanani* do exhibit partitioning in their feeding habitats, but because of macro-tidal activity that mixes the trophic resources throughout the water column, dietary overlap was strongly noticed in this study.

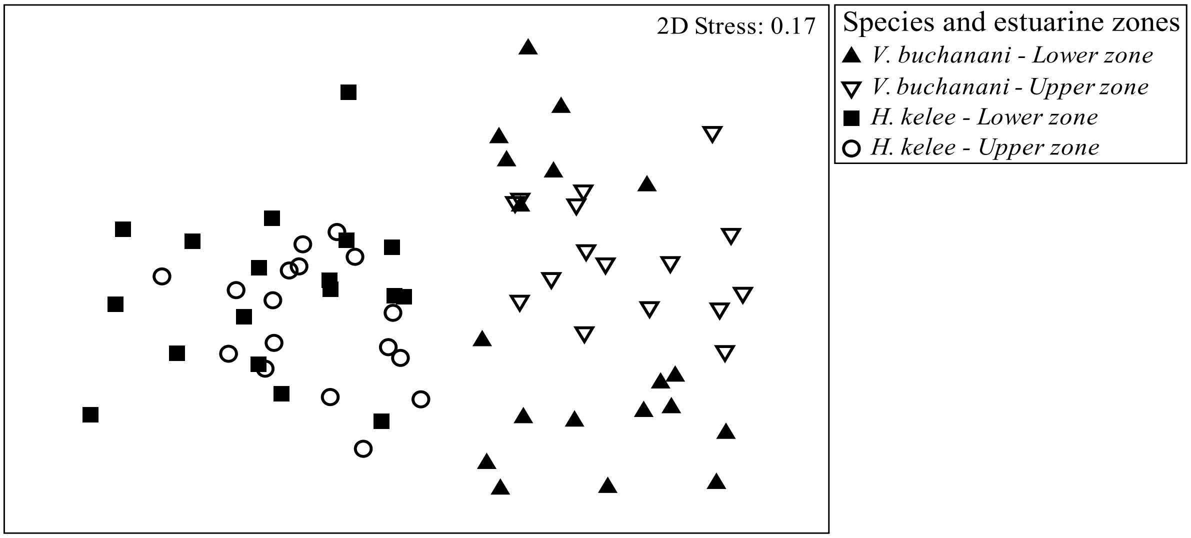

**Figure 4.** Non-metric MDS plot showing the FA compositions in *H. kelee* and *V. buchanani* from upper and lower zones of the Pangani Estuary.

Both species showed a dominance of micro-algae and detritus in their diets, in addition to different volumes of animal input, indicative of a detritivorous and omnivorous feeding mode. The two species differ in the extent to which these feeding modes adhered to. This can be explained by the differences in dietary niche breadth of the species. The analysis of dietary niche breadth, together with the feeding strategy, suggests that the species differ in their ability to access, and ultimately assimilate, the different dietary resources available in the estuary. Such variation in feeding strategy is presumably correlated to the morphological limitations of the two species, restricting them to certain prey items. For instance, the morphological features of *V. buchanani* facilitate easy digestion of vascular plant tissues (Mann, 1988; Cardona, 2016) when compared to *H. kelee*. Similarly, these two analyses indicated that the individuals and population of *H. kelee* exhibit a mixed feeding strategy incorporating both specialization and generalization, and that this contributes to

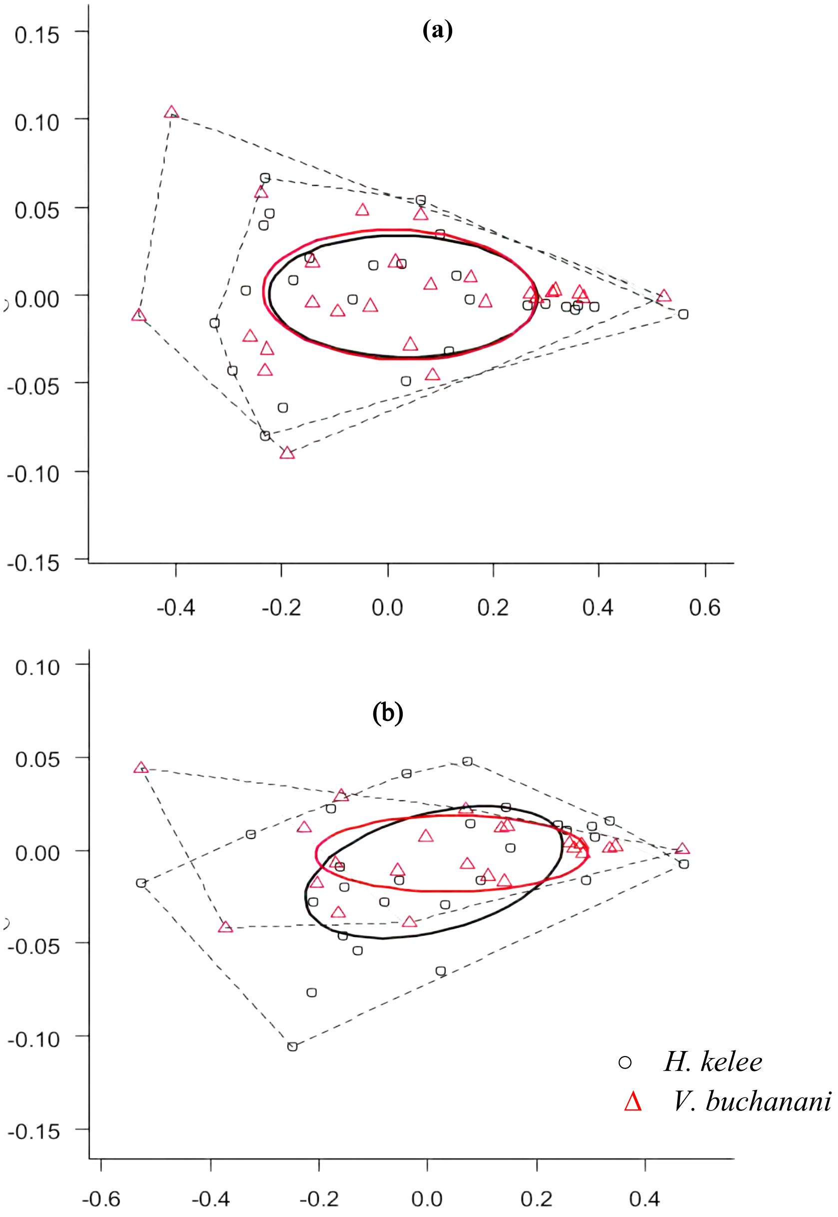

**Figure 5.** Fatty acid (FA) trophic niches of *H. kelee* and *V. buchanani* presented in x and y ordinates of non-metric multi-dimensional scaling (nMDS) for FA profiles of the species (n = 28 FA; Euclidean distance) in (a) upper and (b) lower zones of the Pangani Estuary. The dotted polygons are the convex hulls (TA) and the solid lines are standard ellipse areas (FA SEAc), both indicating FA feeding niche widths of the species.

intermediate niche width of high within-phenotype. This implies that part of the population of *H. kelee* appears to specialize on diatoms, contributing to the narrow diet niche breadth, and part of the population are generalists, comprising moderate generalist individuals that feed on detritus and copepods. In contrast, most of the population of *V. buchanani* displayed a generalist feeding strategy, contributing to greater trophic niche width and diet niche breadth. The generalist feeding strategy and omnivorous foraging mode displayed by both species agrees with previous studies which show that most estuarine fish are generalists (e.g. Pasquaud *et al.,* 2010). Moreover, the present findings emphasize that the degree of generalization and opportunistic omnivorous feeding behaviour tends to differ among marine fish found in estuaries.

### Fatty acid composition and feeding strategy

The FA composition in *H. kelee* and *V. buchanani* follows the normal trend found in marine fish that are commonly dominated by, among others, C16:0, C18:1(n-9), EPA and DHA. Moreover, the significant variations in FA composition between the species were contributed to by the type of food assimilated by the species. The elevated DHA:EPA ratio in *H. kelee* is an indication of the pelagic feeding mode, with pelagic species tending to accumulate and retain higher level of DHA in their tissues *(*Dalsgaard *et al*., 2003; Pethybridge *et al*., 2014). This is possibly due to high abundance of dinoflgellates, the main source of DHA in pelagic habitats (Dalsgaard *et al*., 2003). It is also important to note that DHA is essential, and most elevated, in fish during reproductive periods, as it enhances reproductive performance (Luo *et al*., 2015). Because the high abundance of *H. kelee* in estuaries is related to spawning (Gjosaeter and Sousa, 1983), this could explain why large individuals of the species displayed such high levels of DHA in this study. However, because small immature size classes of *H. kelee* also displayed an elevated level of DHA in comparison to that of *V. buchanani*, it remains relevant for DHA to be used as an indicator of the nature of trophic resources consumed by both species.

The low DHA:EPA ratio in *V. buchanani* suggests an herbivorous feeding mode with the species intensively grazing on diatoms. This also implies that the efficiency of *V. buchanani* to retain and accumulate DHA is lower than *H. kelee*. In contrast, *H. kelee* showed lower herbivorous and higher carnivorous feeding modes as indicated by the higher level of DHA. A high proportion of DHA in animals suggests a carnivorous foraging mode since this FA concentrates higher up the food chain. The FA copepod marker, C20:1(n-9) in *H. kelee*, further confirmed its carnivorous feeding habits. These findings concurred with the dietary composition in *H. kelee* which showed that the species consumes microalgae, copepods and other zooplankton simultaneously. In addition to that, previous studies confirmed that carnivorous fish species tend to accumulate and retain DHA to a greater extent than herbivorous species (Dalsgaard *et al*., 2003; Copeman *et al*., 2009).

