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Thermal tolerance, density, and distribution of mangrove crabs, *Perisesarma guttatum* and *Uca urvillei* at Gazi Bay, Kenya

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Abstract. *Kipyegon JK, Obudho PA, Kairo JG. 2019. Thermal tolerance, density, and distribution of mangrove crabs,* Perisesarma guttatum *and* Uca urvillei *at Gazi Bay, Kenya. Indo Pac J Ocean Life 3: 38-50.* Mangrove crabs are fundamental for the viability of mangrove forests. Therefore, the effects of climate change can impact mangrove ecosystems. The aim of this study was to determine the thermaltolerance, density, and distribution of the mangrove crabs *Perisesarma guttatum* (A.Milne-Edwards, 1869) and *Uca urvillei* (H.Milne Edwards, 1852) within Gazi Bay, Kenya. Field activities included collecting data on the density and distribution of the two crab species and environmental variables in the *Rhizophora mucronata* Lam., *Ceriops tagal* (Perr.) C.B.Rob. and *Avicennia marina* (Forssk.) Vierh. monospecific stands. The crabs were maintained at temperatures between 17-37°C in the laboratory, and respiration rate measurements were performed in closed chamber systems after the crabs were acclimated for 8 hours at a temperature of 27°C. The results indicate the temperature ranges for *P. guttatum* and *U. urvillei* adult crabs were 27-31°C and 27-33°C, respectively, beyond which the crabs got stressed as indicated by increased metabolism. Findings suggest that *P. guttatum* is more sensitive to temperature variation than *U. urvillei*. At the highest average densities of *U. urvillei* and *P.guttatum* crabs were recorded at 66.25±7.7/m² and 11.75±4.1/m², respectively, in the *R. mucronata* zone. The densities of *U. urvillei* and *P. guttatum* were strongly related to the temperature, fine sand, and organic matter using stepwise regression analysis ($P<0.05$). This study has increased the understanding of mangrove crab populations' physiological responses and possible distribution patterns to the expected impacts of climate change on these species.

Keywords: Density, distribution, Gazi Bay, mangrove crabs, *Perisesarma guttatum*, thermal tolerance, *Uca urvillei*

INTRODUCTION

Mangroves support distinctive fauna and flora, dominated by crabs and mollusks. There are 275 species of mangrove crabs globally, with 35 in Kenyan mangroves (Cannicci et al. 2009). In addition, mangrove crabs play an important role in the mangrove ecosystem as a food source (Gillikin et al. 2001; Gita et al. 2015). Thus, their diversity and relative abundance are crucial for the viability of mangrove forests, which in turn support coastal community livelihoods.

Uca urvillei (H.Milne Edwards, 1852) (Family: Ocypodidae) and *Perisesarma guttatum* (A.Milne-Edwards, 1869) (Family: Sesarmidae) are intertidal semi-terrestrial crabs. The *U. urvillei* is detritivorous and digs burrows for shelter. The *P. guttatum* is mainly omnivorous and uses other crabs' burrows and shade in mangroves to minimize thermal stress (Skov et al. 2002). In Gazi Bay, Kenya, both *P. guttatum* and *U. urvillei* occur in the *Rhizophora mucronata* Lam. and *Avicennia marina* (Forssk.) Vierh. zone (Cannicci et al. 2009). Few studies have described the densities of these crabs in the *Ceriops tagal* (Perr.) C.B.Rob. pure stands (Dahdouh-Guebas et al. 2002).

Climate change can threaten mangroves through temperature, sea level, salinity, low pH value, changes in precipitation, and frequency of storms located at the land-sea margins (Macintosh and Ashton 2004). These changes will soon affect the abundance and distribution of aquatic fauna, including crabs, causing local extinctions (Perry et al. 2008). Portner and Knust (2007) reported that thermal changes are the key drivers of ongoing ecosystem changes co-occurring with increasing hypoxia and carbon dioxide accumulation in a climate context. Portner (2010) observed that ecosystem changes have brought out the need to understand the mechanical background underlying physiological responses of aquatic ectotherms to thermal stress. Temperature determines distribution ranges and boundaries for marine and terrestrial species (Gaston 2003; Sanford et al. 2006). Portner et al. (2000) proposed the concept of oxygen and capacity-limited thermal tolerance in aquatic ectotherms. They successfully explained the climate-induced effects of rising temperatures on species abundance in the field (Portner and Knust 2007). However, there is a lack of documented studies on the thermal tolerance of mangrove crabs, *P. guttatum*, and *U. urvillei* in African mangroves.

It is still unknown if there is a link between mangrove crab distribution and thermal determinants (Tewksbury et al. 2008). Meta-analyses of species distribution patterns haveexplained climate-driven effects that have emphasized discovering large-scale patterns without necessarily understanding the mechanisms underlying the physiological processes and their response to abiotic stress. In addition, the abundance of crabs in some mangrove zones, such as the *C. tagal* pure stands, is yet to be fully documented.

The results from this study will allow an appraisal of possible differences in thermal tolerances of crab species that may help explain species distribution patterns within mangroves. The specific objectives were: (i) To establish the optimal thermal tolerance of male adults of *P. guttatum* and *U. urvillei* crabs at Gazi Bay; (ii) To determine the density of *P. guttatum* and *U. urvillei* crabs within the *R. mucronata*, *C. tagal* and *A. marina* mangrove zones at Gazi Bay; (iii). To establish the variation in the distribution of *P. guttatum* and *U. Urvillei*, concerning the environmental factors in the *R. mucronata*, *C. tagal*, and *A. marina* mangrove zones in Gazi Bay, Kenya.

MATERIALS AND METHODS

Study area

Gazi Bay is situated along the south coast of Kenya, between (4°25'S and 39°30'E) (Figure 1). Mangroves of Gazi Bay cover an estimated area of 615 ha (Kairo et al. 2008). That bay is sheltered from strong waves by the presence of the Chale peninsula to the east and a fringing coral reef to the south.

Monsoon winds principally influence the climate in Gazi Bay with two rainy seasons. The rains are heavier during the southeasterly monsoons and fall around April/August, whereas the northeasterly Monsoon winds bring light rains around October/November (Kairo 2001; Bosire et al. 2004). As a result, it is normally hot and humid with an average annual air temperature of about 28°C, with little seasonal variation and a temperature range between 24.8-39°C (Bosire et al. 2006). The seaward mangroves are inundated by tides twice a day, with the highest tidal range of spring tide being about 4.0 m (Bosire et al. 2006).

In Kenya, mangrove forests are facing increasing threats exacerbated by climate change leading to loss of biodiversity; 70% of the mangroves of Gazi Bay are degraded (Dahdouh-Guebas et al. 2004) by several factors, including the effects of 1997/8 El-Niño rains. Trial mangrove plantations were initiated in degraded intertidal areas in 1991 To enhance regeneration (Kairo 2001), and monospecific mangrove stands were planted in denuded mudflats between 1994 and 2000 (Bosire et al. 2004). There are more than 35 species of brachyurans belonging to six families and 4 anomurans associated with the Kenyan mangroves, including Gazi Bay (Cannicci et al. 1997). The two species were chosen because they are abundant and have easy collection and maintenance under laboratory conditions and wide geographic distribution. Further, the two species are strict residents of mangroves throughout their adult life and occupy different niches (Skov et al. 2002).

Sampling design

For crab density data, the sampling design adopted was stratified random sampling. The sampling stations, referred to as zones, were carried out in natural monospecific stands of *R. mucronata*, *C. tagal*, and *A. marina*. Two transects approximately 100-500 m apart, perpendicular to the waterline, were set randomly, cutting across the three mangrove zones to ensure the independence of samples. Four plots per zone of 10×10 m² and at least 20 m apart were randomly selected from a pool of eight plots for each zone, and their positions were marked with GPS. Density surveys were carried out in these plots during October and November 2011 and repeated in December 2011 and January 2012. Each plot was divided into four quarters, and four 1-m² sub-quadrats were randomly selected for the survey from each quarter, making a total of 48 sub-quadrat samples per month. Stratified random sampling protocols were adapted during this study (Chapmanand Tolhurst 2004; Cannicci et al. 2009). Visual observation and burrow counts provide crude estimates of population density at best, even where a single species is concerned (Macia et al. 2001; Skov and Hartnoll 2001).

