

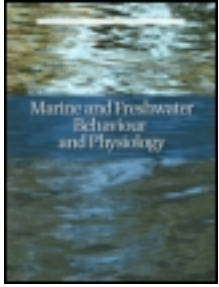
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### Hermit crabs in a mangrove swamp: Clustering dynamics in *Clibanarius laevimanus*

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# HERMIT CRABS IN A MANGROVE SWAMP: CLUSTERING DYNAMICS IN *CLIBANARIUS* *LAEVIMANUS*

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(16 July 1991)

Some dynamic patterns of clustering in the mangrove-dwelling hermit crab *Clibanarius laevimanus* were studied during a semi-lunar tide cycle in Kenya. Clusters composed of hundreds of quiescent individuals occurred at every low tide, developing either on the mangrove prop roots or in the open (but always within a 4-m belt from the mangrove fringe). They disbanded at ebb tide, when most animals migrated in lines towards feeding grounds. There they grazed on vegetable debris during high water. When the tide receded, they came back home in crowded groups. The position of aggregating sites remained constant throughout the tides, as well as their number and size, and the shape of clusters was stable with time. Individual hermits often changed clusters (only rarely they were found scattered), but transfers only occurred between aggregations where shell size range matched the shell worn by the moving crab. Dispersal was slower than predicted by random walk models. Questions were aimed on the proximate and ultimate factors underlying this spatial strategy which contrasts the nomadic behaviour shown by the sympatric *C. longitarsus*.

**KEY WORDS:** Hermit crabs, clustering, activity, intertidal habitats, mangrove swamp.

## INTRODUCTION

Mangrove swamps are characterized by many basic environmental features, most of them common to other intertidal habitats (Hartnoll, 1989). Mangrove-dwelling organisms must be able to avoid or tolerate different forms of stress from physical factors, e.g. extreme temperatures, desiccation, exposure to both salt and fresh water, and very abrupt changes in these extreme conditions. Other risks arise from the biotic realm, where both terrestrial and marine animals may prey upon these intertidal species. Among the advantages of living in a mangrove forest, food does not seem to constitute a limiting factor, especially for scavengers and detritus feeders, since wave action is limited, favouring sedimentation (mangroves flourish only in sheltered areas), and this vegetable assemblage is highly productive (published figures generally cluster around 3 kg/m<sup>2</sup> of organic matter per year; Barnes and Hughes, 1982). In addition, the three-dimensional structure of this habitat and the availability of crevices and shelters within the tangle of trunks and aerial roots provide refuges against risks originating from both abiotic and biotic factors.

In hermit crabs, behaviour associated with shell use has been considered the major adaptation enabling them to successfully exploit stressful environments (Reese, 1969). Moreover, the correct timing of activity within the tidal cycle, the patterns of space use and movement, as well as detritivorous and scavenging habits seem to play important roles in hermit colonization of mangrove ecosystems. Nevertheless, the habit of clumping at low tide still remains enigmatic as far as its adaptive value is

concerned, notwithstanding its wide occurrence among Diogenidae and Paguridae (MacKay, 1945; Hazlett, 1966; Snyder-Conn, 1980, 1981; Gherardi and Vannini, 1989).

This study was undertaken to gather data relative to the clustering behaviour of *Clibanarius laevimanus* Buitendijk, which was before only preliminarily studied (Gherardi et al., 1991). This species, distributed throughout Indonesia and Philippines (Buitendijk, 1937), has only been reported in East Africa before at Gesira (Somalia) (Lewinsohn, 1980). In the mangrove swamp of Mida Creek (Kenya), *C. laevimanus* forms spectacular aggregations consisting of hundreds of quiescent individuals in direct physical contact with each other. Animals aggregate at low tide either on the mangrove prop roots or in open areas. At ebb tide the hermits disperse to feed, migrating in lines towards patches of vegetable debris diffused in the habitat, and return to the clustering sites when the tide recedes.

With the purpose of understanding the clustering dynamics of *C. laevimanus* as a first descriptive step towards the comprehension of clusters' adaptive significance (Gherardi and Vannini, in preparation), two questions were addressed, focusing, first, the clusters, and, second, the hermits:

1. Were the clusters stable in time for number, position, size, and shape?
2. Were the hermits faithful to one particular cluster? Otherwise, how far did they disperse within the habitat?

## MATERIALS AND METHODS

In the mangrove swamp of Mida Creek (20 km south of Malindi, Kenya) the dominant mangrove species are *Avicennia marina* and *Rhizophora mucronata*, on the basal trunk and roots of which red algae such as *Bostrichya tenella* and *Catenella nipae* flourish. Tides are always semi-diurnal, with notable differences in the fluctuations of quadrature (neap, NT) and syzygial (spring, ST) tides. Temperatures ranged from 23°C at night to 32°C at day.

Research was conducted from October to November 1988, during a semi-lunar tidal cycle. Three hundred and fifty and 150 m long (1 m wide) stretches were established as transects along the seaward edge of the mangrove (*C. laevimanus* was never found inside the forest), to evaluate cluster distribution (in relation to scattered individuals and live molluscs), as well as their number, richness of hermits, and size of used shells. We classified as clusters those clumps composed by more than 10 individuals in physical contact with each other. Otherwise, hermits were considered scattered.

Twelve clusters were photographed at low tide (LWs) from 12–31 October. The photographs were later analyzed with an Apple IIGS image digitizer connected to a graphic tablet, to evaluate cluster morphometry (size and shape), following the software suggestions by Mize (1985). The relative position of some clusters was estimated by superimposing a grid system on the pictures and measuring the displacement of the geometric centre from the first position noted.

One hundred and seventy one animals, which all formed part of the same cluster on 17 Oct, were individually marked by attaching plastic tags to their shells, and their location inside a grid system was recorded about once every two days during LWs. In addition, it was noted whether they were clustered or scattered, as well as their faithfulness to a particular cluster. Data were compared with 108 marked hermits

dwelling in a different area. At the end of observations (9 Nov), marked animals, when possible, were captured and sacrificed. They were sexed and measured (shield length) to 0.1 mm with an ocular micrometer. Occupied shells were also measured to 0.1 mm from apex to siphonal canal with a caliper, and extent of breakage noted. In two other clusters, 296 and 198 animals were marked on their shells with spots of nail-polish. Their dispersal within the habitat was evaluated by measuring the distance covered from the previous record for seven times in 22 LWs which followed the marking. Although the shells and not the animals themselves were directly marked, errors incurred by following shell movements were assumed to be very slight because hermits seldom switched their shells even under laboratory conditions.

The timing of hermit dispersal and aggregation at ebb and flood tides respectively was recorded on 19 Oct by placing two 35-cm lines spaced 110 cm apart between aggregating and foraging areas, at a distance of 50 cm from the clustering site. Animals passing through these lines were counted for one min every two min from 7:30 to 13:40.

The text and figures give mean values  $\pm$  standard error (SE). When the scores appeared to be drawn from a normally distributed population, parametric statistical techniques were used. Otherwise, statistical inference was made through nonparametric tests, following the methods described by Siegel (1956). The level of significance under which the null hypothesis was rejected is  $\alpha = 0.05$ .