The C18:1(n-9) FA carnivory index was found to be higher in *V. buchanani* than in *H. kelee*. This is probably linked the different types of food chains that the two species are part of. It is possible that *V. buchanani* has more diverse mechanisms of accumulating C18:1(n-9) than *H. kelee*. *V. buchanani* is likely to obtain C18:1(n-9) through feeding on carnivorous detrital organic matter, through the consumption of benthic macro-algae and meiobenthos rich in C18:1(n-9). In contrast, *H. kelee* accumulates C18:1(n-9) through consumption of pelagic carnivorous zooplankton. Furthermore, vascular plants were part of the sources of nutrition for both species, bearing in mind that this food source is assimilated by most fish species to a limited extent (Mann 1988). The high level of LIN plus ALA in *V. buchanani* emphasizes that the species obtains these dietary FAs by directly browsing on decaying terrestrial plants and through the consumption of bacteria. Bacteria extract and use LIN and ALA from terrestrial plants. Likewise, the proportion of LIN, ALA and bacteria FA in *H. kelee* is an indication that the species extracts these FAs from bacteria. This also depicts different levels of niche breadth and generalization of feeding strategies in the species examined.

The FA trophic niches (measured by SEAc), and the omnivory index, C18:1(n-9)/C18:1(n-7) ratio, suggest that both species are opportunistic omnivores, but the degree of omnivory was found not similar in all estuarine zones. The high FA omnivory index, C18:1(n-9)/C18:1(n-7) ratio, and large FA niche area (SEAc) of *V. buchanani* implies a more generalized diet and opportunistic feeding strategy. Specifically, the wider FA trophic niche width found in *V. buchanani* in the upper estuarine zones could be explained by the presence of a higher diversity of dietary resources and associated dietary FA in this zone. This suggests that the upper part of the estuary has a high level of decomposing vascular plant and algal material, and accompanying bacteria, in the surface sediments, possible due to reduced tidal influences when compared to the lower estuarine zone. To some extent, this disagrees with the patterns of dietary niche breadth showed by *V. buchanani*, which was wider in the lower zone and narrow in the upper estuarine zone. Such contradictory results could reflect the long-term and the instantaneous nature of feeding mode information revealed by FA and gut content analyses, respectively. However, the findings from both methods emphasize that *V. buchanani* has a greater dietary niche width and consequently a more opportunistic omnivore than *H. kelee*.

### Intra-specific trophic resource use variations

The slight spatial differences in diets exhibited by *H. kelee* and *V. buchanani* could primarily be a result of their feeding strategies which involved feeding on the readily available food items in the estuarine system. Most probably, this was influenced by heterogeneity in distribution and abundance of potential diet categories in the longitudinal salinity gradient. The long term spatial intra-specific feeding patterns of both species revealed by their FA profiles justifies the findings of the gut content analyses. The variation in FAs showed by *V. buchanani* collected in different estuarine zones could be linked to periodic migration across the zones. This implies that *V. buchanani* might have spent at least two weeks at a time feeding in one estuarine zone before migrating to other zones. Chang and Iizuka (2012) and Loc'h *et al.* (2015) also reported that mugilidae can experience periodic movement in the estuary. The study by Odom (2012) also revealed that the FA signatures of white mullet were significantly variable within the spatial fine scale sampling zones in the Indian River lagoon, Florida. In contrast, the nature of the movement (moving with the tidal currents) and high swimming speed of the *H. kelee,* presumably explains the spatial intra-specific differences in FA composition. More studies on the movement and foraging pattern of different fish species that differ in mobility and swimming speed in the Pangani estuary are required to better understand these dynamics. Changes in FA composition with fish size were much more evident in *H. kelee* than in *V. buchanani*. This is likely connected to species differences in sexual maturity and spawning period (Taşbozan and Gökçe, 2017). DHA and EPA, which are the most important PUFA during reproduction in fish, were found in the highest proportion in the large sexually mature size classes of *H. kelee*.

## Conclusion

The present study applied the FA trophic marker and stomach content methods to explore the feeding patterns and feeding strategies of *H. kelee* and *V. buchanani* from the Pangani estuary. The non-metric multivariate analyses revealed significant differences in dietary and FA compositions between the species across the estuarine zones. Despite the extreme inter-specific diet overlap indicated by the ecological index, a segregation in trophic resource use pattern (feeding in the benthic habitats versus feeding within the water column) was noticed. The dietary FA signatures and FA trophic niches, the dietary niche breadth ecological index and feeding strategy diagrams, strongly suggest that *V. buchanani* exhibits a generalist feeding strategy, contributed to by most individuals in the population. Contrary to this, *H. kelee* uses a mixed feeding strategy (generalist and specialist) that is more skewed towards a generalist feeding strategy. Because of the presence of a greater dietary and FA niche width, *V. buchanani* is considered a more efficient opportunistic omnivore than *H. kelee* throughout the Pangani estuary. Thus, *V. buchanani* is likely to show a higher degree of resilience to anthropogenic disturbances compared to *H. kelee* in the feeding and nursery grounds of the Pangani estuarine system.

## Acknowledgements

The study was financially supported by the Tanzania Commission for Science and Technology (COSTECH) under a project aiming at building the capacity of human resources in employing institutions. The authors acknowledge the technical support and research facilities offered by the University of Dar es Salaam, College of Agricultural Sciences and Fisheries Technology. Laboratory facilities for FA analysis and technical support was provided by State Key Laboratory of Estuarine and Coastal Research (SKLEC) of the East China Normal University (ECNU) in China through Prof. Zhang Jing, and the services of Wu Ying and Fu Qiang are also appreciated.

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# Reproductive biology of the beaked clam *Eumarcia paupercula* (Bivalvia: Veneridae) from Maputo Bay, Mozambique

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## Abstract

The beaked clam *Eumarcia paupercula* (Holten 1802) (Bivalvia: Veneridae) is an important fishery resource for local artisanal fishers in Maputo Bay. Its annual reproductive cycle was described by following seasonal fluctuations in the condition index of the population occupying a tidal flat, and by analysing fresh gonad smears to confirm that changes in condition were, in fact, due to gonad state. Macroscopic gonad observations and changes in body condition confirmed that *E. paupercula* is a year-round breeder with three spawning peaks, with the major spawning periods occurring during summer. The spawning pattern found in this study is similar to other clams inhabiting similar tropical ecosystems.

**Keywords:** Reproductive activity, condition index, *Eumarcia paupercula*, Maputo Bay, venerid clam

## Introduction

The stages and frequency of gonadal maturation in clams varies among species and are typically dependent on environmental conditions (Laruelle *et al.*, 1994; Adkins *et al.*, 2016). Various studies on reproductive patterns have shown that clams exhibit long spawning periods over the year (Narasimham *et al.*, 1988; McLachlan *et al.*, 1996; Tirado and Salas, 1999; Denadai *et al.*, 2015). This is particularly true in venerids, in which spawning typically peaks one to three times a year (Laruelle *et al.*, 1994; Jagadis and Rajagopal, 2007; Luz and Boehs, 2011).

The venerid clam *Eumarcia paupercula* inhabits sandy and muddy bottoms, and it is usually found 2–3 cm below the surface in the intertidal zone. It is one of the most important commercial clam species in Maputo Bay, Mozambique (Scarlet, 2005; Rosendo, 2008; Vicente and Bandeira, 2014). Effective regulation of this fishery requires understanding of the 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 compensate for its removal by fishing. This study represents the first attempt to describe the reproductive activity of the beaked clam, *E. paupercula*, inhabiting Maputo Bay.

## Methods

### Study area

Maputo Bay is located in southern Mozambique, between 25°55’ and 26°10’S, and 32°40’ and 32°55’ E (Fig. 1). The total area of the 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). Sampling for *E. paupercula* took place at Costa do Sol beach, an intertidal sandflat that is the major fishing area in Maputo Bay and a major source of harvested *E. paupercula*.