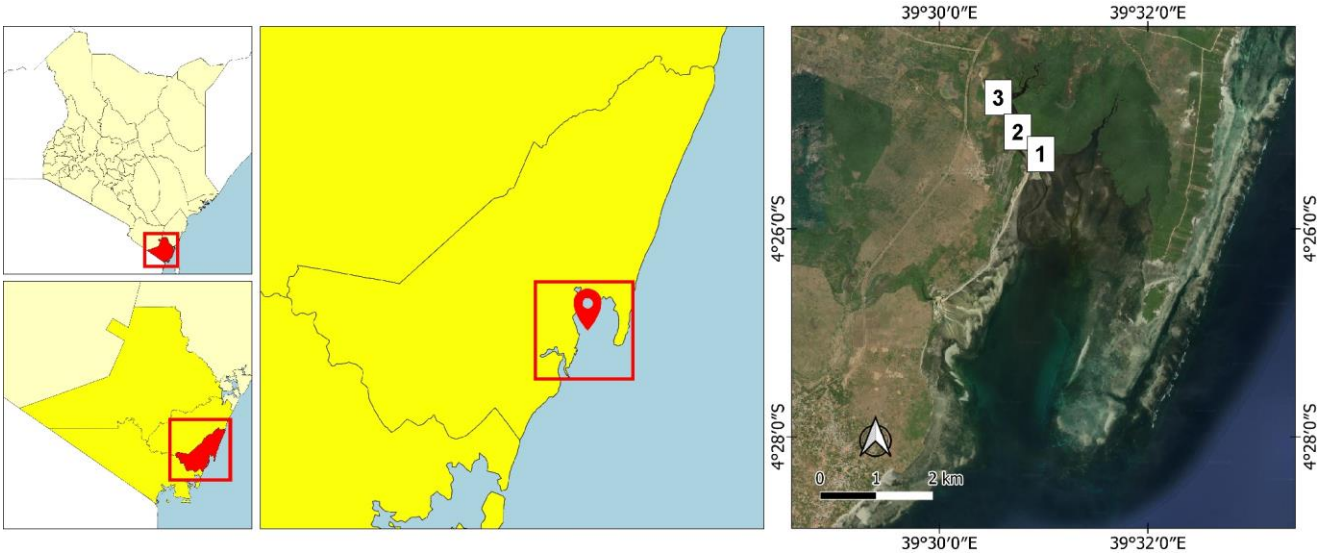

Figure 1. Map of the Kenyan coast showing the study area, Gazi Bay. Adopted from Bosire et al. (2004). Sampling stations: 1. *Rhizophora mucronata* 2. *Ceriops tagal* 3. *Avicennia marina* zones

Figure 2. One (1) m² quadrat (enclosed with a piece of rope round) used to sample crabs in the *Ceriops tagal* zone

Data collection

Determination of density of Perisesarma guttatum *and* Uca urvillei *crabs*

Crab density sampling was carried out across the intertidal area in the threemangrove zones using binoculars in the four 1-m² sub-quadrats per plot (Figure 2) for five days during spring high tides. For *U. urvillei*, density was estimated using visual and burrow counts (Skov et al. 2002; Cannicci et al. 2009). Visual counts of all active crabs were done using binoculars (8x40 magnification) when standing at about 3.5 meters from each quadrat, and crabs were enumerated after the observer remained motionless for 15 minutes to provide sufficient time for resumption of full activity. In addition, crab burrow openings were counted to avoid underestimation of crabs not active on the surface during visual counts (Hartnoll et al. 2002). The density of *U. urvillei* was estimated by the burrow count data and calibrated with the species ratio (all species counted that make burrows observed within the quadrat) obtained from visual counting. For *P. guttatum*, they were counted visually using binocularsthroughout the 1-m² sub-quadrats, as no burrow counts were used for *P. guttatum* because they do not make burrows (Skov et al. 2002).

Measurement of abiotic factors

At each sampling station, data for the following parameters were collected to characterize the crab's habitat: Sediment temperature on the sub-surface was recorded using a digital probe thermometer, and pore water salinity of sediment (determined from centrifuge-extracted interstitial water) was measured using an optical refractometer (Atago brand), in situ data on Redox potential (Eh) and PH was measured using standard electrodes and a combination millivolt/pH meter. Redox potential (Eh) is a quantitative measure of reducing the power that provides a diagnostic index of the degree of anaerobiosis or anoxia (Patrick and Delaune 1977). The pH was measured with fresh samples of sediments to avoid oxidation of iron pyrites to sulfuric acid to avoid giving a much lower pH value than normally occurs. The above samples were taken at 10 cm and 40 cm depths along the core.

Sediment characteristics sampled were; fine and coarse sand, silt and clay, and organic matter of the sediment. In the sediment sampling, 4 cores of 5 cm deep by 2.5 cm wide per plot per sub-quadrat in each zone were taken for granulometric analysis. Sediments were measured by placing a known weight of sediment of about 100-150 grams into an oven at 80ºC for about 24 hours until the constant dry weight was obtained for granulometric analysis. About 25 g for each dry sample from the oven were then weighed and transferred into pre-labeled beakers with 250 mL water and 10ml of aqueous sodium hexametaphosphate $(NaPO_3)_6$) and stirred for 10 minutes and leftfor a minimum of four hours. Afterward, they were subjected to a series of sieves ranging from <63 to 500 µm mesh sizes for wet-sieving to measure cumulative percent weights of soil particle sizes. The organic matter in the samples was obtained by ashing about 20 g of the remaining dry sample from the oven to 450ºC for four and half hours in the furnace and then cooling and weighing. The difference in weight gave an estimate of organic matter (Wartel et al. 1995) as:

$$\% \text{ Organic matter} = \text{Initial weight(g)} - \text{Final weight(g)} \times 100\%$$

Collection of crab specimens for laboratory experiments

The *P. guttatum* and *U. urvillei* specimens for thermal tolerance experiments were collected by hand capture at low tide. At least ten male adults per species per experiment were collected. They were kept and maintained in the laboratory for at least 24 hours (Vernberg 1959) at ambient temperature before the experiments. They were kept in plastic tanks with 5 cm mangrove soil sediment from their habitat area and were not fed. The health of the crabs was determined using the Righting Response Time method (Hogarth 1999), and only those crabs that quickly righted themselves up were used.

Optimal thermal tolerance experiments for male adults of Perisesarma guttatum *and* Uca urvillei

In temperature-controlled rooms, adults of *P. guttatum* and *U. urvillei* were maintained separately at different experimental temperatures (17-37ºC). Respiration rate measurements were performed using a closed chamber system consisting of five partially darkened respiration chambers (using aluminum foil to avoid visual stresses) and connected to single-channel, temperature-compensated oxygen meters (Fibox 3-Presents de), as shown in Figure 3. The Fibox 3 was connected to a PC desktop that recorded all measurements. Each respiration chamber had a single crab, except the control, and was submersed in a constant temperature recirculating water bath heated to the appropriate trial set-point temperature. The control chamber with no crab inside was used to correct bacterial oxygen consumption.