## RESULTS

### *Focus on Clusters*

#### *Distribution over the habitat*

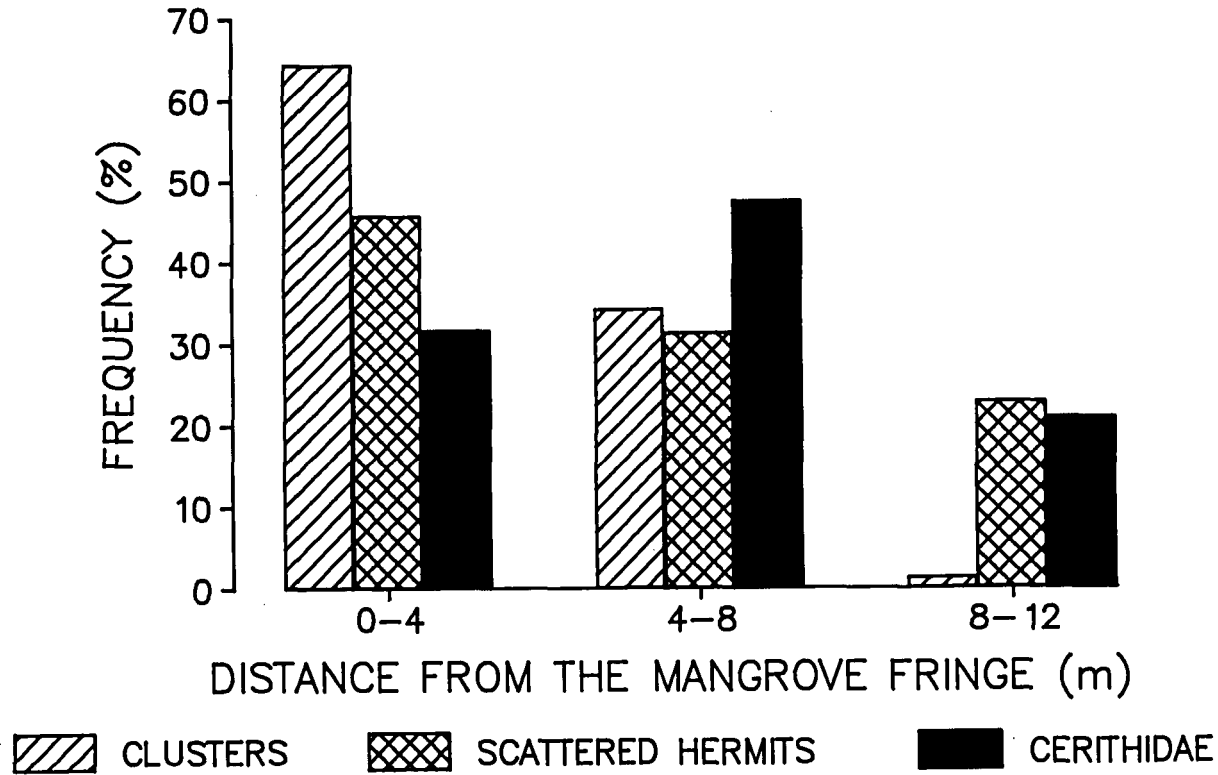
Clusters were mostly found at LW within a 4-m wide belt from the mangrove swamp seawards (comparing three strips ranging 4 m vs a homogeneous distribution,  $\chi^2 = 124.5$ ,  $df = 2$ ,  $P < 0.001$ ) (Figure 1). They prevalently developed on mangrove aerial roots (vertical clusters: VCs), but some also occurred in open areas (horizontal clusters: HCs) (Figure 2). In contrast, live molluscs (mostly Cerithidae, Vannini et al., in preparation), which *C. laevimanus* uses for shells, were more frequent at 4–8 m from the mangrove edge ( $\chi^2 = 10.801$ ,  $df = 4$ ,  $P < 0.05$ ). Scattered hermits were uniformly distributed over the plateau (vs homogeneous distribution:  $\chi^2 = 8.979$ ,  $df = 4$ , ns), but were never found inside the forest. In the latter two cases, statistics were applied on the basis of an arbitrary evaluation of animal frequency (few, some, many), computed for each 80-cm long strip.

Along the x-axis, clusters were patchily distributed over the habitat. However, their distribution reflected both those of live Cerithidae (Spearman's rank test:  $r_s = 0.599$ ,  $t = 4.012$ ,  $df = 18$ ,  $P < 0.001$ ), and scattered conspecifics (Spearman's rank test:  $r_s = 0.609$ ,  $t = 4.13$ ,  $df = 18$ ,  $P < 0.001$ ) (Figure 3).

At 4–8 m from the mangrove fringe, no relationship was found between substrate type (sand, mud, and rock) and mollusc frequency (Kruskal-Wallis one-way analysis of variance:  $H = 1.367$ ,  $df = 2$ , ns). Otherwise, clusters were more frequently found on a hard substrate ( $H = 19.157$ ,  $df = 2$ ,  $P < 0.001$ ), and scattered specimens on sand and rocks ( $H = 12.523$ ,  $df = 2$ ,  $P < 0.01$ ).

### *Number and Position*

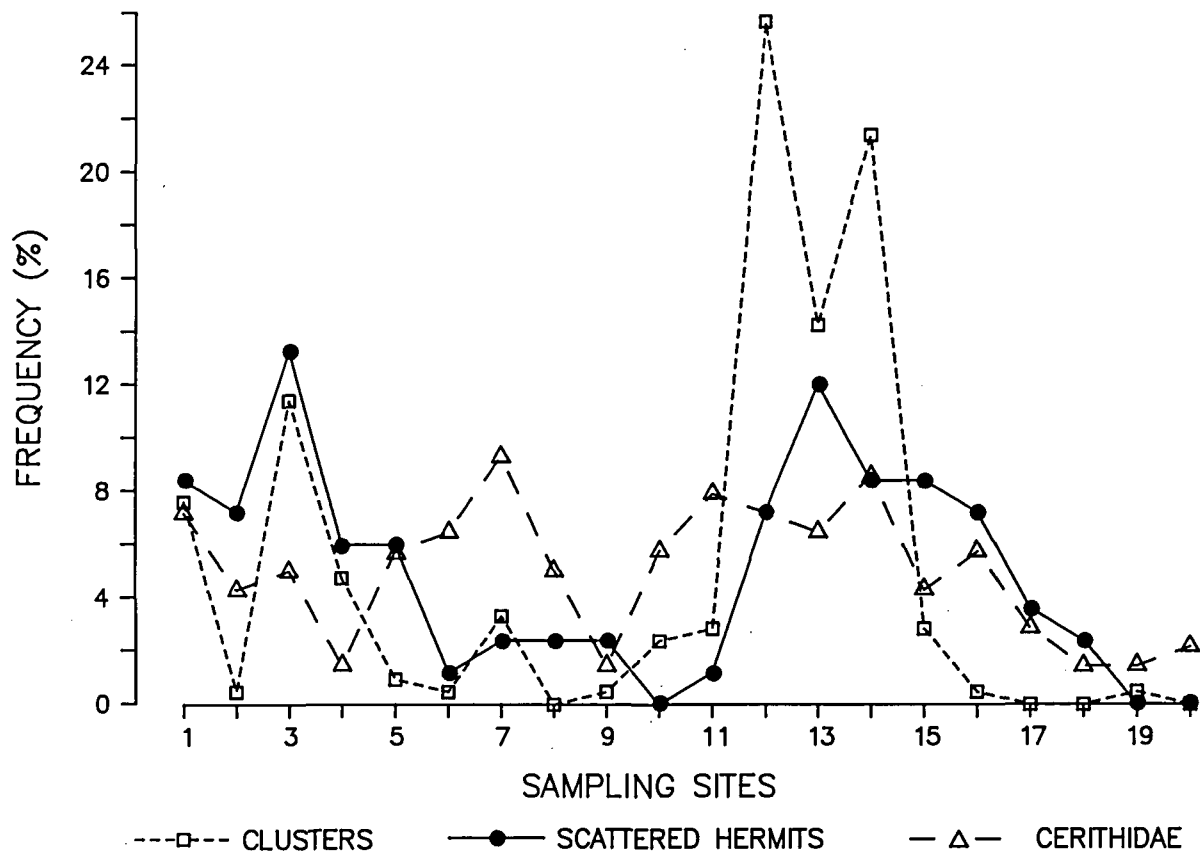
The number of clusters was steady over a synodic cycle (along a 150-m long transect,



