

M. Vannini · R. K. Ruwa · S. Cannicci

Effect of microclimatic factors and tide on vertical migrations of the mangrove crab *Sesarma leptosoma* (Decapoda: Grapsidae)

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Abstract The tree crab *Sesarma leptosoma* Hilgendorf migrates up the mangrove trunks twice a day, both in the morning and in the evening, leaving its refuge near the tree base to feed on fresh leaves. In spite of the 150 cm of tide excursion at the base of the trees, the timing of the migrations seems largely controlled by nontidal factors. The timing of the morning upward migration is controlled by the light level alone. The morning downward migration takes place as soon as the temperature rises and relative humidity falls, with no relationship to tidal cycle or light level. Only the evening upward flow seems primarily controlled by the tide, while the evening downward flow, which ends at twilight, seems to be related to the timing of the evening upward migration, to the tide and again to light levels. During the day, crabs abandon the canopy to avoid low relative humidity, usually coupled with the higher wind speeds, which would quickly dehydrate them. At night, crabs stop migrating, probably because their movements and orientation capability along the trunk and in the canopy are largely vision dependent. Nontidal factors have never previously been shown to influence the migratory behaviour of an intertidal crustacean species so extensively.

Introduction

Intertidal isophasic animals usually migrate across the zone they inhabit according to the tide, always keeping themselves within the same respiratory phase (Vannini and Chelazzi 1985). Mangrove crabs have recently been found in Kenya whose migration, in spite of the wide intertidal excursion affecting their habitat, seems regulated by factors other than the tide (Vannini and Ruwa 1994).

The crab *Sesarma leptosoma* Hilgendorf is an Indo-Pacific Grapsidae Sesarminae that lives on mangrove trees and feeds on fresh leaves (Vannini et al. 1997), similar to the related Central American and West African species, *Aratus pisonii* and *Sesarma elegans*, respectively (Hartnoll 1965; Warner 1967; Jones 1984). In Kenya, *S. leptosoma* lives among the mangrove trunks and roots and undertakes, twice a day, a synchronised mass migration to reach the tree canopy, as high as 12 to 15 m above the ground (Vannini and Ruwa 1994). When not migrating, crabs always stay out of the water: just above the water level during high tide, or among the root crevices and between the roots and the mud during low tide. Between 15:00 and 18:00 hrs, the crabs climb the trees to reach the canopy and feed on leaves; many of them return to the base of the tree before 18:30 hrs, while others spend the night, immobile, without feeding, among the leaves. At about 06:30 hrs, another upward migration takes place after which all the crabs descend again, usually before 10:00 hrs. It was experimentally shown that, at least in the morning, light intensity triggered the upward migration, while temperature and tide had little influence on it (Vannini et al. 1995). Nothing is known about the effects of the various microclimatic factors and tide on this migratory behaviour, nor about the interaction between these and the crab's biological clock.

The aim of the present study was to evaluate these behaviour patterns and to investigate the effect of the tide and such microclimatic factors as light, temperature,

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M. Vannini (✉)
Museo di Zoologia "La Specola",
Università di Firenze, v. Romana 17,
I-50125 Firenze, Italy

R.K. Ruwa
Kenya Marine and Fisheries Research Institute,
P.O. Box 81651, Mombasa, Kenya

S. Cannicci
Dipartimento di Biologia Animale e Genetica "Leo Pardi",
Università di Firenze, v. Romana 17,
I-50125 Firenze, Italy

relative humidity and wind speed on the migratory behaviour of *Sesarma leptosoma*.

Materials and methods

Observations were carried out in the mangrove swamp of Dabaso, a locality within Mida Creek near Malindi, Kenya, in July 1993 (for preliminary observations) and July to August 1994. The tide regularly inundated the study site twice a day, flooding the tree roots for about 3 (10 to 30 cm) or 6 h (up to 150 cm) at neap or spring tide, respectively. Nine *Rhizophora mucronata* trees were chosen which were 11 to 13 m high, 30 to 40 cm in diameter, relatively close to each other (within a 30 m radius), and supported by large root systems. Observations were made with binoculars of only half of the tree's circumference, from a distance of 10 to 20 m, by scanning the visible trunk surface from just above the roots to the first or second main branch bifurcation (3 to 5 m). The number of climbing or descending crabs was recorded every 10 min. On average, crabs crossed the 3 to 5 m distance in 10 min or less. Thus a 10-min recording frequency allowed the observer to record different crabs each time, even if not all of them (Vannini and Ruwa 1994).