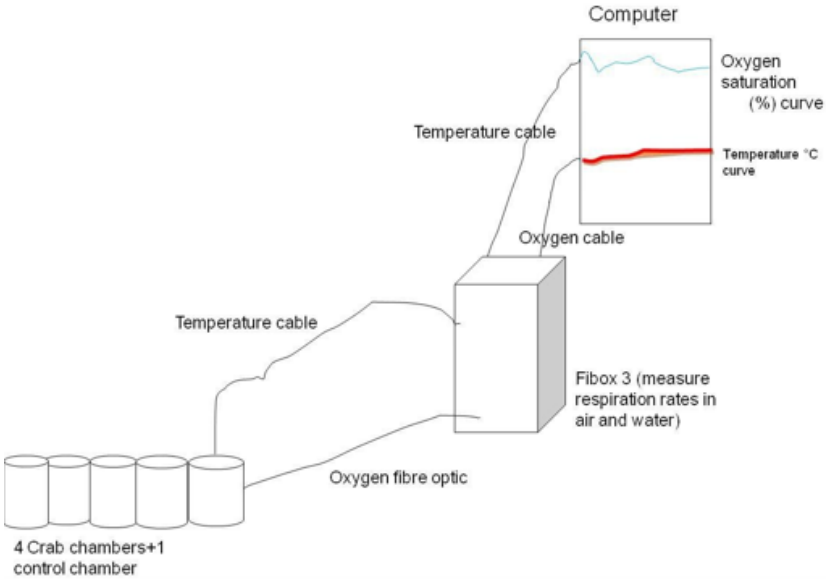

Figure 3. Laboratory crab experimental set-up to measure respiration rates

The air and water experiments were performed separately for each species. For water experiments, caution was taken within the crab chambers to ensure no bubbles were introduced while putting the crab inside the chamber. Sea water was used that had been filtered to remove particulate matter (0.2 µm filter). The water flow from each respirometer was controlled with a screw pinch clamp. The crab chambers were made of glass with removable airtight lids and a screw fitting for the oxygen fiber optic cable, and they had a capacity volume of 450 mL.

The experiments were divided into two parts; (a) increasing temperature from 27 to 37°C in air media per species separately and increasing temperature from 27 to 37°C in water media per species separately (b) decreasing temperature from 27 to 17°C in water media only for each species separately. During each experiment, the crabs were acclimated for eight (8) hours in the respirometry chambers at 27°C, the ambient temperature at Gazi Bay during the study period. The valves were then switched off using a screw pinch valve/clamps to cut off atmospheric oxygen for air experiments and external dissolved oxygen for water experiments, as well as the control chambers to record oxygen consumption rate inside the chambers only. The respiration rate of each crab in the closed chamber was determined by measuring the decline in oxygen saturation (initial 100%) in the known volume of water and the air surrounding the crab in the chamber and was recorded each lasting 5 minutes making a total of 25 minutes for 5 chambers and used as their basal metabolism (Hervant et al. 1998; Frederich and Pörtner 2000). At least two measurements/replicates of oxygen consumption rates per experiment were made for each crab's respiration rates per temperature step to ensure a strong regression line of declining oxygen saturation.

Measurements of oxygen consumption rates were conducted every 20 minutes between each of the two replicate measurements (one replicate here refers to one full measurement in 5 chambers per temperature step) at each experimental temperature per experiment. The declining rate of oxygen content/percent saturation (Y-axis) versus time (X-axis) was calculated as the slope of the regression line fitting the oxygen consumption rates data versus time from the two pooled replicate measurements per temperature level was automatically recorded by the computer. The oxygen content of the water was never allowed to fall below 80-90% saturation to avoid hypoxic stress during recording. All measurements lasted between 4 hours for air experiments and water experiments up to 2 hours. In the case of air experiments, the volume of the chambers was too great to allow feasible measurement of the consumption of 10-20% of the available oxygen, so the volume was decreased by adding glass marbles to the chamber. The volume of glass marbles was recorded after the experiment, and the new volume of the chamber was calculated. The crabs were used only once in each experiment, and water was not changed between replicate measurements. After the respiration rate at the acclimation temperature at 27°C was recorded, the valves were removed, and the crab chambers reaerated again. The temperature was then increased gradually at 2°C intervals every 2 hours to the next experimental temperature. At the same time, oxygen consumption rates were recorded to the maximum and minimum experimental temperatures of 37°C and 17°C, respectively.

At every experimental test temperature, the crabs were left to acclimate to the experimental temperature for a further 30 minutes. The experiment was then repeated at the new temperature, and the respiration rate was recorded. Each experiment lasted about 33 hours. Moreover, 12 and 10 specimens or replicates of *P. guttatum* adult males were used in water and air respiration experiments, respectively. In comparison, for *U. urvillei*, 15 and 12 specimens/replicates of males for water and air respiration experiments were used, respectively. At least two temperature measurements were performed at each temperature level. At the end of each experiment, the mass

and volume of the crabs were recorded and subtracted from the empty chamber to determine the exact amount of respiratory medium of each crab per experiment to get mean weight-specific oxygen consumption rates (µmol). All crabs were released 24 hours post experiment back to their area of collection (Eshky 1999; Addo-Bediako et al. 2000; Jimenez and Bennet 2005). Three incidences of mortalities of *P. guttatum* were reported during the experiments, with two at 33°C and one at 37°C may be due to oxygen bubbles in the chambers. In almost all instances in water experiments, therefore, measurements were made in 2°C increments over a total temperature range of 10°C above and below 27°C, which for every species bracketed its preferred temperature. Assumptions were made that the comparatively brief period spent at each measurement temperature (≤2 hours) provided little or no temperature acclimation. Moreover, the considerable care taken to avoid disturbance during sampling or flushing of the respirometer probably prevented any cumulative stress effects during the experiment.

Oxygen consumption rate recordings were carried out in constant darkness to try to eliminate the effects of diel changes in oxygen consumption rate. In addition, the decreasing temperature in water experiments was performed to understand the physiological responses/cold tolerance of these animals in cold water as these two crab species are naturally known to occur up to their southern latitudinal limit range in subtropical regions on the north coast of South Africa where they are exposed seasonally to chilly weather (Lee 2008).

Only male crabs were used in this study following previous similar crab physiological studies, which showed no differences in responses of either sex (Frederich and Pörtner 2000; Jimenez and Bennett 2005) and thus was a representative model of these crab populations.

Data analysis

General Linear Model (GLM) ANOVA was used to test for the effect of increasing temperature (independent variable) on oxygen consumption rate (dependent variable) for each species. Tukey test was used to show which paired temperatures significantly affected oxygen consumption rates. GLM was also used to test for the effect of temperature, species, and media (independent variables) on oxygen consumption rates (dependent variable). GLM 3-factor ANOVA with species (two levels), zones (3 levels), transects (2 levels), and season (2 levels) as the factors and their interactions was used to test for significant effects of the factors on the densities of the two species. Differences in environmental parameters between zones and season and between zones and transects were tested using a two-way ANOVA with zones, season, and transects as the factors. The relationship between crab density (dependent variable) and environmental parameters (independent variables) was carried out using Backward stepwise multiple regression analysis. Percentage data were arc-sine transformed prior to analysis. For the ANOVAs, the dependent variable crab density was square-root transformed prior to analysis to stabilize variance and ensure normality. All P- Values less than 0.05 ($P<0.05$) were significantly different. All analyses were carried out using Minitab Version14 software.

Q_{10} is the factor by which an ectothermic physiological rate increases over a 10°C interval but also T_1 and T_2 do not need to be exactly 10 degrees apart to use this equation as shown in the formula:

$$Q_{10} = (R_2/R_1^{10/(T_2-T_1)}$$

Where R_2: Final Respiration rate; Respiration rate; R_1: Initial Respiration rate; $^{T}_{2}$**:** Temperature at R_2; ^{T}: Temperature at R_1 (Jimenez and Bennett 2005).

RESULTS AND DISCUSSION

Determination of thermal tolerance of adult males of *Perisesarma guttatum* and *Uca urvillei*

The *P. guttatum* and *U. urvillei* displayed similar respiratory response patterns to increasing temperature in both air and water media (Figure 4). The results show a general increase in oxygen consumption rate with increasing temperature in both media, but not constantly at the range of temperatures tested.

