

# MANGROVE ECOSYSTEM STUDIES IN LATIN AMERICA AND AFRICA

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# Tree-climbing decapods of Kenyan mangroves

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The investigation of arboreal habits in 16 species of Kenyan mangrove decapods indicates that a total of seven are true arboreal species, three of which can be defined as exclusively arboreal (*Sesarma leptosoma*, *S. brocki*, *S. elongatum*) while the remaining four are mainly arboreal (*Metopograpsus oceanicus*, *M. thukuhar*, *Petrolisthes lamareckii* and *Merguia oligodon*). The other species climbed trees only occasionally. Among the true arboreal species, only *S. leptosoma* show the ability to climb the entire length of the tree and feed on its canopy. All the true arboreal species are iso-phasic, while occasional tree climbers are considered iso-zonal. Within the Grapsidae, the tree-dwelling habit is well correlated with morphological adaptations such as the flat and square shape of the carapace, the relative shortening of the dactylus on the walking legs and the lengthening of the propodus.

## Introduction

The various tree-climbing habits of mangrove crabs have been well documented in the West Indies by von Hagen (1977). For the whole Indo-Pacific area there are only scattered quotations, many of which are summarized by von Hagen (1977), Jones (1984) and Hartnoll (1988). Gherardi and Vannini (1992, 1993) record that the hermit crab, *Clibanarius laevimanus*, periodically climbs the mangrove roots and rests on them during the entire low water period, forming dense clusters of up to 5,000 individuals. A description of the vertical migrations between the roots and the canopy by *Sesarma leptosoma* in Kenya is given by Vannini and Ruwa (1994). Apart from these observations, the only previous works on the ecology of East African crabs of Kenya and Tanzania, and in which arboreal behavior of some species has been quoted, are those by Hartnoll (1975) and Ruwa (1990).

In these papers no distinction is made between species that are strictly dependent on trees and those only occasionally found on them. Another aspect which is not clear is the actual level at which crabs may occur on the trees. Since in many cases this can depend strictly on the tidal level, a vertical dynamic zonation of crabs is more useful than a static one; though the former has rarely been attempted. The object of this chapter is to provide quantitative details of the arboreal habits of decapods found on mangrove trees in Kenya to better understand their distribution within the mangrove and their use of its resources.

## Material and methods

The study areas include Mida Creek, near Malindi, Kenya (Fig. 1), a rather large (30 km<sup>2</sup>), round creek with a relatively small entrance and no apparent freshwater inflow; Shimoni, a coastal, fringing mangrove swamp; and Gazi, a funnel-shaped mangrove swamp with two small seasonal streams flowing into the creek.

Dabaso, the site where most of the observations were made is located in Mida Creek. This area is rich in *Rhizophora mucronata* and is more or less mixed with some *Ceriops tagal*. A narrow belt of *Avicennia marina* borders the landward side of the *Rhizophora-Ceriops* zone, while *Rhizophora* and a few *Sonneratia alba* are present on the seaward side of this zone. Observations were made in October 1990, November 1991, July 1992 and August 1993. Crabs were recorded using 10 x 25 binoculars and a powerful waterproof electric torch. Some snorkelling was also required. A rough quantitative estimate of crab abundance and

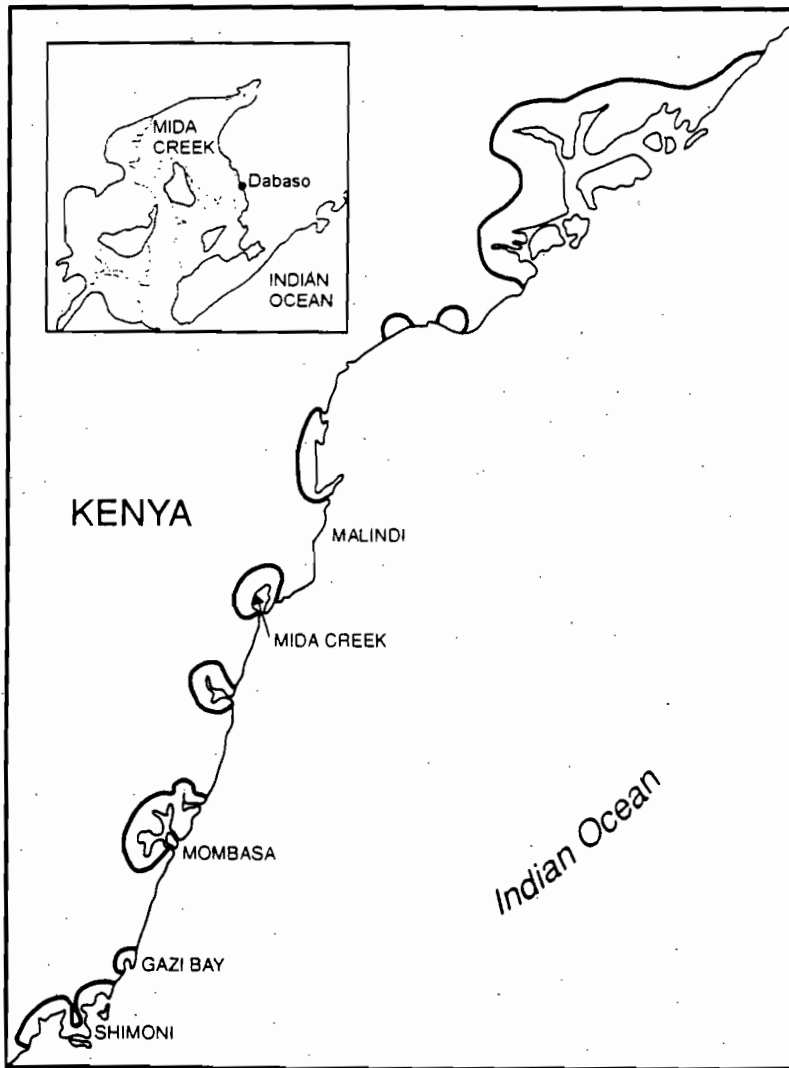


Figure 1. Location of the study sites along the Kenyan coast.

