

Burrowing activity in the sand-bubbler crab, *Dotilla fenestrata* (Crustacea, Ocypodidae), inhabiting a mangrove swamp in Kenya

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Abstract

Several species of crabs belonging to the family Ocypodidae are burrowers; they inhabit tropical sandy and muddy shores, including mangrove swamps, exposed to extreme conditions of intertidal areas. *Dotilla fenestrata*, the only East African representative of the subfamily Scopimerinae, exhibits high flexibility in its burrowing activity. Only part of the population has an exclusively burrow-orientated activity, whereas most individuals form dense aggregations or droves, that during the phase of diurnal low water move away from the normal distribution zone. Burrows are built according to two different architectural designs, the feeding-trench burrow and the igloo, which then constitute their territory. A resident will lose a contest for the burrow when the attacker is larger. When the ground is uncovered at low tide, emergence can be delayed or even fail to occur, and some crabs remain buried during the entire low water period. Only 50% of crabs remain faithful to the original burrow, while the others either leave it to occupy an empty one or dig a new burrow, or join the wandering drove. The spatial distribution of burrows from the high water neap level (our reference point) to the sea, differs during both spring and neap tides, and both diurnal and nocturnal tides. The differences may be due partly to the change of physical conditions, such as drainage and substrate grade (although within a mangrove swamp these do not follow a consistent gradient), but mostly may be related to the trade-off between the benefits and costs of living at different intertidal levels. With its burrowing and feeding activity leading to the re-deposition of excavated and pseudofaecal pellets, *Dotilla* plays a role as a sediment mover in this very specialized habitat. The results obtained from this study are compared with those reported in other ocypodids.

Key words: burrowing, Ocypodidae, *Dotilla fenestrata*, mangrove swamps, East Africa

INTRODUCTION

Species of crabs of the subfamily Scopimerinae (Brachyura, Ocypodidae) are common dwellers of tropical sandy and muddy shores (Hartnoll, 1973). They also inhabit mangrove swamps. During high water these crabs remain buried, emerging only after the tide has receded; they then feed upon surface deposits and produce pseudofaecal pellets. Five of the seven genera of Scopimerinae are restricted to muddy environments, but *Dotilla* and *Scopimera* prefer sandy shores where their specialized mouth-parts enable them to sort sand with high efficiency in order to extract the small amount of organic material (Tweedie, 1950; Ono, 1965). The sand-bubbler crab (*Dotilla fenestrata*), is the only East African representative of the Scopimerinae, occurring on the mainland from South Africa northwards to

Somalia and on Madagascar and the Comoro Islands. Further north in the Red Sea and the Gulf of Aden, this species is replaced by *D. sulcata* (Fishelson, 1971).

A number of morphological, physiological and behavioural adaptations enables these crabs to inhabit the intertidal zone and to adopt an isospacial strategy (i.e. they do not resort to mobility in order to avoid the phase that is unfavourable for them, as isophasic animals do, but remain in the intertidal zone during both high and low water, Vannini & Chelazzi, 1985). First, adaptations for a semi-terrestrial habit include the development of: (1) structures for aerial gas exchange, as tympani or gas windows (Maitland, 1986); (2) tufts or rows of setae for water uptake (Hartnoll, 1973); (3) grooves on the carapace, where water is spread out from the exhalant openings, and behavioural mechanisms for thermal regulation by evaporative cooling (Fishelson, 1983). Secondly, the crabs have adaptations for feeding on 3–4 mm thick surface deposits, with the development of spoon shaped setae on the second maxillipeds for sorting organic matter from the sand (Bigalke, 1921;

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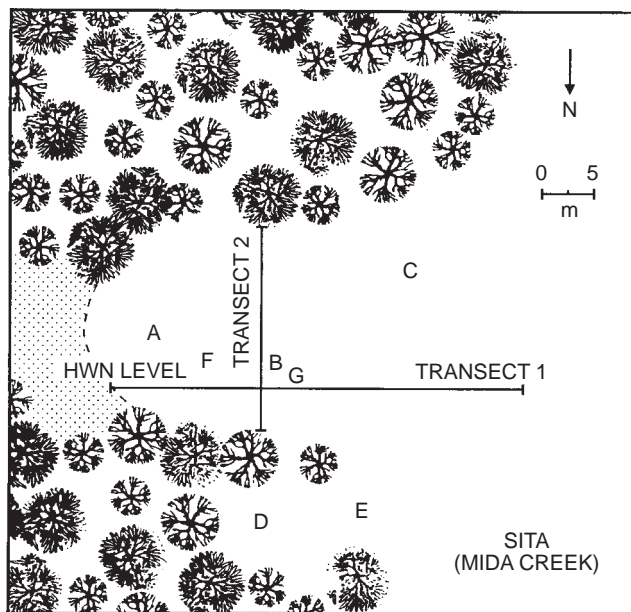


Fig. 1. The study area at Mida Creek, showing the experimental setting. Two transect lines, respectively orthogonal (transect 1) and parallel (transect 2) to the coastline, were laid; the first, 40 m long, started at the high water neap (HWN) level and the second, 20 m long, at 15 m seawards from the HWN level. A–G represent fixed quadrates measuring 60×60 cm. These were located (seawards from point 0): A at 5 m; B at 15 m; C at 30 m; D at 15 m; E at 25 m; F at 10 m; G at 17 m.

Ono, 1965; Vogel, 1984). Thirdly, behavioural adaptations have evolved for digging burrows within the intertidal zone where the sediment is suitable in particle size and organic and water content. Burrows have diverse functions: they provide refuges from disturbance, predation and thermal extremes; assure the renewal of moisture loss; mark the centre of the crabs' feeding range (Ansell, 1988). However, in most species, including *D. fenestrata*, such burrow-orientated activity is abandoned by parts of the population in favour of wandering, generally beyond the confines of the normal zone (Ansell, 1988).

We describe the burrowing activity of *D. fenestrata*, including both spatial and temporal distribution of different types of burrows, in a mangrove swamp habitat where this species has never been analysed before. The degree of the crab's fidelity to a specific burrow was also studied. The results of this study are compared with the burrowing of other representatives of the family Ocypodidae and in particular, other crabs in the subfamily Scopimerinae (genera: *Dotilla*, *Ilyoplax* and *Scopimera*) and some in the subfamily Ocypodinae (genera: *Ocypode* and *Uca*).

MATERIALS AND METHODS

Fieldwork was carried out in the mangrove swamp of Mida Creek (20 km south of Malindi, Kenya) in

November, 1995, and March–April, 1997. A small gulf facing the village of Sita was chosen because its sand banks were inhabited by a large population of *D. fenestrata*. Figure 1 illustrates our experimental setting in that area. Two transect lines were laid at this site: the first orthogonal (transect 1) and the second parallel (transect 2) to the coastline. The first, 40 m long, started at the HWN (high water neap) level (= point 0) and the second, 20 m long, started 15 m seawards from the HWN level. A–G represent fixed quadrates measuring 60×60 cm. These were located (seawards from point 0): A at 5 m; B at 15 m; C at 30 m; D at 15 m; E at 25 m; F at 10 m; G at 17 m.

Burrows were counted within 30 cm of the line at low tide: transect 1 at diurnal spring (November 8, 1995), nocturnal spring (November 23, 1995), diurnal neap (November 16, 1995), and nocturnal neap (November 16, 1995) tides; and along transect 2 the count was done at diurnal spring tide (November 9, 1995).

A, B and C are the areas where the observer recorded the behaviour of *D. fenestrata*, including spontaneous exchange of burrows, abandonment of burrows and fighting, both occasionally (using the technique of the focal animal), and *in continuum*, during the entire low water phases of November 21, 23 and 24, 1995, respectively. At A, *D. fenestrata* shared the area with 1 species of fiddler crab (*Uca annulipes*), and the substrate was mostly sand; at B, *Dotilla* was alone and the substrate was mixed between sand and mud; at C, the species changed its habitat with a second species of fiddler crab *U. vocans*, and the substrate was prevalently muddy. Behavioural observations were possible as the crabs rapidly adapt to the presence of an observer. However, we were unable to capture crabs, mark them and record either their sex or their size.

The directions of the main feeding-trenches (four 90° -wide categories were distinguished: seawards (= West); North; landwards (= East); and South) were recorded during the diurnal low waters of both spring (November 10, 1995) and neap tides (November 16, 1995), as well as during the nocturnal low water of neap tide (November 17, 1995). We used a mobile 60×60 cm quadrate (10 replications in randomly selected areas) and measured the directions with a compass.