**Figure 1** Frequency distributions of clusters, scattered hermits and live *Cerithidae* (whose shells were the most often used by *C. laevimanus*) along 350 m-long transect alongshore compared among 4 m-wide stretches from the mangrove fringe seawards. Records were taken during LW. The overall number of clusters recorded in this stretch was 35, while the frequency of scattered hermits and *Cerithidae* was scored on the basis of a qualitatively estimation (none=0, few=1, some=2, many=3).



**Figure 2** Clusters harbouring on the prop roots of mangroves (vertical clusters, VCs) (top), and those developing in open areas (horizontal clusters, HCs) (bottom).



**Figure 3** Frequency distribution along the x-axis of clusters (overall number=110), scattered hermits, and live Cerithidae at LW. Sampling sites were spaced 80 cm apart.

14 at NT vs 15 at ST), and did not differ for diurnal and nocturnal LWs (on 13 Oct: 20 vs 20).

The relationship between the relative position of VSs and the time lag from ST was not significant ( $r=0.039$ ,  $df=152$ , ns) (Figure 4), and also remained constant during diurnal and nocturnal LWs ( $t=1.16$ ,  $df=202$ , ns). On the contrary, animals which clumped in the open seemed to have different clustering sites at day and night, usually moving under cover during the day or joining nearby VCs.

### *Size and Shape*

Cluster size was taken as a measure of the frequency of clumping hermits (in fact, it was significantly related with the number of constituent specimens,  $r=0.89$ ,  $df=34$ ,  $P<0.005$ , as it was revealed by counting the hermits of each cluster the last day of study and comparing it with clusters' size). Cluster size did not significantly change over a semi-lunar tide cycle in either VCs (ANOVA, considering the days for each row and diurnal and nocturnal LWs for each column:  $F=0.35$ ,  $df=120$  &  $11$ , ns) or HCs (ANOVA:  $F=1.08$ ,  $df=11$  &  $96$ , ns) (Figure 5). Accordingly, the number of aggregating animals per cluster (ranging from 100–2500) analyzed along a 150-m long transect did not differ between neap and spring tides (NT, Oct 20: average number =  $176.4 \pm 53.6$ ,  $n=14$ ; ST, Oct 26: average number =  $119.8 \pm 36.6$ ,  $n=15$ ; Student's t-test:  $t=0.88$ ,  $df=27$ , ns). While cluster size on mangrove roots remained unchanged for diurnal and nocturnal low tides (diurnal LWs: average size =  $494.1 \pm 49.5$  cm<sup>2</sup>,  $n=72$ ; nocturnal LWs: average size =  $507.0 \pm 46.6$  cm<sup>2</sup>,  $n=66$ ; Student's t-test:  $t=0.19$ ,  $df=136$ , ns; ANOVA:  $F=0.01$ ,  $df=1$  &  $120$ , ns), there was a significant difference in HCs (diurnal LWs: average size =  $144.58 \pm 15.82$  cm<sup>2</sup>,  $n=60$ ; nocturnal LWs: average size =  $213.12 \pm 17.3$  cm<sup>2</sup>,  $n=60$ ; Student's t-test:  $t=2.92$ ,  $df=118$ ,  $P<0.01$ ; ANOVA:  $F=8.64$ ,  $df=1$  &  $96$ ,  $P<0.01$ ).

On the mangrove roots, cluster shape remained extraordinarily constant during the study period (Figure 6), which cannot be explained by substrate constraint alone.

### *Focus on Hermits*

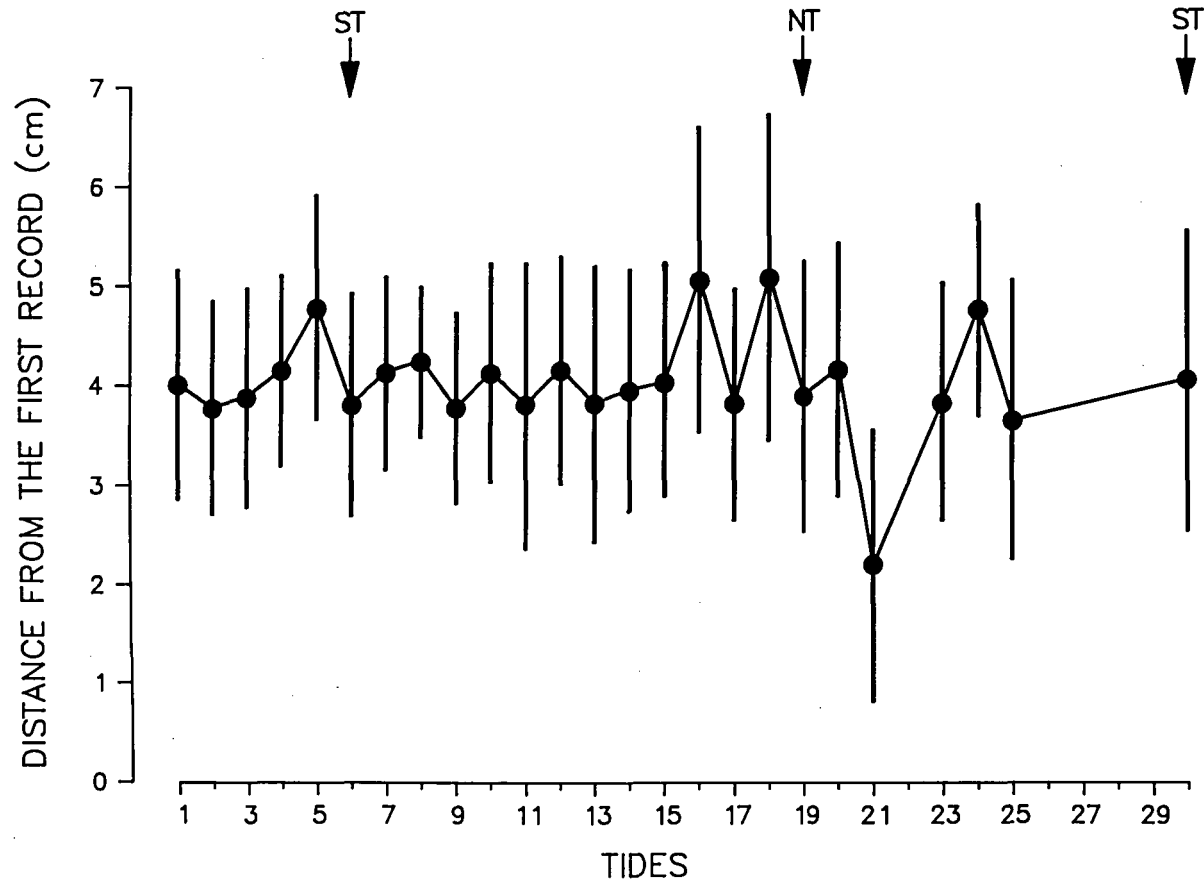
#### *Cluster membership*

Within each cluster, shell size (we measured at least 50 randomly collected shells per cluster) seemed to be homogeneous, varying little from the mean value (Figure 7). In 22 monitored clusters, frequency distributions of mean size ( $\chi^2=8.426$ ,  $df=2$ ,  $P<0.02$ ) and standard deviations ( $\chi^2=15.319$ ,  $df=1$ ,  $P<0.001$ ) significantly differed from those obtained with a simulation model where observed shell sizes were randomly distributed among the different aggregations.