Quantitative observations were carried out during seven sessions (one could not be completed because of heavy rain), during different tidal periods, from 06:00 to 19:30 hrs. During most of the days, 5- to 10-min showers commonly occurred every 1 to 2 h. At night, both the crabs spending the night among the roots and those remaining in the canopy were inactive, and only very few individuals were seen wandering along the tree trunks (Vannini and Ruwa 1994).

The following abbreviations are used to indicate the four types of migratory flows: MU (morning upward), MD (morning downward), EU (evening upward), ED (evening downward). The average time of each migratory flow, for each day and for each tree, was calculated by averaging the mode and the four or eight adjacent records on both sides of the mode (four, for the more concentrated flows, MU and ED, and eight for the less concentrated ones, MD and EU).

Microclimatic parameters were measured both on the highest branch bifurcation of a *Rhizophora mucronata* tree (where a platform was built 12 m above the ground and on which crabs were not recorded) and among its roots. Temperature and relative humidity (RH) were recorded with a portable thermo-hygrometer (error range ± 0.5 °C and 5% RH). A portable light meter was used to record the light intensity and a hand anemometer to record the wind speed. Measurements were made every 30 min throughout the observation period. Confidence limits were computed at the 95% probability level.

For each migratory flow, the total number of crabs recorded was extremely variable between different days (see Table 1). This could be due to an intrinsic crab number variability or to other sources as well. Crabs prefer to walk on the darker side of the trunk, the position of which may change at different heights on the trunks; furthermore, this preference is affected by the hour of the day and the amount of cloud cover. A further source of error in the estimation of crab numbers is crab speed, which appears to be affected by both temperature and wind, especially during the MD migration. Crab speed may thus lead to underestimation (when crabs accelerate during the hottest hours) or overestimation (when crabs nearly stop walking, as in the case of strong wind).

Results

Migratory flow patterns – quantitative analysis

The variations in relative frequency of migrating crabs during each observation session are reported in Figs. 1(A–G) and 2(A–G), together with the variations

in temperature and water level. The average time of day for each flow and the relative number of crabs involved in it are presented in Table 1, along with an estimate of the variability. In Figs. 1 and 2, the relative frequency of crabs for each migration is related to the total number of observed crabs in each flow (as reported in Table 1).

Two-factor analysis of variance ANOVA was applied to the average migration times (expressed in decimals) to test for differences in the timing of the four migrations between the nine trees and among the seven days (Table 2). Between trees, only a slight difference exists for the MU flow, while in the other three migrations, the crabs on all nine trees appear well synchronised, with little variability among trees. Even for MU, the variability among trees is very low (SD = 4 min; Table 1) and the seven daily averages of the nine trees are all between 06:22 and 06:35/hrs. The differences between days, on the contrary, are highly significant for all four migratory flows. Consequently, all data relative to one flow and one day of observations represent the cumulation of measurements from the nine trees.