vertical zonation was attempted by counting the animals visible on the roots and trunks bordering a transect (80 m x 2 m), oriented land-seawards. A total of 18 daily and 20 nocturnal inspections were carried out, on different days, during different tidal phases. Zonation data have been analyzed with less accuracy since there is strong evidence that the visibility of the diverse species is quite different and may even vary for the same species under different light conditions and tidal levels. Furthermore, recording activities were unbalanced (the greatest effort was during the nocturnal high waters).

Morphometric measures were obtained for each species by averaging the measurements of three adult males and three adult females (for legs, both left and right elements were measured and averaged). Class distributions of crab vertical zonation were compared using the G-test with Williams correction (Sokal and Rohlf, 1981). For each of the mangrove decapods commonly found in Mida creek, a Tree-dwelling Adaptation Score (TAS; values between 1 to 7), was assigned as an indication of their degree of tree-adaptation, on a scale ranging from 1 (no dependence) to 7 (absolute dependence). We have not followed the system proposed by von Hagen (1977) because we prefer to compare littoral decapods alone, which periodically face tidal excursions, without taking into account inland tree decapods (i.e. as *Metapaulias*, *Birgus latro*), living on trees other than mangroves and not subject to tidal inundation. As a sort of control, three species common in Mida Creek, which have never been seen climbing trees, have also been included in the assessment of tree adaptation and have been given a TAS value of 1.

The taxonomic problems within the subfamily Sesarminae are still unresolved and the genus *Sesarma* may only refer to New World species. Although *Sesarma elongatum* and *S. brocki*, have sometimes been attributed to the genus *Selatium*, the six Sesarminae species recorded in this study have been attributed to genus *Sesarma* until an updated taxonomic revision of the group can provide a better solution. All of the specimens collected and studied are located in the Nairobi National Museum and the Museo Zoologico dell'Università di Firenze, "La Specola". The abbreviations used in the text and figures are as follows: EHWST, extreme high water of spring tide; HW, high water; HWNT, high water of neap tide; IP, isophasic; IZ, isozonal; LW, low water; ns, not significant; NT, neap tide; ST, spring tide; TAS, tree-dwelling adaptation score

## Results and discussion

The decapod crabs observed during the study have been divided into two groups. Group A includes those species which are typical of the semi-exposed and exposed hard substrata found in mangroves and on rocky cliffs, such as those in Kenya, Somalia and Tanzania (Hartnoll, 1975; Vannini and Valmori, 1981; Vannini, 1987; Ruwa 1990); group B comprising those species which are usually called "mangrove crabs" and which are more or less constantly associated with mangrove swamps (Table 1).

Table 1. List of Kenyan decapods observed on mangrove trees.

GROUP A: Species typical of rocky habitats, occasionally found on mangrove trees.	
Grapsidae - Grapsinae	
(1) <i>Grapsus tenuicrustatus</i> (Herbst)	*
(2) <i>Grapsus fourmanoiri</i> Crosnier	(1,2) *
(3) <i>Geograpsus stormi</i> De Man	(2) *
Xanthoidea - Menippidae	
(4) <i>Lydia annulipes</i> (H. M.-Edw.)	*
(5) <i>Eriphia sebana</i> (Shaw and Nodder)	(2) *
(6) <i>Eriphia smithi</i> McLeay	(2)
GROUP B: Species typical of sheltered shores, occasionally or permanently found on mangrove trees	
Grapsidae - Grapsinae	
(1) <i>Metopograpsus thukuhar</i> (Owen)	(1,3,4,5) *
(2) <i>Metopograpsus oceanicus</i> (Jacquinot)	(1) *
(3) <i>Metopograpsus messor</i> (Forskål)	(1,2,4)
Grapsidae - Sesarminae	
(4) <i>Sesarma brocki</i> (De Man)	(1,6) *
(5) <i>Sesarma elongatum</i> (A. M.-Edw.)	(1,2) *
(6) <i>Sesarma meinerti</i> De Man	(2,7) *
(7) <i>Sesarma guttatum</i> A. M.-Edw.	(2,3) *
(8) <i>Sesarma leptosoma</i> (Hilgendorf)	(6) *
(9) <i>Sesarma impressum</i> (H. M.-Edw.)	(2)
Xanthoidea - Pilumnidae	
(10) <i>Eurycarcinus natalensis</i> (Krauss)	*
Xanthoidea - Oziidae	
(11) <i>Epixanthus dentatus</i> White	*
(12) <i>Ozius guttatus</i> H. M.-Edw.	*
Anomura - Porcellanidae	
(13) <i>Petrolisthes lamarckii</i> (Leach)	*
Anomura - Diogenidae	
(14) <i>Clibanarius longitarsus</i> (De Haan)	(8) *
(15) <i>Clibanarius laevimanus</i> Buitendijk	(9) *
Natantia - Hippolithidae	
(16) <i>Merguia oligodon</i> (De Man)	(10) *

(1) Hartnoll 1975; (2) Ruwa 1990; (3) Lewinsohn 1979; (4) Holthuis 1977; (5) Vannini and Valmori 1981; (6) Davie 1985; (7) Verwey 1930; (8) Macnae 1968; (9) Gherardi *et al.* 1991; (10) Vannini and Oluoch 1994; \* present study.

