Jörundur Svavarsson, Melckzedeck K.W. Osore and Emil Ólafsson

Does the Wood-borer *Sphaeroma terebrans* (Crustacea) Shape the Distribution of the Mangrove *Rhizophora mucronata*?

Field surveys were conducted to evaluate the occurrence of the isopod borer *Sphaeroma terebrans* (Crustacea) in aerial roots (prop roots) of the red mangrove *Rhizophora mucronata* on several different spatial scales (m to 100 km) in East Africa. In 6 out of 17 sites studied in Kenya and on Zanzibar Island, Tanzania, no signs of the isopods were found. When the isopods were present the frequency of infestation was high. Trees in muddy substrates in the lower intertidal, in particular at fringing channels or the open sea, showed high prevalence and intensity of infestation, with large part of their roots damaged or dead. Trees at the upper range of *Rhizophora*, in sandy and muddy areas, showed no signs of isopod infestation. This pattern recurred in mangrove forests on large spatial scales and there was no indication that island forests differed from the mainland forests. This indicates that sediment characteristics, vertical height in the tidal zone, and direct exposure to incoming water are the major factors controlling the abundance of *S. terebrans*. The isopod may play an important role in determining the lower intertidal limits of *R. mucronata*. Trees with numerous dead or nongrowing roots, as result of *Sphaeroma* attack, are likely to tumble due to a lack of root support and this is most likely to occur along channels at the lower, muddy intertidal. Tumbled trees were frequently observed along channels in the lower, muddy intertidal, but rarely in the mid or high intertidal. Implications for management of mangrove forests are discussed.

INTRODUCTION

Tidal mangrove forests cover a vast area in the tropics. These forests are believed to play an important role in the support of estuarine and coastal food webs. They act both as a nursery ground and habitat for commercially important fish species (1–3). Unfortunately, these forests are now diminishing in many parts of the world due to exploitation of various kind (4–6). Mangrove trees are popular as building material because of their resistance against fungus and termites, they are logged for tannins used in leather treatment, and increasing aquaculture has resulted in the demand for space within these forests (5). Understanding of the dynamics and natural variation of the mangrove forests is becoming progressively more important, as their utilization increases. In addition, mangroves will probably be affected by altered sea level due to climate change (7).

In addition to human impact, mangrove trees are damaged by a variety of wood-boring organisms (8). These include insects, bivalves and in particular marine isopods (Crustacea), which burrow into the aerial roots (prop roots) of a number of mangrove species in search for food or shelter. The isopod *Sphaeroma terebrans* Bate utilises aerial roots of a variety of mangrove trees, among them species of the genus *Rhizophora* (9–13). They burrow with their mandibles into newly formed aerial roots, creating hollow channels within the roots up to 5-cm long. They do not feed on the wood itself, but filter particles from the water column with their front of legs (14).

It has been suggested that *S. terebrans* was causing an “eco-catastrophe” by destroying the aerial roots of red mangroves (*Rhizophora mangle* L.) along the southwestern coast of Florida to such an extent that the Ten Thousand Islands and mangrove fringes of the mainland were steadily shrinking (15). Similarly, it was concluded that the isopods were a serious threat to the mangroves of the Kerala coast, India (16). Other authors have questioned the catastrophic effects of *Sphaeroma* on *Rhizophora* (17, 18) and proposed that burrowing of aerial roots may even be advantageous to the mangroves (18). The beneficial effects of burrowing are doubtful (19), since it has been shown that net root production of burrowed roots was 62% below that of non-burrowed roots and that the stimulation of new root-tip growth did not compensate for the loss in growth rate (20). It has also been shown that the most common response to damage is the replacement of root tissue, rather than the stimulation of new tissue formation (21).

Even though the potential threat of the isopod to mangrove forests has been highlighted by several researchers, there is a huge gap in our ecological knowledge of this borer. There is little or no information about their occurrence over extensive geographical areas, the nature of their distribution within and between areas, and only a few attempts to link their distribution with co-occurring physical or biological factors. Here we report on the first field survey in eastern Africa on the distribution patterns of *S. terebrans* in *Rhizophora* stands. Our main questions were: *i*) Are the isopods restricted to a certain habitat (upper or lower intertidal; muddy or sandy mangroves)? *ii*) If they are restricted to a certain habitat, that environmental factors are most likely to control their distribution? *iii*) Are some trees, within in the same habitat, more infested than others? *iv*) Does the local isopod distribution pattern vary between distant areas?

