Shell selection of the hermit crab *Clibanarius africanus* (Aurivillus, 1898) (Decapoda: Diogenidae) in the Lagos lagoon: Aspects of behavioural and bio- ecology of benthos.

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Abstract. Size and shell species preferences of *Clibanarius africanus* was determined and compared for most occupied shell in the intertidal area of the Lagos lagoon, between March and August, 2008 at five study sites. A total of 663 specimens of hermit crab in gastropod shells were collected. Shell occupation of *C. africanus* was limited to gastropod shells belonging to *Pachymelania* and *Tympanotonus* spp. The gastropod shell most inhabited was *Pachymelania* spp, which accounted for 60.96% of inhabited shells, while about 39% of the shell inhabited belonged to *Tympanotonus* spp. Shell preferences were characterized by shell length, weight and aperture width. Positive and statistically significant correlations were obtained between morphometric characteristic of *C. africanus* and those of the shells inhabited, suggesting that fitness of shell to crab dimension constitutes mainly the determinant for *C. africanus* shell utilization. Spatiotemporal variations in the type of shell occupied were not significant in this study. Analysis of the abundance of *C. africanus* in the study area indicates that, a relatively higher abundance of *C. africanus* was observed in site 3, due probably to the favourable environmental conditions provided by large percentage of sand fractions in the sediment. From the data recorded in this study, it may be concluded that shell selection by hermit crabs involves individual preferences related to the shell features that best provide protection, survival and opportunity for the enhancement of behavioural attributes that are necessary for the maximization of bio-ecological relationships.

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1. Introduction

Bioecological relationship is an important phenomenon in benthic assemblages and therefore plays significant roles in the pattern of structural parameters of benthic communities such as density, biomass, richness, species diversity and spatiotemporal distribution (Tait and Dipper, 1998). Benthic taxocoenosis of the Lagos lagoon system is controlled by the populations of two gastropod mollusc taxa; *Tympanotonus* and *Pachymelania* spp (Oyenekan, 1975; Brown, 2000; Uwadiae, 2009), which provide important biotope for encrusting benthic species and cover for hermit crabs.

Hermit crabs (Anomura: Diogenidae) are crustaceans adapted to use empty gastropod shells as shelter, preventing mechanical damage to their abdomen (Barnes, 2003), and as protection against predation (Leonard *et al*., 2001). They need increasingly larger shells during their life cycle, a fact that keeps them in constant activity searching for suitable shells (Bertness, 1981). The life cycle of hermit crabs, therefore depends mostly on the availability of suitable gastropod shells (Hazlett, 1981). Shell selection behavior appears to be based on a complex and interactive factors, including shell weight, architecture, volume, height, width, colour and aperture size (Brown *et al.,* 1993; Garcia and Mantelatto 2001; Briffa and Elwood, 2006).

Often, availability of empty gastropod shells is a limiting factor to populations of many species of hermit crabs (Fotheringham, 1976; Scully, 1979) and the sizes of shells occupied by hermit crabs are usually well correlated with crab size owing to mechanisms such as mutual gain shell exchange (Hazlett, 1981, 1983). Hermit crabs seem to select among the available empty gastropod shells the most suitable one for their size and shape (Koutsoubas *et al*., 1993). Shell selection is not by chance, but based on adequacy and availability of resources (Reese 1962, Conover 1978), and is affected by both shell size and species (Conover, 1978; Lively 1988; Ohmori *et al.*, 1995; Rodrigues *et al.* 2000; Mantelatto and Dominciano, 2002; Mantelatto *et al*., 2007).

Moreover, the fitness of a particular shell may differ between hermit crab species, reflecting several selection pressures associated with different habitats which act in different ways on each crab species

(Bertness, 1981) in different areas. As hermit crabs grow they require larger shells. Since suitable intact gastropod shells are sometimes a limited resource, there is often vigorous competition among hermit crabs for shells. The availability of empty shells at any given place depends on the relative abundance of gastropods and hermit crabs, matched for size. An equally important issue is the population of organisms that prey upon gastropods and leave the shells intact (Tricarico and Gherardi, 2006).