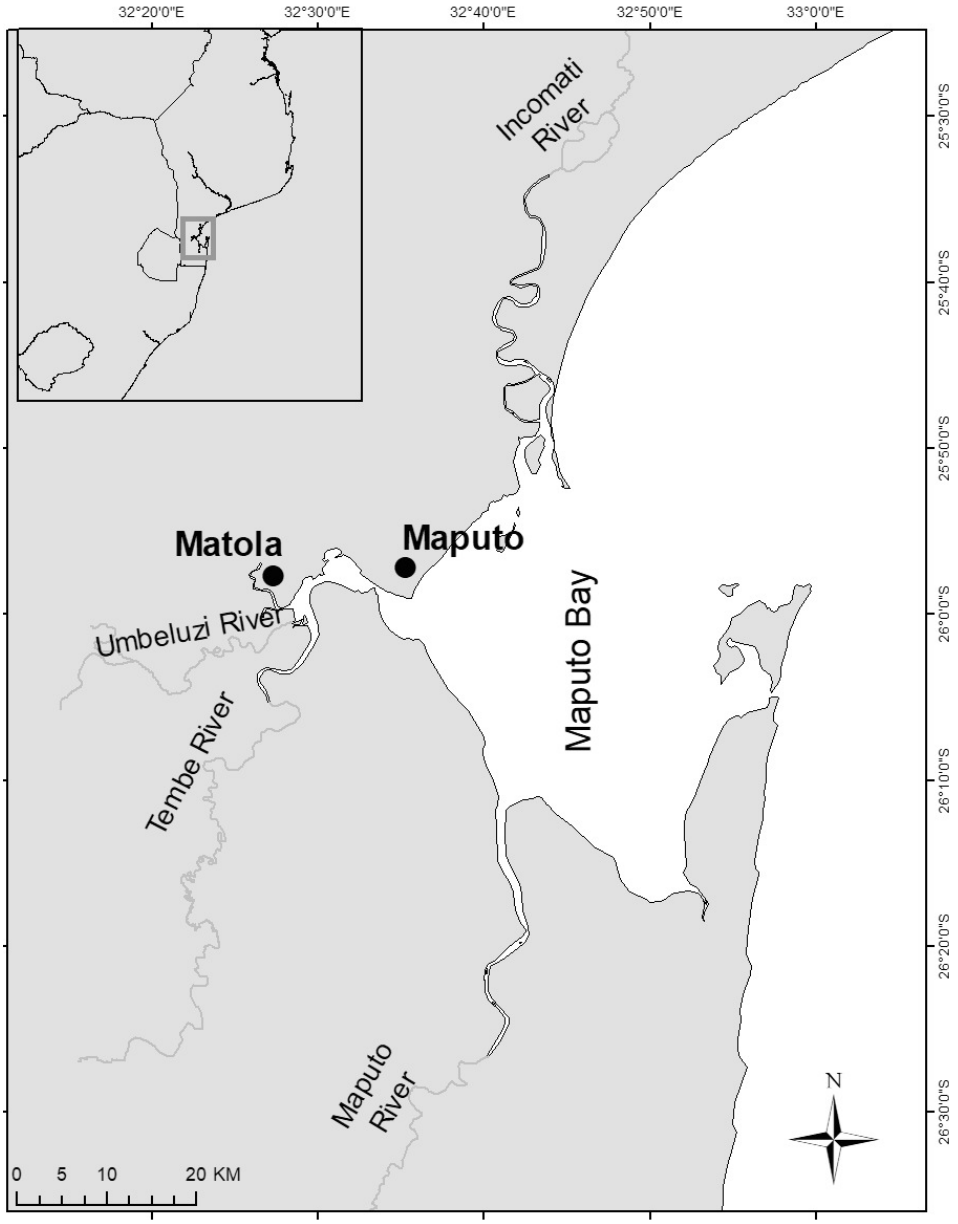

**Figure 1.** Maputo Bay, with rivers discharging into the Bay and main cities marked as black dots (Matola and Maputo).

## Sample collection

Sixty clams measuring ≥ 20 mm in length were collected during low spring tides each month between November 2012 and April 2014. Thirty of these clams were used for gonad smear observations and macroscopic gonad analysis, and the other 30 for measuring the condition index (CI). In addition, three replicate water temperature (°C) and salinity measurements were made *in situ* on each day of sampling. A hand-held digital thermometer and refractometer were used to record temperature and salinity, respectively. Total monthly rainfall data for the study period were obtained from the Mozambican National Institute of Meteorology, Maputo.

## Description of reproductive cycle

Two methods were used to describe the reproductive activity of *E. paupercula*. The first was a measure of condition index, expressed as the fluctuation in flesh dry weight (FDW) of a standard sized (30 mm shell length) individual. The changes in FDW of the standard 30 mm individual were calculated from monthly length/condition regressions of 30 individual clams, which were fitted using a power function ($FDW = aL^b$). The weight of a standard sized individual was determined using each monthly regression. Regressions were fitted using the SPSS 22.0 statistical package.

The second method was based on a macroscopic examination of gonad maturation for 30 clams in which the reproductive state of each clam was scored following a visual scale of stages, developed from a combination of scales defined for other venerids (Shafee and Daoudi, 1991; Baron, 1992; Jagadis and Rajagopal, 2007), 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 become 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 in colour. Sex remains identifiable when cutting the gonad tissue. At this stage, all mature gametes have been released.

Sexual products were also taken and sex determined by performing a smear and observing this at 400 X magnification, and sex ratio was presented as percentages of males and females. To determine if the sex ratio differed from 1:1, a Chi-square test ($\chi^2$) was conducted each month.

### Data Analysis

Pearson's correlation was used to compare relationships between environmental variables and CI. One-way analysis of variance (ANOVA) followed by a post hoc Tukey test, was used to test for significant differences in CIs among the 18 study months. The correlation between environmental factors and reproductive

**Table 1.** Monthly regression equations of length-weight relationships. FDW = Flesh Dry Weight (g), L = length (mm), a = intercept and b = slope at $\alpha = 0.05$.

| Month-Year | Regression Equation ($FDW = aL^b$) | FDW (30 mm individual) |
|---|---:|---:|
| N – 12 | $y = 0.001x^{2.68}$ | 6.4 |
| D – 12 | $y = 0.037x^{1.41}$ | 4.4 |
| J – 13 | $y = 0.002x^{2.33}$ | 5.6 |
| F – 13 | $y = 0.053x^{1.39}$ | 6.1 |
| M – 13 | $y = 0.082x^{1.32}$ | 7.5 |
| A – 13 | $y = 0.024x^{1.66}$ | 6.8 |
| M – 13 | $y = 0.001x^{2.64}$ | 6.3 |
| J – 13 | $y = 0.002x^{2.39}$ | 6.5 |
| J – 14 | $y = 0.004x^{2.19}$ | 6.6 |
| A – 13 | $y = 0.0001x^{3.3}$ | 5.6 |
| S – 13 | $y = 0.0001x^{3.21}$ | 5.6 |
| O – 13 | $y = 0.0002x^{3.05}$ | 6.3 |
| N – 13 | $y = 0.087x^{1.23}$ | 5.8 |
| D – 13 | $y = 0.009x^{1.88}$ | 5.1 |
| J – 14 | $y = 0.041x^{1.46}$ | 5.8 |
| F – 14 | $y = 0.008x^{1.95}$ | 6.5 |
| M – 14 | $y = 0.001x^{2.62}$ | 7.7 |
| A – 14 | $y = 0.004x^{2.21}$ | 6.0 |

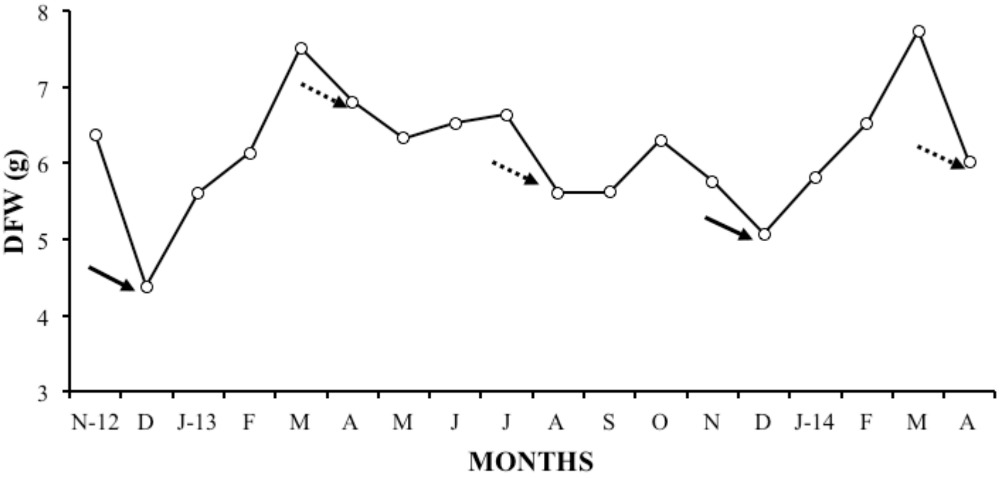

**Figure 2.** Average monthly changes in condition ($n$ = 30) of *Eumarcia paupercula* at Maputo Bay from November 2012 to April 2014. Solid and doted arrows indicate major and minor spawning peaks, respectively at $\alpha$ = 0.05.

cycles was assessed using changes in CI as an indicator of spawning events. All statistical analyses were performed in SPSS 22.0.

## Results

The mean sex ratio of males to females in the 18 monthly samples was 275:253, (12 indeterminate). The overall sex ratio did not differ significantly from 1:1 ($x^2$ = 0.60, $df$ = 1, P = 0.44) over the 18 months; however, it differed from unity during three individual months, namely November 2012 (19:11), July 2013 (20:10), and August 2013 (19:11).

The monthly equations relating FDW to shell length, and the FDWs of standard sized (30 mm) individuals, are presented in Table 1. Changes in FDW in a standard sized individual (30 mm shell length) over the study period are presented in Fig. 2. The FDW dropped in December 2012 and increased rapidly until March 2013, after which a slight drop was observed. Significant drops in FDW (F = 25.45, P < 0.05) were observed during December 2012, August and December 2013, and April 2014.

The monthly distributions of gonad stages are illustrated in Fig. 3. Ripe individuals were present during all sampling months, although they occurred in more than 50% of individuals in the sample only during four months (November and December 2012, and August and November 2013). These periods preceded the

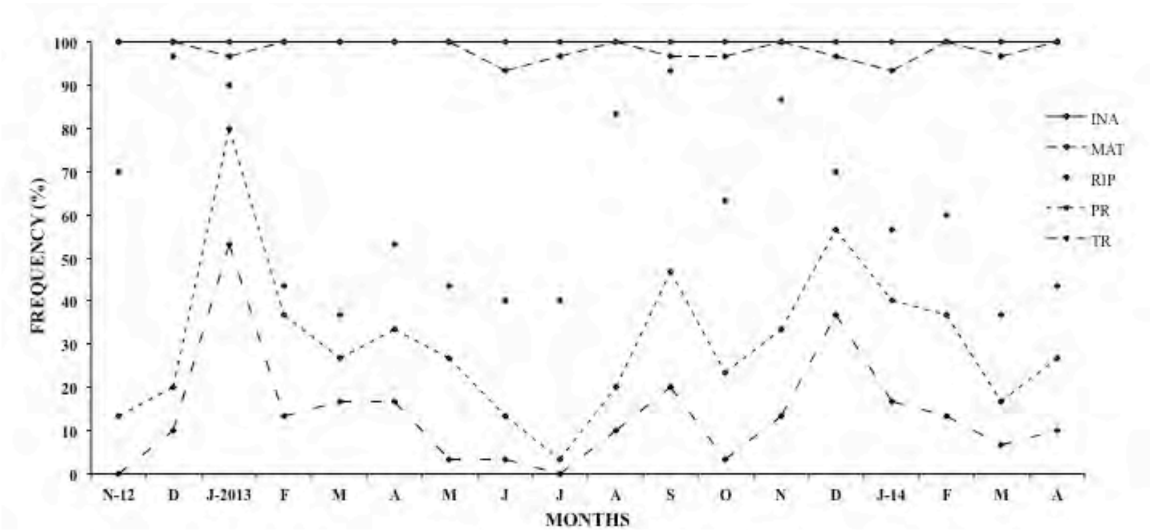

**Figure 3.** Percentages of mature *Eumarcia paupercula* in Maputo Bay showing various stages of gonad maturation as derived from macroscopic observations of gonads. INA - indeterminate; MAT - Maturing; RIP - Ripe; PR - Partial Release; and TR - Total Release stages.

months in which the highest percentages of individuals releasing gametes (individuals in PR and TR phases) were recorded. Similarly, individuals in maturing stages (MAT) were present throughout the sampling period, comprising over 50% of the sample towards the the end of summer (February and March 2013) and the greater part of winter (April – July 2013). Over the course of the 18 sampled months, inactive or sex indeterminate individuals (INA) were only recorded in eight months, and they always represented less than 10%.