At D and E, emergence and disappearance of the crabs were analysed at rising and ebbing tides (November 9, 18 and 23, 1995), as well as at sunrise and sunset when these occurred during low water (November 16, 17 and 18, 1995). On November 7 (diurnal spring tide) and November 15 (diurnal neap tide) 1995, at the same quadrates, the number of different types of burrows was counted throughout the low water period, once every 15 min, with 1 h of interruption. During diurnal low tide of November 25, 1995, we counted burrows opening within three 30×30 cm areas randomly chosen at distances of 5, 15 and 30 m seawards from point 0. From the same site, we dug to a depth of 10 cm and collected the crabs after washing the sand through a 1.5 mm mesh sieve. On March 27 and 28, 1997, at F and G, we measured the quantity of

sediment moved at the end of the low water phase and related this to the density of the crabs.

To analyse the sand particle size, on November 22, 1995, 10 samples of the upper 5 cm of substrate were collected every 4 m along a gradient from point 0 to the sea. In the laboratory, the sediment samples were dried at 60°C and then sieved on an automatic shaker through meshes of 500, 250, 125 and 53 µm. The quantity retained by each sieve was then weighed.

Some crabs were killed using ethanol in order to evaluate both their size (measuring the antero-lateral angle width (ALW), Clayton & Al-Kindi, 1998) and their sex. Killing was necessary to get the precise size of these very small crabs and to distinguish sex, both procedures requiring a microscope with an ocular micrometer. Otherwise, for live crabs, 3 classes of size were arbitrarily distinguished by a well-trained observer as: small (< 4 mm ALW); medium (between 4 and 7 mm ALW); large (> 7 mm ALW).

The text and figures give mean values and standard error (SE). When the scores appeared to be drawn from a normally distributed population, parametric statistical techniques were used (Zar, 1984). Otherwise, statistical inference was made through non-parametric tests, following Siegel (1956). The level of significance under which the null hypothesis is rejected is $\alpha = 0.05$.

RESULTS

Types of burrow

We distinguished four types of *D. fenestrata* burrow:

- (1) Burrows with simple apertures, nearly circular, the diameter of which averaged 8 mm (SE = 0.2, $n = 42$).
- (2) Non-structured burrows, i.e. irregular burrows with excavated pellets scattered around the aperture. The mean number of excavated pellets was 29 (SE = 2, $n = 34$) and they were oval in shape, composed of grey-black reduced sand (though the colour soon fades as a consequence of oxidation). The maximum axis of these averaged 5.1 mm (SE = 0.3, $n = 34$).
- (3) Feeding-trench burrows, i.e. well structured burrows with a nearly circular aperture circumscribed by excavated pellets (both the diameter of aperture and the number and dimension of excavated pellets were as above) plus a single trench produced by the crab's feeding activity with a mean length of 4.5 cm (SE = 0.3, $n = 42$) and limited by one or two dry-walls built with its pseudofaecal pellets. These pellets are formed by the mouth parts, from which the crab sorted out organic matter. These are picked off by one of the chelae and passed back beneath the body, being thrust posteriorly by the last two legs on the same side as the cheliped. In 43 burrows the depth of the tunnel averaged 6.3 cm (SE = 0.3).
- (4) Igloos, characterized by a 2 cm deep enlarged chamber covered by a dome composed of 2–6 superimposed rows of bricks (mean number: 32, SE = 4, $n = 13$; mean diameter: 11 mm, SE = 0.7, $n = 13$).

In addition, it was frequently observed that wandering crabs buried their bodies directly in the semi-fluid or fluid surface to protect themselves after having perceived a danger (the approaching of potential predators, e.g. birds); but after a few minutes, the crabs emerged from the mud and then re-engaged in surface activities.

Type 1 and 2 burrows were usually not inhabited during low water, and were left as the crab emerged to wander or switch burrow. Instead, type 3 and 4 burrows were occupied by *Dotilla* for the whole, or at least part, of the low tide, and are considered as active burrows. Igloos are constructed erecting a dome above the mouth of a pre-existing burrow. Following the terminology of Altevogt (1957), we also call them igloos, while Hartnoll (1973) suggests the term 'domes'. Recently, Takeda *et al.* (1996) distinguished in *D. myctiroides* vertical burrows, constructed in well-drained and firm sand, and igloos, which crabs build in semi-fluid, unstable sand. Similar constructions of wandering crabs constitute refuges from the high water. In such instances they are built on loose moist sand or in the waterlogged area, at the edge of the approaching tide; the crab rotates in the wet sand (either clockwise or anticlockwise, 49% vs. 51%, Willk test, $G = 0.04$, d.f. = 1, ns), producing a wall around and roofing this over to form a complete dome. At the approach of the tidal front, crabs inhabiting feeding-trench burrows retreat into the tunnel and plug the entrance by either a heap of pellets dragged into the opening with their trailing legs, or with sand pellets from within.

On each study site, the number of burrows does not correspond exactly with the number of crabs. Burrows were 87% (20 vs. 23) at 5 m, 69% (38 vs. 55) at 15 m and 69% (63 vs. 91) at 30 m seawards from point 0, with respect to the crabs sieved in three 30 × 30 × 10 cm turfs (the average was 75%). This difference could be the result of sharing the same burrow by more than one individual, as observed in *Scopimera proxima* (Ansell, 1988) and *Ilyoplax pusillus* (Wada, 1981). Nevertheless, our records for *D. fenestrata* showed that burrows are usually occupied and defended by a single crab.

The *Dotilla*'s digging activity results in the movement of a large quantity of sediment, which we estimated at around 900 ml/m² per day at sites where crab density averaged 120 per m² ($n = 12$).

Details of feeding-trench burrows

Feeding-trench burrows are the result of the burrow-orientated activity of *D. fenestrata*. The crab feeds along the trench, beginning next to the opening and slowly working away from it in a straight line.

These burrows aggregate, as shown by the frequency distribution of the number of burrows in 160 randomly selected sample units (15 × 15 cm quadrates) compared with the expected Poisson distribution ($\chi^2 = 17.209$, d.f. = 7, $P < 0.02$) (Fig. 2).

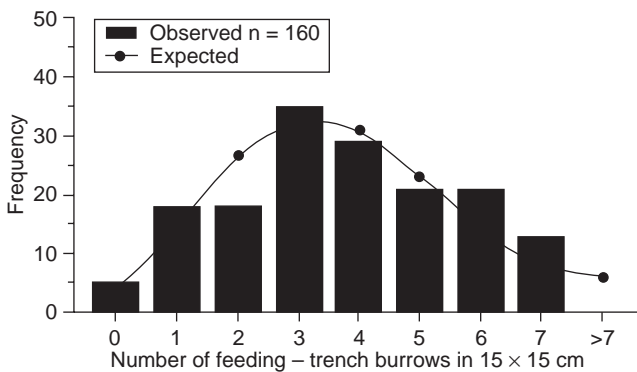


Fig. 2. The frequency distribution of the number of burrows *D. fenestrata* in 160 sample units (15×15 cm quadrates) randomly selected and compared with the expected Poisson distribution.

Aperture

A positive correlation was found between the resident's size and the hole diameter (Pearson correlation test, $r = 0.722$, d.f. = 24, $P < 0.01$).

Tunnel

This is a simple vertical tube. Out of the 38 tunnels analysed, 13% were orthogonal, 42% presented smooth loops, 39% had one sharp loop and 5% two sharp loops. The depth of the tunnel is not significantly correlated with the resident's size (Pearson correlation test, $r = 0.267$, d.f. = 27, ns), while a positive correlation was found in relation to the distance from the HWN level ($r = 0.317$, d.f. = 41, $P < 0.05$) (Fig. 3, bottom), which follows the increase in depth of the reduced layer (Fig. 3, top). Under this layer, the soil is fibrous, being composed largely of the remains of roots and other woody structures, and the crabs do not dig in it. Tunnels never reach the water table.

Trench

During the first 10 min of emergence, *D. fenestrata* may experiment with different directions in building the feeding-trench, but soon one direction is chosen and maintained throughout the whole low water period (except when the burrow's owner is replaced). As shown by recording of behaviour *in continuum*, out of 13 animals that changed the direction of the trench at least once (up to a maximum of 6 times), the angle of displacement was wide, with a mean of 73° (SE = 11°) and a range of 30 – 160° .