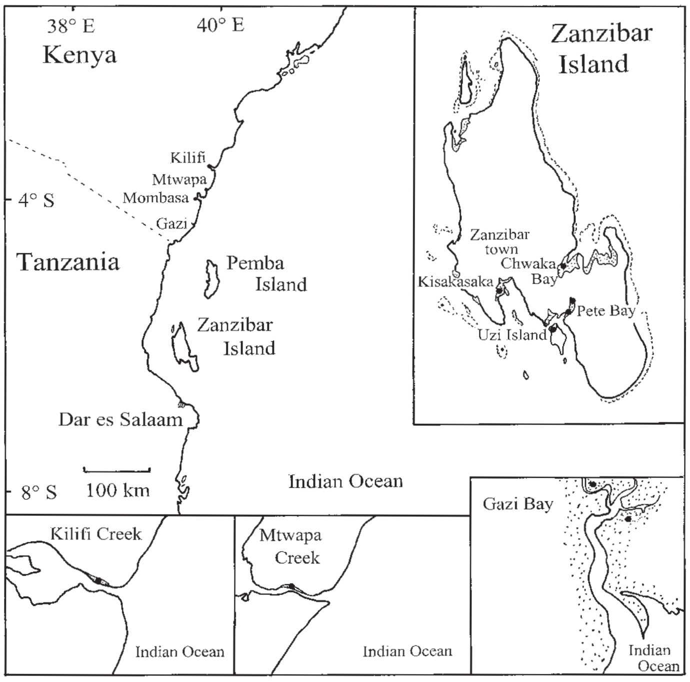
MATERIALS AND METHODS

Study Sites

Three mangrove stands were studied along the coast of Kenya (Fig. 1). Gazi Bay (4° 25'S, 39° 30'E) 50 km south of Mombasa, harbors extensive mangrove forest (around 660 ha). *Rhizophora mucronata* (L.) is the dominant mangrove species followed by *Sonneratia alba* Smith, *Bruguiera gymnorrhiza* (L.) Lamarck and *Avicennia marina* (Forskål) Vierh. *R. mucronata* also forms stands of its own that can cover considerable areas and of the total mangrove its coverage accounts for 75% (22). It is mainly found at medium water height, though it may extend to high water levels, and often fringing the main bay, creeks, and channels. Kilifi Creek (3° 37'S, 39° 50'E) 60 km north of Mombasa provides a narrow belt (ca 20 m) of mangrove trees where *R. mucronata* is common. The trees are in isolated patches and show a variable degree of exposure to the open water. Mtwapa Creek (3° 56'S, 39° 25'E) 20-km north of Mombasa is another small mangrove stand where *R. mucronata* is the dominant species in a narrow belt (50 m) which extends from high to medium/low water levels. The trees fringing the creek are almost all *R. mucronata* with only the odd *A. marina* tree.

On Zanzibar Island, approximately 50 km off the Tanzanian coast, 5 mangrove areas were studied (Fig. 1). Chwaka Bay (6° 10'S, 39° 26'E) on the east coast of Zanzibar provides the larg-

Figure 1. Map of studied localities in Kenya and Tanzania. Dotted areas indicate mangrove forests.



est mangrove forest on the island (3000 ha). Here *R. mucronata* is the dominant mangrove species making up 25% of the total mangrove coverage (23). As in Gazi Bay, *R. mucronata* is mainly found at medium high water levels, with trees fringing large parts of the various creeks and channels. Kisakasaka (6° 14'S, 39° 18'E) on the south coast of Zanzibar harbors a large mangrove stand, about 460 ha with about 30% *R. mucronata* coverage. Pete Bay (6° 18'S, 39° 25'E) is also on the south coast of Zanzibar, where mangrove cover is about 320 ha with 35% *R. mucronata* cover. Here *R. mucronata* is found both at high intertidal levels more than 1 km from the bay and also at much lower intertidal levels fringing the bay. Finally, on the northern part of Uzi Island (6° 19'S, 39° 23'E) a fairly narrow fringe of *Rhizophora* occurs among *Sonneratia* trees. The area is open the sea and the substrate is sandy.