The mean monthly sea temperature and salinity readings in the study area are presented in Fig. 4. Monthly temperature recorded during sampling (mean ±SD) ranged from a minimum of 22.1±0.26$^{0}$C in August 2013 to a maximum of 30.9±1.11$^{0}$C in January 2014. The average salinity recorded during sampling ranged from a low of 33.0±0.8 in November 2013 to a high of 38.2±0.5 in September 2013. There was no rainfall in June and July 2013, nor in March and April 2014, and the maximum monthly rainfall (262.1 mm) throughout the study period was recorded in January 2013 (Fig. 5). Pearson's 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).

## Discussion

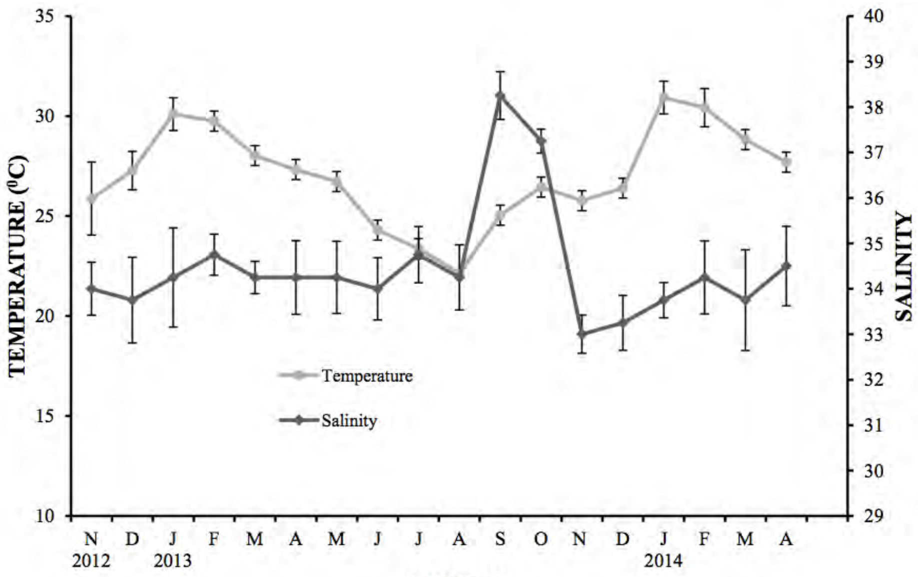

**Figure 4.** Monthly mean (±SD) water temperature (0C) (black line) and salinity (grey line) in Maputo Bay from November 2012 to April 2014.

**Figure 5.** Monthly rainfall (mm) recorded for Maputo Bay from November 2012 to April 2014.

## Sex ratio

Although reproductive cycles of venerids have been studied for tropical and temperate waters globally, the majority of these studies have taken place in the northern hemisphere, and the present study is the first for *E. paupercula*. Table 2 shows reproductive characteristics of venerids from the literature. From 8 other studies (on 6 different species) that presented sex ratio data, all reported sex ratios as being close to parity (the M:F ratio varying from only 1:1 to 1: 1.3). This means that regardless of species and study site, the sex ratio of venerids is close to 1:1. Nevertheless, it is of interest to note that some minor variation in sex ratio with latitude was reported for *Marcia opima* from India by Suja and Muthiah (2007).

## Reproductive cycle

Both methods used to quantify the reproductive cycle of *E. paupercula* detected three spawning peaks. The major spawning occurs in December-January, and two minor events occur in March-April, and August-September. PR individuals were found during all 18 months in which samples were collected, suggesting that *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 to have already spawned, as a complete spawning would have recently occurred. Consequently, September 2013 was also considered a spawning peak, and the drop in the condition in the previous month (August 2013) supports this. Although TR and PR individuals were present throughout the sampling period, their highest percentage occurrence was in summer. 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. Table 2 shows the seasonal spawning peaks for several venerid species, and while some species spawn during winter, most tropical and subtropical clams follow a similar spawning pattern to that seen in this study.

When venerids from tropical and subtropical areas are analysed, it is apparent that species found furthest from the tropics spawn two or three times a year for prolonged periods (Jayabal and Kalyani, 1987; Barreira and Araujo, 2005; Suja and Muthiah, 2007; Luz and Boehs, 2011), while others exhibit year-round spawning (Jagadis and Rajagopal, 2007; Denadai *et al.*, 2015). Thus, the spawning pattern of *E. paupercula* in Maputo Bay is similar to those of most other tropical and subtropical clam species (but see Denadai *et al.*, 2015). The limited number of species from tropical-subtropical areas referred to in this table reflects a lack of studies on venerids from these regions.

### *Reproductive cycle in relation to environmental parameters*

No significant correlation between reproductive activity and any of the environmental parameters measured was found. The effect of salinity on reproduction of bivalves is not well understood. For most of the study period, salinity was between 32 and 35 and remained stable at levels considered normal for coastal marine habitats, with insufficient variation to affect animal physiology. This fact has been confirmed for *Austrovenus stutchburyi*, which maintained high CI even at salinities <20 (Adkins *et al.*, 2016).

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). However, in June 2013, the PR and TR stages accounted for only 13% of individuals, and INA for 7%. An absence of a 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.

Rainfall is often indirectly considered as a driving factor of reproductive cycles in clams inhabiting tidal flats, because of its ability to reduce salinity (Riascos and Jose, 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.

All in all, the reproductive season of *E. paupercula* in Maputo Bay is characterized by a long spawning season with three annual peaks. The presence of only a few individuals in indeterminate stages during sampling may be indicative of a very short resting period before recuperation. Literature discussing the beaked clam *E. paupercula* is limited, particularly with regards to the management of stocks and understanding the reproductive cycle. In Maputo Bay this species is being heavily exploited for food, emphasising that it is important to start considering the implementation of management practices. These could be based on the reproductive pattern, which seems to be linked to environmental factors during the summer such as increased food availability and elevated temperatures, and which may regulate spawning intensity.

**Table 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 & Araujo, 2005 |
| *A. brasiliana* | Brazil | 20 – 35 | 1:1.2 | Two: Jan – May; Sep - Nov | Luz & Boehs, 2011 |
| *Cyclina sinensis* | China (37°84' N) | 2.0 – 30.0 | - | One: Aug | Yan *et al.*, 2010 |
| ***Eumarcia paupercula*** | **Mozambique (25°54' 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 & Rajagopal, 2007 |
| *M. opima* | India (08°45' N) | 26.0 – 32.3 | 1:1 | Two: May – Jul; Sep – Dec | Suja & Muthiah, 2007 |
| *M. opima* | India (09°28' N) | 24.0 – 34.0 | 1:0.7 | Two: Mar – May; Sep – Dec | Suja & Muthiah, 2007 |
| *Mercenaria mercenaria* | USA (41°67' N) | 17.5 – 25.5 | - | One: June | Rice & Goncalo, 1994 |
| *M. mercenaria* | USA (38°.77' - 39°06' N) | - | - | One: Jul - Sep | Marroquin-Mora & Rice, 2008 |
| *M. mercenaria* | USA (40°55' - 41°01' N) | - | - | One: May Sep | Doall *et al.*, 2008 |
| *Meretrix meretrix* | India (11°17' N) | - | 1:1 | One long: Feb – Sep | Jayabal & Kalyani, 1987 |
| *Ruditapes decussatus* | UK (47°40' N) | - | - | One: Jul – Oct | Laruelle *et al.*, 1994 |
| *R. decussatus* | France (43°23' N) | - | - | Two: Jun – Aug | Borsa & 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* | 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 & Yakolev, 1992 |
| *Tawera gayi* | Argentina (54°50'S) | 3.4 – 8.2 | 1:1.1 | One: Oct | Morriconi *et al.*, 2007 |
| *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

## Acknowledgements

This study was supported by the International foundation for Science (A5497-1), and partially by the WIO-RISE programme and the Mozambican Ministry of Science and Technology. Field support was provided by Sara Tembe and Flora Manjate. The Laboratory of Aquatic and Marine Ecology of the Department of Biological Sciences in Maputo provided logistical support.