At spring tide, 38% of feeding-trenches were directed towards the sea (vs. a uniform distribution: Willk test, $G = 59.355$, d.f. = 3, $P < 0.001$), contrary to diurnal neap tide ($G = 4.674$, d.f. = 3, ns). As a consequence, distributions were significantly different between spring and neap tides ($G = 21.798$, d.f. = 3, $P < 0.001$), but not

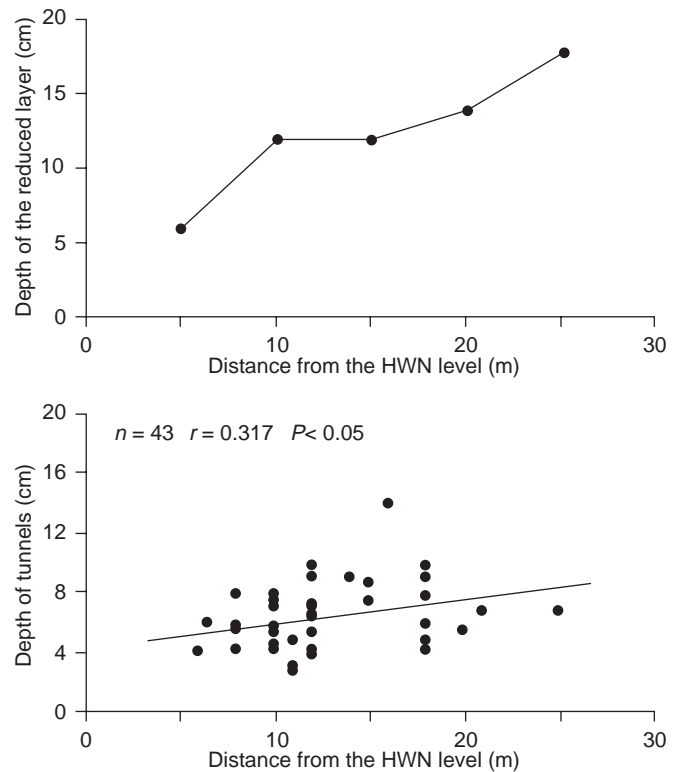


Fig. 3. Depth of the reduced layer plotted against the distance from the high water neap (HWN) level (top), compared with the relationship between the distance from the HWN level and the depth of the burrow tunnels (bottom).

between diurnal and nocturnal neap tides ($G = 1.192$, d.f. = 3, ns), as the nocturnal neap tide distribution did not differ from a uniform distribution ($G = 1.642$, d.f. = 3, ns).

Plotting the number of crabs counted in each 60×60 cm quadrate against the SE of the average direction of trenches for each quadrate, a negative correlation was obtained (Pearson correlation test, $r = 0.876$, d.f. = 18, $P < 0.01$) (Fig. 4). This suggests that the increase of crab density is accompanied by a tendency to build parallel (or anti-parallel) trenches.

The lengths of 163 trenches were measured with a vernier caliper at the end of the low water phase and related to the resident's size. One-way ANOVA showed that the larger the individual crab, the longer the trench in which it feeds ($F = 30.16$, d.f. = 2 and 160, $P < 0.01$) (Fig. 5, top). In addition, the trenches lengthen with time from the aperture opening (Spearman rank correlation: $t = 6.116$, d.f. = 39, $P < 0.001$) (Fig. 5, bottom).

Spatial distribution

Counting all the burrows along both transects at low tide, neither of the transects exhibited a uniform distribution (transect 1: at diurnal spring tide: Willk test, $G = 1429.712$, d.f. = 7, $P < 0.001$; at nocturnal spring tide: $G = 1224.673$, d.f. = 7, $P < 0.001$; at diurnal neap tide: $G = 869.903$, d.f. = 7, $P < 0.001$; at nocturnal neap

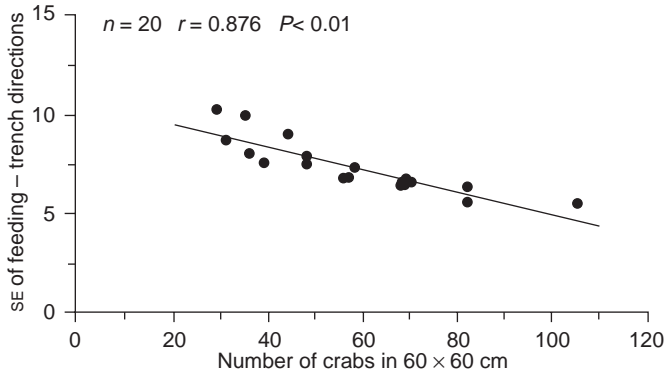


Fig. 4. Relationship between the density of crabs and the standard error (SE) of the feeding-trench directions.

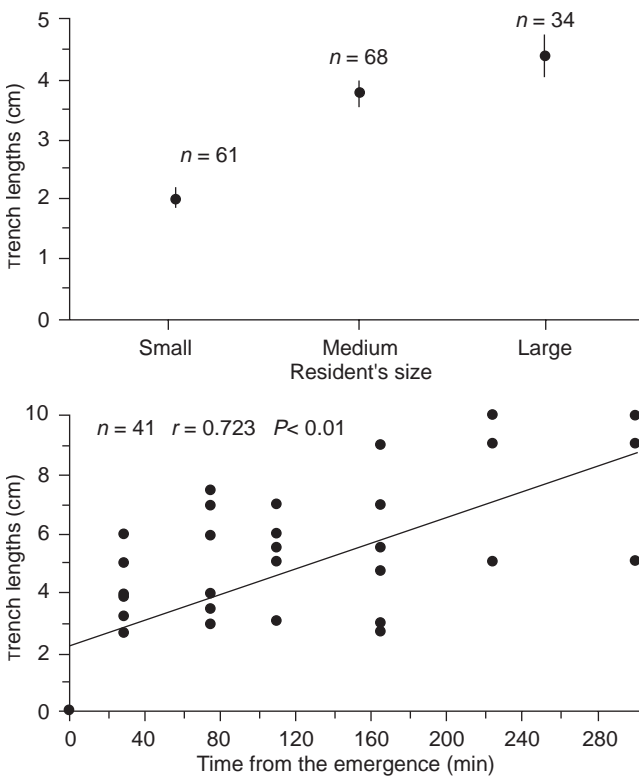


Fig. 5. Resident's size (three classes: small, medium and large) plotted against the feeding-trench length (average \pm SE) (top) and the relationship between the time from emergence and the feeding-trench length (bottom).

tide: $G = 775.046$, d.f. = 7, $P < 0.001$; transect 2: $G = 52.955$, d.f. = 6, $P < 0.001$; Fig. 6). The two types of active burrows (feeding-trench burrows and igloos) (Figs 7 & 8) had significantly different spatial distributions (diurnal spring tide: $G = 358.988$, d.f. = 6, $P < 0.001$; diurnal neap tide: $G = 715.993$, d.f. = 6, $P < 0.001$; nocturnal neap tide: $G = 81.817$, d.f. = 7, $P < 0.001$), except during nocturnal spring tide ($G = 12.328$, d.f. = 6, P ca. 0.05).

Figure 9 shows the substrate grade along transect 1, ranging from coarse sand to silt. The latter fraction significantly increases with the distance from the HWN

level (Spearman correlation test, after arcsine square transformation: $r = 0.658$, d.f. = 8, $P < 0.05$), in contrast to the other fractions (very fine sand: $r = -0.425$, d.f. = 8, ns; fine sand: $r = 0.307$, d.f. = 8, ns; medium sand: $r = 0.049$, d.f. = 8, ns; coarse sand: $r = 0.078$, d.f. = 8, ns).

Temporal distribution

When both ebb and flood tides occur in daytime, apertures are opened when the front of the ebb tide is on average at a distance of 228 cm (SE = 20, $n = 84$) (i.e. 14 min from the receding tide) and are sealed when the front of the flood tide is at 133 cm (SE = 22, $n = 75$) (i.e. 8 min from the incoming tide), these two distances differing significantly (Student's t -test, $t = 3.193$, d.f. = 157, $P < 0.01$). The distance from the front of the flood tide was not related to the crab's size (small: 384.8 cm, SE = 134.9, $n = 5$, medium: 265 cm, SE = 184.7, $n = 5$, large: 239.5 cm, SE = 77.7, $n = 8$; one-way ANOVA, $F = 0.37$, d.f. = 15 and 2, ns).