Estimation of Burrowing Activity

Field studies were undertaken in January 1999 when around 200 trees and 2715 nongrounded aerial roots were examined. Two different sampling strategies were adopted depending on the size of the area and the expansion of the *Rhizophora* zone. In areas with extensive *Rhizophora* cover (Gazi Bay) transects from the lowest shore, perpendicular to the shore, were taken. A tree at the lowest shore was randomly selected, and closest trees were then subsequently analyzed along a line into the forest. Where the *Rhizophora* zone was narrow (Kilifi Creek, Mtwapa Creek, parts of Gazi Bay), trees were randomly selected at the lower fringe, exposed to the open sea and, for comparison, trees in the upper zone.

Each tree was analyzed in the following manner. The maximum diameter of the stem was measured, the maximum extension of the aerial root system estimated in meters, and the number of intact roots, roots with burrows and root ends with no obvious growth (roots without a growing tip/dead roots), were counted. The total number of grounded aerial roots was counted or estimated, when these were more than 100. Information was gathered regarding the sediments and the surrounding vegetation, and also the extent of exposure to open areas.

Estimating the height of areas above sea level can be difficult in mangrove forests. In some cases, the mangrove trees obstruct the view to the sea or seawater is retained in creeks and channels complicating water height measurement. To overcome this problem, biological indicators were used to estimate the vertical height of the *Rhizophora* zone. For this the highest barnacles (Cirripedia) and/or oysters (Bivalvia, Ostreidae) were estimated on each examined tree, when present. This methodology may raise criticism since the different current regimes at the edge and within forests may also strongly affect the height of the epibiota.

Additionally, for a number (N = c. 30; Kilifi Creek, Mtwapa Creek, Kisakasaka, Chwaka Bay) of *Rhizophora* trees the height of individual aerial roots above the substrate was measured, i.e. the distance from the tip of the aerial root to the substrate/water surface. Each of these roots was examined for burrows and root ends with no growth.

A total of 286 roots with burrows were cut from trees and brought to the laboratory. The distance of each burrow from the distal tip of the root and the diameter of the burrow opening was measured with a sliding ruler. Then the burrow was carefully opened and the presence of *Sphaeroma* or any other animal noted. The number and developmental stage of the animals within each burrow were noted. The length of each burrow was measured and the size of the animals was measured using eyepiece graticule in a dissecting microscope, and their sex and developmental stage noted. Specimens were preserved in 90% ethanol.

Table 1. Number of trees and roots examined and the number and frequency of infested (damaged, dead) trees and roots at different locations in Kenya and Tanzania.

Area	Site	Position	Substrate	No. of trees examined	No. of trees infested	% of trees infested	No. of roots examined	No. of roots infested	% of roots infested
Kenya									
Kilifi Creek		low intertidal, fringe	muddy	9	9	100	130	105	80.8
Mtwapa Creek	1	low intertidal, fringe	muddy	5	5	100	140	101	72.1
Mtwapa Creek	2	mid intertidal, fringe	muddy	5	1	20	182	2	1.1
Gazi Bay	1	low intertidal, fringe	muddy	21	21	100	732	610	83.3
Gazi Bay	2	mid intertidal, inside	muddy	9	9	100	270	141	52.2
Gazi Bay	3	high intertidal, inside	sandy	31	0	0	200	0	0
Tanzania									
Uzi Island		mid intertidal, fringe	sandy	5	4	80	90	9	10.0
Pete Bay	1	high intertidal, inside	muddy	37	0	0	133	0	0
Pete Bay	2	mid intertidal, fringe	sandy	5	2	40	66	7	10.6
Chwaka Bay	1	low intertidal, fringe	sandy	around 10		0	100	0	0
Chwaka Bay	2	low intertidal, fringe	muddy	15	4	27	100	4	4
Chwaka Bay	3	low intertidal, fringe	muddy	around 10		100	205	159	77.6
Chwaka Bay	3	high intertidal, inside	muddy	around 10	0	0	50	0	0
Chwaka Bay	4	low intertidal, fringe	muddy	6	6	100	150	110	73.3
Chwaka Bay	4	high intertidal, inside	muddy	around 10	0	0	30	0	0
Kisakasaka	1	mid intertidal, inside	muddy	5	0	0	35	0	0
Kisakasaka	2	low intertidal, fringe	muddy	around 10		100	102	75	73.5