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# Codend mesh size of beach seine nets influences fish species and size composition in Lamu, north coast, Kenya

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## Abstract

Beach seine nets are commonly used in reef lagoons in Kenya, with potentially destructive impacts on reefs and other habitats. The species composition and size frequency of catches made by nets with codend mesh sizes of 25 mm, 38 mm and 44 mm were evaluated for samples collected during three sampling trips in the Lamu area between 2014 and 2016. A total of 98 fish species belonging to 41 families were recorded. Most species with highest diversity ($D$ = 10.67) were caught by the 25 mm codend mesh, followed by the 38 mm ($D$ = 6.69) and 44 mm meshes ($D$ = 3.04), respectively. Size frequencies of dominant species *Leptoscarus vaigiensis*, *Siganus sutor* and *Lethrinus lentjan* depended on the codend mesh size sampled, with the 25 mm mesh retaining more immature individuals than the other two meshes. It is concluded that codend mesh size influences catch properties of beach seine nets used in Lamu, and that introducing a minimum mesh size would reduce the proportions of juvenile fishes landed.

**Keywords:** Beach seine, Species composition, Size frequency, Codend mesh size, Fisheries management, Kenya.

## Introduction

Fishing with beach seine nets in reef lagoons contributes substantially to food security and economic activity in coastal villages in Kenya (FAO, 2011). Beach seining is particularly common in the Lamu area on the north coast, where it has been assimilated into the fishing culture after being introduced by migrant fishers about 30 years ago (FiD, 2015). Beach seining is considered to be a destructive fishing gear, and its use has been banned in Kenya since 2001 (Kenya Gazette Notice No. 7565 Vol. CIII. No. 69, 2001). Nevertheless, many artisanal fishers do not comply with the ban (McClanahan *et al.,* 2005), and the number of beach seine nets in the marine artisanal fishery has remained relatively constant, with frame surveys reporting 139 nets (2008), 211 nets (2012) and 193 nets (2014) over the past decade (FiD, 2015). Cinner *et al.* (2009) suggested that fishers do not comply with the ban because of lack of alternative employment opportunities. Noncompliance with regulations undermines the effectiveness of fisheries management (Madrigal-Ballestero *et al.,* 2013; Turner *et al.,* 2014; Pomeroy *et al.,* 2015).

The physical effects of beach seining on reefs and associated habitats have been well documented (McClanahan & Mangi, 2001). Areas affected by beach seining often have significantly smaller corals and a lower density of coral colonies (Mangi & Roberts, 2006). Dragging a net across the seafloor leads to resuspension of bottom sediment, increasing turbidity and smothering benthic organisms (Jones, 1992). It also removes or crushes epibenthic organisms such as corals, seagrasses and sponges (Sainsbury *et al.,* 1997). Beach seine nets are long and mobile, and can therefore affect large areas of seafloor habitats where they are frequently used (McManus, 1997; Auster, 1998; Watling & Norse, 1998).

Beach seining captures a range of fish species and sizes that occur in the intertidal and shallow subtidal zones (Gough *et al.,* 2009), and the codend mesh size used will determine the selectivity of the gear (FAO, 2011). Using a small mesh size is likely to capture a larger proportion of juvenile fishes (Nunoo & Azuma, 2015), and the lead line of the net may also destroy fish spawning grounds while being dragged over the seafloor. Fisheries regulations that specify a minimum mesh size can be used to manipulate the selectivity properties of gear, to reduce the proportion of juvenile fishes smaller than a given size in catches. Mesh size can also be adjusted to reduce catches of non-target species, through size selectivity (MacLennan, 1992; 1995). Knowledge of fishing gear selectivity is therefore important within the context of fisheries management. The effects of codend mesh sizes on the species composition and size of fish caught by beach seine nets in Lamu was assessed.

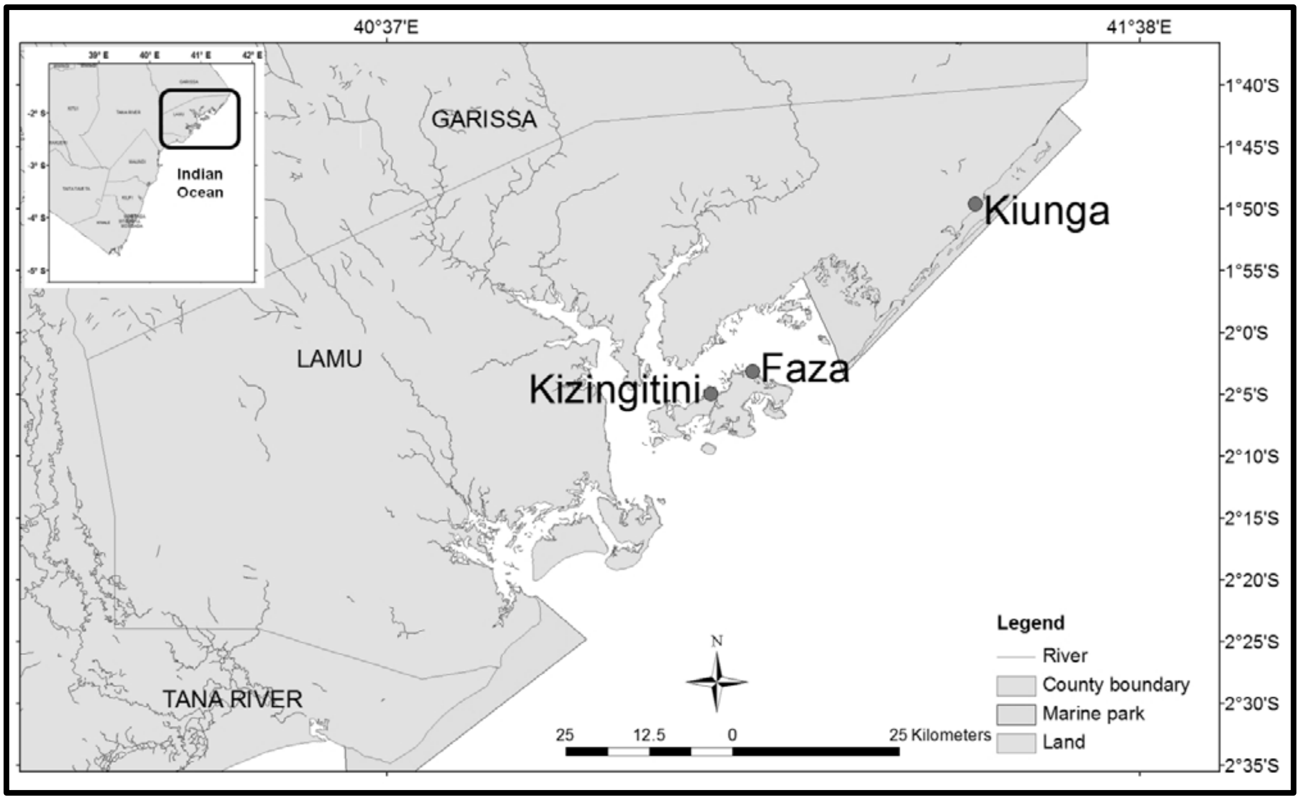

**Figure 1.** A map of the north coast Kenya, with dark filled circles showing the sampling sites in Lamu.

## Materials and methods

Catch assessment surveys were carried out on 1st–7th May 2014, 6th–12th March 2015, and 9th–14th May 2016 at the main beach seine fishing grounds in Lamu (Kiunga, Faza, Kizingitini) (Fig. 1). The area is highly productive with rich fishing grounds influenced by northeast and southeast monsoon winds. The sampled beach seines comprised of a seine body with different nominal codend mesh sizes of 25mm, 38mm and 44 mm, with anterior and posterior wings attached, which is hauled by up to 30 fishers at a time. The upper part of the net is maintained on the surface by a float line (150 – 400 m long) and the footrope on the seafloor comprises a lead line with sinkers to prevent fish from escaping the enclosure. The wings are attached to hauling ropes (FAO, 2011).

A representative catch sample was collected with a bucket from 33 hauls (Table 1), after removing marine litter. The sub-sample of the catch was identified to species level using field guides (Smith & Heemstra 1986; Lieske & Myers, 1994). Fish total length (TL) was measured to the nearest 1 mm using a fixed ruler on a fish measuring board, and individual weights were recorded to the nearest 0.01 g using a weighing balance. Fish were grouped into length class categories to enable a comparative analysis between codend mesh sizes.

Simpson's Diversity Index was used as a measure of diversity for individual mesh sizes, because it takes into account the number of species present, as well as the relative abundance of each species. The index was calculated using the equation:

$$D = \sum (n(n-1))/((N(N-1)),$$

where $n$ is the number of individuals of each species, and $N$ is the total number of individuals of all species. A non-parametric Kruskal–Wallis test was used to compare the fish retained by the three mesh sizes, based on the mean ranks of groups. Mesh selectivity was also determined from size frequencies of the dominant species caught by the different codend mesh sizes, based on the assumption that the community is the same. The length at maturity ($L_{mat}$) of dominant species was obtained from Hicks & McClanahan (2012) and the proportion of fish smaller than $L_{mat}$ retained by the different mesh sizes was calculated.

## Results

Species composition included bony fishes, crustaceans, mollusks, cephalopods and echinoderms. Some 98 species belonging to 41 families were collected and the catch was dominated by three major families; namely Scaridae, Siganidae, and Lethrinidae. The main families that were caught and retained by the 25 mm mesh, but escaped from 38 mm and 44 mm mesh, were small-bodied fish species including Apogonidae (*Apogon fragilis*, *Ostorhinchus taeniophorus*, *Taeniamia fucata*), Monocanthidae (*Cantherhines fronticinctus*), Clupeidae (*Amblygaster sirm*) and Labridae (*Stethojulis strigiventer*).

In terms of numbers of fish, 25 mm and 38 mm meshes caught mostly *Leptoscarus vaigiensis,* followed by *Siganus sutor* and *Lethrinus lentjan,* whereas similar numbers of *L. vaigiensis* and *S. sutor* were caught by the 44 mm mesh (Table 2). In term of weight, *S. sutor* dominated the catch made with the 44 mm mesh, followed by *L. vaigiensis and L. lentjan*. Catches made by the 38 mm mesh were dominated by *L. vaigiensis,* followed by *S. sutor* and *L. lentjan* (Table 3). The Simpson index indicated that the samples caught with the 25 mm mesh had the highest diversity ($D$ = 10.67), followed by the 38 mm mesh ($D$ = 6.69) and the 44 mm mesh ($D$ = 3.04).