Oxygen consumption rate at an initial temperature of 27°C differed for each species per media. At 27°C in water, *P. guttatum* and *U. urvillei* had 0.08±0.04 and 0.06±0.02 µmol/gmin, respectively, while at 27°C in air, *P. guttatum* and *U. urvillei* had 0.14±0.03 and 0.51±0.02 µmol/gmin respectively. At 37°C in water, oxygen consumption rates for *P. guttatum* and *U. urvillei* were 0.14±0.02 µmol/gmin and 0.09±0.01 µmol/gmin, respectively. While at 37°C in air 0.23±0.11 µmol/gmin and 0.13±0.04 µmol/gmin for *P. guttatum* and *U. urvillei*, respectively.

Results in Figure 5 indicate oxygen consumption rates increased with increasing temperature in water media from 17-37°C in both species, but not constantly at the range of temperatures tested. The graphs showed three major levels giving astaircase pattern; the lower temperature level of 17-27°C and middle level of 27-31°C for *P. guttatum* and of 27-33°C for *U. urvillei*, where there was an apparent regulation of respiration rate and lastly the high-level temperature 31-37°C. In the low-level temperature, very low oxygen consumption rates with an increase in temperature between 17-23°C were recorded, indicating low metabolism for both species. Then oxygen consumption rate increased exponentially with temperature rise from 25-27°C. At the middle level, oxygen consumption rates did not increase with increasing temperature (oxygen consumption rate is temperature independent). In contrast, for *P. guttatum*, this temperature range was 27-31°C while that of *U. urvillei* range was 27-33°C. Finally, the third level indicates increased oxygen consumption rates by both species with increasing temperature, with *P. guttatum* rates nearly more than doubling that at 37°C.

The average rate of oxygen consumption of *P. guttatum* was 0.012±0.007 µmol/gmin, half that for *U. urvillei* of 0.02±0.008 µmol/gmin at 17°C. On the hand, oxygen consumption rates for *P. guttatum* and *U. urvillei* at 37°C

were 0.14±0.02 µmol/gmin and 0.08±0.01 µmol/gmin, respectively, which suggests that at low temperatures *U. urvillei* tend to have higher metabolic rates than *P. guttatum. In contrast,* at high temperatures, it is the opposite.

Temperature variation significantly affected oxygen consumption rates ($F_{5,244}$=15.95, P<0.05) of P. guttatum and U. urvillei in air and water media. In addition, oxygen consumption rates were significantly different between the two species ($F_{1,244}$=155.39, P<0.05) and significantly different between air and water media ($F_{1,244}$=27.64, P<0.05).

Temperature variation showed a significant effect on oxygen consumption rates ($F_{5,125}$=10.81, P<0.05) in *P. guttatum* and *U. urvillei* ($F_{5,134}$=9.32, P<0.05) in both air and water. There was a significant difference in oxygen consumption rates between air and water in *P. guttatum* ($F_{1,125}$=61.35, P<0.05). At the same time, there was no significant difference in oxygen consumption rates between air and water in *U. urvillei* ($F_{1,134}$=0.12, P>0.0.05). The *P. guttatum* consumed higher oxygen consumption rates in the air than in water throughout the tested temperatures, while it is the opposite for *U. urvillei,* with higher oxygen uptake in water than in air except for between 33-35°C, where there was a drop and then it rose again from 35-37°C (Figure 5).

For the respiration rate of *P. guttatum* in air and water, temperature variation showed a significant effect on oxygen consumption rates ($F_{5,125}$=10.81, P<0.05). Further analysis, by the Tukey test, a low oxygen consumption rate which did not vary with increasing temperature was observed between the temperature range 27-31°C, where temperature variation had no significant effect on oxygen consumption rates (P>0.05) in both air and water (Figure 4 and 5). However, temperature variation showed a significant effect on oxygen consumption rates between 33-37°C (P<0.05) and between 17-27°C (P<0.05) (Figures 4 and 5).

For the respiration rate of U. urvillei in air and water media, temperature variation significantly affected oxygen consumption rates ($F_{5,134}$=9.32, P<0.05). The temperature range between 27-33°C did not show any significant effect on oxygen consumption rate (P>0.05) in both air and water (Figures 4 and 5). However, temperature variation showed a significant effect on oxygen consumption rates between 33-37°C (P<0.05) and between 17-27°C (P<0.05).

Q_{10} over the whole temperature range of 17-37°C for *P. guttatum* was 3.31, while for *U. urvillei* was 2.02. Aquatic oxygen consumption rates of *P. guttatum* and *U. urvillei* increased from 17-27°C with a Q_{10} value of 6.58 and 3.11, respectively, thus clearly showing that Q_{10} of *P. guttatum* was higher than the latter, in fact, by double value. Over the temperature range of 27-37°C in water media, the Q_{10} of oxygen uptake was not similar for the two species, with *P. guttatum* having 1.7 while that of *U. urvillei* was 1.3. Q_{10} for *P. guttatum* and *U. urvillei* in the air over 27- 37°C was 1.6 and 2.6, respectively, opposite for *U. urvillei* to that recorded in water. Within the optimal temperature range for *P. guttatum* of 27-31°C, the Q_{10} was 1.5, while for *U. urvillei,* at the optimum temperature range of 27-33°C, Q_{10} was 1.4.

In summary, the optimum temperature range for *P. guttatum* was 27-31°C, while that of *U. urvillei* was 27-33°C, where the temperature had no significant effect on oxygen consumption rates (P>0.05). The optimal thermal ranges of the two species are significantly different ($F_{3,161}$=4.02, P<0.05).

Crab density and distribution in mangroves

Figure 6 generally indicates a higher density of U. urvillei than *P. guttatum* in the *R. mucronata* zone compared to other zones. The *P. guttatum* density was highest in the *R. mucronata* zone, followed closely by the *C. tagal* zone, and lowest in the *A. marina* zone. The highest mean density (Number (No)/m²±SE) of *U. urvillei* and *P. guttatum* was 66.25±7.7 and 11.75±4.1, respectively, in the *R. mucronata* zone. The *A. marina* zone recorded the lowest mean density (No/m²±SE) of the two species, *U. urvillei* was 0.18±0.7, and that of *P. guttatum* was 1.9±1.8. The density (No/m²±SE) of *U. urvillei* and *P. guttatum* in the *C. tagal* zone was 0.47±0.28 and 8.03±1.8, respectively.

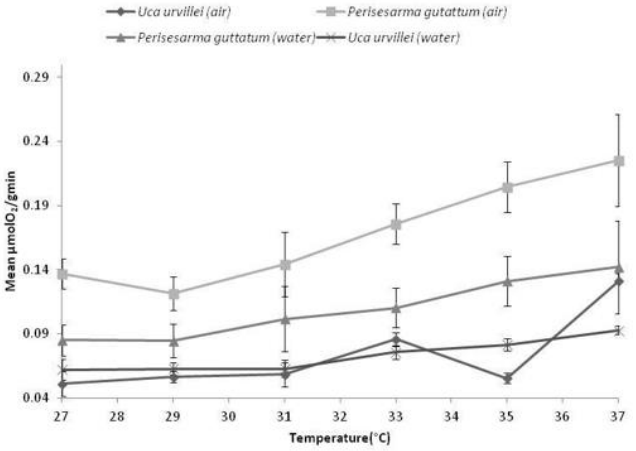

Figure 4. Relationship between temperature (mean±SE) and oxygen consumption rates of *P. guttatum* and *U. urvillei* crabs in air and water media

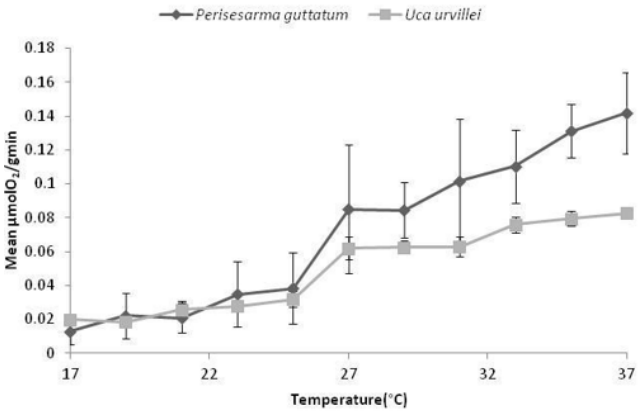

Figure 5. Relationship between temperature (mean±SE) and oxygen consumption rates of *P. guttatum* and *U. urvillei* crabs in water media

There were significant differences in the density of the two species between the three mangrove zones ($F_{2,47}$=402.95, P<0.05) for *U. urvillei* and ($F_{2,47}$=65.04, P<0.05) for *P. guttatum*. Further analysis showed that *U. urvillei* density was significantly different between; *R. mucronata* and *A. marina* zones (T=-28.75, P<0.05), *R. mucronata*, and *C. tagal* (T=-27.66, P<0.05) but was not significantly different between *A. marina* and *C. tagal* zones (T=1.088, P>0.05). For *P. guttatum*, there was a significant difference indensity between; *R. mucronata* and *A. marina* zone (T=-9.996, P<0.05), *C. tagal* and *A. marina* zones (T=7.994, P<0.05) but was not significantly different between *R. mucronata* and *C. tagal* zone (T= -2.003, P>0.05). The season transects and neither interaction between zones, transects, and seasons did not show any significant effect on the density of these crabs (P>0.05) (Figure 6).