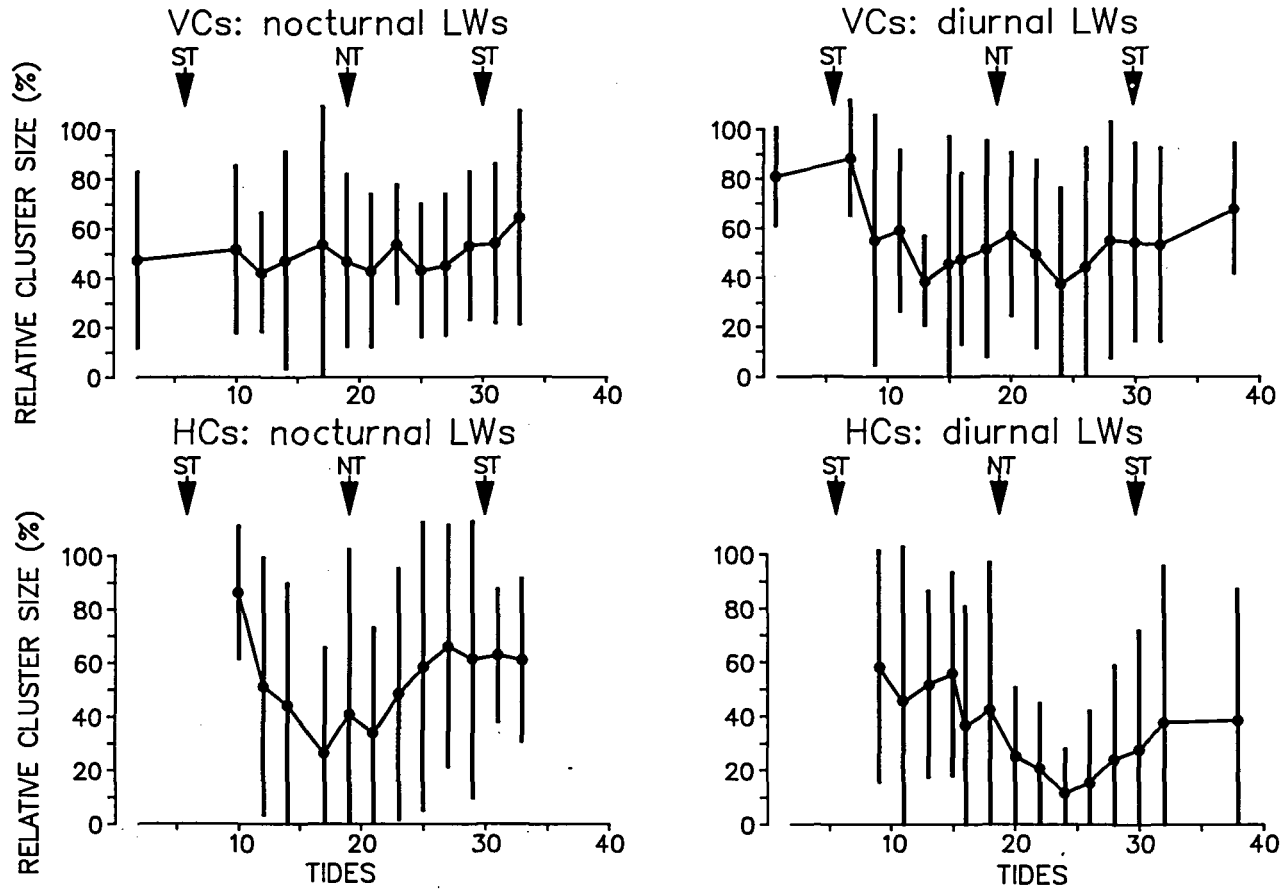
In 91.18% of LWs ( $\pm 2.16$ ,  $n=95$ ), marked animals (only specimens captured more than five times were considered) were found clumped, with no difference between sexes (males:  $90.08 \pm 3.45\%$ ,  $n=13$ ; females:  $92.13 \pm 2.80\%$ ,  $n=15$ ; after arcsine square transformation:  $t=0.4$ ,  $df=26$ , ns). However, cluster attachment was negatively related to hermit size ( $r=-0.319$ ,  $df=26$ ,  $P<0.05$ ) and shell size ( $r=-0.395$ ,  $df=26$ ,  $P<0.025$ ), but did not depend on shell breakage (Sperman's rank correlation test:  $t=1.739$ ,  $df=26$ , ns).

In one monitored area, the frequency of hermit transfer from one cluster to another was about 56%, regardless of sex (males:  $59.6 \pm 7.40\%$ ,  $n=11$ ; females:  $51.02 \pm 7.97\%$ ,  $n=9$ ;  $t=0.86$ ,  $df=18$ , ns). Neither was transfer correlated with hermit size ( $r=-0.03$ ,  $df=18$ , ns), shell length ( $r=0.118$ ,  $df=18$ , ns) or shell



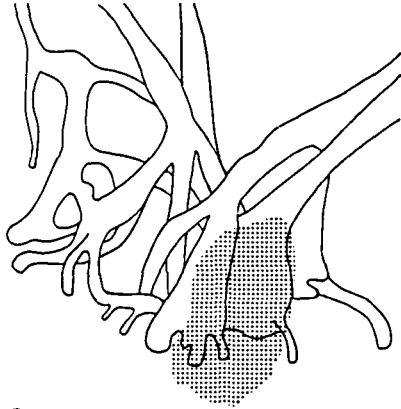


**Figure 4** Relative position of the central point of vertical clusters (average  $\pm$  SE,  $n=5$ ) along a semi-lunar tide cycle. ST= spring tide. NT= neap tide.

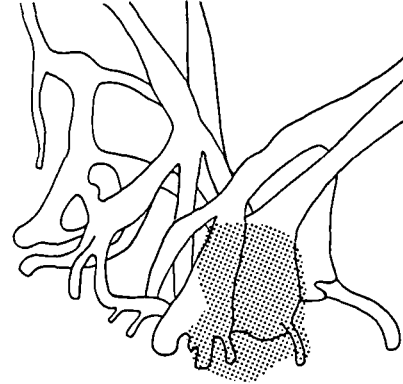


**Figure 5** Relative cluster size, i.e. the percentage with respect to the maximum size recorded during the study period (average  $\pm$  SE,  $n=5$ ) along a semi-lunar tide cycle, compared between vertical clusters (VCs) and horizontal clusters (HCs) during nocturnal and diurnal LWs. ST=spring tide. NT=neap tide.