Mesh selectivity for the three dominant species differed significantly (Kruskal-Wallis test, $p<0.05$; *L. vaigiensis* H = 87.09, *S. sutor* H = 34.61, and *L. lenjan* H = 179.82*)*. Some 48.0% of *L. vaigiensis* retained by the 25 mm mesh were smaller than the 15.1 cm $L_{mat}$. Similarly, 90.2% of *S. sutor* caught with the 25 mm mesh were smaller than the $L_{mat}$ of 20.2 cm, and 88.7% of *L. lentjan* were also smaller than the $L_{mat}$ of 20.3 cm (Fig. 2).

Some 53.1% of *L. vaigiensis* landed by the 38 mm mesh, 50% of *S.sutor*, and 60% of *L. lentjan* were smaller than

**Table 1.** Summary of the field surveys.

| Year | Season | Haul No. | Sampled amount (A, kgs) | Catch amount (B, kgs) | Sampling ratio (A/B) | Nominal codend mesh sizes (mm) |
|---|---|---|---|---|---|---|
| 2014 | SEM | 1 | 9,0 | 20,0 | 0,45 | 25 |
| 2014 | SEM | 2 | 20,74 | 250,0 | 0,08 | 38 |
| 2014 | SEM | 2 | 19,26 | 150,0 | 0,13 | 44 |
| 2015 | NEM | 1 | 6,2 | 100,0 | 0,06 | 25 |
| 2015 | NEM | 4 | 17,42 | 93,0 | 0,19 | 25 |
| 2015 | NEM | 2 | 4,94 | 120,0 | 0,04 | 38 |
| 2015 | NEM | 3 | 27,76 | 65,0 | 0,43 | 38 |
| 2015 | NEM | 2 | 10,7 | 50,0 | 0,21 | 38 |
| 2015 | NEM | 1 | 4,2 | 15,0 | 0,28 | 44 |
| 2016 | SEM | 9 | 25,5 | 250,0 | 0,10 | 25 |
| 2016 | SEM | 3 | 13,3 | 227,0 | 0,06 | 38 |
| 2016 | SEM | 3 | 21,0 | 1530,0 | 0,01 | 38 |

**Table 2.** Species composition by count (%) by codend mesh sizes.

| | **Numbers** | **1367** | **789** | **229** |
|---|---|---|---|---|
| | **D** | **10,67** | **6,69** | **3,04** |
| **Family** | **Species** | **25 mm** | **38 mm** | **44 mm** |
| Scaridae | *Leptoscarus vaigiensis* | 18,6 | 26,1 | 40,2 |
| Lethrinidae | *Lethrinus lentjan* | 13,8 | 6,3 | 1,7 |
| Siganidae | *Siganus sutor* | 13,2 | 25,9 | 40,2 |
| Lethrinidae | *Lethrinus mahsena* | 10,8 | 5,1 | 7,9 |
| Terapontidae | *Pelates quadrilineatus* | 5,2 | 0,8 | 0,0 |
| Gerreidae | *Gerres oyena* | 4,9 | 1,3 | 0,0 |
| Scaridae | *Scarus psittacus* | 3,8 | 1,0 | 0,0 |
| Siganidae | *Siganus canaliculatus* | 3,7 | 5,3 | 0,0 |
| Scaridae | *Scarus ghobban* | 3,2 | 1,3 | 0,4 |
| Lethrinidae | *Lethrinus nebulosus* | 2,6 | 1,6 | 2,6 |
| Sphyraenidae | *Sphyraena flavicauda* | 2,3 | 5,4 | 1,7 |
| Mullidae | *Parupeneus rubescens* | 2,1 | 0,3 | 0,0 |
| Lutjanidae | *Lutjanus fulviflamma* | 1,7 | 0,6 | 0,4 |
| Scombridae | *Sarda sarda* | 1,7 | 0,1 | 0,0 |
| Labridae | *Stethojulis strigiventer* | 1,4 | 0,0 | 0,0 |
| Haemulidae | *Plectorhinchus gaterinus* | 1,0 | 0,9 | 0,0 |
| Hemiramphidae | *Hemiramphus far* | 0,7 | 1,9 | 0,0 |
| Labridae | *Cheilio inermis* | 0,4 | 1,6 | 2,6 |
| Plotosidae | *Plotosus lineatus* | 0,4 | 0,1 | 0,0 |
| Gobiidae | *Priolepis cincta* | 0,4 | 0,0 | 0,0 |
| Scaridae | *Scarus sordidus* | 0,4 | 0,0 | 0,0 |
| Sphyraenidae | *Sphyraena jello* | 0,4 | 0,0 | 0,0 |
| Haemulidae | *Plectorhinchus flavomaculatus* | 0,4 | 1,9 | 2,2 |
| Clupeidae | *Amblygaster sirm* | 0,3 | 0,0 | 0,0 |
| Leiognathidae | *Karalla daura* | 0,3 | 0,1 | 0,0 |
| Siganidae | *Siganus stellatus* | 0,3 | 0,1 | 0,0 |
| Sepiidae | *Squid* | 0,3 | 0,0 | 0,0 |
| Scaridae | *Calotomus spinidens* | 0,3 | 3,2 | 0,0 |
| Apogonidae | *Apogon fragilis* | 0,2 | 0,0 | 0,0 |
| Lethrinidae | *Lethrinus microdon* | 0,2 | 0,0 | 0,0 |
| Apogonidae | *Ostorhinchus taeniophorus* | 0,2 | 0,0 | 0,0 |
| Haemulidae | *Scolopsis ghanam* | 0,2 | 0,1 | 0,0 |
| Apogonidae | *Taeniamia fucata* | 0,2 | 0,0 | 0,0 |
| Monacanthidae | *Cantherhines fronticinctus* | 0,2 | 0,0 | 0,0 |
| Carangidae | *Caranx ignobilis* | 0,2 | 0,1 | 0,0 |
| Apogonidae | *Cheilodipterus quinquelineatus* | 0,2 | 0,3 | 0,0 |
| Carangidae | *Gnathodan speciousus* | 0,1 | 0,3 | 0,0 |
| Tetraodontidae | *Arothron hispidus* | 0,1 | 0,3 | 0,0 |
| Chanidae | *Chanos chanos* | 0,1 | 0,3 | 0,0 |
| Fistulariidae | *Fistularia petimba* | 0,1 | 0,3 | 0,0 |
| Lutjanidae | *Lutjanus gibbus* | 0,1 | 0,4 | 0,0 |
| Monacanthidae | *Paramonocanthus frenatus* | 0,1 | 0,3 | 0,0 |
| Clupeidae | *Sardinella gibbosa* | 0,1 | 0,3 | 0,0 |
| Scombridae | *Rastrelliger kanagurta* | 0,0 | 0,3 | 0,0 |
| Ephippidae | *Platax teira* | 0,0 | 0,5 | 0,0 |
| Labridae | *Halichoeres scapularis* | 0,0 | 0,3 | 0,0 |
| Lethrinidae | *Lethrinus harak* | 0,0 | 0,4 | 0,0 |
| Serranidae | *Dermatolepsis striolata* | 0,0 | 0,5 | 0,0 |
| Serranidae | *Epinephelus coioides* | 0,0 | 0,5 | 0,0 |
| Serranidae | *Epinephelus malabaricus* | 0,0 | 0,3 | 0,0 |
| Pomacentridae | *Abudefduf sexfasciatus* | 0,0 | 0,5 | 0,0 |