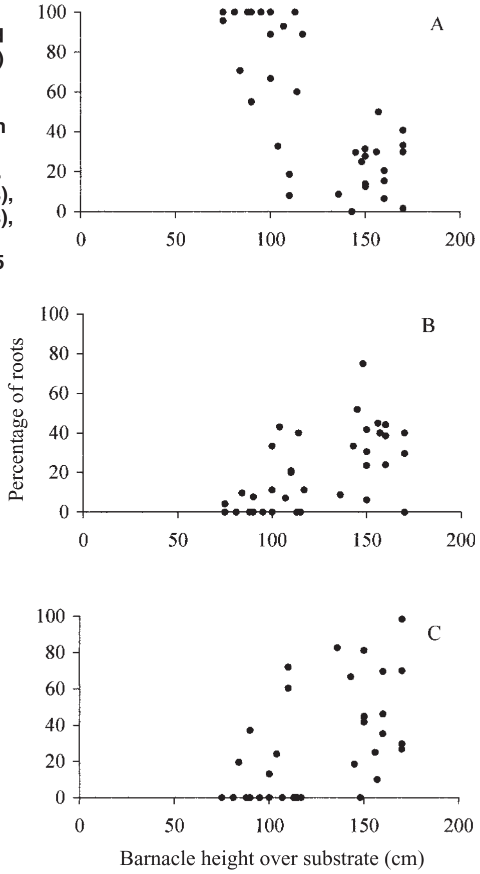


Figure 2. Frequency of intact (A), damaged (B) and dead roots (C) on individual trees in *Rhizophora* forests in Kenya and Zanzibar in relation to height of uppermost barnacles. Gazi bay (N = 25 trees), Uzi Island (N = 4 trees), Pete Bay (N = 5 trees) and Kisakasaka (N = 5 trees). Low barnacle height over substrate indicates the upper intertidal and high barnacle height the lower intertidal.

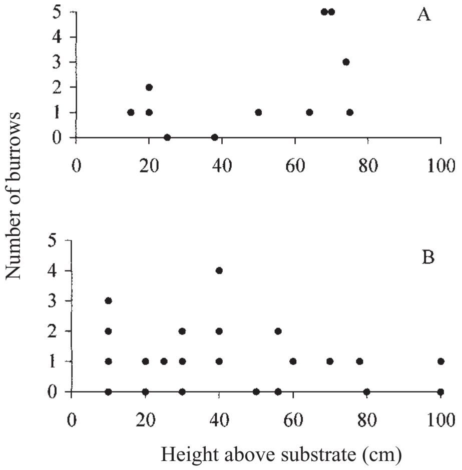


Figure 3. Height above substrate and the number of burrows on two *Rhizophora* trees in Kilifi. Highest oysters were at 130 cm (A) and 133 cm (B) height above the substrate.

Table 2. Number of *Rhizophora* aerial roots at different height intervals above the substrate in Kilifi forest. The height was measured at the tip of the respective roots.

Height range above sediment (cm)	Area 1				Area 2					Total	%	Cumulative %
	Tree 2	Tree 3	Tree 4	Tree 5	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5			
151–160						1				1	0.8	
141–150										0	0	
131–140										0	0	
121–130	1									1	0.8	
111–120										0	0	
101–110			1							1	0.8	
91–100			1							1	0.8	97.9
81–90										0	0	97.1
71–80				2					2	4	3.1	97.1
61–70	1		1	3				2	1	8	6.2	94.0
51–60			1		2		1	1	5	10	7.8	87.8
41–50	1		3	1	1			2	1	9	7	80.0
31–40				1	2		3	3	5	14	10.9	73.0
21–30	5		2	1	2		3	1	8	22	17.1	62.1
11–20		3	6	3	7	2	4	9	2	36	27.9	45.0
0–10		6	5		2	6	1	2		22	17.1	17.1

RESULTS

Infestation of *Rhizophora*

Rhizophora trees infested by *Sphaeroma* were found in all studied mangrove forests in Kenya and Tanzania (Table 1). Within the same mangrove forests there was a considerable difference in prevalence (% of infested trees) at different sites, ranging from noninfested localities to places with 100% prevalence. The intensity of *Sphaeroma* infestation (estimated by the number of damaged roots) ranged from 0 to > 70 % of nongrounded roots. Despite a high prevalence, a few sites had low intensity (e.g. Uzi Island and Pete Bay, lower fringe). At these sites only a few roots had burrows, but most trees had at least one burrow.