*Metopograpsus messor* and *Sesarma impressum* are the only two tree-climbing crabs which have been recorded outside Mida Creek, along the Kenyan coast (Ruwa, 1990). *Ozius guttatus* is quite common in Kenyan mangrove swamps but it is also very common on semi-exposed rocky shores, at the base of cliffs (Vannini, pers. obs.) and it could be included in group A as well. Typically, crabs of group A were found in mangrove areas where no rocky habitats existed in the surrounding area. Sometimes species of group A (especially *Grapsus fourmanoiri*) and group B (especially *Sesarma elongatum* and *Metopograpsus oceanicus*) were seen on the same tree, as was the case at Shimoni, where the coast is straight, the site is protected from the direct influence of ocean waves and wind by the nearby island of Wasini. The mangrove swamp is a coastal belt of *Sonneratia alba* that grows in front of a 2-4 m limestone cliff. In the remaining part of this paper little attention will be given to crabs of group A.

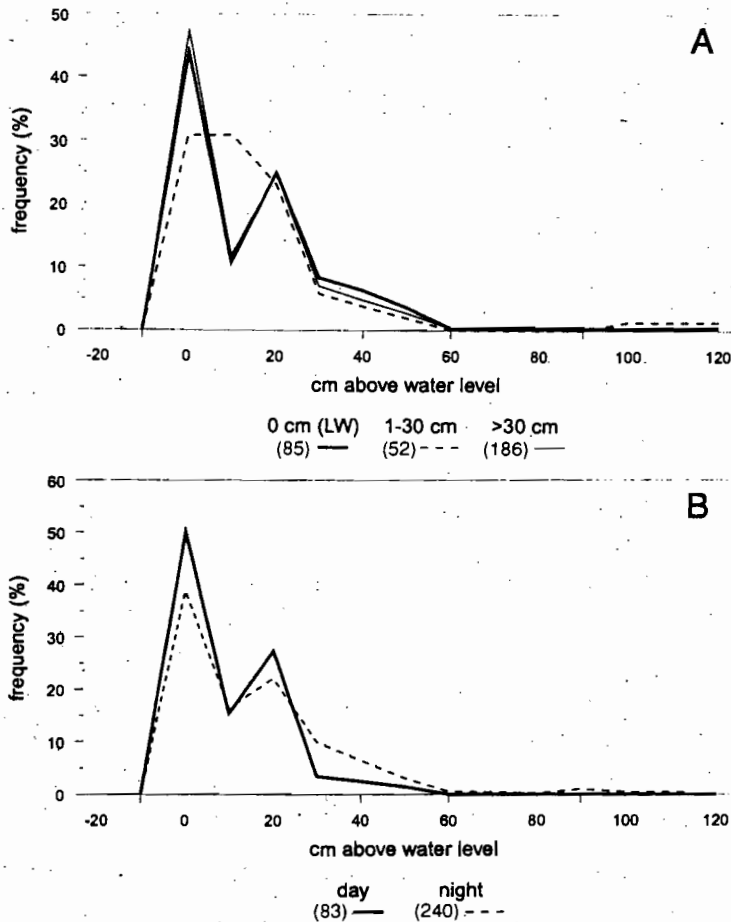


Figure 2. Vertical zonation on mangrove roots and trunks of *Metopograpsus thukuhar* showing the frequency of occurrence of crabs at A) different tidal levels and B) different times of the day. The total number of animals recorded is presented in parentheses. For the x-axis, the 0 value corresponds to the distance of the observed animals from the actual water level and not from the muddy floor. The 0 level obviously corresponds to the mud surface only at LW.

#### Vertical zonation

Most of the time *Metopograpsus* spp. graze on the trunk surface. At HW they often gather on the roots near the water level, ready to collect any sort of edible matter floating on the water surface. During the day, at LWs, *M. thukuhar* and *M. oceanicus* are commonly seen resting on the roots near the floor, then suddenly running across the mud to capture small prey (usually a fiddler crab of the genus *Uca*) and then running back onto the root. Regardless of the water level, *M. thukuhar* was always found 0-60 cm above the water

(Fig. 2). At LW (when the water level equals zero) it occurred at a mean level of 15.0 cm, rising to 16.2 cm when the water level was greater than zero, but less than 30 cm; and descending to 12.9 cm when the water level was greater than 30 cm ( G-test, 6.72, df= 6; P= ns). At night, the crab was found at a slightly higher mean level on the trunk than during daytime (Fig. 2B; G-test, 11.67, df= 3; P<0.01). *M. thukuhar* was never observed under water and only moved into the water when threatened.