A hermit crab with a shell that is too small cannot grow as fast as those with well-fitted shells, and is more likely to be eaten if it cannot retract completely into the shell (Angel, 2000). Most species of hermit crabs have long, spirally curved abdomens, which are soft, unlike the hard, calcified abdomens seen in related crustaceans. The vulnerable abdomen is protected from predators by shell carried by the hermit crab, into which its whole body can retract (Ingle, 1997). The tip of the hermit crab's abdomen is adapted to clasp strongly onto the columella of the gastropod shell (Chapple, 2002).

This habit of living in a second hand shell gives rise to the popular name "hermit crab", by analogy to a hermit who lives alone. Several hermit crab species use “vacancy chains” to find new shells: when a new, bigger shell becomes available, hermit crabs gather around it and form a kind of queue from largest to smallest. When the largest crab moves into the new shell, the second biggest crab moves into the newly vacated shell, thereby making its previous shell available to the third crab, and so on (Randi *et al*., 2010).

Although the utilization and selection process of gastropod shells by hermit crabs have been conducted by many authors (Bertness, 1980, 1981a, b, 1982; Blackstone, 1985, 1989; Gherardi and Vannini, 1989; Hazlett, 1989, 1990, 1992; Gherardi, 1991; Elwood *et al*. 1979; Bertness, 1980; Hazlett, 1992, 1996; Ohmori *et al*.1995; Garcia and Mantelatto, 2001; Meireles and Mantelatto, 2005) around the world, there is scarcity of studies on the shell preferences and utilization of hermit crabs in Nigerian aquatic environment. *Clibanarius africanus* (Aurivillus, 1898) is a species of hermit crab in the family Diogenidae common on the shores of the Lagos lagoon. Despite its abundance, wide distribution and easy accessibility to its habitat, ecological information on the organism is still scarce. Here, the shell selection and species preferences of *C. africanus* in a stretch of intertidal area in the western part of the Lagos lagoon are evaluated.

2. Description of study area

Lagos lagoon is located in the West African Coast of Nigeria. It lies between longitude 3° 54" and 4 ° 13"E and latitude 6 ° 25" and 6 ° 35" N. This Lagoon is more than 50 km long and between 3 to 13m in width, it is separated from the Atlantic Ocean by a long sand spit of 2 to 5km wide (Brown, 1999). The lagoon is characterised by fresh and brackish water conditions occasioned by the heavy input of rainfall run-offs and river discharges during the rainy season, and the influences of tidal incursion and increased surface water evaporation during the dry seasons. The Lagoon is fed by a number of rivers and creeks including Ogun, Majidun, Osun rivers and Agboyi creek. These water bodies altogether have a drainage area of 103, 637 km^2 (Oyewo, 1998).

The study sites (Figure 1) used for this study were selected along the inter tidal area of the lagoon close to the University of Lagos. This part of the lagoon has been under the stress of human activities because of its accessibility to man. Major stressors include garbage overload arising from indiscriminate dumping of litter during major events such as picnics and students’ activities around the lagoon. Modification of the shoreline arising from the construction of brick wall to serve as shoreline protection is evident in the study area. Another prominent feature of the study area is the presence of burrows of crabs scattered all over the shoreline which are most visible at low tides. This area was chosen for this study because of the high biological activities that can be observed in this area. Table 1 presents some physical characteristics of the study sites.

3. Materials and methods

Collection and analysis of samples

Specimens of *C. africanus* in gastropod shells were collected using a van Veen grab at five locations along the lagoon. Three grab hauls were taken from each site and the collected materials washed through a 0.5mm mesh sieve. The residue in the sieve for each station was preserved in 10% formalin solution and kept in labelled plastic containers for further laboratory analysis. Preserved benthic samples were washed with tap water to remove the preservative and any remaining sediment and specimens of *C. africanus* were sorted out, counted and recorded for all the sampling months and study sites. Specimens of *C. africanus* and gastropod species were identified based on the works of Edmund (1978), Olaniyan (1978), Yoloye (1994), and Uwadiae (2009). Specimens of *C. africanus* in gastropod shell and after removal from the shell were weighed with an electronic scale of 0.001g sensitivity. Prior to weighing, the animals were drained on a fine sieve, air dried for 5 minutes on absorbent paper and exposed to air until liquid is no longer visible. The lengths of gastropod shell, width of aperture and length of *C. africanus* were measured in centimeter using a graduated meter rule. Collection of sediment samples and grain size analysis followed the methods described in Uwadiae (2009).