Where high incidence of infestation occurred the substrate was invariably muddy (Table 1), while low infestation sites were either with muddy or sandy sediments (Table 1). There was no infestation at sites located in the upper intertidal of the forests.

The level of infestation was dependent upon the intertidal height of the sites. There was a significant negative correlation (Spearman rank correlation, $r = -0.71$, $P < 0.001$) between the percentage of intact roots and the height of barnacles above substratum (Fig. 2a), while the inverse relationship was found between the percentage of damaged roots and barnacle height (Spearman rank correlation, $r = 0.52$, $P < 0.001$; Fig. 2b) and the percentage of dead/nongrowing roots and barnacle height ($r = 0.64$, $P < 0.001$, Fig. 2c).

Within the same site most trees had quite similar frequency of infestation. We found no differences in infestation, which could be related to differential response of individual trees towards a *Sphaeroma* attack.

Vertical Distribution of Burrows on Individual Trees

The aerial roots start to grow from the stem of the plants at various heights above the substrate, some well-above the intertidal. Nearly half (45%) of the roots had at the time of study in January in Kilifi forest their tips developing close to the sediments (0 to 20 cm from the tip of the roots to sediments; Table 2), but not yet rooted in the sediment. There was considerable variation among trees with respect to the vertical distribution of infested roots/intact roots on individual trees and the number of burrows on the roots. Good examples are 2 trees in Kilifi forest (lower fringe) (Fig. 3) where isopod burrows were found within a relatively large height range (> 1 m).

The average heights above the sediment/water level (i.e. the distance from the tip of the root to the sediment/water level) (see methods) of dead roots (roots heavily infested by various organisms and without a growing tip), damaged roots (roots with one or more *Sphaeroma* burrows) and intact roots (roots without burrows) are shown in Figure 4 for 3 different areas (Kisakasaka, Mtwapa Creek and Chwaka Bay). In Kisakasaka and Chwaka no biological height-indicator was available and the relative height of intact, damaged and dead roots was estimated above low-water level in a canal close to a fringe of trees. In all 3 areas the average height of intact roots was significantly higher above the sediment/water level than the damaged or the dead roots (1-way ANOVA, $P < 0.001$; Tukey test, $P < 0.05$). In 2 of the areas (Mtwapa Creek and Chwaka Bay) there was also a significant difference between the average height of dead and damaged roots, dead roots being closer to the sediment (Tukey test, $P < 0.05$).

Number of *Sphaeroma* Burrows

The number of burrows on individual aerial roots was similar in different mangrove forests. Most frequently, about two thirds of damaged roots had one to 3 burrows, but up to 15 burrows were seen on a single root (Table 3). The pattern of burrowing was consistent, with the burrows most often lined along the ventral margin of the roots. The first burrow was almost always within the first 5 cm of the tip of the root, with subsequent burrows occurring with increasing distance from the tip of the root. On average the first 2 burrows were of similar distance from the tip and significantly closer to the tip than subsequent burrows (1-way ANOVA, $P < 0.001$; Tukey test, $P < 0.05$; Fig. 5).

Sphaeroma terebrans was found within most of the burrows examined (average 61.3%, range 50–72%, N = 795, Mtwapa Creek, Gazi Bay, Kilifi Creek). Presence of juveniles with adults was frequently observed (extended parental care; *sensu* 11, 12). The size of *Sphaeroma* burrows were similar in different forests (e.g. Gazi Bay 2, average length = 1.62 ± 0.73 cm S.D., N = 124; Mtwapa, 1.78 ± 0.86 cm S.D., N = 110), and burrows < 0.5 cm in length were relatively rare. There was a significant relationship between the size of the isopods and the length of the burrow (e.g. Mtwapa Creek and Gazi Bay; Spearman rank correlation, r = 0.561, N = 87, $P < 0.001$).