When dawn and dusk occurred during low waters, observations at D and E were made from 5:30 to 6:30 and from 17:45 to 18:45, respectively. Both the apertures of tunnels and the active crabs (crabs still active around the burrow) were counted. At sunrise (4 replications), a positive correlation with time was found in both the number of apertures (starting from 40 holes already opened, Spearman rank correlation test, $r_s = 0.88$, $t = 13.132$, d.f. = 50, $P < 0.001$) and the number of active crabs (starting from 0, $r_s = 0.888$, d.f. = 63, $P < 0.001$) (Fig. 10, top). Contrary, at sunset (3 replications), a negative correlation with time was found in both the number of apertures ($r_s = -0.575$, $t = 4.276$, d.f. = 37, $P < 0.001$) and the number of active crabs ($r_s = -0.868$, $t = 10.646$, d.f. = 37, $P < 0.001$). However, at 18:45, while the active crabs were 0, an average of 100 apertures were still open (Fig. 10, bottom).

When all the types of burrows counted along transect 1 at low tide were considered, active burrows were more numerous during spring tide (night: 1628 vs. 1199, Willk test, $G = 65.342$, d.f. = 1, $P < 0.001$; day: 2147 vs. 1538, $G = 101.098$, d.f. = 1, $P < 0.001$) and during daytime (spring tide: 2147 vs. 1628, $G = 71.079$, d.f. = 1, $P < 0.001$; neap tide: 1538 vs. 1199, $G = 42.088$, d.f. = 1, $P < 0.001$). A similar trend was observed for igloos (night, spring vs. neap tides: 1209 vs. 163, $G = 901.379$, d.f. = 1, $P < 0.001$; day, spring vs. neap tides: 1278 vs. 265, $G = 723.455$, d.f. = 1, $P < 0.001$; spring tide, day vs. night: 1278 vs. 1209, $G = 1.914$, d.f. = 1, ns; neap tide, day vs. night: 265 vs. 163, $G = 24.515$, d.f. = 1, $P < 0.001$). By contrast, feeding-trench burrows were more numerous during neap tides (night, spring vs. neap tides: 11 vs. 722, $G = 901.321$, d.f. = 1, $P < 0.001$; day, spring vs. neap tides: 204 vs. 856, $G = 430.977$, d.f. = 1, $P < 0.001$), but again were more abundant during daytime (spring tide, day vs. night: 204 vs. 11, $G = 210.736$, d.f. = 1, ns; neap tide, day vs. night: 856 vs. 722, $G = 11.389$, d.f. = 1, $P < 0.001$).

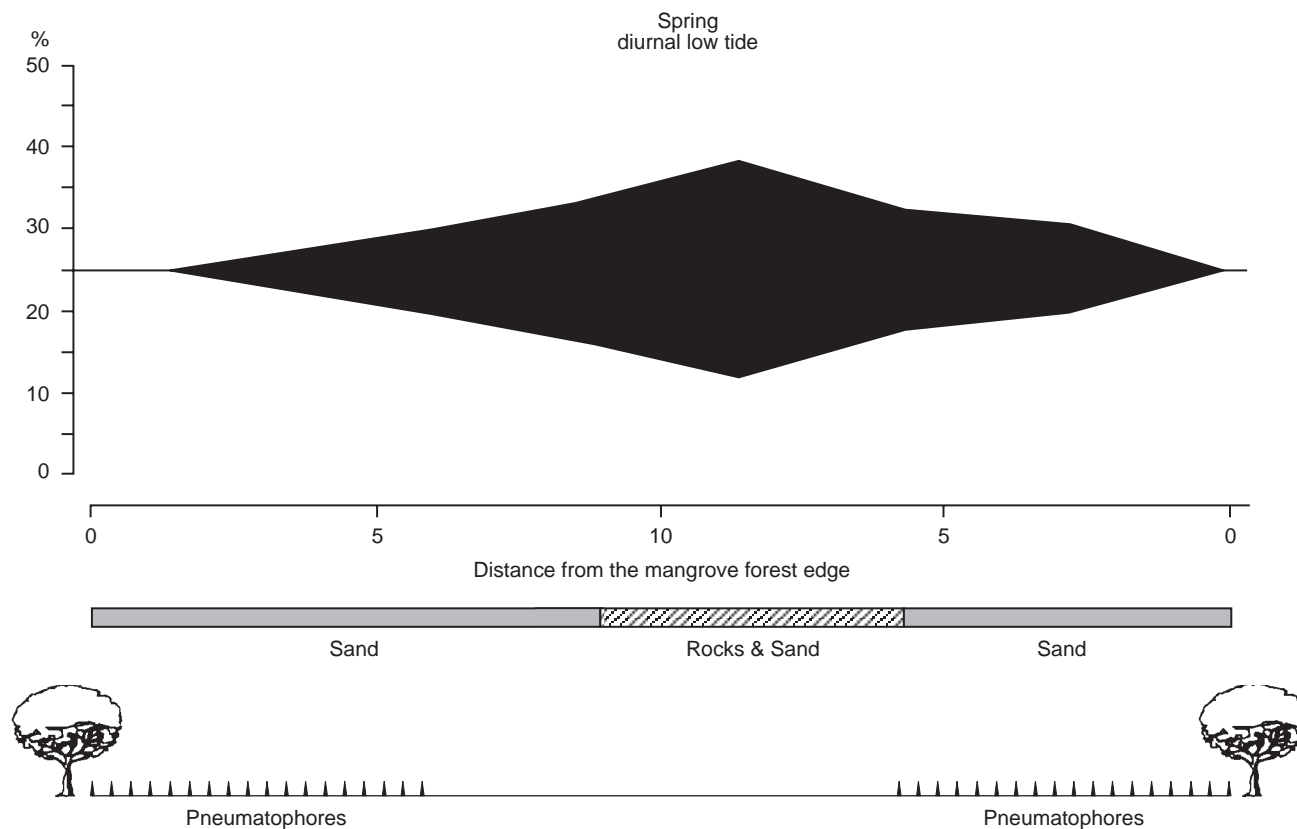


Fig. 6. Spatial distribution of burrows at spring tide during diurnal low tide as related to the distance from the mangrove forest edge.

Igloos were more frequent than feeding-trench burrows during spring tides (day: $G=866.587$, d.f. = 1, $P<0.001$; night: $G=1565.146$, d.f. = 1, $P<0.001$), but the latter prevailed during neap tide (day: $G=327.762$, d.f. = 1, $P<0.001$; night: $G=381.172$, d.f. = 1, $P<0.001$).

Figure 11 shows the relative frequency of feeding-trench burrows (top) and igloos (bottom) plotted against the time from the low tide at spring (left) and neap (right) tides. The relative frequency is calculated as the percentage of occurrence of each type of burrow on a scale with the minimum and maximum values at the two extremities. It is thus possible to pool data obtained from areas at different distances from the HWN level (because burrows are not spatially homogeneous). Both feeding-trench burrows at neap tide (Pearson correlation test, $r=0.683$, d.f. = 10, $P<0.02$) and igloos at spring ($r=0.766$, d.f. = 11, $P<0.01$) and neap ($r=0.785$, d.f. = 10, $P<0.01$) tides increase in number with time; the exception is feeding-trench burrows at spring tide.

Faithfulness to the burrow

During behavioural observations, we saw 140 crabs spontaneously leaving their burrows, either to occupy an empty one or to dig a new one. No relation was found with size class (Kruskal–Wallis one-way ANOVA, $H=3.535$, d.f. = 2, ns) or with time from either low tide

($H=1.250$, d.f. = 3, ns) or noon ($H=5.573$, d.f. = 4, ns), but switches of burrows were strangely more frequent in the intermediate phase between spring and neap tides ($H=6.847$, d.f. = 2, $P<0.05$). On 20 occasions, we recorded crabs spontaneously leaving their burrows and disappearing from the area.

Fighting for a burrow was observed 28 times; the winner was equally either the resident or the invader (14 vs. 14, $G=0$, d.f. = 1, ns), but the victor was most often the larger crab ($G=12.509$, d.f. = 2, $P<0.01$). Direct competition for the burrow also occurred with the fiddler crab, *Uca annulipes*, on sites where the distributions of the two species overlapped (quadrant A). In five recorded incidents, *Uca* replaced *Dotilla* twice and buried *Dotilla* with its excavating pellets on three occasions.

When the size of one *Dotilla*, which either spontaneously left the burrow or lost it after a fight, was compared with a crab being faithful to the same burrow over the entire low water phase, we found that the larger *Dotilla* individual, the more faithful it was to its original burrow (Willk test, $G=13.401$, d.f. = 2, $P<0.01$) (Fig. 12).