Environmental variables

The results revealed significant environmental parameters and soil particle characteristics differences between the three mangrove zones (P<0.05). However, the environmental factors did not significantly vary with seasons and transects (P>0.05).

Salinity

The highest porewater salinity recorded during the study period was 63‰ in the *A.marina* zone, and the lowest was 21‰ in *R. mucronata*. The results in Figure 7 indicate mean porewater salinity in *A. marina* zone ranged from 42.25 to 51.75‰, for *R. mucronata*, it ranged from 27.152 to 34.13‰ while for *C. tagal*, it ranged from 34.53 to 44.75‰. There were significant differences in salinity between the three mangrove zones ($F_{2,47}$ =31.40, P<0.05) but not between seasons ($F_{1,47}$=4.73, P>0.05), and neither interaction between season nor zones ($F_{2,47}$=0.72, P>0.05). There was no significant difference in salinity between transects ($F_{1,47}$=0.07, P>0.0.5) and neither interaction between transects and zones ($F_{2,47}$=0.29, P>0.05).

Temperature

The highest temperature recorded during the study period was 36.8°C in December in the *A. marina* zone, while the lowest temperature recorded was 29.0°C in the *R. mucronata* zone in November (Figure 8). There were significant differences in temperature between the three mangrove zones ($F_{2,47}$=6.11, P<0.05). Analysis revealed a significant difference between *R. mucronata* and *A. marina* zones (T=2.548, P<0.05) and between *R. mucronata* and *C. tagal* (T=3.371, P<0.05), while the temperature was not significantly different between *A. marina* and *C. tagal* zones (T=0.8225, P>0.05). There was no significant difference in temperature between seasons ($F_{1,47}$=0.72, P>0.0.05) and neither interaction between season and zone ($F_{2,47}$=1.21, P>0.05). There was no significant effect of temperature on transects ($F_{1,47}$=,4.95, P>0.05) and neither interaction between zone nor transects ($F_{2,47}$= 1, P>0.05).

pH

The mean PH value ranged between 5.6-6.67 in the *R. mucronata* zone. In the *A. marina*, the pH ranged from 5.6 to 6.4, while in C. tagal, it ranged from 6.0 to 6.3 (Figure 9). There was no significant difference in pH between the three mangrove zones ($F_{2,47}$=0.43, P>0.05) nor the interaction between season and zones ($F_{2,47}$=0.32, P>0.05). Likewise, there was no significant difference in PH between zones and transects ($F_{1,47}$ =,0.24 P>0.0.05) and neither interaction between zones nor transects ($F_{2,47}$=,0.30, P>0.05).

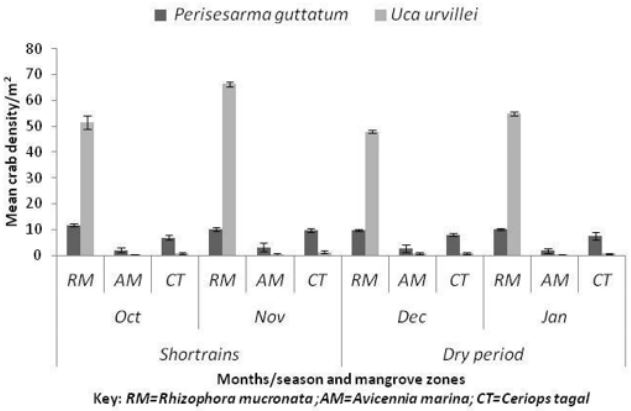

Figure 6. Mean density (±SE) of *P. guttatum* and *U. urvillei* in mangroves zones

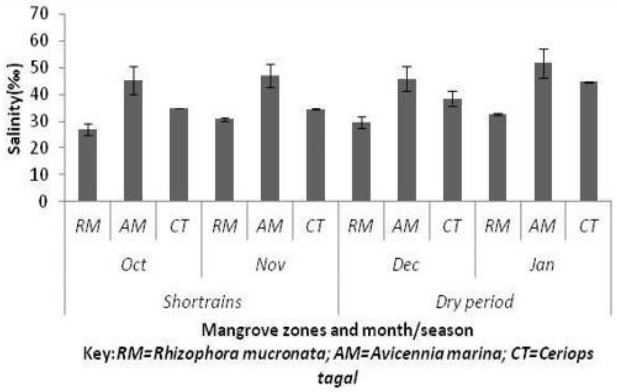

Figure 7. Mean (±SE) monthly salinity in mangrove zones

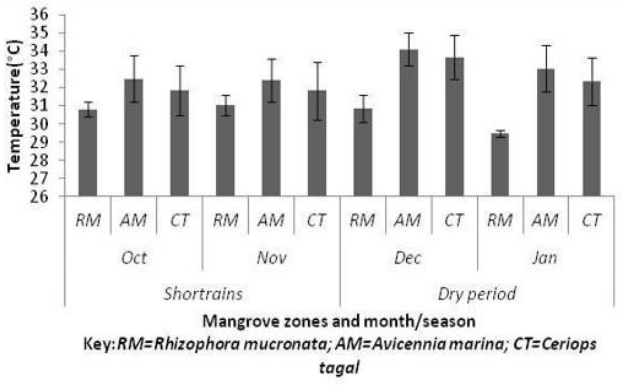

Figure 8. Mean (±SE) monthly temperature in different mangrove zones pH

Redox potential (eH)

The highest redox potential recorded during the study period was 155.6 in *A. marina*, and the lowest was -229.9 in the *R. mucronata* zone (Figure 10). There was a significant difference in Redox potential between the three mangrove zones ($F_{2,47}$=28.3, P<0.05), and analysis revealed a significant difference in redox between; *R. mucronata* and *A. marina* (T=7.176, P<0.05), *A. marina* and *C. tagal* (T=-5.546, P<0.05) while redox potential was not significantly different between

The *R. mucronata* and *C. tagal* zones (T=1.630, P>0.05). Redox potential did not show any significant difference between seasons ($F_{1,47}$=4.01, P>0.05), neither interaction between zone nor seasons ($F_{2,47}$=3.21, P>0.05). Likewise, there was no significant difference in Redox potential between transects ($F_{1,47}$=1.78, P>0.05) and neither interaction between transects and zones ($F_{2,47}$=1.81, P>0.05).

Soil characteristics

The *C. tagal, R. mucronata,* and *A. marina* recorded the highest percent silt of 68.2±8.02%, 52.7±4.05%, and 31.3±18.8%, respectively (Table 1). There were significant differences in silt between the three zones ($F_{2,47}$=125, P<0.05), and analysis revealed significant differences between; *R. mucronata* and *A. marina, R. mucronata,* and *C. tagal* and between *C. tagal* and *A. marina* zones (P<0.05). There was no significant difference in silt between transects ($F_{1,47}$=0.01, P>0.05) nor the interaction between transects and zone ($F_{2,47}$=0.01 P>0.05).