DISCUSSION

From this survey it is clear that *Sphaeroma terebrans* is a frequent inhabitant of *Rhizophora mucronata* aerial roots in both Kenya and Tanzania. Extensive damage on the aerial roots of *Rhizophora* was observed in most of the studied mangrove forests in Kenya and Tanzania, similar to what has been observed in Florida (15) and in India (16, 24). The intensity of *Sphaeroma* damage varied from 0 % to > 50 % dead and damaged aerial roots within only a single meter of vertical height in the *Rhizophora* forests, but the damage was more or less restricted to low-water muddy sites where trees were directly exposed to the sea. There was consistency in this pattern among different mangrove forests along the coast of Kenya and the island of Zanzibar.

The occurrence of *Sphaeroma* in *Rhizophora* aerial roots in Kenya and Zanzibar seems to be dependent upon at least 2 different factors, i.e. water level and the sediment type. Obviously, with increasing intertidal height the isopods are less time submerged in water which will not only limit their feeding time but also their time to attack new roots. The water above the muddy sites is likely to contain much more organic matter than at sandy sites and was normally murky and in strong contrast to

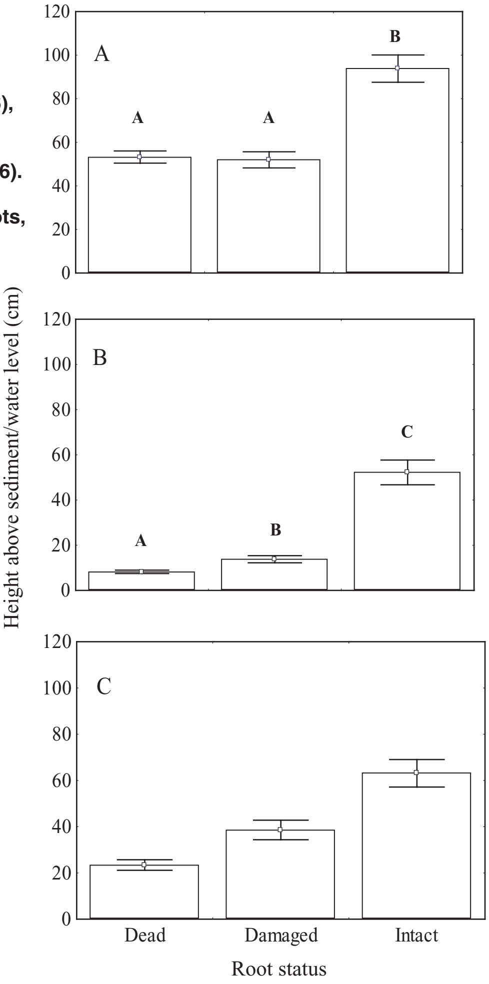


Figure 4. Average height of dead, damaged and intact roots on trees in Kisakasaka (A; N = 6), Mtwapa creek (B; N = 9), and Chwaka Bay (C; N = 6). Mtwapa (dead roots, N = 45; damaged roots, N = 49; intact roots N = 40). Kisakasaka (dead roots, N = 26; damaged, N = 13; intact, N = 5), Chwaka Bay (dead roots, N = 79; damaged, N = 31; intact, N = 40). On the trees in Mtwapa Creek the height of each nongrounded root above substrate was measured and these values then standardized for all 9 trees using height of oysters.

Table 3. Frequency of roots with 1, 2, ...15 *Sphaeroma* burrows at Gazi Bay sites 1 and 2 and in Mtwapa Creek.

Number of burrows	Gazi Bay 1		Gazi Bay 2		Mtwapa Creek		Cumulative
	Number of roots	% of roots	Number of roots	% of roots	Number of roots	% of roots	%
1	16	19.5	8	19.5	10	26.3	20–26
2	24	29.3	12	29.3	7	18.4	45–49
3	13	15.9	7	17.1	9	23.7	65–68
4	8	9.8	7	17.1	3	7.9	74–83
5	3	3.7	2	4.9	2	5.3	78–87
6	6	7.3	3	7.3	3	7.9	85–95
7	4	4.9			1	2.6	90–95
8	4	4.9	1	2.4	2	5.3	95–98
9					1	2.6	95–100
10		1	1.2	1	2.4		96–100
11							96–100
12	2	2.4					96–100
13							96–100
14							96–100
15	1	1.2					100
	82	100	41	100	38	100	