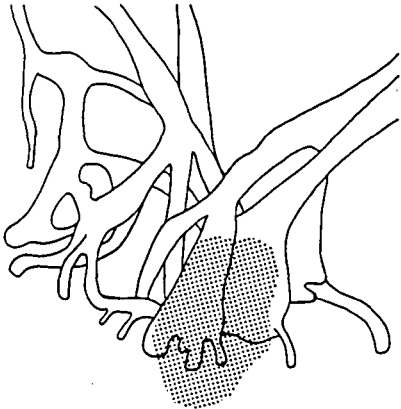
16 October: diurnal LW



18 October: diurnal LW



24 October: nocturnal LW

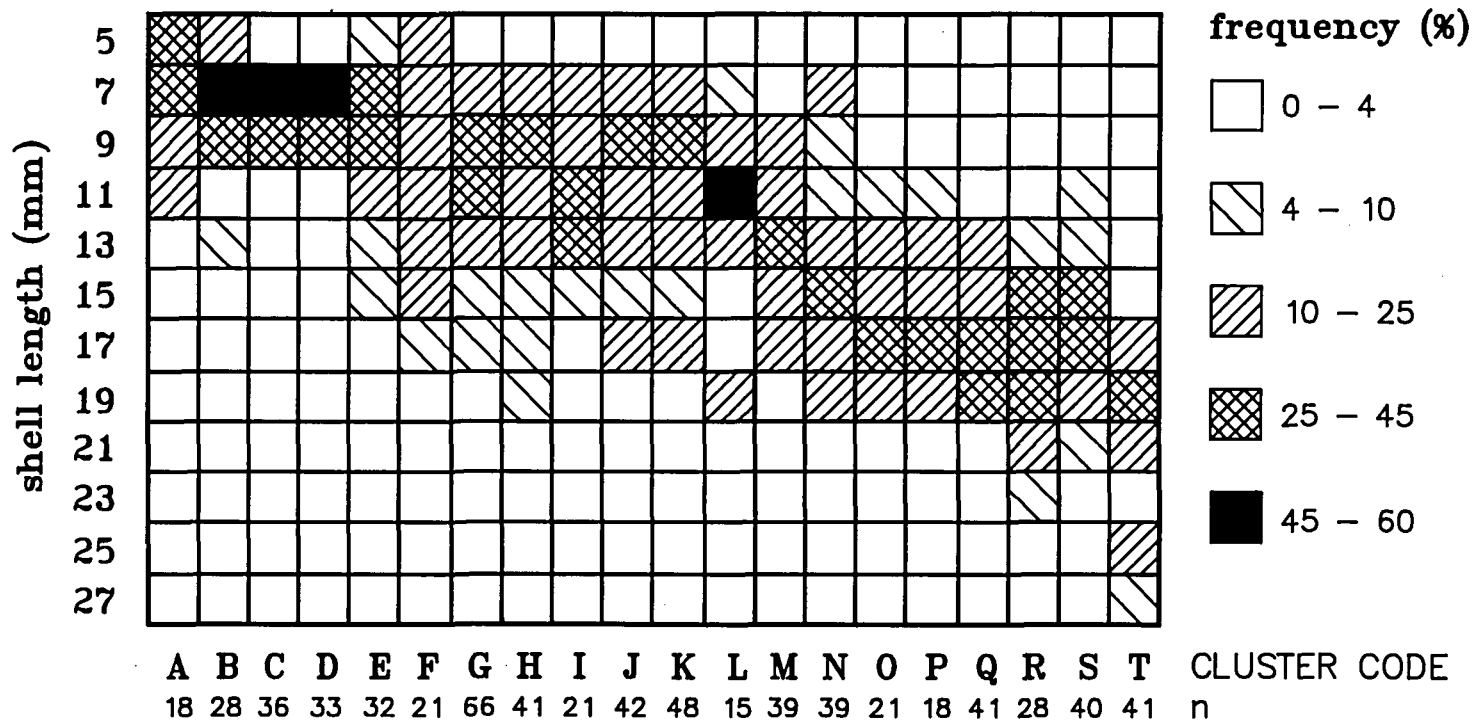


28 October: nocturnal LW



30 cm

**Figure 6** Constancy of shape of a vertical cluster during the study period.



**Figure 7** Frequency distribution (%) of length of those shells used by hermits taking part to the same cluster (columns). For each of the 20 clusters examined, code and sample size are indicated.

breakage ( $r=0.226$ ,  $df=18$ , ns). Similar results were obtained in a second monitored area (males vs females:  $18.66 \pm 5.63\%$  vs  $17.31 \pm 4.32\%$ ,  $t=0.06$ ,  $df=41$ ; hermit size:  $r=-0.098$ ,  $df=40$ , ns; shell length:  $r=0.02$ ,  $df=40$ , ns; shell breakage:  $r=-0.13$ ,  $df=40$ , ns). In the latter case, however, a significantly lower exchange rate was recorded ( $55.74 \pm 5.37\%$ ,  $n=20$ , vs  $17.82 \pm 3.39$ ,  $n=42$ ;  $\chi^2=42.692$ ,  $df=4$ ,  $P<0.001$ ).

### *Movement and Dispersal*

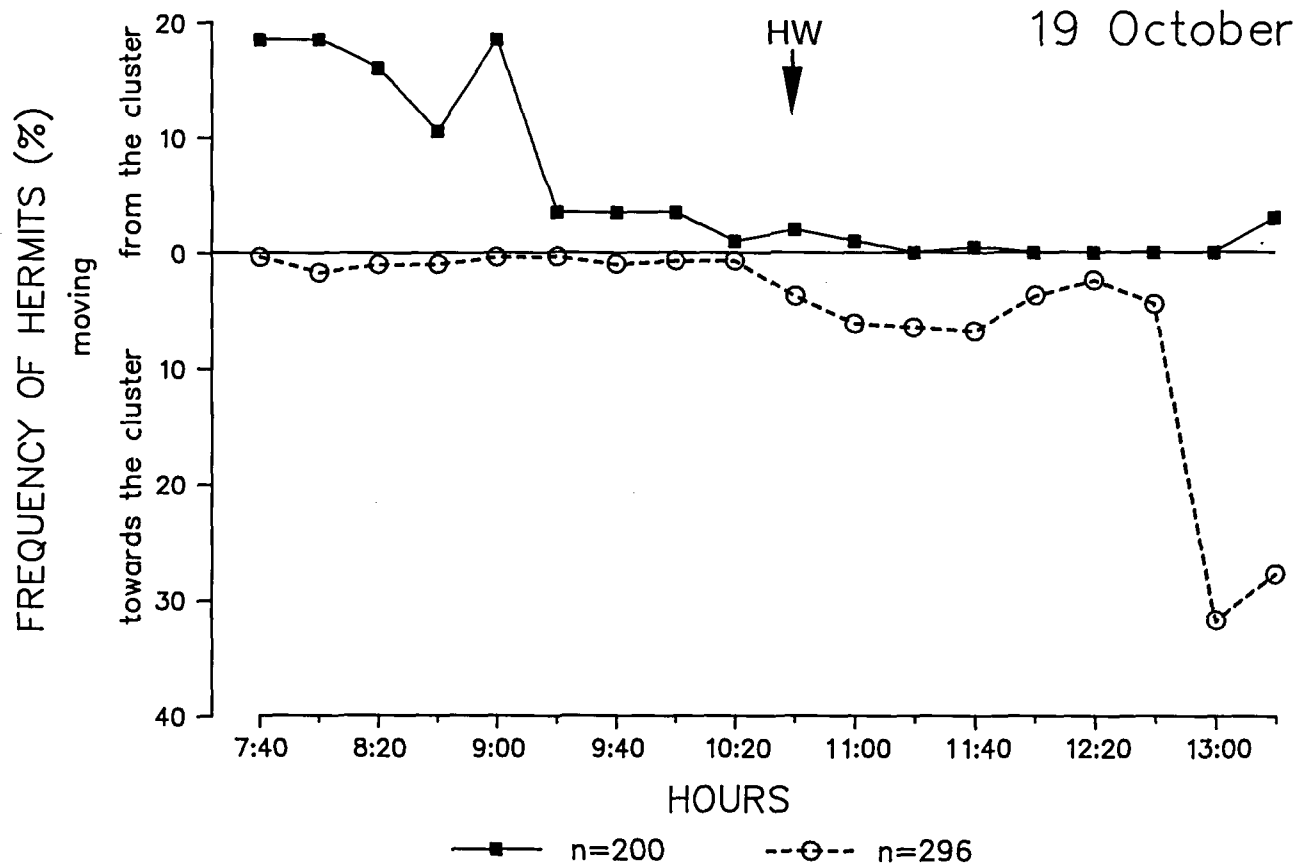
Tidal rhythms account for the formation and dispersal patterns of *C. laevimanus*' clusters. The animals began to move as soon as their clusters were sprinkled with water, first walking over conspecifics, touching their shells and sometimes performing rapping motions (the initiator holds the other crab by its shell with its ambulatory legs and lifts its own shell 4–10 mm above its partner, then it rapidly brings it into contacts with that of the other crab; Hazlett, 1966). Then, as the depth of water increased, they left their clusters, marching in line towards their foraging areas. These were spots of vegetable debris 3–5 m from the aggregating sites, whose dry weight organic content averaged 39% and 0.58% for carbon and nitrogen respectively (Vannini et al., in preparation). At HWs, the clusters sometimes broke up completely, but more often a number of animals (ranging from 20–350) remained behind on the mangrove roots, either keeping still or foraging on the encrusting red algae. Foraging activity on vegetable debris was more intense when the water level increased, it stopped around maximum HW and recommenced when the water slowly receded. About 2 h after the highest tide level, most hermits returned to the aggregating site, following similar routes to their outgoing journey (Figure 8). When the area was completely exposed to air, a few animals were seen resting in the foraging places either isolated or in small and temporary clumps.