Statistical analysis

To determine morphometric relationships and correlations between characteristics of hermit crabs and their preferred shells, regression analyses were computed. All statistical analyses were performed using SPSS 10 and Microsoft Excel 2003 for Windows.

4. Results

Shell type preference of C. africanus

The spatial and temporal variations in the frequency of shell type selected by *C. africanus* are presented in figure 2. A total of 663 specimens of hermit crab in gastropod shells were collected. Shell occupation of *C. africanus* was limited to gastropod shells belonging to *Pachymelania* and *Tympanotonus* spp. The gastropod shell most inhabited was *Pachymelania* spp, which accounted for 60.96% of inhabited shells, while about 39% of the shell inhabited belonged to *Tympanotonus* spp. Occurrence of *C. africanus* in the shells of *Pachymelania* spp shell was highest (43) in the month of March while its lowest occurrence (30) in the same shell type was observed in the months of August and April. The number of shells of *Tympanotonus* spp inhabited by *C. africanus* was highest (34) in the month of April and least number (9) of shells occupied in June. There were slight variations (41-64) in the total monthly number of individuals of *C. africanus* recorded during the sampling months. The month of April recorded the highest number (64) of *C. africanus* in monthly samples, while the least number of individuals of *C. africanus* was observed in June. Sixty - one and forty - eight individuals were recorded in the months of July and August respectively, while 59 specimens of *C. africanus* were observed for the months of March and May respectively.

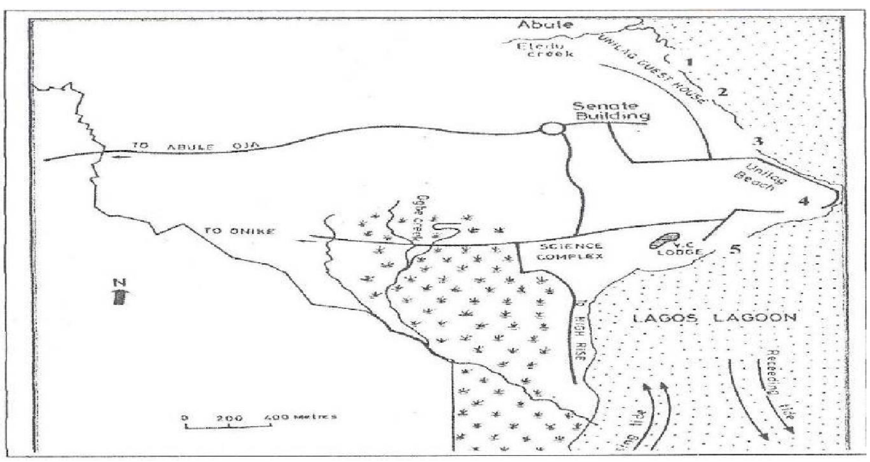


Figure 1: Map showing sampling sites (1-5)

Table 1: Some physical characteristics of the study sites.

Station	Longitude	Latitude	Water colour	Sediment colour
1	003º24´01E	06º31´42"	Brown	Brown
2	003º24´ 02E	06º31´13"	Brown	Brown
3	003º24´06E	06º31´07"	Brown	Brown
4	003º24´08E	06º31´04"	Brown	Brown
5	003º24´ 10E	06º31´00"	Gray	Black