DISCUSSION

Strict intertidal limits set the distribution of *D. fenestrata*. As surface deposit feeders they need an area regularly

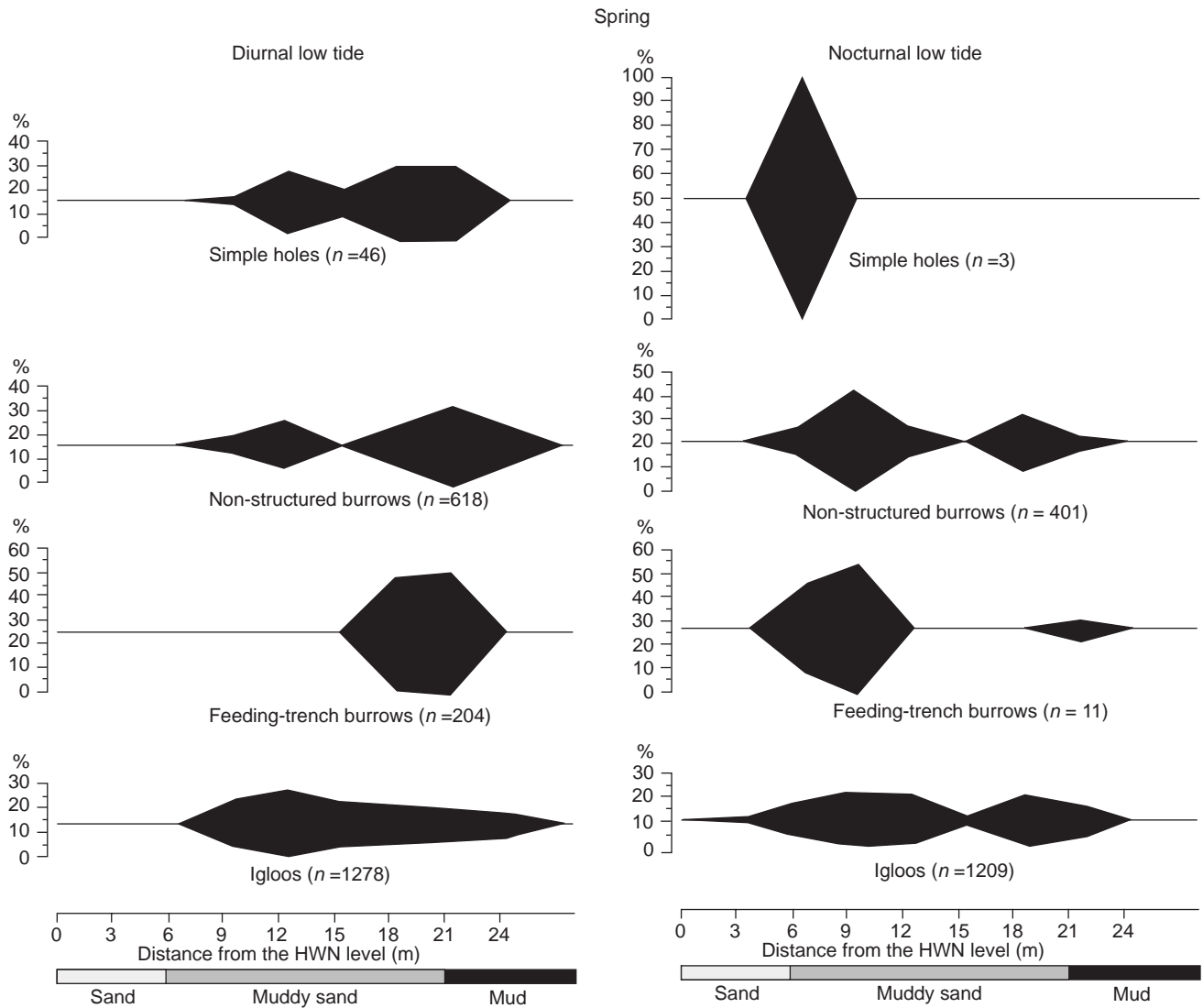


Fig. 7. Spatial distribution of different types of burrows at spring tide during diurnal (left) and nocturnal (right) low tide as related to the distance from the high water neap (HWN) level.

covered by the tide so that their surface food supply is renewed – as ‘air breathers’ they need an area regularly uncovered during low tide to provide sufficient time for feeding. Subsidiary requirements, i.e. sediments of a type suitable for both burrowing and feeding and shelter from wave action during the immersed period, lead to considerable habitat separation, by sediment type, tidal zonation, type of beach exposure, etc. (Ansell, 1988).

After the tide has receded, crabs begin to emerge at a distance from the water front of about 2 m. However, this emergence can occur (with the exception of feeding-trench burrows at spring tide, the number of burrows progressively increases with time) or not (some crabs remain buried during the entire low water phase). A comparison with other Scopimerinae shows great diversity in emergence time: *D. mictyroides* emerges close behind the receding tide (Tweedie, 1950; McIntyre, 1968); 50% of *Scopimera intermedia* emerge 1.5 h after uncovering (Tweedie, 1950); *S. inflata* (Fielder, 1970)

and *S. proxima* (Silas & Sankarankutty, 1967) emerge between 3 and 4 h after uncovering. During neap tide, nearly all *D. fenestrata* studied by Dray & Paula (1998) in Inhaca Island (Mozambique) were at the surface after 30 min of uncovering, while more than 60% of crabs at the low level are at the surface after 15 min. At spring tide, emergence is again faster at the low level, taking 45 min for most crabs to open the burrow, while at mid and high water level the delay is about 90 min (Dray & Paula, 1998). Hartnoll (1973) observed that emergence occurs over a long period in every species, probably in response to an endogenous rhythm. To anticipate changes in the environment and react appropriately may be of particular adaptive value to burrowing animals (Atkinson & Naylor, 1973). The sealing of the burrow occurs only a few minutes in advance of the flood tide, at a distance of around 1 m from the water front. This action is so accurately timed to the approach of the water that it is difficult to postulate that an endogenous rhythm alone initiates such a precise