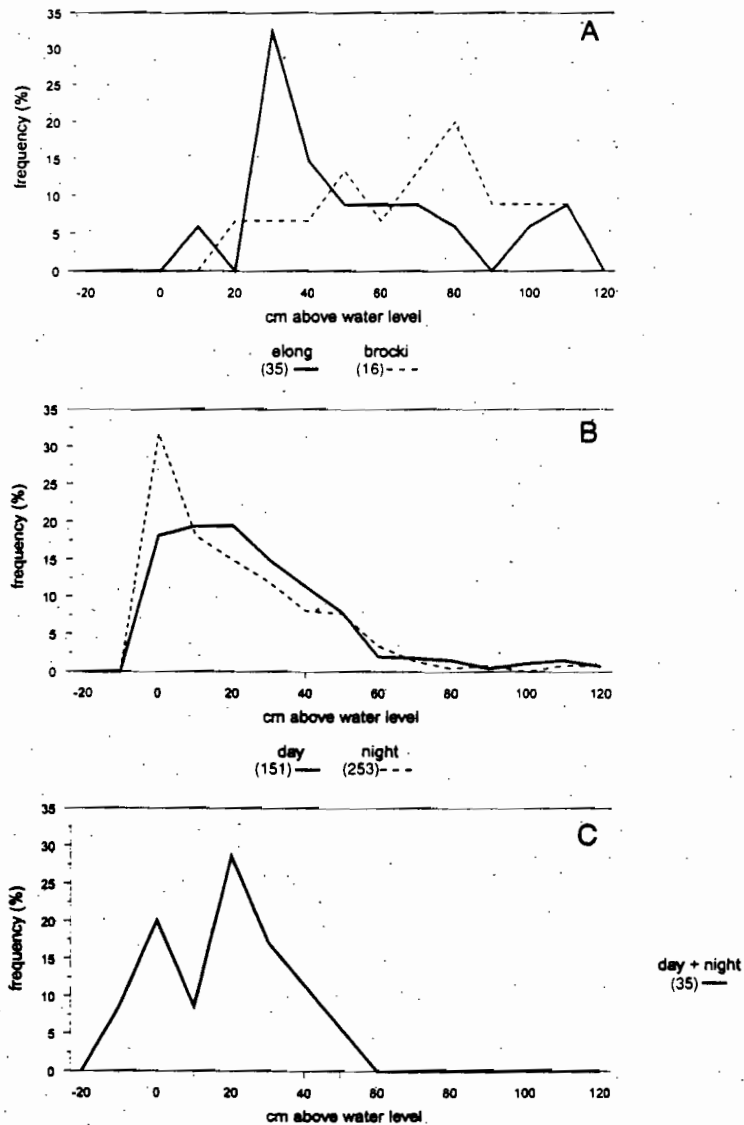


Figure 3. Vertical zonation on mangrove roots and trunks of A) *Sesarma elongatum* and *S. brocki* Baie de Málaga) *S. lempdosoma*, during its non-migratory phase and C) *Epixanthus dentatus*.

In Mida Creek *M. thukuhar* and *M. oceanicus* were collected from living trees and from under dead trunks with no apparent segregation. The former species was much more common than the latter (ratio of 132:1). *M. messor* was not recorded from this site.

In Gazi, along the main channel, which has a consistent water current for most of the time, *M. oceanicus* was very common on trees while *M. messor* was very common, together with *Sesarma guttatum* on the floor (especially among the dead roots of *Ceriops tagal*). While at the Shimoni site, a coastal mangrove swamp, only *M. oceanicus* was recorded and seemed to prefer inhabiting *Sonneratia*.

In Mida Creek, fifteen *Sesarma brocki* were seen on *Avicennia marina* (colonizing the landward mangrove belt) and only one on a seaward *Rhizophora mucronata*. In contrast, *S. elongatum* was concentrated on the seaward *Rhizophora* and *Sonneratia* belt, where all thirty-four specimens were observed. *S. elongatum* was never recorded on *Avicennia*. Both species were usually found at levels higher than 50 cm (Fig. 3), and their zonation patterns did not show a significant difference (average level 52.3 (*brocki*) and 68.7 cm (*elongatum*); G-test, 5.11, df= 2; P= ns).

Neither species was observed under the water level. At HW, when pursued, *S. elongatum* may drop down the trunk and, actively beating its legs (noticeably flattened), swim on the water surface to reach another trunk. During daily LWs, *S. elongatum* has been observed to crawl on the floor, moving from one tree to the nearest one. Scattered records of this species in pools (Fourmanoir, 1954) may refer to this occasional behavior. *S. brocki* were not recorded beneath stones as Hartnoll (1975) has occasionally found them in Tanzania. While, under the stones near the *Avicennia* inhabited by *S. brocki*, many *S. longipes* and *S. villosum* were found.

Many *Sesarma meinerti*, which is basically not a tree crab, have often been seen climbing the base of *Avicennia* trees, high enough to keep themselves out of the water during EHWST. However, many of these crabs (perhaps the majority) were observed crawling on the bottom, under 10-20 cm of sea water. Tree climbing, for this species, probably only represents a mechanism for avoiding very rare long-lasting immersions. They are terrestrial crabs, spending the great majority of their time out of the water, and are well-adapted to air breathing. Part of their usual zone (the landward fringe of the *Avicennia* belt), where they partially overlap with *Cardisoma carnifex* (Gecarcinidae) (Hartnoll 1975; Micheli and *et al.* 1991), is in fact fully submerged only a few times a year (aequinoctial spring tides).

*Sesarma guttatum* is the most common Sesarminae species on the floor between the *Avicennia* belt, inhabited by *S. meinerti*, and the seaward *Rhizophora* edge, where both mangroves and Sesarminae disappear. The floor, especially under *Ceriops* trees, is all riddled with an anastomosing system of tunnels (Jones 1984), probably dug by *S. guttatum* itself and *S. smithi*. The holes are inhabited by other species too (*Eurycarcinus natalensis* and *Thalamita crenata*) but it is not clear if they participate in the digging activity or simply occasionally exploit the available holes. *Metopograpsus* species surely do not dig but exploit these holes when they wander too far from their tree while escaping from danger. Fiddler crabs, *Uca chlorophthalmus* and *U. urvillei*, quite commonly mix with *S. guttatum* in this zone, but if pursued, only retreat into their own holes.