The *A. marina* zone generally had higher fine sand compared to the other two zones (Table 1). There were significant differences in fine sand between the three mangrove zones ($F_{2,47}$=27.37, P<0.05). In further analysis, fine sand showed significant differences between *R. mucronata* and *A. marina* zones (T=2.552, P<0.05), between *R. mucronata* and *C. tagal* zones (T=3.372, P<0.05), while there was no significant difference in fine sand between *C. tagal* and *A. marina* zones (T=0.8198, P>0.05). There was no significant difference in fine sand between transects ($F_{1,47}$=0.72, P>0.5) nor the interaction between transect and zone ($F_{2,47}$=0.15,P>0.05).

The *A. marina* generally had the coarsest mean sediment or sand and recorded the highest value of 19.3±7.0%, followed by *R. mucronata* 12.6±7.4% and finally *C. tagal* 8.4±0.6% (Table 1). There were significant differences in percent coarse sand between the three mangrove zones ($F_{2,47}$=71.00, P<0.05). Analysis revealed significant differences in coarse sand between *R. mucronata* and *A. marina* (T=3.331, P<0.05), *C. tagal*, and *A. marina* zones (T=-3.41, P<0.05), while no significant difference was observed between *R. mucronata* and *C. tagal* zone (T=-1.307, P>0.05). There was no significant difference in coarse sand between transects ($F_{1,47}$=0.63, P>0.05) nor the interaction between transects and zones ($F_{2,47}$=0.52, P>0.05).

The highest percent organic matter content was recorded in the *R. mucronata* zone at 24.2±2.4%, followed by *C. tagal* at 14.7±11.4% and *A. marina* zone at 12.3±8.1% (Table 1). The organic matter content revealed significant differences between the three mangrove zones ($F_{2,47}$=152.60, P<0.05) and the interaction between zones and transects ($F_{2,47}$=150.70, P<0.05) but not between transects ($F_{1,47}$=62.53, P>0.05). Tukey test revealed significant differences in percent organic matter between; *R. mucronata* and *C. tagal* (P<0.05), *R. mucronata* and *A. marina* (P<0.05), but there was no significant difference in the organic matter between *A. marina* and *C. tagal* zones (P>0.05).

Environmental variables and crab density

Table 2 indicates that temperature, salinity, silt, fine sand, and organic matter significantly affected *U. urvillei* density (P<0.05) and accounted for 69.82% of the variations in density. The lowest mean temperature, salinity, and higher organic matter content, silt, and fine sand were recorded in the *R. mucronata* zone, which also recorded the highest densities of this species.

Table 3 indicates that temperature, fine sand, and organic matter significantly affected *P. guttatum* density (P<0.05) and accounted for 67.92% of the variations in density. However, silt could have a marginal effect on the density of the species (P>0.074).

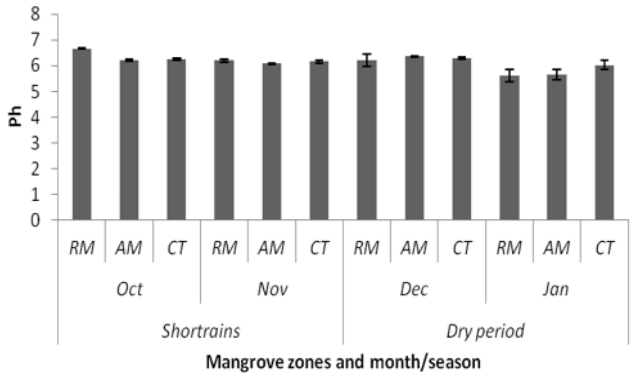

Figure 9. Mean (±SE) monthly pH in different mangrove zones. Note: RM: *Rhizophora mucronata*; AM: *Avicennia marina*; CT: *Ceriops tagal*

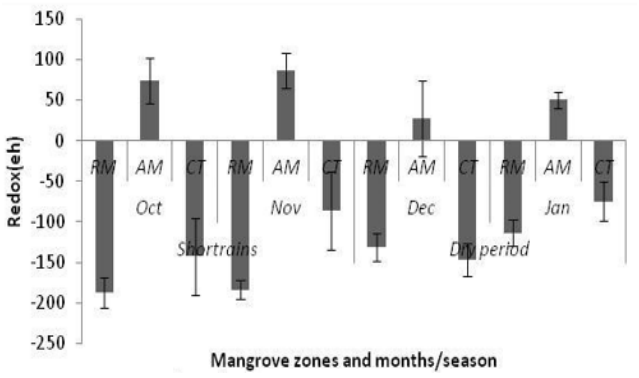

Figure 10. Mean (±SE) monthly Redox potential (eH) in different mangrove zones. Note: RM: *Rhizophora mucronata*; AM: *Avicennia marina*; CT: *Ceriops tagal*

Table 1. Particle sizes (%) variation over months/seasons and mangrove zones

Season	Month	Zone	Silt %	Fine sand (>63µm)%)	Coarse sand (>500µm)%	Organic matter (%)
Short-rains	OCT	RM	52.7±4.05	36.3±4.1	10.95±4.5	22.7±2.6
		AM	20.1±8.15	63.2±14.7	16.7±6.6	12.3±8.1
		CT	68.2±8.02	24.8±5.8	6.9±2.3	14.6±10.7
	NOV	RM	34.6±10.7	52.8±6.7	12.6±7.4	24.2±2.4
		AM	23.8±4.6	56.9±4.2	19.3±7.0	10.9±5.3
		CT	54.27±5.1	37.3±12	8.4±0.6	13.8±10.2
Dry-period	DEC	RM	51.2±20.9	39.4±15.6	9.3±6.7	24.1±0.9
		AM	31.3±18.8	53.9±17.8	14.8±9.1	9.7±5.7
		CT	60.3±15.4	32.9±12.8	6.8±2.7	14.7±11.4
	JAN	RM	42.4±25.2	51.1±1.3	6.5±23.9	23.6±1.6
		AM	13.1±3.3	73.6±7.5	13.4±10.2	11.8±6.4
		CT	48.8±17.4	43.6±2.4	7.6±15.0	12.6±9.1

Note: RM: *Rhizophora mucronata*; AM: *Avicennia marina*; CT: *Ceriops tagal*

Table 2. Stepwise regression analysis (Backward) of the effects of dependent variable *Uca urvillei* density on the independent variables

Variable	Constant	T-value	P-value
Silt (<63 µm)	-27.4	-4.0	0.000
Fine sand (>63µm)	-26	-4.13	0.000
Organic matter	0.155	-4.16	0.001
Temperature	-0.433	-3.66	0.001
Salinity	-0.086	5.01	0.000

Note: S=0.442, R^2=69.82, R-Sq(adj)=66.23, Mallows C-p=4.1, r^2=69.82%, P<0.05, *U. urvillei* density (Y)=35.9(C), -27.4 Silt, –26 Fine sand, +0.155 Organic matter, -0.433 Temperature, -0.086 Salinity

Table 3. Stepwise regression analysis (Backward) results in the effects of dependent variable *P. guttatum* density on independent variables

Variable	Constant	T-value	P-value
Fine sand (>63µm)	1.96	-2.05	0.047
Organic matter	4.3	3.80	0.000
Temperature	-0.074	-2.53	0.015

Note: S=0.200, R^2=67.92, R-Sq(adj)=64.10, Mallows C-p=3.4, r^2=67.92%, P<0.05. The *P. guttatum* density (Y)=2.221(C), +1.96 Fine sand, +4.3 Organic matter, -0.074 Temperature

Discussion

Determination of thermal tolerance of adult males of Perisesarma guttatum *and* Uca urvillei

The study indicated that the metabolic rates of *P. guttatum* and *U. urvillei* increased over the temperature range of 17-37°C indicating the animals were displaying standard metabolic rates (Bennett, 1988). However, within a certain temperature range of each species in both media, the oxygen consumption rate was less independent of temperature, suggesting the optimum temperature range. This temperature range of no metabolic change with increasing temperature for *U. urvillei* was 27-33°C, while that of *P. guttatum* was 27-31°C, suggesting the latter's thermal tolerance window is narrower, thus indicating that the two species have different optimal thermal ranges. That clearly showed a difference in the thermal sensitivity of the two species, which agrees with the general observation by Angilletta et al. (2009).