Specimens spent 1–5 h away from their clusters. Locomotory speed was the same in outgoing and return journeys ( $t=1.35$ ,  $df=9$ , ns), averaging  $8.6 \pm 1.6$  cm/min ( $n=5$ ) and  $11 \pm 3.9$  cm/min ( $n=6$ ) respectively.

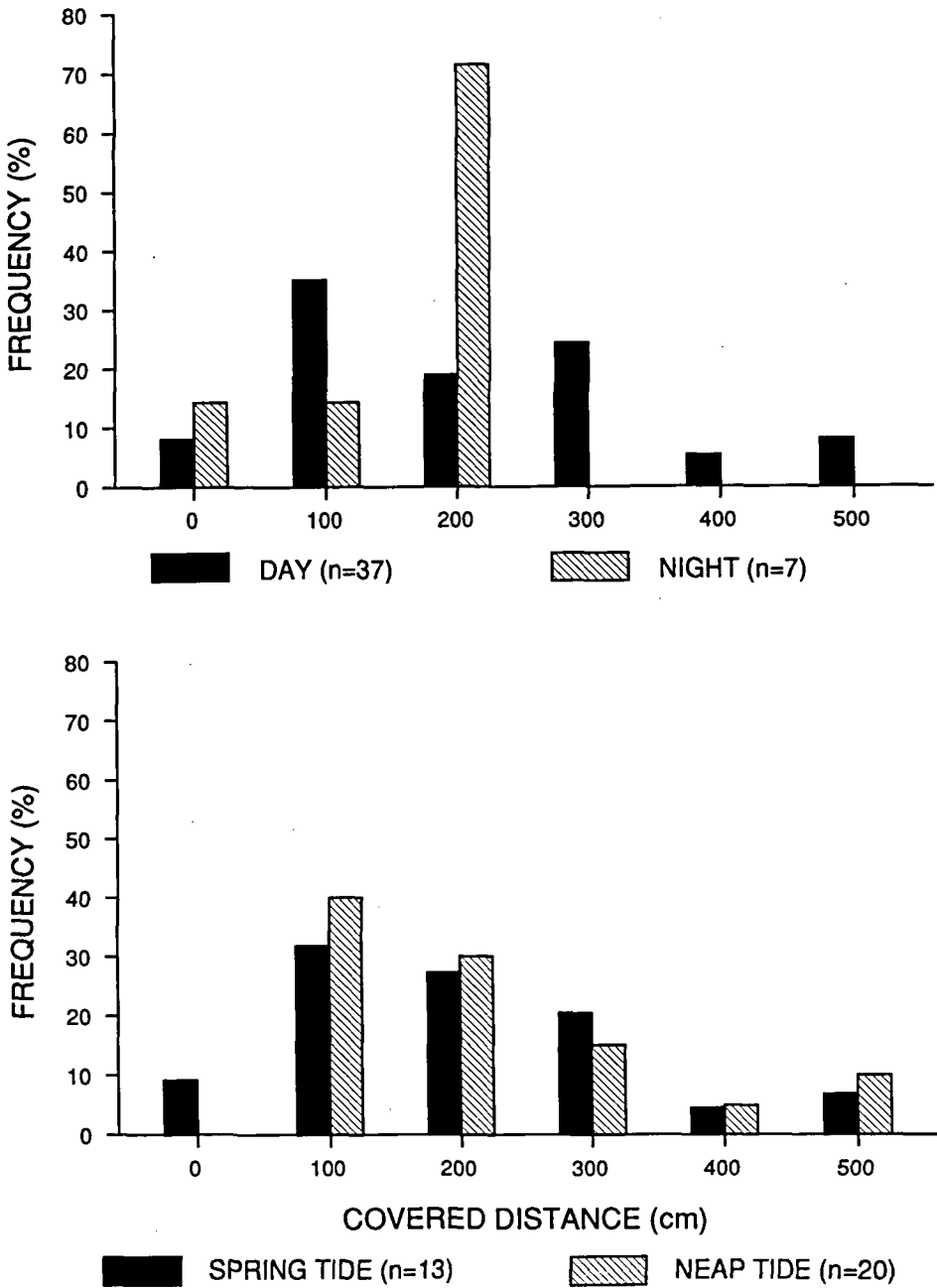
The extent of displacements between successive tides did not depend on the time of day (night: average =  $104 \pm 19$  cm,  $n=7$ ; day: average =  $151.3 \pm 20.9$  cm;  $t=0.95$ ,  $df=42$ , ns), or the position within the synodic month (spring tides: average =  $165.7 \pm 36.1$  cm,  $n=13$ ; neap tides: average =  $150.3 \pm 28.1$  cm,  $n=20$ ;  $t=0.33$ ,  $df=31$ , ns) (Figure 9).

The percentage of marked hermits still participating in their original cluster decreased significantly with successive tides, from 76.19% one tide after the first capture to 14.55% after 11 tides (after arcsine square transformation:  $r=-0.75$ ,  $df=4$ ,  $P<0.05$ ), but about 99% animals always remained within 2-m<sup>2</sup> area around their original aggregating sites ( $r=-0.212$ ,  $df=4$ , ns).