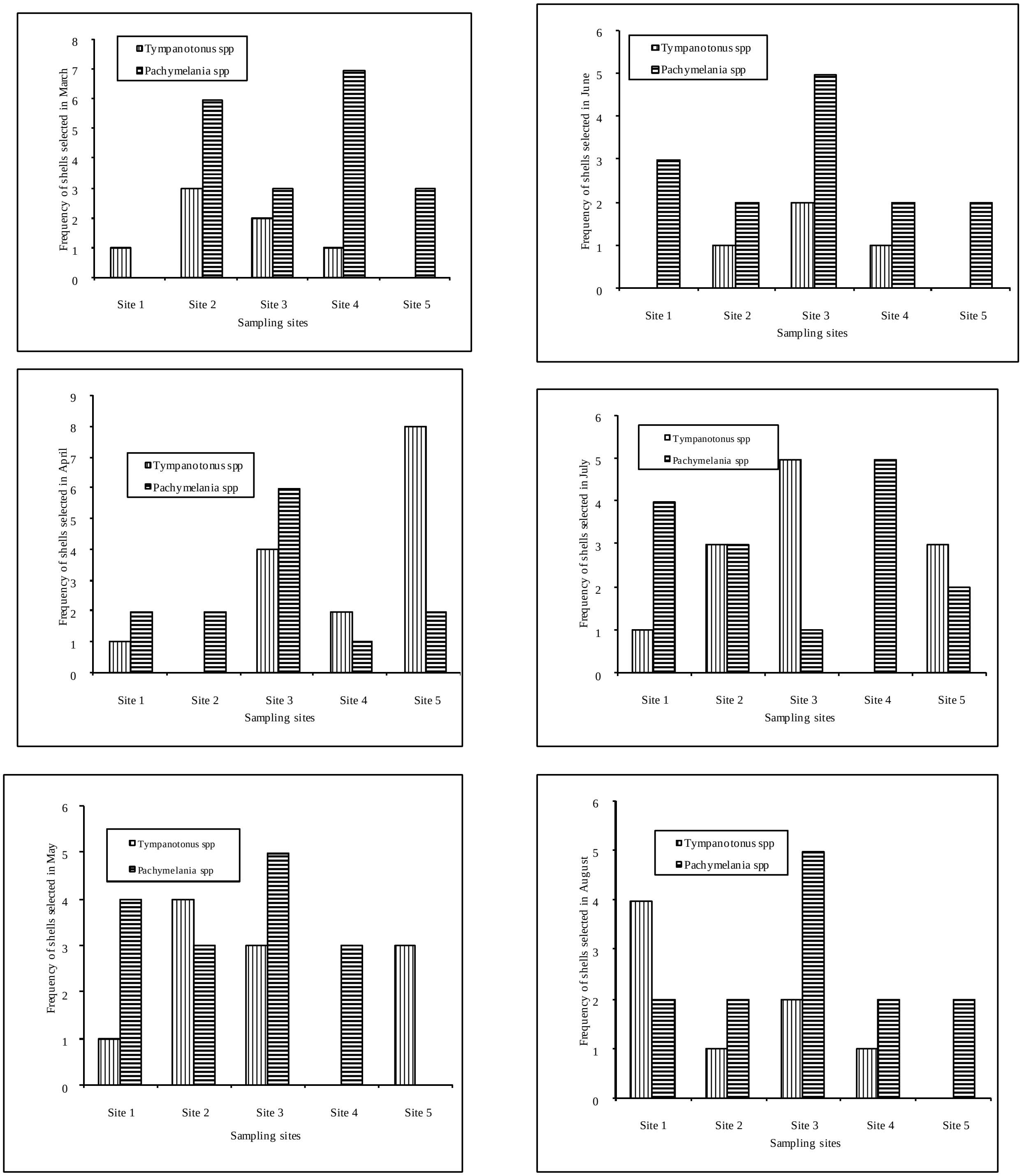


Fig. 2. Spatial and temporal variations in the frequency of shell type selected by *C. africanus*.