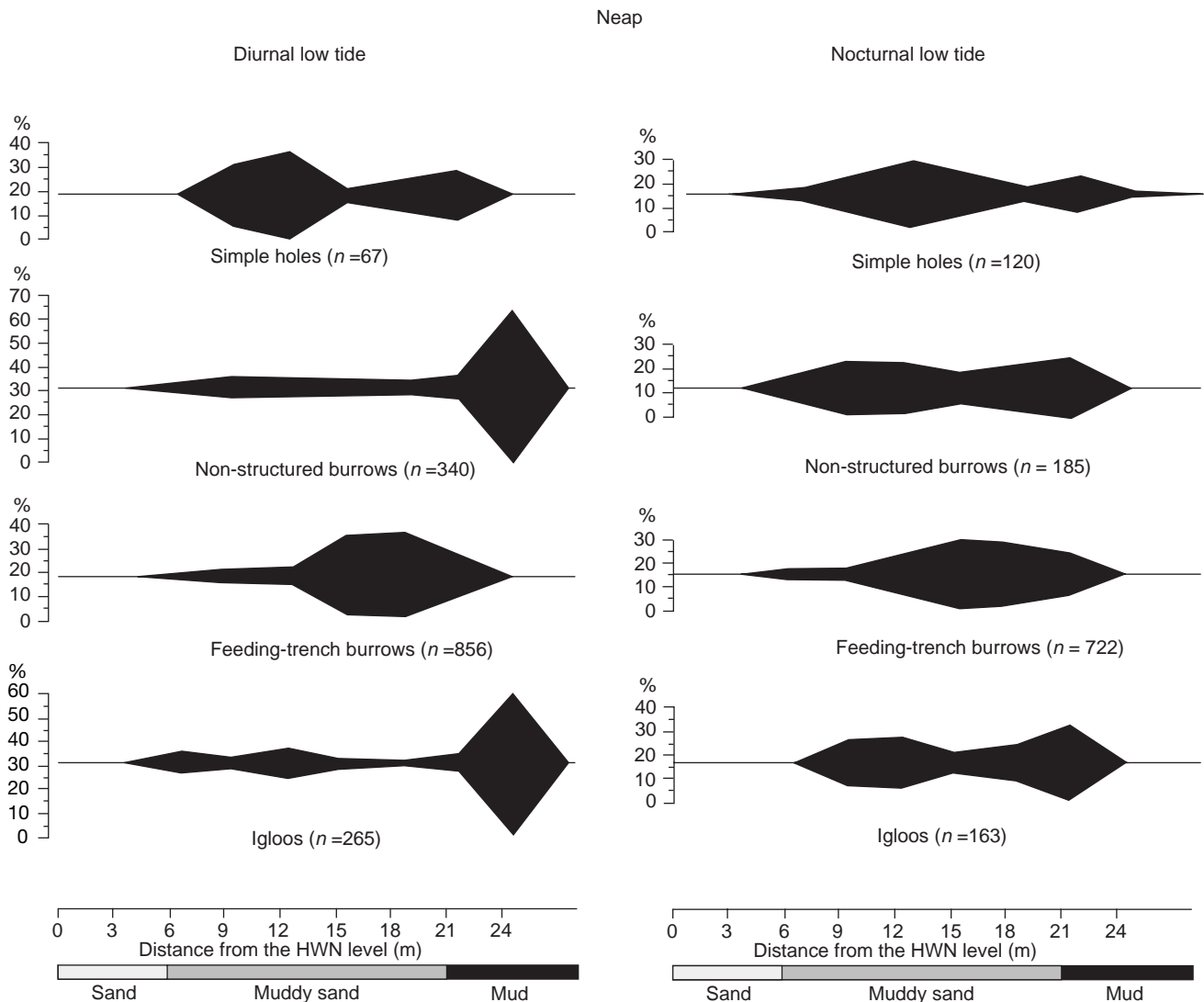


Fig. 8. Spatial distribution of different types of burrows at neap tide during diurnal (left) and nocturnal (right) low tide as related to the distance from the high water neap (HWN) level.

reaction. It is more likely that a mechanical stimulus from the rising tide, possibly in combination with an endogenous rhythm, determines the precisely phased behaviour pattern (Hartnoll, 1973).

Several species of the families Ocypodidae and Mictyridae are burrowers, but not all of them appear to have an exclusively burrow-orientated activity. At least some Ocypodinae and Scopimerinae, and most soldier crabs (*Mictyris longicarpus*) form dense aggregations or droves moving away from the normal distribution zone during the phase of diurnal low water. With the incoming tide, wandering crabs construct igloos in loose moist sand or in the waterlogged area, never coming back to their original burrow (in accordance with Hartnoll, 1973; but contrary to Fishelson, 1983). In *D. fenestrata*, one alternative is to steal burrows from smaller residents.

The use by burrow-centred crabs of two architectural types of burrow (the feeding-trench burrow and the igloo) represents an additional example of the flexibility

of this species' mode of life. Both burrows are more numerous during the diurnal hours and at spring tide, with feeding-trench burrows prevailing at neap tide and igloos at spring tide. In both types, the aperture diameter is related to the resident's size. In the feeding-trench burrow, the tunnel is nearly a vertical tube, sometimes with a sign of spiralling, while the igloo mostly presents a dilatation at its base. A tunnel's depth is related to the profundity of the reduced layer. Thus, while in *Scopimera inflata* (Fielder, 1970), the tubes descend to the water table and serve as a reservoir, those of *D. fenestrata* fail to do so and the crab must depend upon interstitial water, to which it has access through capillarity (see also Hartnoll, 1973).

Igloos are constructed by *D. blandfordi* (Altevogt, 1957), *S. inflata* (Fielder, 1970) and *D. mictyroides* (Tweedie, 1950), but the reason for their construction is still obscure. One hypothesis is that the igloo traps air for the subsequent high water period, assuring that the crab remains at the air/water interface which allows

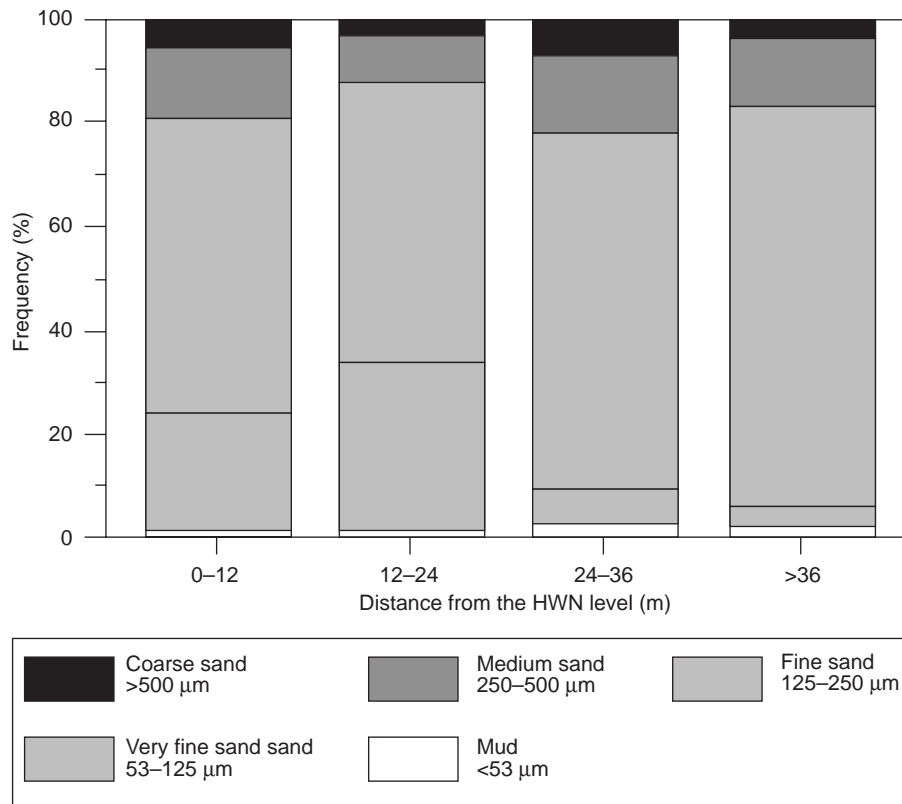


Fig. 9. Substrate grade at different distances from the high water neap (HWN) level.

aerial gas exchange to take place (however, the maintenance of air within igloos during the phase of immersion, asserted first by Cowles, 1915, later by Tweedie, 1950, and more recently by Fishelson, 1983, Maitland, 1986 and Ansell, 1988, has been refuted by Altevogt, 1957 and Hartnoll, 1973). This question has been experimentally solved by Takeda *et al.* (1996), who, at least in *D. myctiroides*, found a small quantity of air together with the crab itself inside igloos. In these air-filled chambers beneath the sand surface, the crab continued to scoop up the sand from the lower surface of the chamber and attached the scooped pellets to the ceiling. Consequently, the crab, together with the chamber, continually moved deeper into the sand until it was below the water level (Takeda *et al.*, 1996). The making of the igloo seems thus an adaptation enabling the construction of an air chamber in semi-fluid sand, where vertical tunnels cannot be constructed, but collapse. The descent of the crab into the sand may prevent encounters with predators arriving with flood tide, such as the moon crab, *Matuta* sp., and the swimming crab (*Portunus* sp.) (Takeda *et al.*, 1996).

Among other functions, igloos can be seen as permanent displays involved in territorial and sexual behaviours. The social function of structures made of mud or sand excavated from the burrow by some ocyropodids has been suggested, e.g. sand piles in several species of *Ocypode* (Vannini, 1980) the value of which in courtship and territorial defence has been demonstrated in *O. saratan* (Linsenmair, 1967), and mounds in *Ilyoplax pingi* (Wada *et al.*, 1994) and *I. pusilla*

(Kitaura & Wada, 1996) deterring the approach of neighbours. Indeed, several large *D. fenestrata* have been seen displaying over their domes.