Dispersal was not related to time in either sex (males:  $r=0.078$ ,  $df=75$ , ns; females:  $r=0.122$ ,  $df=49$ , ns), neither did the sexes differ in dispersal extent (males:  $b=0.67$ ; females:  $b=1.749$ ;  $t=0.528$ ,  $df=126$ ). No difference in distance covered was recorded between the two sexes 39 tides after the first capture (males: average =  $232.1 \pm 33.4$  cm,  $n=9$ ; females: average =  $257.9 \pm 74.1$  cm,  $n=9$ ;  $t=0.32$ ,  $df=16$ , ns). Distance only increased with hermit size in the males ( $r=0.608$ ,  $df=7$ ,  $P<0.025$ ; in females:  $r=-0.117$ ,  $df=7$ , ns), but with the degree of shell breakage in both sexes (males:  $r=0.585$ ,  $df=7$ ,  $P<0.05$ ; females:  $r=0.641$ ,  $df=7$ ,  $P<0.05$ ), while it was not influenced by the shell length (males:  $r=0.327$ ,  $df=7$ , ns; females:  $r=-0.373$ ,  $df=7$ , ns).



**Figure 8** Frequency distribution (%) of hermits moving from the clustering site (top) during flood tide, and towards it (bottom) during ebb tide. HW fell at 10:42.



**Figure 9** Frequency distributions (%) of the displacement performed by individually marked hermits during diurnal and nocturnal HWs (top) and spring and neap tides (bottom).

To understand whether space utilization resulted from random dispersal within the habitat or, on the contrary, it was ruled by active maintenance of position, we simulated two random walks with the computer (100 iterations for 40 successive tides), taking the frequency distribution of distance covered between two successive LWs as unitary steps. The first model was run assuming there were no constraints on hermit movement, i.e., it could develop in all the directions of the mangrove swamp. In the second, the edge of the forest (fixed 5 m from the starting point) represented an obstacle to hermit displacement: collisions against it were considered elastic, causing a rebound towards the sea. We then plotted average displacements against time and compared the curves obtained from the computer with the field data (Figure 10). The two models significantly differed from each other in their parameters (b:  $t=13.187$ ,  $df=78$ ,  $P<0.01$ ; a:  $t=12.004$ ,  $df=79$ ,  $P<0.01$ ). Expected values for the first random walk differed from those observed in dispersal speed (b: 0.023 vs 0.315,  $t=12.075$ ,  $df=54$ ,  $P<0.01$ ) and distance from first position recorded (a: 1.196 vs 4.162,  $t=14.747$ ,  $df=55$ ,  $P<0.01$ ). The second model, on the contrary, seemed to forecast that zonal constraints alone could account for the low dispersal speed observed in the field (b: 0.023 vs 0.06,  $t=1.704$ ,  $df=54$ , ns), but could not justify the short distance covered from the starting point (a: 1.196 vs 4.358,  $t=14.477$ ,  $df=55$ ,  $P<0.01$ ). Similar results were obtained when the mangrove fringe was set at 3 m from the aggregating site (a: 1.195 vs 3.651,  $t=13.923$ ,  $df=55$ ,  $P<0.01$ ; b:  $t=1.866$ ,  $df=54$ , ns).

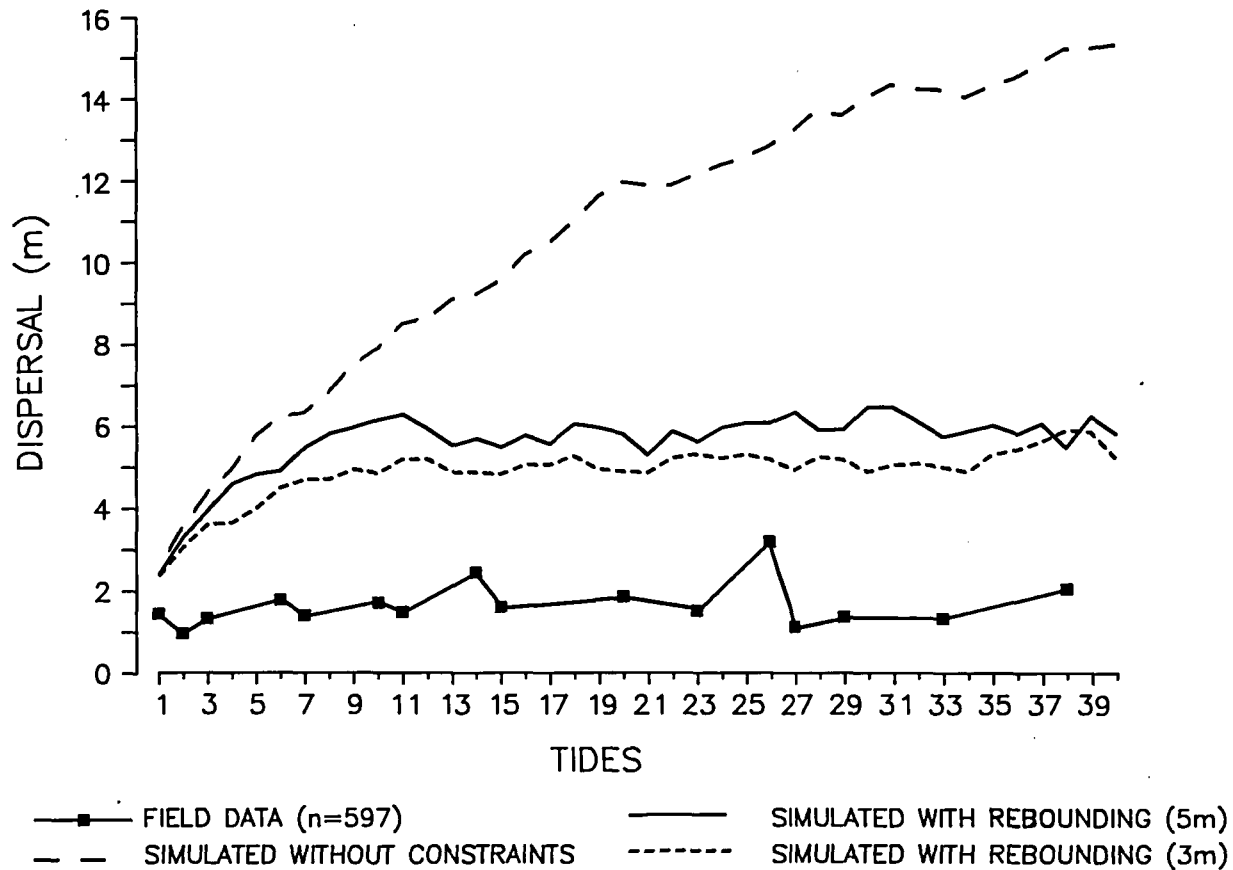
## DISCUSSION

In the Mida Creek mangrove swamp (Kenya), the dense aggregations composed of hundreds of *C. laevimanus* were subject to rhythmical breakdown and buildup with the rise and fall of the tides. The short-term activity of clustering behaviour can be divided into temporal units scheduled in the following sequence:

- 1) Clumping when exposed at low tide, either on the aerial props of mangroves or in the open. Animals were seen resting in physical contact with each other.
- 2) "Social" activity with the incoming flood tide, when hermits moved around the disgregating cluster, and could be seen grazing on conspecifics (shell cleaning), touching their shells, and sometimes performing rapping motions. Mating and shell exchange are presumed to occur in this phase (Snyder-Conn, 1981).
- 3) Dispersal when the water was still shallow, most animals migrating in lines towards foraging areas along paths up to 10-m long. There, they were seen scavenging on patches of vegetable debris (mangrove leaves, seeds, and twigs) which were relatively site-constant during the study period. Foraging was interrupted when the water level reached its maximum.
- 4) Returning home with receding tides, when hermits moved in crowded groups towards the aggregating sites and rebuilt their clusters.