Shell size preference

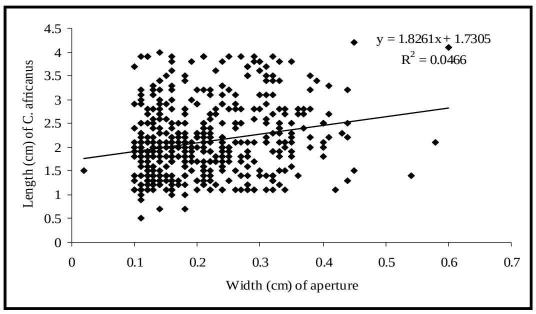
Specimens of *C. africanus* collected during this study varied between 0.5 and 4.3 cm in length while the length of shell occupied ranged from 1.8 to 5.5 cm. These figures show an overlap indicating that the lengths of *C. africanus* observed are closely related to the length of gastropod shell inhabited. This relationship is clearly depicted in figure 3a where a positive correlation between lengths of shell and that of *C. africanus* is shown in a regression model. Statistically, the relationship between the length of *C. africanus* and the length of shell it occupied was found to be significant (F= 145.58, df =1, *P* <0.001).

The length of *C. africanus* was also found to be related to the width of the aperture of the mollusc shell it occupied. Regression analysis indicates that length of *C. africanus* correlated positively (Fig. 3b) with width of shell aperture, and this relationship was observed to be statistically significant (F = 38.58, df = 1, P<0.05).

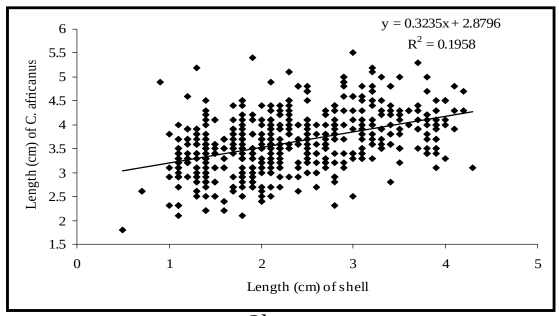
This study also revealed that another factor of importance in the selection of shell by *C. africanus* is the weight of the gastropod shell. The study observed a positive correlation (Fig. 3c) between the weight of *C. africanus* and the weight of gastropod shell selected. This relationship was also found to be of statistical significance (F = 27.540, df = 1, P<0.005).

Sediment characteristics and abundance of C. africanus.

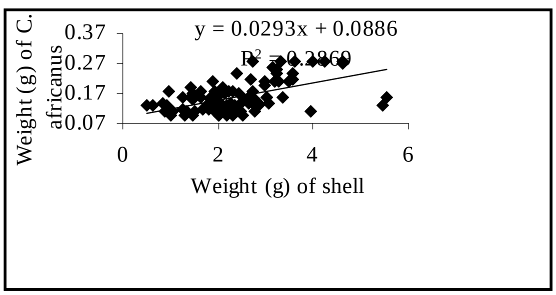
In the study area, it was observed that sand and mud intermixed in varying proportions (Figure 4). The percentage of sand ranged from 45.7 to 99.4% while mud varied between 0.5 and 63.9%. In station 1, sand ranged between 45.7 and 87.4%, and mud between 5.7 and 63.9%. Lowest values observed for sand in sites 2 to– 5 were 58.8%, 66.2%, 63.7% and 65.2% respectively, while those of mud for the same stations were 4.3%, 0.5%, 3%, and 1.5% respectively.



3a



3b



3c

Figure 3a-c. Relationships between morphometric characteristic of *C. africanus* and those of the shells inhabited.

Variation in the percentage of sand fractions in the sediment of the study area was a major physical parameter that affected the abundance of *C. africanus* recorded in the study sites. Figure 5 depicts a positive correlation between abundance of the animal and percentage sand in sediment. The overall results indicate that, although there were higher percentage sand fractions than mud in sediment of all the study sites, values for site 3 were relatively higher. Site 3 also recorded the highest number of individuals of *C. africanus*. The lowest mud content was recorded in site 1.

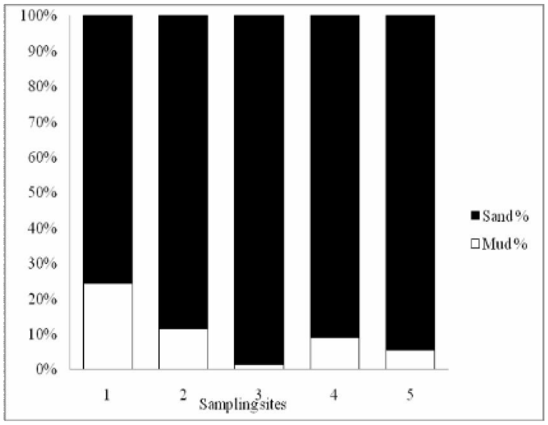


Figure 4 . Grain size composition of the study sites.