These results are like Frederich and Pörtner (2000), who determined the optimum temperature range for spider crab, *Maja squinado* (Herbst, 1788), to be between 8-17°C for maximum aerobic scope. Other similar studies by Teal (1959) for seven *Uca* species observed that oxygen consumption rates were relatively temperature-insensitive within a given optimum temperature range; for example, *Uca minax* (Le Conte, 1855) and *Uca pugilator* (Bosc, 1801) consumed oxygen at the same rate between 11.1-15.9°C and 13.2- 19.4°C respectively, and the temperature had little effect on their metabolism. A discontinuous metabolic response was observed at certain points in the range despite the increasing temperature. In this case, *P. guttatum* corresponds to the temperature range of 27-31°C with a Q_{10} of 1.5, while that for *U. urvillei* was at 27-33°C with a Q_{10} of 1.4. These Q_{10} values are closer to 1, which indicates thermal insensitivity. Relatively low Q_{10} values indicate wide thermal tolerance of the species (Katsanevakis et al. 2007). Within the normal environmental temperature range, the Q_{10} values for oxygen consumption rates are consistently less than or equal to 2. Q_{10} over the whole temperature range of 17-37°C for *P. guttatum* was 3.31, while for *U. urvillei* was 2.02. That agrees with studies by Katsanevakis et al. (2007), who reported that most crustaceans have a Q_{10} of between 2 and 3.

These studies have shown that, for both species, values of Q_{10} are lower in the temperature range normally experienced but increase at temperatures outside this range. This reduction in the sensitivity of metabolic rate to changing temperature has been interpreted as a mechanism by which energy could be conserved despite the increase in environmental temperature. Newell (1969) reported that the metabolic rate in response to acute temperature change varies very little over a wide portion of the physiological temperature range in intertidal animals. The adaptive significance of this is that the standard rate of respiration of intertidal invertebrates is relatively

independent of fluctuations in temperature and is not only lower but often has a low-temperature coefficient. Some organisms may temporarily decrease metabolism below these levels or even enter ametabolic states in response to unfavorable environmental conditions. However, they are not fully functional organisms under these conditions and must return to normal metabolic levels to proceed with normal processes of life (Bennett 1988). Thus, a comparatively stable oxygen consumption rate over that range of temperature fluctuation encountered daily is of significant value to these intertidal organisms. As a result, adaptation to intertidal life in these crabs entails high metabolic flexibility and efficient regulation of metabolism in a wide range of environmental temperatures. The difference in Q_{10} values for oxygen consumption rates between the two species *P. guttatum* and *U. urvillei*, may reflect differences in the range of temperatures that they normally experience in the field. Although both species occur at the same location, differences in their lifestyle in occupying different niches and behavior may result in the two species experiencing somewhat different temperature regimes (Eshky 1999).

The temperature ranges of 27-31°C (*P. guttatum)*and 27-33°C (*U. urvillei)* infer the temperature window of maximum scope for aerobic activity, which suggests the range of optimum performance supporting successful survival where availability of aerobic energy is maximal for all physiological functions in the natural environment. That is in agreement with studies by Weinstein (1998) on the ghost crab *Ocypode quadrata* (Fabricius, 1787), who reported a temperature range of 24-30°C, which did not display a significant change in resting metabolic rate suggesting the maximal rate for aerobic scope. However, further studies on the measurement of oxygen tension in crab hemolymph, heart rate, anaerobic products, and LT_{50} (Lethal Temperature at which 50% of animals experimented die) need to be done to validate optimum temperature range and establish critical temperature ranges.

The results suggest that *P. guttatum* is more sensitive to temperature variation than *U. urvillei*. That could be interpreted to mean that excessive oxygen demand causes insufficient oxygen levels in the body fluids to compensate for increased metabolic rates at high temperatures. Higher oxygen demand is limited by oxygen availability as the solubility of oxygen in warm water decreases with increasing temperature leading to stress in the crabs. The limited capacity of the circulatory and ventilatory systems to keep pace with the increased oxygen demands of basal metabolism at higher temperatures causes a reduction in aerobic scope, allowing less energy to be devoted to, for example, feeding, growth, and reproduction. Portner and Knust (2007) suggested that a reduced aerobic scope is the key physiological mechanism determining ectotherms' response to increased ocean temperature. Oxygen consumption rates decreased in the decreasing temperature from 27 to 17°C for both animals, which could be interpreted to mean that at low temperatures, even in fully aerated waters, there is limited capacity by the ventilatory and circulatory systems to match oxygen demand for basal metabolism. Also, the aerobic capacity of mitochondria may become limiting and could cause a reduction in aerobic scope where the animals could resort to anaerobic metabolism.

The rate of metabolism of both species in water and air displayed different patterns, whereby the oxygen consumption rate for *P. guttatum* was consistently lower in water compared to the rate in the air. In comparison, for *U. urvillei*, the rate in water was higher than in air media. This observation in *P. guttatum* agrees with studies by Jimenez and Bennett (2005) on the fiddler crabs *U. vocans* (Linnaeus, 1758), *U. tetragonon* (Herbst, 1790), and *U. crassipes* (White, 1847) who reported similar patterns. That further suggests that *P. guttatum* uses more energy in air than in water to meet metabolic costs and hence must spend more time in the air as compared to *U. urvillei*, as evidenced by the more than twice the oxygen consumption rates by *P. guttatum* than *U. urvillei*, which could mean a better tolerance to temperature change in the air than in water by *P. guttatum* and is less dependent on anaerobic respiration. It may not need to pay back oxygen debt rapidly. The *U. urvillei* showed that oxygen uptake in the air was lower concerning water (except at temperatures 33-35°C), suggesting that *U. urvillei* is more sensitive in the air than in water. This low oxygen uptake in the air was interpreted to be the direct consequence of the lower metabolic cost of extracting oxygen from the air than from the water. This observation on

Eshky et al. (1990) and Jimenez and Bennett (2005) reported that the difference in relative oxygen uptake in water and air by these semi-terrestrial crabs exhibiting bimodal respiration is often used to ascertain how these organisms are adapted to the aquatic or terrestrial environment. Due to low dissolved oxygen tension, crabs have adopted several methods to maintain a constant oxygen uptake rate (Eshky et al. 1990). Skov et al. (2002) noted that in their natural environmental conditions, *P. guttatum* is a free-roaming species found in shaded mangrove areas and not often in open areas and is active throughout the day and night at low tide to feed and utilize other crab burrows or crevices during high tide and only burrows when shelter such as root systems is unavailable for protection from temperature fluctuations and predators. On the hand, *U. urvillei* is a known burrower and active during daytime only at low tide, emerging from its burrow to feed, and can be found in both exposed and shaded areas in the mangroves. That implies that it can withstand wide temperature variation. Thus *P. guttatum* spends more time in the air than *U. urvillei.*

Most activities of these crabs take place in the air, and the oxygen concentration of air is 20% higher than in water (Hogarth 1999), even at saturation levels. Because *P. guttatum* spends most of its time in the air, it is less dependent on anaerobic respirationand may not need to pay back oxygen debt rapidly. Portner (2002) and Cannicci et al. (2011) reported that the leading advantage of evolving a terrestrial development is the thirty-fold abundance and 10,000 times higher diffusiveness of oxygen in the air than in water. Therefore, adopting aerial respiration could reduce the problems described for marine species due to the limiting oxygen demand in water as it warms due to

increased temperatures. The temperature tolerances of this *P. guttatum* and *U. urvillei* could reflect their distribution in the mangrove forests as the laboratory optimal temperature range of 27-33°C established falls within the normal field environmental temperature ranges of these animals observed**.** Therefore, small changes in temperature of a few degrees Celsius from the current optimal limits suggest it could influence these crabs' physiological condition, developmental rate, growth rate, and reproductive performance. If the environmental temperature rises beyond these optimal ranges, *P. guttatum*, which is more thermally sensitive than *U. urvillei*, will be more vulnerable to thermal stress. That is because they live in constant shade, are not generally adapted to the high temperatures found in warmer open habitats, and have few behavioral options available to evade rising temperatures. Consequently, any climate-induced increase in operative temperature could cause thermal performance and fitness declines.