**Table 3.** Species composition by weight (%) by codend mesh sizes.

| Family | Species | 25 mm | 38 mm | 44 mm |
|---|---|---|---|---|
| Carangidae | *Caranx ignobilis* | 24,5 | 0,0 | 0,0 |
| Siganidae | *Siganus sutor* | 15,3 | 18,9 | 38,0 |
| Scaridae | *Leptoscarus vaigiensis* | 15,1 | 26,2 | 33,3 |
| Lethrinidae | *Lethrinus lentjan* | 11,9 | 5,9 | 1,2 |
| Lethrinidae | *Lethrinus mahsena* | 4,1 | 1,6 | 2,8 |
| Siganidae | *Siganus canaliculatus* | 3,2 | 5,6 | 0,0 |
| Gerreidae | *Gerres oyena* | 2,6 | 0,6 | 0,0 |
| Sphyraenidae | *Sphyraena jello* | 1,9 | 0,0 | 0,0 |
| Hemiramphidae | *Hemiramphus far* | 1,8 | 3,0 | 0,0 |
| Terapontidae | *Pelates quadrilineatus* | 1,8 | 0,3 | 0,0 |
| Scombridae | *Sarda sarda* | 1,7 | 0,1 | 0,0 |
| Sphyraenidae | *Sphyraena flavicauda* | 1,5 | 9,5 | 4,8 |
| Scaridae | *Scarus psittacus* | 1,3 | 0,2 | 0,0 |
| Scaridae | *Scarus ghobban* | 1,3 | 1,1 | 0,1 |
| Lutjanidae | *Lutjanus fulviflamma* | 1,3 | 0,7 | 0,1 |
| Sphyraenidae | *Sphyraena putnamae* | 1,0 | 0,0 | 0,0 |
| Mullidae | *Parupeneus rubescens* | 1,0 | 0,1 | 0,0 |
| Chanidae | *Chanos chanos* | 1,0 | 0,5 | 0,0 |
| Haemulidae | *Plectorhinchus flavomaculatus* | 0,8 | 6,7 | 6,3 |
| Lethrinidae | *Lethrinus nebulosus* | 0,6 | 2,2 | 7,0 |
| Tetraodontidae | *Arothron hispidus* | 0,4 | 0,5 | 0,0 |
| Carangidae | *Gnathodan speciousus* | 0,4 | 0,0 | 0,0 |
| Labridae | *Cheilio inermis* | 0,3 | 1,8 | 4,8 |
| Siganidae | *Siganus stellatus* | 0,3 | 0,0 | 0,0 |
| Scombridae | *Scomberoides tol* | 0,3 | 0,0 | 0,0 |
| Sepiidae | *Squid* | 0,3 | 0,0 | 0,0 |
| Scaridae | *Calotomus spinidens* | 0,1 | 0,9 | 0,0 |
| Haemulidae | *Plectorhinchus schotaf* | 0,1 | 0,8 | 0,0 |
| Chirocentridae | *Chirocentus dorab* | 0,1 | 0,2 | 0,0 |
| Gobiidae | *Amblygobius albimaculatus* | 0,1 | 0,1 | 0,0 |
| Monacanthidae | *Cantherhines fronticinctus* | 0,1 | 0,0 | 0,0 |
| Scaridae | *Scarus sordidus* | 0,1 | 0,0 | 0,0 |
| Lethrinidae | *Lethrinus elongatus* | 0,1 | 0,0 | 0,0 |
| Plotosidae | *Plotosus lineatus* | 0,1 | 0,7 | 0,0 |
| Fistulariidae | *Fistularia petimba* | 0,0 | 0,2 | 0,0 |
| Lutjanidae | *Lutjanus gibbus* | 0,0 | 0,3 | 0,0 |
| Albulidae | *Albula glossodonta* | 0,0 | 2,8 | 0,0 |
| Serranidae | *Epinephelus coioides* | 0,0 | 2,1 | 0,0 |
| Ephippidae | *Platax teira* | 0,0 | 1,0 | 0,0 |
| Scaridae | *Calotomus carolinus* | 0,0 | 0,8 | 0,0 |
| Lethrinidae | *Lethrinus borbonicus* | 0,0 | 0,8 | 0,0 |
| Lethrinidae | *Lethrinus harak* | 0,0 | 0,7 | 0,0 |
| Haemulidae | *Diagramma pictum* | 0,0 | 0,6 | 0,0 |
| Acanthuridae | *Acanthurus dussumieri* | 0,0 | 0,6 | 0,0 |
| Toxopneustidae | *Tripneustes gratila* | 0,0 | 0,0 | 1,6 |

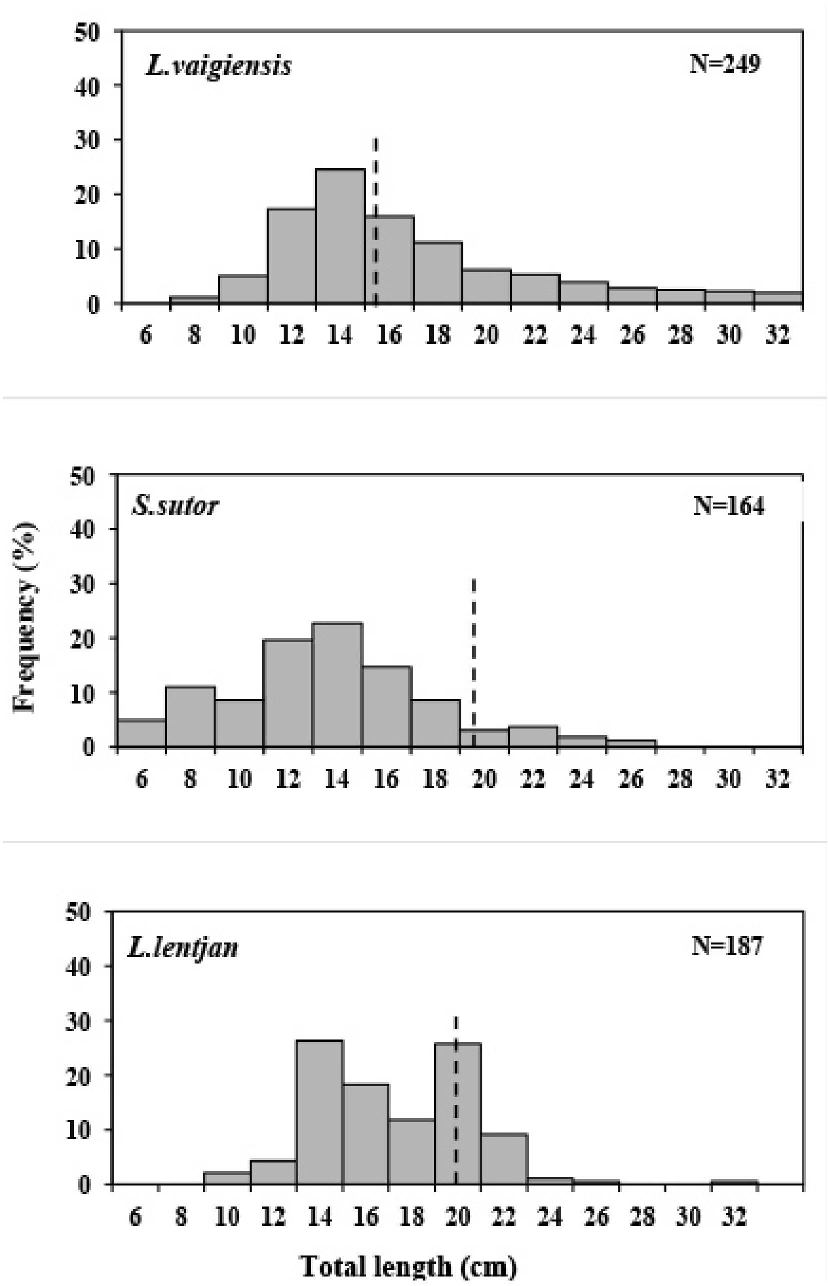

**Figure 2.** Comparative size frequency graphs for 25 mm codend mesh size of the three dominant species. Dotted lines designated the size of $L_{mat}$.

the respective $L_{mat}$ estimates (Fig. 3). Only 14.1% of *L. vaigiensis* retained with the 44 mm mesh were smaller than $L_{mat}$. However, the 44 mm mesh also retained substantial proportions of immature (< $L_{mat}$) *S. sutor* (76.9%) and *L. lentjan* (60%) (Fig. 4). The sample size of *L.lentjan* was small, and may have affected the results. Overall, the results confirm that the 25 mm mesh size retained proportionally more individuals smaller than the $L_{mat}$ than the 38 mm and 44 mm meshes (Fig. 5).

## Discussion

Comprehensive studies on the species composition and size structure of beach seine catches and the effects of gear selectivity on target species are limited in Kenya, where the use of beach seines are prohibited, although not strictly enforced. Attempts to replace beach seine nets with other gear types have been ineffective, and the use of beach seines persists. As an alternative to prohibiting beach seines, implementing a larger mesh size might reduce the impacts on exploited fish populations. Therefore, we analyzed fish caught with different codend mesh sizes, to assess species and size selectivity.

Beach seines with fine mesh codends are active fishing gears known for efficiently capturing a wide range of fish sizes including small, immature individuals

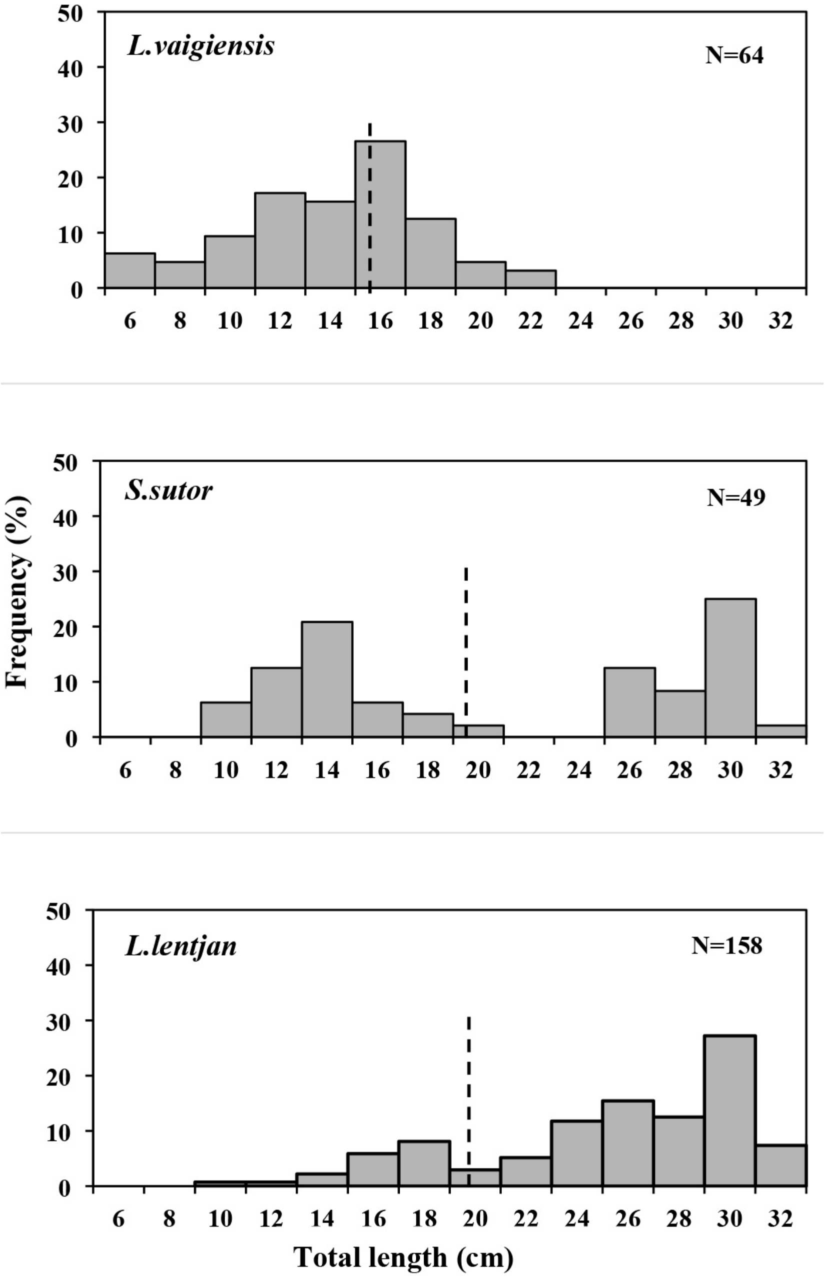

**Figure 3.** Comparative size frequency graphs for 38 mm codend mesh size of the three dominant species. Dotted lines designated the size of $L_{mat}$.