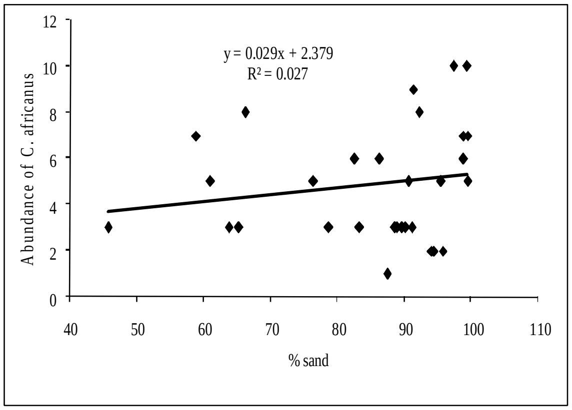


Figure 5. Relationship between percentage of sand in sediment and abundance of *C. africanus*

5. Discussion

The most striking feature of the result obtained in this study is the positive and significant relationships between *C. africanus* variables and morphometric qualities of the gastropod shell inhabited. This is a vivid corroboration with the very popular theory among crustacean biologists that shell selection in hermit crabs is based on suitability for specific purposes (Hazlett, 1981, 1983, Koutsoubas *et al.*, 1993, Ates *et al.*, 2007, Mantelatto *et al.*, 2007, Nakin *et al.*, 2007). Suitability for the intended purposes is a major factor underlying the choice of close associations that can be observed among different species in benthic assemblages (Nybakken, 1988), and form the basis for most bioecological relationships.

This study reveals that shell dimension constitutes mainly the determinant for *C. africanus* shell selection and utilization. In hermit crabs a well-fitted shell is essential for maintaining low evaporation rates and carrying ample water (Angel, 2000). An appropriately sized shell in good condition allows for effective movement and provides competitive edge than ill – fitted shells. Hermit crabs with broken, ill-fitted shells are restricted to the coast and appear to be in relatively poor conditions (Angel, 2000; Koutsoubas *et al.*, 1993, Ates *et al.*, 2007).

Bertness (1980), reported that hermit crabs do not necessarily live in shells they prefer, the availability of different shell types and contact with competitors for empty shells influences shell occupation. This study revealed that shells of *Tympanotonus* spp provided a low specimen adequacy to *C. africanus*, this may be related to the relatively higher abundance and availbilty of *Pachymelania* spp in the study area (Oyenekan, 1975, 1979, 1988, Brown, 2000; Uwadiae, 2009), which provided larger number of shells for *C. africanus*. Although, Yoshino *et al.* (1999), posited that there is a trade-off between shell size and species preference and that less preferred shell species are actively chosen when the more preferred shell species the crabs encounter frequently in the field are of a less suitable size, in this study, considering the great availability (in size and number) of shells of *Pachymelania* spp in the study area , we may infer that the assertion proposed by Yoshino *et al.* (1999) may not be applied because availability of shell was considered as the overriding factor determining shell usage in this particular study. Shell morphology and morphometric qualities of *Pachymelania* and *Tympanotonus* spp would not have been significant in preferential selection of shell by *C. africanus* since the two taxa bear similar qualities. Previous studies including Völker (1967) found that shells generally used by hermit crabs were found in the same frequency as the gastropod fauna, revealing a close relationship between shell use and availability of the resources.

The availability of shells in the environment plays a fundamental role in the population dynamics and distributional pattern of hermit crabs (Meireles *et al.* 2003), although we did not evaluate the shell availability to the hermit crab community in this present study. The availability of empty shells at any given place depends on the relative abundance of gastropods and hermit crabs, matched for size. An equally important issue is the population of organisms that prey upon gastropods and leave the shells intact (Tricarico and Gherardi, 2006).