From this organized activity, two main facets of space utilization in *C. laevimanus*' clustering emerge. On the one hand, hermits adopt an "isospacial" strategy (Vannini and Chelazzi, 1985), because they remain within a narrow belt along the sea-land axis, with alternating exposure to air and water. In contrast to "isophasic" animals, which follow oscillations in the medium, energy expenditure for locomotion is reduced in isospacial species. Actually, hermits seem to be preadapted to this





**Figure 10** Comparisons between hermit dispersal recorded in the field and those obtained through simulated random-walks where either no constraints impeded hermit movement or the mangrove fringe (at 5 or 3 m from the starting point) were fixed to be an obstacle to hermits' displacement. In these latter cases, collision were thought to be elastic.

strategy due to their ability to cope with both physical environmental factors (dehydration and overheating) and abrupt changes in these extreme conditions (Reese, 1969). On the other hand, feeding in *C. laevimanus* can be classified under the "central place foraging" model first proposed for intertidal chitons and gastropods (Chelazzi et al., 1988), because the hermits rest in a definite spot to where they home after each feeding move. Ecological significance and operational aspects relative to "homing behaviour" in *C. laevimanus* still remain puzzling features of this spatial strategy.

Similar clustering and dispersal tidal rhythmicity is reported in *C. digueti* at Puerto Peñasco, Mexico (Snyder-Conn, 1980), and in *C. virescens* and *Calcinus laevimanus* at Gesira, Somalia (Gherardi and Vannini, 1989), but these species inhabit rocky shores and hide in crevices (sometimes taking refuge in mass in the same hole) at HW. They probably thus avoid predatory pressure there (from fishes, octopuses, and crabs; Reese, 1969), as well as their removal and drift caused by wave action.

In contrast, in the habitat we are concerned with here, current strength is low and there is certainly no risk to foraging hermits of being washed away at HW. However, they are vulnerable to predators active during high tide. The most proficient is the portunid *Thalamita crenata*, which was seen adopting a sit-and-wait strategy, attacking *C. laevimanus* as it moved away from its aggregation site to foraging areas. Moreover, hermit remains were also found in the stomach content of the sedentary xanthid *Ozius guttatus* (Vannini, personal communication). Aquatic predation was similarly high for *C. panamensis* dwelling in mangrove estuaries in Costa Rica where puffer fishes, as well as portunid, xanthid and grapsid crabs were presumed to come into contact with hermits as they forage among the mangrove roots (Borjesson & Szelistowski, 1989). Shore birds might feed on hermit crabs, but in the study area they all foraged over 4-m away from the mangrove fringe. Hermit crab remains have never been reported in bird stomachs in literature (Reese, 1969).

The rationale here is that in *C. laevimanus* the advantages coming from longer available feeding times outweigh the costs of higher predation risks incurred from long exposure to the most formidable predators. In turn, the time actually devoted to foraging and the quality of food sources seem critical parameters in the energy balance of these intertidal hermits.

Contradicting any general pattern, the outstanding feature of this species' spatial behaviour is its flexibility: first, some crabs (mostly ovigerous females, Vannini et al., in preparation) did not leave their aggregating site and were content to graze on lower energy-providing algal layers covering mangrove roots; second, the time spent by hermits outside a cluster varied highly among individuals, ranging from 1–5 h; then, when the tide receded, several remained scattered or clung to one another in small clumps within the foraging areas. Moreover, some individually marked animals which had been constantly followed in their movements for successive tides were found isolated from their conspecifics in about 10% of LWs, and most frequently they were the largest in size and wore the longest shells.

Environmental stimuli appeared to play primary roles in determining the rhythm of activity within tidal cycles. Clustering animals were activated by sprays of water (also artificially induced), their migration was triggered off by submergence in a critical depth of water, and foraging activity was heightened during ebb and flood tides when the current was more intense. In the laboratory, both submersion and current enhanced activity on substrate surfaces in *C. digueti* (Snyder-Conn, 1981) and in the Mediterranean *C. erythropus* and *Calcinus ornatus* (Gherardi, 1990). Whether these factors work for *Zeitgeber*n or are merely releasing stimuli, and how

endogenous and exogenous patterns interact to regulate correct timing of activity are however still unexplored questions.

If we look at the mangrove swamp from a diachronous view, the habitat can be depicted as a "sea" of variability, like other intertidal ecosystems (Hazlett, 1988). The temporal and predictable pattern of regular variation in water level superimposed on a lunar cycle is complicated by seasonal and annual patterns, in addition to storms and other climatic events which are not easily foreseen by organisms. The physical location of the intertidal zone can also move quite easily, sometimes slowly and under a regular regime, but often over great distances as a result of current patterns and physical features nearby (river inputs, rocky promontories, etc.).

In this setting which has often changed as a result of spatio-temporal variability of environmental parameters, the regular clustering in *C. laevimanus* seems to be an odd exception. Over a semilunar tidal cycle at least, aggregations remained stable in number and were strictly site-constant (certain cluster sites lasted for several months in *C. digueti*; Snyder-Conn, 1980; space stability was also shown in *C. virescens* and *Calcinus laevimanus*; Gherardi and Vannini, 1989). If we exclude clumps developing in the open, cluster size was relatively independent of both daily timing and tidal progression (in contrast, clusters were significantly more crowded during both nocturnal and syzygial tides in *C. virescens* and *Calcinus laevimanus*; Gherardi and Vannini, 1989), and their shape appeared extraordinarily stationary with time. When our focus shifted to individual hermits, it was apparent that the animals frequently changed their aggregations regardless of sex, size and shell status, but they always moved to another group whose range of shell sizes matched the one they wore. Displacements between clusters also occurred within a limited space in the habitat (dispersal never exceeded 2 m), even though both sexes were capable of covering more than 10 m during their foraging excursions. However, the average distance covered each tide seemed to be positively related to hermit size (by contrast, lack of a size effect has been reported by Hazlett, 1983, in *C. tricolor* and *Calcinus tibicen*) and shell status (the species of shell inhabited significantly affected *C. tricolor*'s extent of movement, Hazlett; 1983).

Our last remark is that the main outcome of this descriptive analysis on clustering in *C. laevimanus* is that more problems have been raised than answered, and consequently new avenues of research have been opened on the proximate and ultimate factors underlying this behaviour.

First, homing accuracy (often deterministic; Chelazzi et al., 1988) raises the question on the nature of the cues involved in the orienting performance of hermits, whether they are internal, pertain to the macrosystem, or are related to the microsystem onto which the animals move. Behavioural mechanisms working against passive diffusion within the habitat must be summoned to explain the differences between field data and the results from random walk models. These anti-dispersal mechanisms certainly allow long-term stability in *C. laevimanus*' zonation, as well as its contagious distribution over the mangrove swamp. Use of the habitat also tended to be patchy in other hermit crab populations dwelling in both sandy and rocky tropical shores (Vance, 1972; Vannini, 1976; Scully, 1979).

Second, the constancy of *C. laevimanus*' clusters in time and space seems to be opposite to habitat use found in the sympatric *C. longitarsus* (Gherardi et al., 1989), whose movement patterns consist of high locomotion speed, path linearity, and "one way" displacement along shore. Future research must further compare the life histories of these taxonomically related species which are subject to similar

environmental pressures. Besides, more intense efforts must be devoted to open the ecological black box of the adaptive value of spatial strategies (either site-attachment or nomadism) in mangrove-dwelling hermit crabs.

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