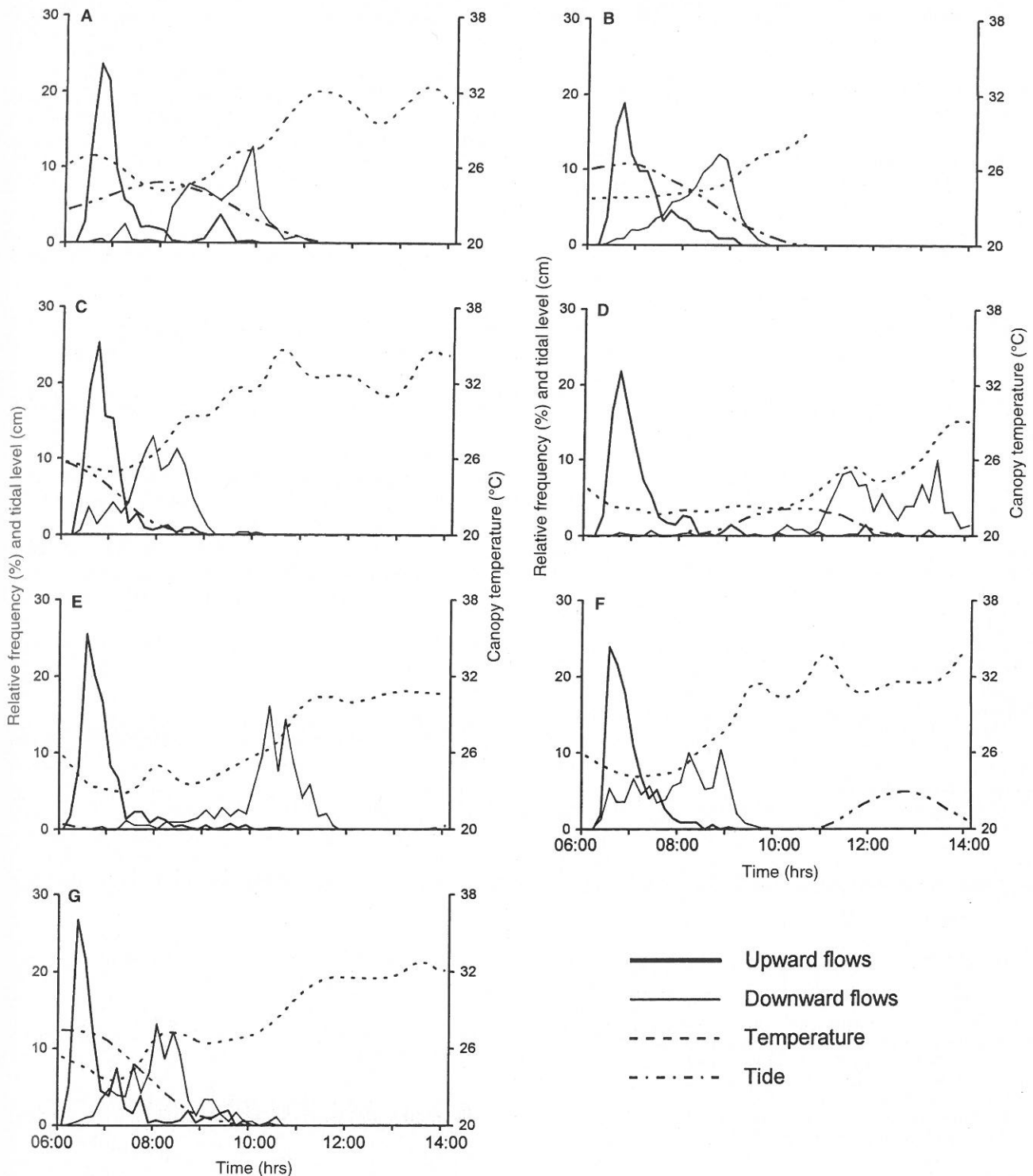
An analysis was performed to answer two preliminary questions: which flow is more concentrated around its mean and which flow average is more constant in time.

Flow concentration

From Figs. 1 and 2, it appears that the time distributions of the crabs during the various morning and evening migratory flows are quite different from one another but relatively constant from day to day for each kind of flow. To compare this distribution variability, a graph of average occurrence time (determined by overlapping the seven daily modes and then averaging the data) for each migratory flow was calculated and the four resulting plots were then superimposed in Fig. 3. Furthermore, to compare the pattern and variability of the different flows on different days, the SD for each flow was used as a measure of flow concentration (Table 3). One-factor ANOVA of the SD data from Table 3 shows that the four SDs are not homogeneous ($F = 15.16$, $df = 3$ and 22 , $P < 0.001$). The MU and ED flows appear to be concentrated around their average time, and thus crabs are likely to be more synchronised during these two periods, while during EU and especially MD they appear less so.