Several hypotheses have been put forward to explain the discrepancy in gastropod shell occupancy in hermit crabs (Bertness, 1980; 1981a, b, 1982): 1) Gastropod life cycle – availability of different shell types (species) in nature is determined by the relative abundance of different live gastropods and their mortality rates (Meireles *et al.*, 2003); 2) Environmental conditions –

differences in abiotic characteristics of the area in terms of water dynamics (wave activity, intensity of currents, food supply) are determinant of installation of some invertebrate species (Fransozo and Mantelatto, 1998); 3) Predation pressure – several combined actions from natural and artificial predators can act in different ways to reduce the diversity of gastropod shells in the region.

According to the energy savings hypothesis, proposed by Osorno *et al.* (1998), hermit crabs may prefer shells of gastropods because it is light thus reducing the cost of bearing and carrying a shell. Large sized crabs might have modified their shell preference and occupied other species when large shells are no longer available. The energy saved by carrying a light shell may be used to increase growth rate and egg production of intertidal hermit crabs, which ultimately improve fitness (Guillén and Osorno, 1993; Bertness, 1981). Also, crabs occupying shells large enough that, they can withdraw completely and block the shell aperture with the chelipeds are much harder to extract from their shells than crabs which are too large to withdraw completely, and for this reason they would presumably be less vulnerable to predators (Randi, *et al*., 2010).

Shells that are modified by previous hermit crab use are also occupied. The new shells in some cases are small to accommodate big crabs, so relatively bigger crabs may inhabit shell whose internal volume have been modified by the occupation of another hermit crab (Wolcott, 1988). This may account for the reason why the majority of the shells occupied by *C. africanus* in this study seem to have their columella and callosity altered (Ball, 1972). A similar observation has been made by Kinosita and Okajima (1968) on shells of *Nerita striata* occupied by *Coenobita rugosus* from Japan. Abrams (1978) suggested that hermit crabs show "shell facilitation"; that is, larger populations of crab generate, through wear, larger numbers of shells suitable for adult crabs.

Differences in gastropod shells utilization can occur as a function of the area of occurrence of the hermit crabs (Garcia and Mantelatto, 2000). *Clibanarius africanus* are frequently found in areas, such as sandy beaches, where shells are extremely scarce (Ball, 1972). This fact probably indicates the resource competition/partition occurring mainly to guarantee a good adequacy of individual size to shells available in the area. Differences in shell utilization between sexes observed by Imazu and Asakura (1994) and Bertini and Fransozo (1999) were not investigated in this present study. The observed shell occupation were due to differences in body size of *C. africanus*.

Clibanarius africanus was found in places with small percentage of mud, and high concentrations of sand. The nature of the substratum influences the frequency and ability of the hermit crabs in burying themselves, in a way, that they rarely choose another substrate that is not sand (Oyenekan and Adediran, 1987). This fact corroborates our observations in the present study, *C. africanus*, a species which has the habit to bury itself (Mantelatto ***et al.*** 2004), was registered principally in locations with the highest percentage of sand.

Besides the interactions with the abiotic factors, the animals share the environment with other organisms from the benthic fauna. The individuals of a community are in various ways interdependent, and some organisms thrive only in the presence of particular associated fauna. These inter-relations can interfere in the distribution of the organism (Pardo *et al*., 2007). *Clibanarius africanus* is always found in close proximity with *Pachymelania* and *Tympanotonus* spp since they depend on the shells of these organisms for protection. Several animals are sometimes found on the back of these shells in the study area, the most common are the barnacles *Balanus tintinabulum* (Olaniyan, 1978). Tait and Dipper (1998) reported that worms sometimes bore shells inhabited by hermit crabs and also may live alongside hermit crabs in their shells. These worms feed on fragments of food dropped by the crab. These interactions have played significant roles in the structural features of the population of *C. africanus* in this study.

The populations of *C. africanus* like other benthic organisms are threatened by the intensive unregulated human activities in the Lagos lagoon. This suggests that the data gathered may be reflecting both responses to biotic and abiotic environmental features. Further studies are encouraged to analyse the consistency of the patterns depicted here and explore the causal mechanisms.

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