The pattern of substrate collection and thus the spatial organization of the feeding-trench is similar in most species. When resources are distributed homogeneously or with such a complexity that animals cannot efficiently sample or interpret food gradients, a circular area that is progressively sampled, with the hole as the centre and a radius that allows for a rapid escape into the hole, optimizes net resource yields (Zimmer-Faust, 1990). Systematic deposit-feeding of this type reduces the chances that a crab will feed in areas previously explored and it is thus a commonly observed phenomenon among other invertebrate and vertebrate grazers and deposit feeders (for a review, see Zimmer-Faust, 1990). In the population of *D. fenestrata* studied by Hartnoll (1973) in Tanzania, a crab would excavate and sort an increasing sector of a circle, following either a clockwise or anticlockwise course around the hole. It always maintained a clear trench for rapid escape into the burrow entrance and covered the excavated area with pseudofaecal pellets. Seldom was a circle completed in the course of a tidal cycle, while this happens more frequently in *D. wichmanni* (Luschi *et al.*, 1997) which sorts a sector of 60° per hour. The systematic excavation along a sector of a circle has been recorded in other Scopimerinae (Tweedie, 1950; Altevogt, 1957; Silas & Sankarankutty, 1967; McIntyre, 1968; Fielder, 1970). The alternative pattern is one in which a number of narrow trenches radiate from the hole, these being

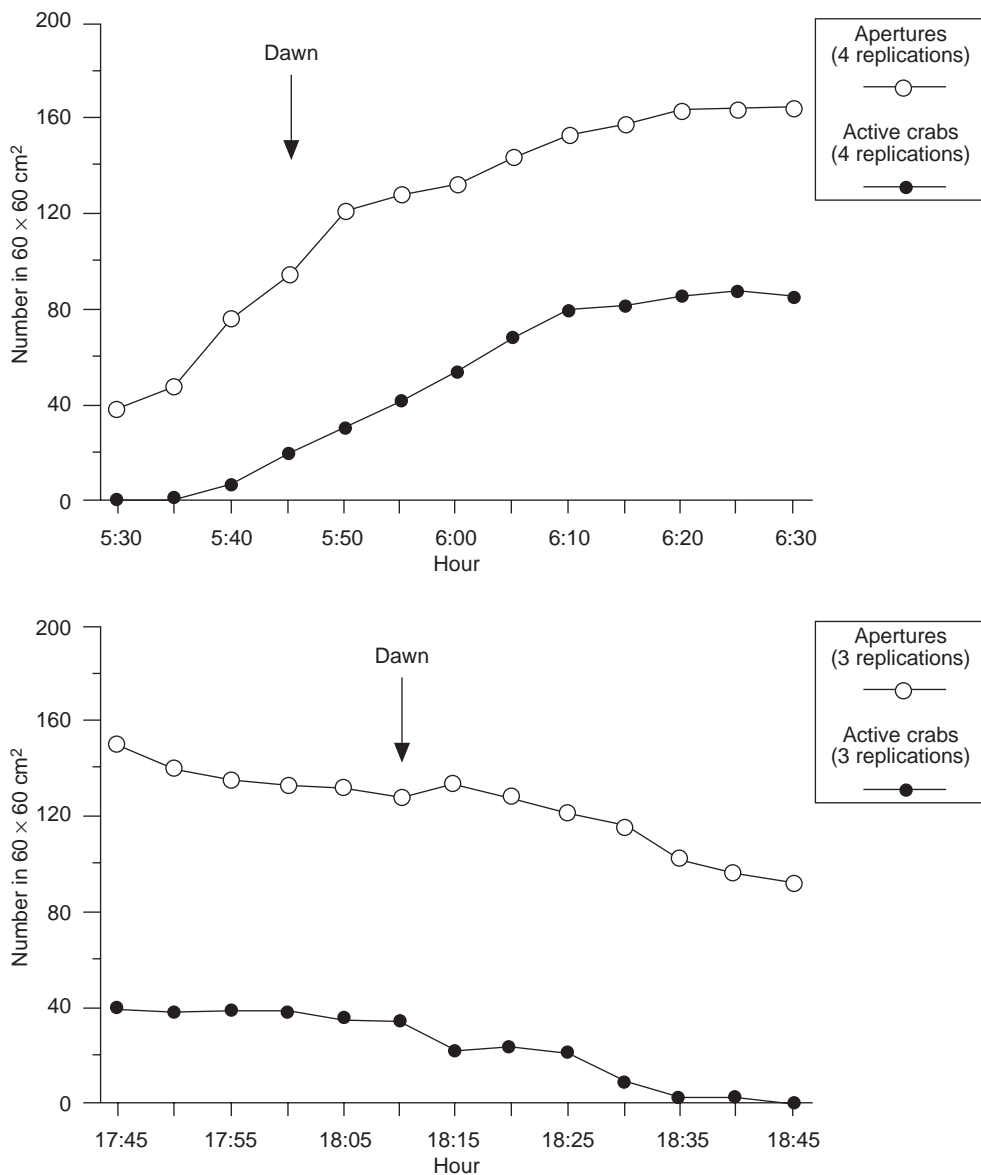


Fig. 10. Number of either apertures or active crabs with time when either dawn (top) or dusk (bottom) occur during low water.

generally longer than in the sector-feeding pattern, with the discarded pellets scattered on either side of the trench (Altevogt, 1957; Silas & Sankarankutty, 1967). In the population of *D. fenestrata* inhabiting Mida Creek, one single feeding-trench, walled on either one or both sides by pseudofaecal pellets, spreads out from the burrow entrance following an apparently random direction (with the exception of the spring tide when feeding-trenches are mainly directed seawards). The trench is longer when the resident is large, being possibly related to the higher metabolic requirements of larger individuals, and it lengthens with time, i.e. the crab excavates and sorts at an increasing distance from the aperture. The latter strategy seems to be less efficient, according to Zimmer-Faust (1990), not because it reduces the substrate biomass that can be harvested but because it increases the exposure to predation.

The burrow, including the feeding-trench, constitutes the territory of *Dotilla*, which is defended against

intrusion by con- and heterospecific crabs. However, the resident will be the loser in a contest if the attacker is larger. Territorial behaviour against neighbours is less frequent than described by Wada (1993) in *Ilyoplax pusilla*. We have never observed barricade-building (Wada, 1984) or neighbour burrow plugging (Wada, 1987); the latter was, however, performed by the fiddler crab (*Uca annulipes*) on neighbouring *Dotilla*'s burrows. One geometrical system to reduce time- and energy-consuming aggression among neighbours is the construction of trenches that do not overlap or intersect, as occurs with the increase of parallel or anti-parallel trenches following an increase in crab density.

In *D. fenestrata* studied by Hartnoll (1973), the burrow is defined as a semi-permanent structure, retained from one activity cycle to the next, from which the crab seldom strays further than the limits of its feeding-trench. Contrary to this, in *D. mictyroides* (Altevogt, 1957), the original burrow is a very temporary