From Figure 4A it is evident that most of the *S. guttatum* disappear during HW (0.5 crab/inspection at HW, instead of 10.7 at LW). Among the crabs counted at LW, at 0 level, were all the *S. guttatum* visible on the mud surface, within 10 cm from the nearest root. *S. guttatum* retreats into its hole before HW and frequent snorkeling surveys failed to reveal any individuals visible on the mud surface during the whole HW. Like *S. meinerti*, this species is basically a ground dweller and may occasionally try to avoid long-lasting submersion. Instead of being submerged only at EHWST, *S. guttatum* is submerged at most HWs; however a small number are seen every HW since instead of retreating into their holes, they remain out of the water, and move away from it, by climbing *Ceriops* and *Rhizophora* trees.

During HW, less crabs are seen but they are at higher levels (average levels 1.5, 25.8 and 70.0 cm for the three water levels; G-test, 66.74, df= 6; P<0.001). A difference seems to exist between day and night, in the vertical zonation of these crabs as they reach relatively higher levels during day time (Fig. 4B; 27.3 and 16.3 cm, respectively; G-test, 22.95, df= 3; P<0.001).

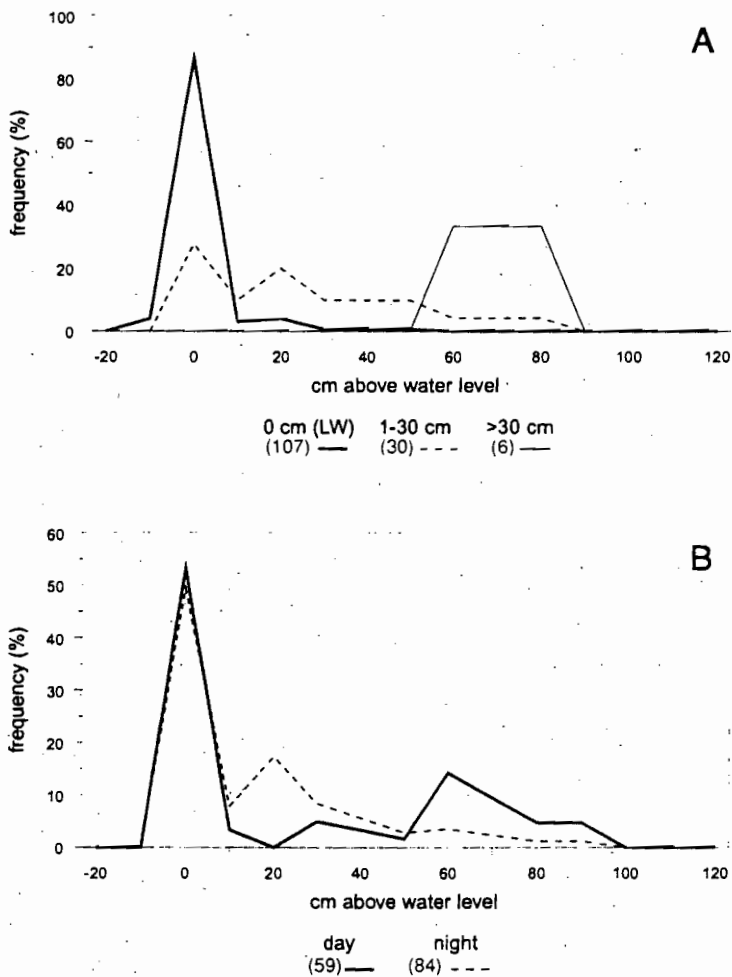


Figure 4. Vertical zonation on mangrove roots and trunks of *Sesarma guttatum* showing the frequency of occurrence of crabs at A) different tidal levels and B) different times of the day.

*Sesarma leptosoma* was recorded climbing the entire tree to feed on fresh mangrove leaves (Vannini and Ruwa, 1994). Until now, among all the mangrove crabs, only the West-Atlantic Sesarminae, *Aratus pisoni*, was known to feed on fresh leaves directly from the tree branches (Hartnoll, 1965; Warner, 1967; Jones, 1984). On the trees, the zonation of this crab (Fig. 3B), when not migrating (i.e. for about 16-17 hrs a day), overlapped with that of *M. thukuhar* (Fig. 2A). At low tide *S. leptosoma* never ventured onto the floor and rarely came in contact with the mud. A difference in zonation between day and night was also observed (Fig. 2B; 26.4 and 21.0 cm, respectively; G-test, 9.95,  $df=3$ ;  $P<0.02$ ). As for *M. thukuhar*, *S. leptosoma* was never recorded submerged by the water and always kept itself within a 50 cm belt above the water level (at HW).

The zonation of *Epixanthus dentatus* (Fig. 3C) follows a pattern quite similar to that of *M. thukuhar* and *S. leptosoma* (average level, 18.3 cm), but this species does not avoid being submerged: about 10% of the observations were made at a level of -10 cm. These crabs are permanently more or less hidden and are always encrusted with mud. When submerged, they usually remain still, with fully extended claws, waiting to capture prey (quite often individuals of the above two species). Small specimens are quite common under root bark.

Only four specimens of *Eurycarcinus natalensis* were recorded and these were all found on *Rhizophora* roots. Two very small individuals (less than 1 cm carapace length) were found under the root bark. Although specimens of *E. natalensis* have been seen to be active on the floor at HW and at LW, more or less overlapping in distribution with *Sesarma guttatum*, nothing can be said about its vertical zonation.



During the resting phase at LW, *Clibanarius laevimanus* congregated to form large clusters around the base of the *Rhizophora* roots. At HT individuals dispersed, feeding on the mud surface. They were never recorded more than 70-80 cm above the ground. *C. longitarsus* is also active at HW and rests at LW, but its activity was mostly on the floor, occasionally venturing out to explore and graze along the *Bostrichia* felt growing on the aerial *Rhizophora* roots, as has also been observed by Macnae (1968). Like most hermits, *C. longitarsus* is a good climber and was occasionally found, at HW, up to 60-80 cm above the floor, though always submerged.