Flow time stability

Table 1 (SD column) shows that the variability of the MU flow around its average time, expressed by the SD, is 4 min, followed by ED (23 min), EU (37 min) and MD (1 h 43 min). Comparison of the four flows reveals that MU is significantly more constant than the others, and ED more than MD (two-tailed F -test, $P < 0.02$).

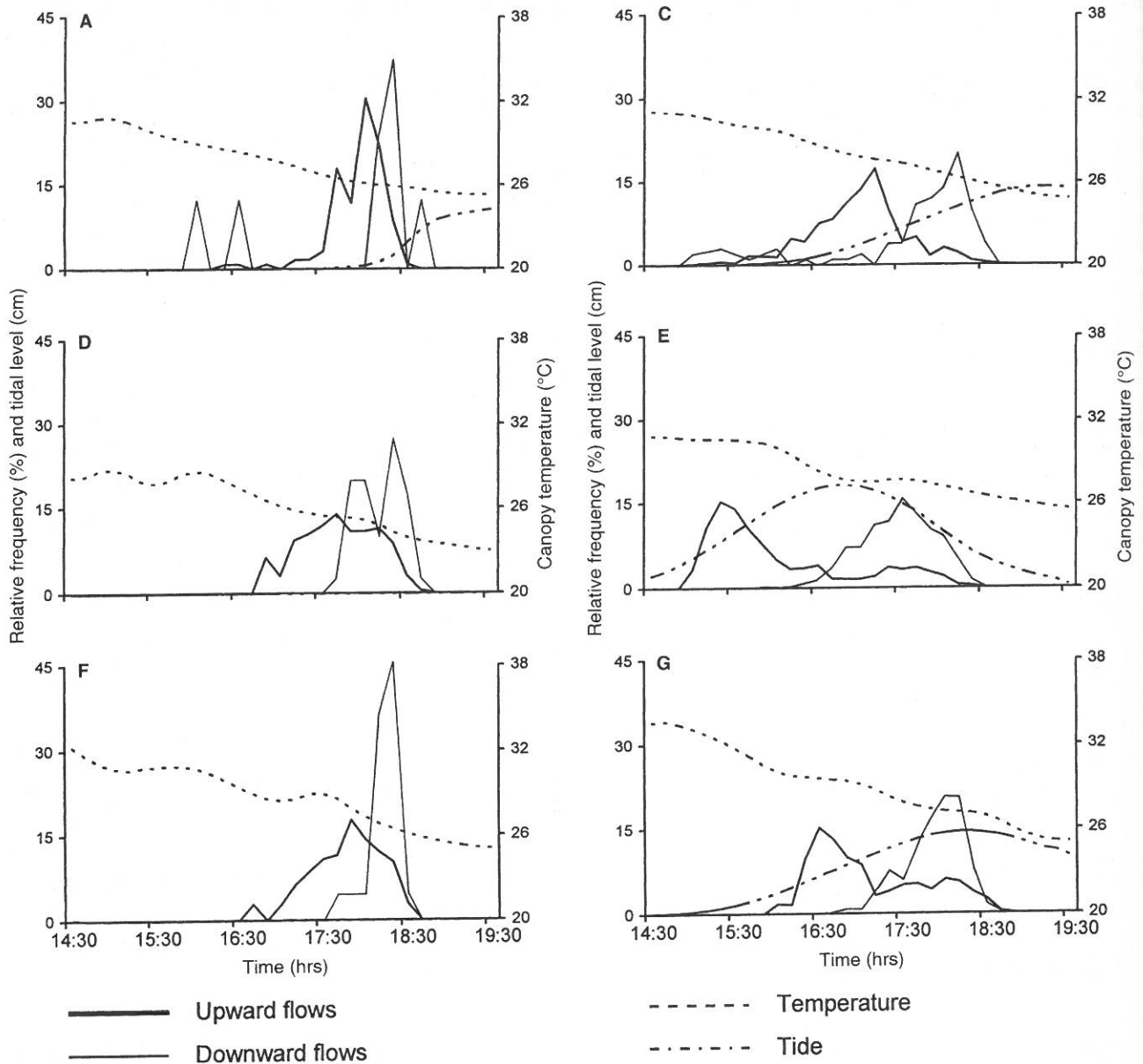


Relationships between the average time of migration and microclimatic factors

The timing of crab migration was not correlated with wind speed, since the wind was very irregular and gusty. To correlate temperature, relative humidity and light with migratory behaviour, time intervals had to be chosen, during which the examined variables could be relevant in triggering the various migratory flows. For