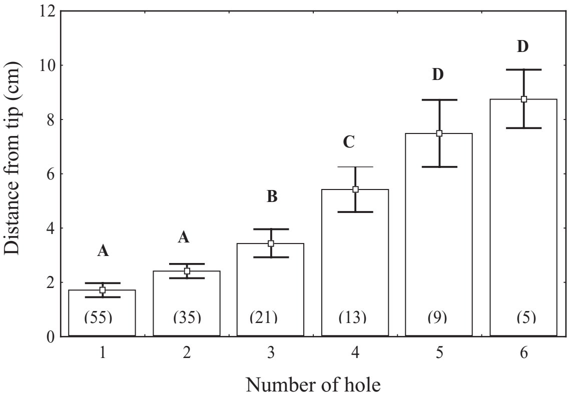


Figure 5. Location of burrows on roots (N = 138) in Gazi Bay. Average distance of hole from the tip of the root. Columns with common letter codes are not significantly different (Tukey test, $P > 0.05$). Numbers in brackets represent number of roots analyzed.

The destruction caused by the wood-borer *Sphaeroma* on the aereal roots of *Rhizophora*. Photo: J. Svavarsson.

the clear water often observed at the sandy sites. This is likely to result in higher food availability for this filter feeder (14) at muddy sites and, therefore, will limit the distribution of the isopods to such an environment. It has been suggested, without any data to support the notion, that *Sphaeroma* destruction in Florida was influenced by tides, temperature, and salinity (25). While the effects of temperature and salinity remain to be evaluated, it has recently been shown with experimental manipulations that submergence is an important physical factor for the colonization of *Sphaeroma terebrans* onto the red mangrove, *R. mangle* (13). Still there is a need for further information concerning the ecology of the isopod. Little data exist on the survival at different submergence and the interactions between submergence time and feeding/food availability.

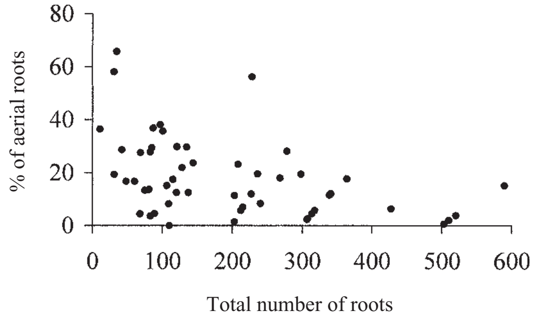
The pattern of infestation and the distribution of *Sphaeroma* indicate that *Sphaeroma* is setting the lower limits of the distribution of *Rhizophora*, rather than being a catastrophic event. *Sphaeroma* presumably weakens the stability of the *Rhizophora* trees at the lower intertidal. Trees with numerous dead or nongrowing aerial roots are likely to tumble due to a lack of root support and this is most likely to occur along channels in the lower, muddy intertidal. Tumbled trees were frequently observed along the channels in Gazi Bay and in Chwaka Bay, but rarely in the mid or upper intertidal.

Conflicting information has been reported regarding both the beneficial and destructive consequences of *Sphaeroma* burrowing activities. It has been suggested that *Sphaeroma* burrowing activity may benefit the mangrove by increasing lateral branching of the aerial roots (18). This has been questioned (19). The burrowing activity of the limnoriid isopod *Phycolimnoria clarkae* does not increase lateral branching, but only reduces the relative growth rate of the roots (26). *Sphaeroma peruvianum* Richardson had extensive effects on the growth rate of *R. mangle*, and the net root production was 62% below that of unburrowed roots (20). In *R. mucronata* the burrowing may result in extensive damage to the inner part of the roots as the isopods place their burrows in the center of the roots and this leads to a later impregnation of fungus (27). The burrows were most frequently between 0.5 and 3 cm (average around 1.6 to 1.8 cm) in length and with the most common frequency of 1 to 3 burrows, resulting in < 2 to 5 cm of burrows within a single aerial root, usually within the tip (first 5 cm) of the roots. The high frequency of dead or nongrowing roots at the lowest sites clearly indicates that the effects are at least nonbeneficial at the lowest sites.