The filter feeder, *Petrolisthes lamarckii*, was very active at HW on the submerged surface of the *Rhizophora* trees. At LW it retreated under bark and root crevices, together with the *Merguia oligodon*, with which it was usually found.

Table 2. Correlation between Tree-dwelling Adaptation Score and various morphometric characters.

Character	df	t	P
carapace thickness/carapace length	8	-3.410	<0.01
carapace length/carapace width	8	2.772	<0.05
2nd leg length/carapace length	8	-0.763	ns
2nd merus length/2nd leg length	8	1.480	ns
2nd merus width/length	8	1.480	ns
2nd carpus length/2nd leg length	8	2.449	<0.05
2nd propodus length/2nd leg length	8	3.163	<0.01
2nd dactylus length/2nd leg length	8	-6.172	<0.001

t = evaluation or r, parameter of Spearman rank correlation test

#### Feeding and morphological adaptations

The stomachs of several specimens of the various species were dissected and a rough classification of predominant feeding habits was attempted by distinguishing, in the stomach, the remains of plant and animal origin. More details of predator-prey relationships and feeding specializations are found in Dahdouh-Guebas *et al.* (1993). Several morphological parameters were correlated with the TAS score and a few proved to be highly correlated (Table 2). The more the species seems to conduct an arboreal life, the more the carapace appears flat and square (Fig. 5), the carpus (somewhat irregularly) and the propodus of the ambulatory legs appear relatively long (Fig. 6B, C respectively), and the dactylus appears short (Fig. 6D). The TAS value does not appear to be correlated with the relative length of the whole leg (Fig. 5C) nor with the merus width/length ratio or merus relative length (Fig. 6A).

#### Spatial strategy

Among the species for which enough data have been collected, a distinction could be made between species occupying average levels (10 - 30 cm) on the trunks above the water level (*Metopograpsus thukuhar*, *Sesarma guttatum*, *S. leptosoma* and *Epixanthus dentatus*) and species living higher than this average (50 to 70 cm) (*S. brocki* and *S. elongatum*). In some cases the zonation seems higher during day-time (for *S. guttatum* and *S. leptosoma*) while in other cases the opposite seems to be true (*M. oceanicus*). However, to understand the meaning of these variations in level, detailed studies must be carried out for each species.

A more important distinction among the vertical zonation patterns of the mangrove crabs was that some species always keep themselves above water level by migrating vertically (*M. thukuhar*, *M. oceanicus*, *S. brocki*, *S. elongatum* and *S. leptosoma*), whereas others tend

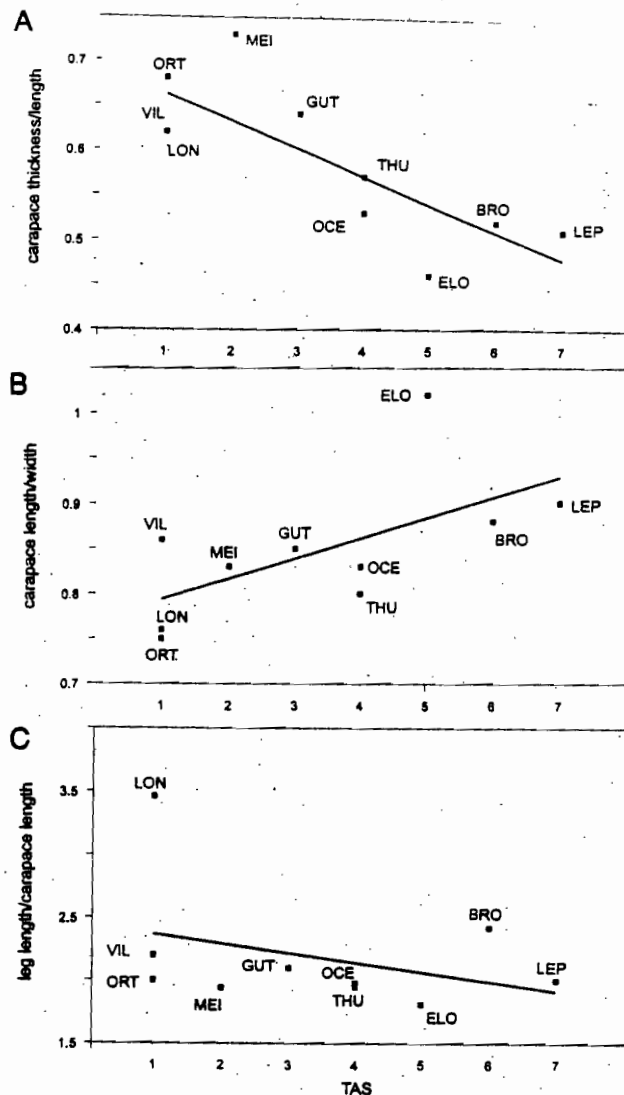


Figure 5. Correlation between TAS (x-axis) and the ratio of A) carapace thickness to carapace length B) carapace length to carapace width and C) leg length to carapace length. BRO: *Sesarma brocki*; ELO: *S. elongatum*, GUT: *S. guttatum*; LEP: *S. leptosoma*; LON: *S. longipes*; MEI: *S. meinerti*; ORT: *S. ortmanni*; OCE: *Metopograpsus oceanicus*; THU: *M. thukuhar*; VIL: *S. villosum*. See text for explanation of TAS values.

to remain in the same zone despite the tidal events; either retreating into their holes (*S. meinerti*, *S. guttatum*) and under crevices (*Petrolisthes lamarckii*) or simply resting on the floor (*Clibanarius longitarsus*, *C. laevimanus*) when the tidal phase is unsuitable for them (resting at HW, as *S. guttatum*, or at LW, as *Petrolisthes lamarckii*, *C. longitarsus*, *C. laevimanus*).