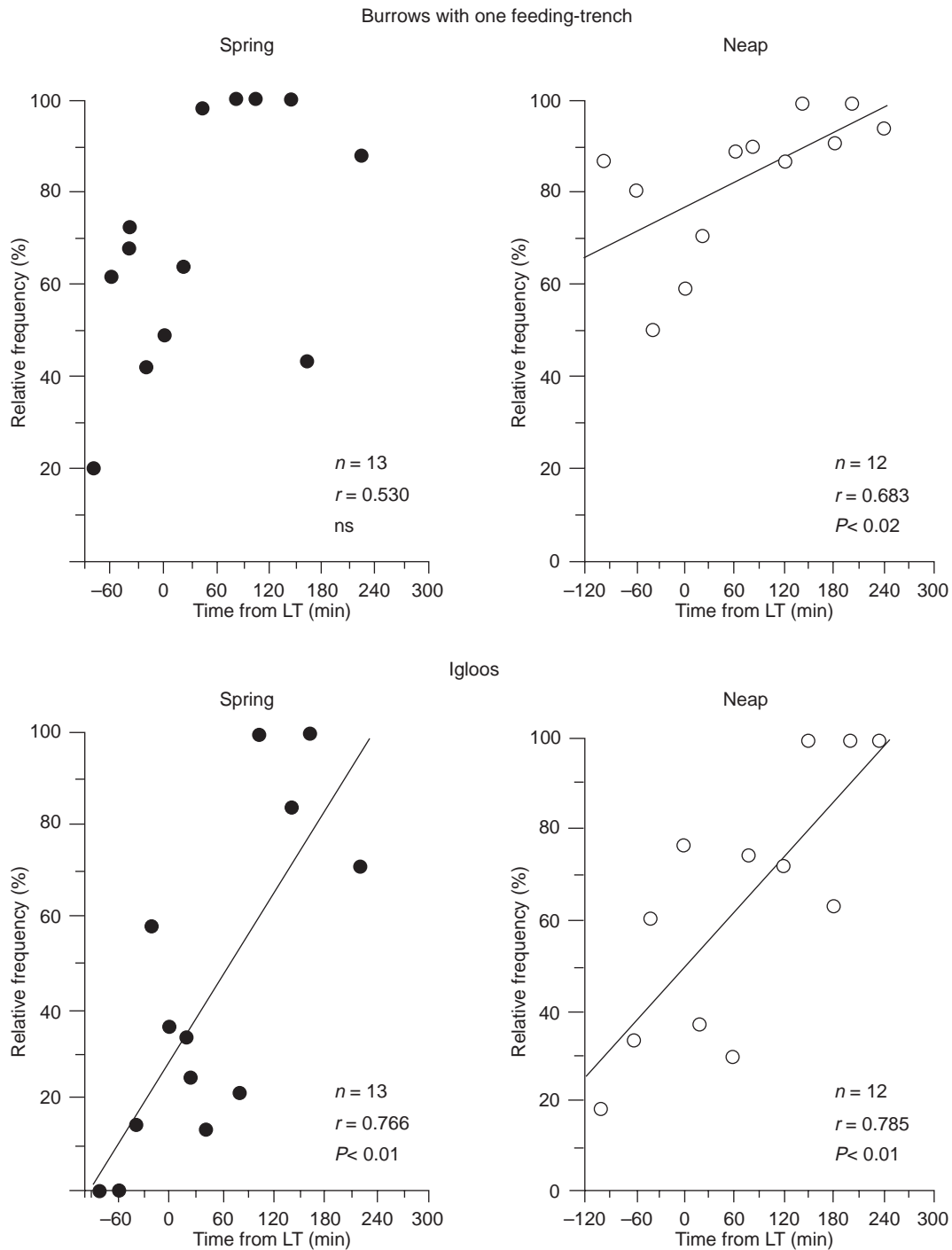


Fig. 11. Relationships between the time from low tide (LT) and the relative frequency of feeding-trench burrows (top) and igloos (bottom), at spring (left) and neap (right) tides. Relative frequencies are calculated as the percentage of occurrence of each type of burrow on a scale with the minimum and maximum values at the two extremities; this allows one to pool data obtained from areas at different distances from the high water neap (HWN) level (because burrows are not spatially homogeneous).

habitat and the crab constructs several burrows during its wandering in a single low water period before finally settling in one when the tide rises. *Dotilla fenestrata* of Mida Creek showed an intermediate behaviour; around half of 50 crabs followed throughout the entire low water phase remained faithful to the original burrow, while the others either left the burrow to occupy an

empty one or to dig a new one, or joined with the wandering drove. This occurs at varying substrate hardness, contradicting Fielder (1970), according to whom permanent burrows are proper to firmer substrates, whereas less territoriality is exhibited by crabs inhabiting softer substrates. Contrary to the observation made by Hartnoll (1973) that large males regularly leave

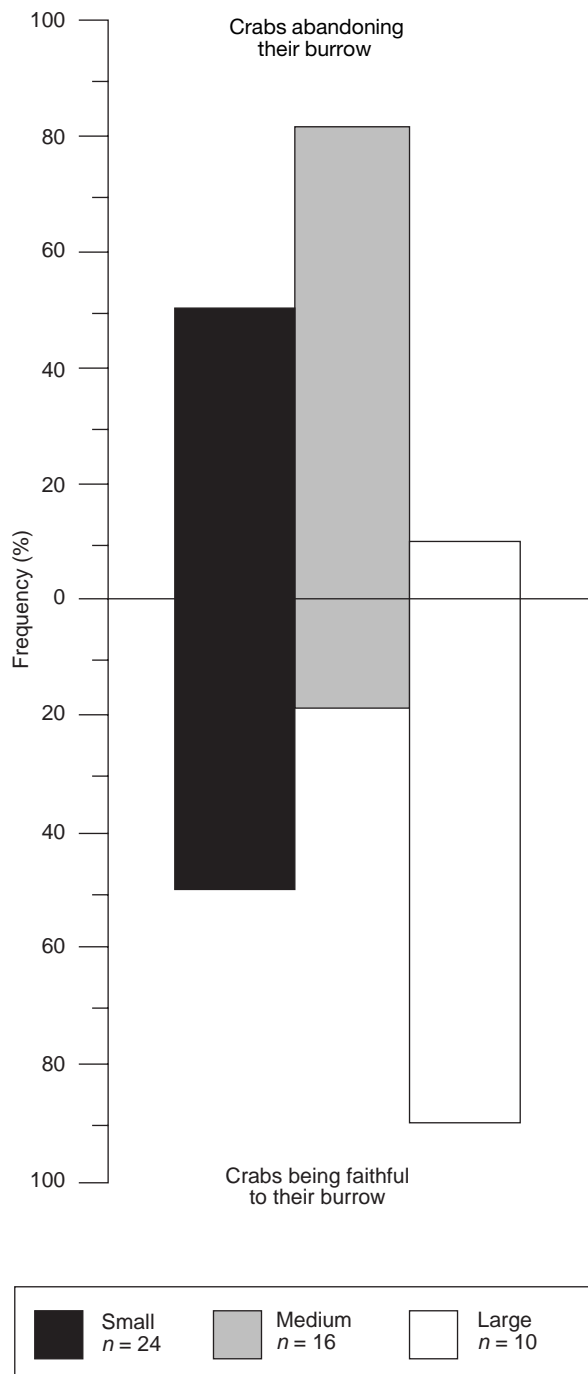


Fig. 12. Frequency of crabs abandoning or faithful to their original burrows.

their burrows marching over the sand in large groups, in the present study individuals of larger size appeared to be more faithful to their original burrow.

The spatial distribution of the different types of burrows from the HWN level to the sea is significantly different, both during the spring and neap tides and during the diurnal and nocturnal tides. At spring tide, feeding-trench burrows are more concentrated seawards in the daytime and landwards at night, while igloos are dispersed between 6 and 24 m seawards from point 0. At neap tide, both burrows are distributed between 3 and

24 m seawards. It is difficult to explain the differences. Inhabiting higher intertidal sites may be related to the trade-off between the benefits (more time is available for feeding; during high waters, fish predators are not able to swim in the shallower water) and costs (the crabs are more exposed to extreme temperatures and evaporation; flood tide is shorter and slower, causing the deposition of fewer algae and detritus), while the opposite is true for crabs inhabiting lower intertidal sites (see also Fishelson, 1983). Other factors that condition spatial distribution are obviously physical conditions. The types of burrow depend on both drainage and substrate grade, although within a mangrove swamp these do not regularly follow a gradient (we found a gradient only in the silt fraction).

As shown by the transect parallel to the coastline, burrows are concentrated far from the mangrove edges, possibly to avoid the strong predation by other crabs living within the mangrove forest, like *Metopograpsus thukuhar*. The aggregation of burrows is certainly caused by the nature of the substrate, but in part may be also explained by its anti-predator efficiency. The proximity of conspecifics might, first, reduce the time devoted to being alert against predators (other crabs, but also birds, like *Threskiornis aethiopicus* and *Dromas ardeola*), thus maximizing foraging, and, secondly, decrease the probability (by 'dilution') of being the prey.

Ocypodid crabs (with the exception of most species of *Ocypode*, see Vannini, 1976) are generally active during daytime (Hartnoll, 1988) and *D. fenestrata* also emerges only at sunrise even when it occurs during the low water phase. Some exceptions are temperate species of fiddler crabs showing some nocturnal activity (Hartnoll, 1988) and other species from the Philippines, which may perform some activity on bright moonlit nights (Pearse, 1912). To a certain extent, *D. fenestrata* may be also considered an exception – during nocturnal low waters the crab builds a limited number of feeding-trench burrows and numerous igloos. At sunset during the low water phase, the crabs' activity stops but most apertures remain unsealed. One reason might be to renew air before the following high water (but see above the debate concerning air retention within igloos). It is still unclear why the activity of ocypodids is so predominantly diurnal. Hartnoll (1988) hypothesized that either this is a mechanism to avoid predators (but the risk would seem to be greater during the day) or possibly the main factor is the importance of visual stimuli for the biology of these species.

There is no doubt that the burrowing and feeding activities of *D. fenestrata*, with the deposition of both excavated and pseudofaecal pellets, play a basic role in the movement of sediment in this very specialized habitat. In the southern Red Sea, at sites where the density of *D. sulcata* reaches 400 per m², Fishelson (1983) reported that the amount of sediment moved was approximately 6 kg/m² per day (at our sites, we estimated around 900 ml/m² per day where crab density averaged 120/m²). Tons of sand are therefore moved on

shores with extensive populations of *Dotilla*. This activity changes the texture and layering of the upper 1–2 cm of sediment, the result of which will be a decrease in organic content and an increase in oxidative decomposition (Fishelson, 1983).

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