The number of new aerial roots varied considerably between individual *Rhizophora* plants and there was no correlation found between the number of grounded roots and the number of newly forming aerial roots. Younger plants have relatively many aerial roots compared to roots having reached the substrate, while aerial roots may be relatively rare on elder trees (Fig. 6). The effects of *Sphaeroma* are consequently most pronounced on young trees found on the lower fringe of the *Rhizophora* zone, facing channels and thus directly exposed to the ocean. These often had only few roots reaching the bottom, while new roots were extensively damaged. The effects were less pronounced on elder trees with extensive root system (> 300 roots in the bottom). Hence, the general effects of *Sphaeroma* on *Rhizophora* may be partly dependent upon the age structure of the trees in the mangrove forest.

In the present study, quite a high percentage of the holes on the roots were occupied by isopods. This is in accordance with other studies (12, 20). The burrow vacancy may vary between seasons. Empty burrows were most frequently found during the

Figure. 6. Relationship between the percentage of aerial roots and the total number of roots.



summer months in Florida (12), while in Costa Rica the vacancy of *S. peruvianum* burrows in *R. mangle* was lower during the wet season (July; 62%) than during the dry season (February; 68%) (20). There was also a good correlation between the hole diameter and the size of the occupant. Some few outliers (small animals in a large burrow) have been observed elsewhere and this is presumably an indication of a reoccupation of burrows (12). The high percentage of occupied holes generally observed is presumably also partly due to the short life span of the roots as aerial roots. There is no information that we know of on the rate of formation of new aerial roots on *Rhizophora* and their growth rate in the mangrove forests in Kenya and Tanzania. The formation of new roots and the growth rate of aerial roots of the red mangrove, *R. mangle*, were highly seasonal in Florida (M. Thiel, pers. comm.). New roots formed mostly between May and November and the average growth rate was corresponding to 2–5 cm month^{-1} (M. Thiel, pers. comm.). Similar growth rates have been provided by others (28, 29). Applying these measurements on *Rhizophora* in East Africa indicates that most of the roots (example from Kilifi Creek) will reach the sediments within the next year and some within several months, making much of the roots unavailable to isopods. Still more information is needed on growth rates, in particular of the younger *Rhizophora*, which may be more subject to *Sphaeroma* attack than elder plants, simply due to a higher proportion of aerial roots.

Uniformity in the effects of *Sphaeroma* in different forests suggests that there are no population-based differences in response of *Rhizophora* towards *Sphaeroma* burrowing activity. However, no information on genetical relationship between trees in individual forests is available to support that notion. The effects of *Sphaeroma* are restricted to only a small proportion of the whole *Rhizophora* population in the larger forests and most likely the propagules disperse quite widely, indicating that selection pressure for protective means may be limited.

With diminishing mangroves in many parts of the tropics, mangrove rehabilitation and restoration is becoming increasingly important. In at least 20 countries, mangrove rehabilitation projects are ongoing (4), and in some places, for instance in Kenya, the local population is encouraged to plant mangroves simultaneously with logging activities. Mangrove logging and rehabilitation should take into account the distribution and habitat preferences of *Sphaeroma terebrans* (this study) and even the distribution of the species off the mangrove forests, where it may be common in driftwood (30). Minimal logging should take place in the lower, muddy intertidal, where restoration may prove to be impractical.

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Jörundur Svavarsson has a PhD in zoology and is professor at the Institute of Biology at the University of Iceland. His research areas include systematics and biology of isopods (Crustacea) and environmental issues, in particular the effects of pollutants on marine organisms. His address: Institute of Biology, University of Iceland, Grensásvegur 12, 108 Reykjavik, Iceland.
E-mail: jorundur@hi.is

Melckzedeck K.W. Osore has a PhD from the Vrije University in Brussels and holds a research position at the Kenya Marine and Fisheries Research Institute. He has mainly studied zooplankton. His address: Kenya Marine and Fisheries Research Institute, P. O. Box 81651, Mombasa, Kenya.
E-mail: mosore@recoscix.com

Emil Ólafsson has a PhD from the Heriot-Watt University in Edinburgh. He is a senior researcher at the Department of Zoology, University of Stockholm. His research has mainly been focused on ecological aspects of benthic invertebrates, such as competition, community organisation and resource allocation . He has extensive experience in tropical research. His address: Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden.
E-mail: emil.olafsson@zoologi.su.se