More generally, among all the intertidal non-sessile animals, a distinction can be made between iso-phasic (IP) and iso-zonal (IZ) (or iso-spatial) species (Vannini and Chelazzi 1985). Iso-phasic species are able to rest and forage, keeping themselves always in the same respiratory phase, migrating up and down along the substratum, in synchrony with the tidal oscillation. The iso-zonal species can forage, even for long distances, remaining in the same zonal belt, regardless of the tidal oscillation, and seeking refuge during the adverse tidal phase.

Many Ocypodidae (several *Macrophthalmus*, *Uca* and *Dotilla* species) have an typical IZ behavior in which they avoid high water by retreating into holes (which in many cases can even be plugged). This IZ behavior is also exhibited by some swimming crabs, such as *Thalamita crenata* (Cannicci *et al.*, 1993), which retreat into burrows and suitable small pools that remain permanently filled with water during low tide. This is in contrast to other portunid crabs which migrate offshore, prior to LW, to avoid the lack of water (Macnae, 1968; Hill, 1978; Jones, 1984).

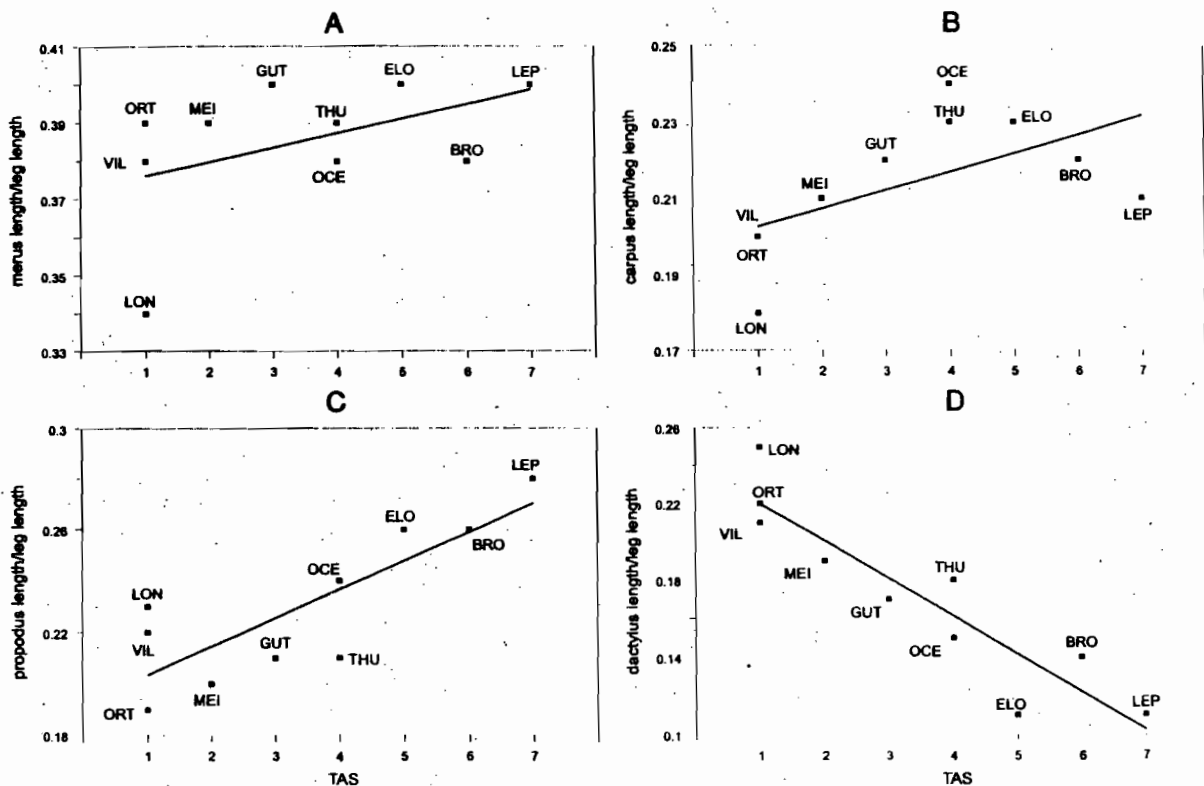


Figure 6. Correlation between TAS and the ratio relative to leg length of A) merus length B) carpus length C) propodus length and D) dactylus length. Abbreviations in Figure 5.

An IP spatial strategy in a mangrove swamp can lead to two different behaviors: horizontal migration across the mangrove belt or vertical migration along the tree trunks. The zonation pattern of the several species examined and the direct observations of the animals seem to indicate that none of the mangrove decapods migrates horizontally across the forest, while many of them can be seen moving up and down the trees, usually in accordance with the tide. In other words, the first reason for climbing the trees, for IP species, is related to the need to avoid submersion. IP strategy is typical of most of Grapsinae and of many Sesarminae.

Possible phylogenetic or physiological reasons why some species would permanently remain above the water level, while others may tolerate, prefer or even need periodical submersion include escape from flooding, escape from predators, search for food and search for shelter (von Hagen, 1977). Although it seems clear that none of these reasons alone can explain the complicated behavior of mangrove decapods, the lack of ecological and physiological information for these crabs makes further discussion of this problem somewhat difficult.

Among Grapsinae of the western Indo-Pacific, the *Metopograpsus* species seem to have a role similar to that of *Grapsus* species. Species of both these genera are IP species, migrating vertically according to the tide, keeping themselves well above water level, feeding mostly by grazing on the substratum and catching matter floating on the water surface (Kramer, 1967; Hartnoll, 1975). At LW, they may forage by moving horizontally on the rocky (*Grapsus*) or muddy (*Metopograpsus*) substratum.