When conditions change rapidly, resistance mechanisms are important, and oxygen limitation has been demonstrated in the present study to be the mechanism dictating survival limits which agrees with Pery et al. (2008) under adaptational limitation. Although death may not be the immediate response, sublethal effects such as the decrease in the number of offspring may contribute to the species' eventual decline or demise.

Determination of density and distribution of Perisesarma guttatum *and* Uca urvillei *crabs*

The current study recorded almost similar densities of these crabs to those recorded by Cannicci et al. (2009). The results clearly show that the *U. urvillei* and *P. guttatum* reported high densities in the *R. mucronata* zone, suggesting it is a preferred habitat. However, densities of *P. guttatum* in the *R. mucronata* and *C. tagal* zone were comparable, but very low densities were recorded in the *A. marina* zone. The results further indicated that the *P. guttatum* and *U. urvillei* were not evenly distributed within the three mangrove zones and varied widely from very low densities in the *A. marina* and *C. tagal* zones to very high densities in the *R. mucronata* zones. On the other hand, *P. guttatum*, despite having a much lower density than *U. urvillei*, was found in all three mangrove zones in shaded areas.

The very low densities of *U. urvillei* in the *A. marina* and *C. tagal* zone could be attributed to high temperatures, high salinities, high coarse sand particles, and low organic matter content. These factors could also contribute to the stunted trees, which were observed during the study as the landward *A. marina* and *C. tagal* trees are stunted and have a less dense canopy. In addition, hypersalinity has been shown to induce stunted growth of *A. marina* (Kathiresan and Bingham 2001).

Salinity was highest in the landward *A. marina* zone and lowest in the lower shores of *R. mucronata*. The high salinity in the landward *A. marina* and *C. tagal* zone could be attributed to a less dense shade canopy which is more open, leading to high water evaporation due to high-temperature rates resulting in concentration of salts, thus high soil salinity. There is also the restricted exchange between tidal and interstitial water as these areas are rarely inundated except only during high spring tides. Mangrove vegetation is more luxuriant in lower salinities (Kathiresan and Bingham 2001) which is true for *R. mucronata* compared to the other two mangrove species. That clearly indicated that *U. urvillei* is intolerant to higher salinities, which pose serious physiological problems.

There was no variation in pH between the three mangrove zones, and Middelburg et al. (1996) reported similar results. Kathiresan and Bingham (2001) observed that mangroves achieve maximum root growth at an acidic pH of 6, indicating normal mangrove soil pH. Acidic conditions can occur in mangrove sediments that are regularly flooded, and mangroves are known to affect the acid-base balance of their sediments (Middelburg et al. 1996) which could explain the similarity in pH in the three mangrove zones during this study in spring high tides. The *U. urvillei* are the least advanced toward a terrestrial existence and are mostly confined to firmer mud (Crane 1975). Similar distribution patterns were observed for this species in this study. Thus, the presence of vegetation is an important factor affecting the distribution of *U. urvillei* (Edney 1962). The results of this study demonstrated a strong relationship between the density of *U. urvillei* and environmental variables such as temperature, salinity, and soil characteristics such as organic matter, silt, and fine sand.

The high density of *U. urvillei* in the *R. mucronata* zone could be attributed to low sediment temperature and salinity compared to the other two zones, as these factors are known to affect their physiological responses and behavior, which concurs with past studies by Hartnoll et al. (2002), Ashton et al. (2003), Bosire et al. (2004) and Cannicci et al. (2009) who reported the existence of a correlation between abundance and distribution of mangrove crabs with soil salinity, temperature, and soil organic carbon. However, Ashton et al. (2003) indicated that environmental measurements should be treated with caution as they only give a general indication of conditions because they vary with the time of day and concerning tidal inundation, seasons, and weather. During the study period, sediment temperature within the mangrove forest varied from 29.01 to 36.8°C and was significantly different between the three mangrove zones. However, there was no clear pattern of temperature effect on these crabs' density over the season. *U. urvillei* require fine grain size to sort their food; thus, it strongly relates to the densities of these crabs. Therefore, substrate characteristics may be very important in influencing crab distribution (Seiple 1979). However, silt was also abundant in the *C. tagal* zone, which recorded very low densities of *U. urvillei*, suggesting that silt may not be the only variable explaining their abundance but could be occurring in combination with the other factors. That agrees with Frith and Brunenmeister (1980), who observed the absence of *U. urvillei* from non-mangrove shores around Phuket Island.

Bosire et al. (2004) observed that organic matter content varies concerning substrate type; thus, the finer substrates of silt and fine sand observed in *R. mucronata*,

and *C. tagal* zone contained more organic material than the coarser substrates of landward *A. marina* zone. The correlation of particle size with organic matter is appropriate for a deposit feeder with a sorting mechanism attuned to a certain particle grade (Cannicci et al., 2009). Thus sediment quality with high organic matter content is more relevant to *U. urvillei*. Further, the high organic matter content encourages the growth of algae and diatoms, serving as the food for these detritivore fiddler crabs. The presence of *P. guttatum* species in the *C. tagal* pure zone in almost equal densities as in the *R. mucronata* zone in the present study, clearly indicates that this zone is an equally important preferred habitat for this species, hence explaining their abundance patterns.

The stunted *C. tagal* and *A. marina* zones have less dense shade canopy. The *P. guttatum* density was significantly related to temperature, organic matter content, and fine sand. Their low densities in the *A. marina* zone could have been affected by the high temperature and the low organic matter content, as these crabs are known to occupy shady areas to avoid thermal stress. The *P. guttatum* like other *Perisesarma* spp. supplement their diet with mangrove leaves in addition to sediment with high organic matter (Skov and Hartnoll 2002), which was quite low in the *A. marina* zone to sustain *P. guttatum* populations. *P. guttatum* is an omnivore, although most of its diet through stomach content analysis (Hogarth 1999) indicates it is mostly an herbivore and its ability to collect fallen leaves is very dependent on prolonged exposure to air within the shaded mangrove areas inundated by tides most of the time with high organic matter content. The high densities of *P. guttatum* in the *C. tagal* and *R. mucronata* zone suggest it plays a big role in these mangrove zones.

An important observation from these results is that the optimum temperature range established for *P. guttatum* and *U. urvillei* crabs were 27-31ºC and 27-33ºC, respectively. The results indicate that *P. guttatum* is more sensitive to temperature variation and displayed a slightly narrower thermal tolerance window, probably to minimize maintenance or energetic costs. Thus, the null hypothesis that the two species have no preferred optimum thermal range was rejected. The alternative hypothesis accepted that the two species have a preferred optimal thermal range. Given the prevailing global warming trends as projected by the IPCC, the results suggest that thermal extremes will affect the performance of the two species differently, as indicated by the metabolic rates and the difference in thermal tolerance between the two species. As a result, *P. guttatum* will be more vulnerable to an increase in temperature, while *U. urvillei* are likely to persist at higher temperatures.

This study showed that *U. urvillei* and *P. guttatum* were not evenly distributed in the three mangrove zones. Temperature, fine sand, and organic matter strongly influenced the density and distribution of these crabs. The landward shores of *A. marina* are rarely inundated, except during spring high tides, and have higher temperatures, salinity, and low organic matter content. That could explain these two species' observed low abundance patterns in this zone.

Temperature showed significant influence, as supported by laboratory experiments. Information on thermal tolerance levels is important for conserving crabs to ensure the right community structure of mangrove trees. In addition, monitoring these animals will increase the knowledge and understanding of mangrove ecosystems' structure, dynamics, and resilience, particularly in climate change scenarios.

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