(Mangi & Roberts, 2006). Beach seines are also known to catch a high diversity of fish species, but with only a few species dominating by weight or numbers (Gell & Whittington, 2002). The results from the present study support the findings by Cinner *et al.* (2009) and Unworth & Cullen (2010) that beach seine catches are dominated by seagrass fish assemblages and coral reef affiliated species that utilize sea grass meadows for feeding.

Catches made with 25 mm mesh were most diverse, because the finer mesh retained small-bodied species, such as *A. fragilis*, *O. taeniophorus*, and *T. fucata* which may escape through the 38 mm and 44 mm meshes. Similar results were observed in various studies in South Africa (Lasiak, 1984), Ghana (Nunoo et *al.,* 2007) and the western Aegean Sea (Stergiou *et al.,* 1997). Lasiak (1984) confirmed that the species diversity reflects differences in sampling techniques, length and mesh size of gears used, and the differences in the shore-zone fish assemblage.

The 25 mm mesh caught both mature and immature *L. vaigiensis, S. sutor* and *L. lentjan*. These are the most abundant and commercially important species for the Kenyan artisanal fisheries (Hicks & McClanahan,

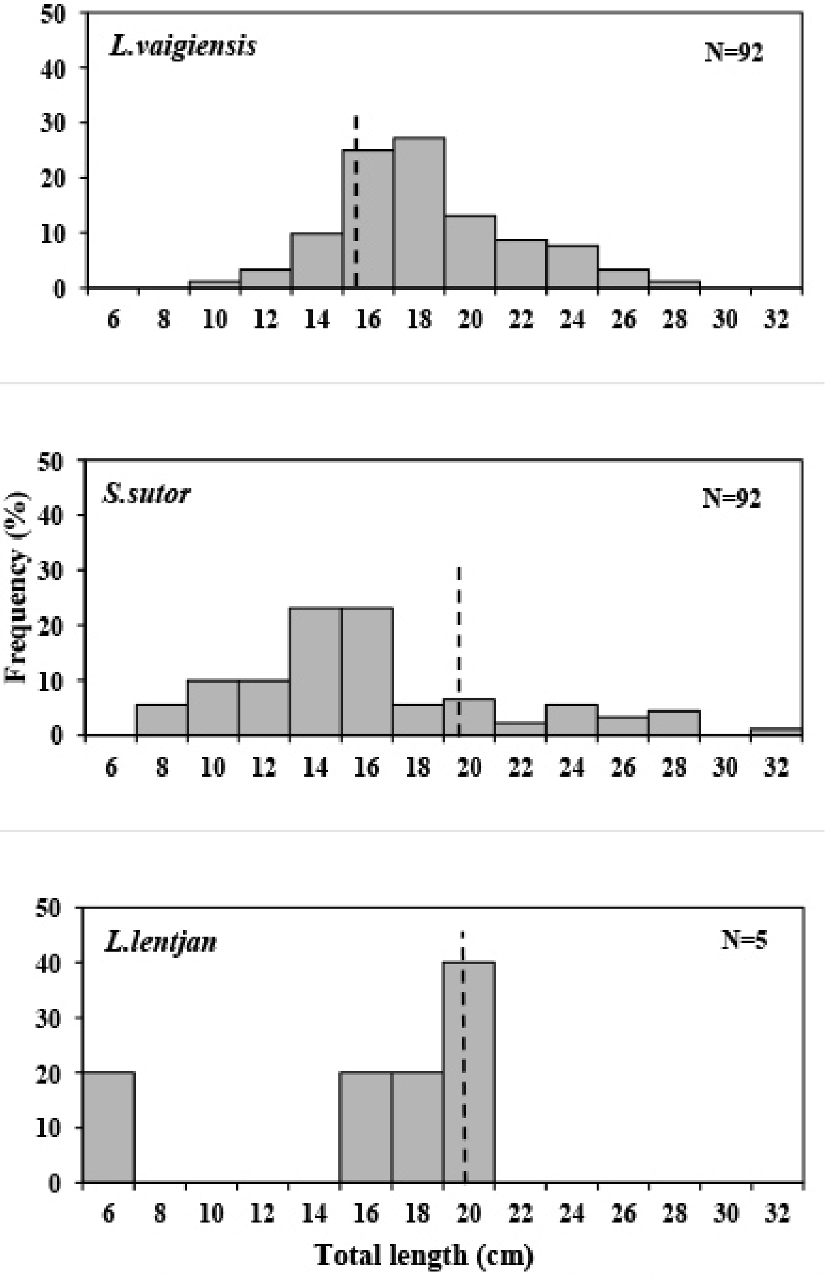

**Figure 4.** Comparative size frequency graphs for 44 mm codend mesh size of the three dominant species. Dotted lines designated the size of $L_{mat}$.

2012). Using the 38 mm and 44 mm meshes generally increased the size at first capture of these species, but also reduced the quantity of fish caught by the gear. This poses a conundrum, because the Lamu fishing communities depend on fish for food security and economic activity, and reducing catch rates by increasing mesh size may affect their income. At the same time, the natural resource-base may be under stress from over-harvesting of juvenile fish by small mesh sizes. The concerns surrounding the capture of juvenile fish are that potential yields may be reduced by growth overfishing, or that too few individuals survive to maturity, resulting in recruitment overfishing (Hutchings & Lamberth, 2002).

It is suggested that an appropriate mesh size is introduced (not a biological optimum, but larger than 25 mm mesh) through stakeholder agreements or voluntary action by fishers. This is already practiced by some fishers in Lamu, who use nets with 38 mm and 44 mm codend mesh sizes. An experimental procedure to collect sufficient data to support robust selectivity analysis is suggested. Reliable measurements of mesh size should be considered during stock assessments, when

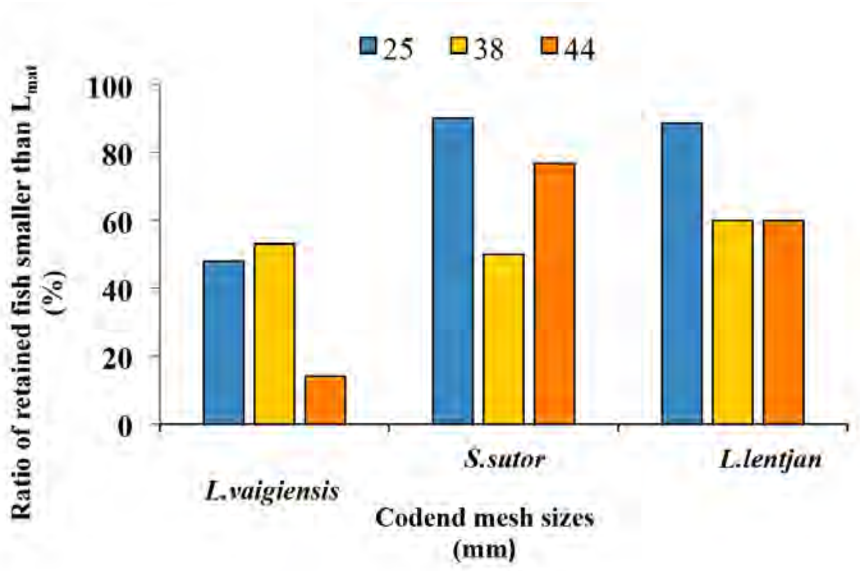

**Figure 5.** Ratios (%) of the three dominant species <$L_{mat}$ retained by different codend mesh sizes.

estimating fishing mortality rates. Moreover, enforcement officers and net makers should ensure fishers use recommended codend mesh sizes. By regulating mesh sizes, and without outright banning of beach seine nets, fisheries managers should be able to control fishing mortality of smaller species and immature individuals of dominant larger species. It is recommended that further research on selective fishing methods, including standardization of codend mesh sizes, is carried out.

## Acknowledgements

We are indebted to the Kenya Coastal Development Project (KCDP) for funding this research work. Special thanks to Dixon Odongo, Rashid Anam, Boaz Orembo, James Gonda, Masud Zamu, Lenjo Mrombo, Nicholus Gichuru, Jacob Ochiewo, Fridah Munyi, Edward Waiyaki, Horace Owiti, Faith Kimanga, Stephen Oluoch, George Waweru, Nicholas Karani, Hassan Bwanamkuu and Captain Ali Salim for the assistance during data collection. We are grateful to the World Wide Fund (WWF) for logistical support. We also thank the county director for fisheries, Mr. Simon Komu, and all the field personnel including fisheries officers from the State Department for Fisheries and the Blue Economy, Beach Management Unit officials, fish traders and fishers for their participation during surveys. Ms. Khyria Swaleh Karama is grateful to the Ministry of Education, Culture, Sports, Science and Technology (MEXT), Japan, for providing a PhD scholarship. We thank two anonymous reviewers for improving the quality of this article.

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