Among Sesarminae both IP (*S. leptosoma*, *S. brocki* and *S. elongatum*) and IZ (*S. guttatum*) spatial strategies are represented. *S. meinerti* exhibits both IZ and IP behaviors, since it always remains in the same zone, always having access to air except during a few HWs a year. During these rare events most of the crabs behave as an IZ species, while a few climb the trees like an IP species.

Table 3. Tree-dwelling Adaptation Score (TAS) for the different decapod species observed.

Living:	Species	TAS
1. only on the floor	<i>Sesarma longipes</i> <i>S. ortmanni</i> , <i>S. villosum</i>	1
2. on the floor, on roots only occasionally	<i>S. meinerti</i> <i>Ozius guttatus</i>	2
3. usually on the floor, often climbing roots	<i>S. guttatum</i> , <i>Epixanthus dentatus</i> <i>Clibanarius longitarsus</i> <i>C. laevimanus</i>	3
4. usually on the roots, often on the floor	<i>Metopograpsus oceanicus</i> <i>M. thukuha</i>	4
5. on or just above the roots, occasionally on the floor	<i>S. elongatum</i> <i>Merguia oligodon</i>	5
6. only on or just above the roots	<i>S. brocki</i> <i>Petrolisthes lamarckii</i>	6
7. only on trees, branches and leaves included	<i>S. leptosoma</i>	7

#### Degree of adaptation

The mangrove tree-dwelling decapods display different degrees of tree-dependence (Table 3) which can be considered as an assessment of their adaptation to tree-dwelling. In comparison to Hartnoll's system (1988) which distinguishes 5 different grades of terrestrial adaptation, our system does not include species which dwell on trees outside the mangrove area. On our scale of 1 to 7, all the TAS values correspond to species that are either intertidal species active during low tide, or species resident out of the water but needing regular access to it (Hartnoll, 1988).

**Feeding specialization.** Tree dependence does not seem to be correlated with feeding habit which seems more related to phylogenetic constraints; Xanthoidea are nearly exclusively predators, Grapsinae are omnivorous, Sesarminae are mostly detritivorous, feeding on plant remains, Hermit crabs are exclusively detritivorous and Porcellanidae are filter feeders.

**Physiological adaptation.** Among the mangrove crabs, Edney (1961) and Macintosh (1978, 1988) have shown a correlation between zonation and metabolic responses to temperature in *Uca*, but nothing is known about physiological adaptation of the mangrove tree crabs in relation to temperature or other ecological factors.

**Morphological specialization.** Tree dependence, at least within the relatively homogeneous Grapsidae taxon, seems to be correlated to some morphological features such as carapace shape, the length of the dactylus and the length (relative to leg length) of the propodus. In other words, the leg is becoming a real climbing instrument, improving its function; the dactylus is transformed into a sort of short claw and there is more space for the adductor muscles inside the propodus.

**Ecological specialization.** Among many littoral taxa, a distinction can be made between species inhabiting muddy, well-protected shores and those living on exposed shores, beaten by high energy waves. It is not known whether the mangrove forests simply offer suitable conditions to typical species of the protected shore fauna or whether they host a truly specialized fauna, strictly dependent on the trees (Jones, 1984). Within the species studied here, *S. meinerti* could be considered as dependent on mangrove swamps (Ruwa, 1990), although their presence along the muddy banks of the Giuba river, under mango trees (Vannini and Valmori, 1981), and on a sheltered muddy shore bordered by *Casuarina* trees, in the islands of Mauritius and Rodriguez (Vannini, pers. obs.), may contest this.

In Tanzania, *S. leptosoma* has been found on trees, *S. brocki* on trees and under stones (Hartnoll, 1975), and *S. elongatum* on a floating tree, about 15 km away from the nearest mangrove swamps (Vannini and Valmori, 1981). Since these species have never been recorded on the mangrove floor and have been observed to feed on the leaves on the mangrove canopy, it would seem that they are possibly ecologically specialized for living in the mangrove trees. Many of the species recorded here as being somewhat dependent on the mangrove trees, including *M. thukar* which had a relatively high TAS value, have been seen in biotopes other than mangrove swamps, such as semi-exposed and exposed rocky shores and rocky-sandy shores (Alexander *et al.*, 1973; Crosnier, 1965; Haig 1984; Hartnoll, 1975; Holthuis, 1977; Macnae 1968; Sakai, 1976; Snelling, 1959; Vannini and Valmori, 1981).

No records seem to exist in the literature of *S. guttatum*, *E. natalensis* and *E. dentatus* being totally independent of mangroves. However, Ruwa (1990) found the above species in areas with no mangrove trees left, but only with mangrove peat. *Petrolisthes lamarckii* seems to be commonly found also on rocky shores (Lewinsohn, 1979). Little is known about the habits of *C. laevimanus* away from Mida Creek but the more common mangrove hermit crab, *C. longitarsus*, has surely been found on sheltered shores, with no mangroves in the surroundings area (Gherardi, pers. comm.). *M. oligodon* was common among the Mida Creek mangroves but in the eastern Indian Ocean it is known from sites with no mangroves at all (Holthuis, pers. comm.).

For the moment *Sesarma elongatum*, *S. brocki* and *S. leptosoma* seem to be the only tree species which can be considered as exclusive inhabitants of mangrove swamps which also fits nicely with their habits and morphology. At least among the Kenyan Grapsidae, they are the species most constantly associated with the trees and the most morphologically adapted to this style of life.

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