Fig. 1 *Sesarma leptosoma*. Morning flows: **A** 13 July 1994; **B** 23 July 1994; **C** 25 July 1994; **D** 30 July 1994; **E** 6 August 1994; **F** 16 August 1994; **G** 22 August 1994. Frequency of crabs (%) recorded every 10 min relative to total number of recorded crabs for each flow is plotted against time of day; tidal level in 5-cm intervals and canopy temperature are also indicated

the MU flow, the period 06:00 to 06:30 hrs appeared to be crucial since the whole mass of crabs migrated toward the end of that period. For the MD flow, which was



much more variable in time (see Table 1), the period between 07:00 and 07:30 hrs was chosen, since a major MD flow never occurred prior to that time. For similar reasons, the periods 14:00 to 15:00 hrs and 17:00 to 18:00 hrs were chosen for the EU and ED flows, respectively.

The relationships between the average climatic values during those periods and the average times of migration flows are shown in Table 4. The timing of the MU flow appears to be negatively correlated with the light level alone: crabs delay their morning upward migration when there is not enough light. The timing of the MD flow appears to be related both to the relative humidity and temperature: crabs migrated earlier when the temperature was too high and/or the relative humidity was too low. The difference between the two correlation coefficients was not significant ($r = 0.741$ – with the negative sign removed – compared with $r = 0.814$;

Fig. 2 *Sesarma leptosoma*. Evening flows: dates for panels as in Fig. 1. The 23 July record (B) is missing because of heavy rain

$\chi^2 = 0.216$, $df = 1$, $P = ns$) and it is impossible to state which of the two factors (obviously also correlated with each other) plays the major role. Finally, both the EU and ED flows appear to be completely unrelated to any of the microclimatic factors measured.

Relationships between the times of the different migrations

We examined whether the average time of EU might be related to that of MU (on certain days crabs might climb earlier both in the morning and in the evening), to that of MD (crabs might climb later in the evening if they descend later in the morning), or to the difference

Table 1 *Sesarma leptosoma*. Quantitative description of the four migrations (*MU* morning upward; *MD* morning downward; *EU* evening upward, *ED* evening downward). Total number of crabs observed in the nine trees (*N*) and average time of occurrence of the migration are given (*SD* standard deviation; *CV* coefficient of variation; *CL* 95% confidence limits; *nd* no data)

Flow	13 Jul	23 Jul	25 Jul	30 Jul	6 Aug	16 Aug	22 Aug	Grand mean	SD	CV	CL	
											Lower	Upper
<i>MU</i>												
<i>N</i>	373	328	109	537	572	347	357	374	152.2	38.0	239	515
Time (hrs)	06:31	06:28	06:35	06:31	06:28	06:32	06:22	06:29	00:04		06:26	06:34
<i>MD</i>												
<i>N</i>	452	283	372	562	514	435	398	431	92.2	21.0	346	516
Time (hrs)	09:08	07:31	08:10	12:08	10:11	07:25	08:02	08:56	01:43		07:22	10:32
<i>EU</i>												
<i>N</i>	128	nd	788	97	743	175	688	436	334.5	76.7	85	787
Time (hrs)	17:34		16:35	17:25	16:01	17:28	17:04	17:01	00:37		16:23	17:40
<i>ED</i>												
<i>N</i>	8	nd	100	20	576	22	339	177	231.8	131.0	0	421
Time (hrs)	18:12		17:35	18:06	17:16	18:08	17:31	17:48	00:23		17:23	18:13

Table 2 *Sesarma leptosoma*. Differences in the average times of the four migratory flows between the nine different trees and among the seven daily observation sessions. ANOVA (two-factor, with no replication); $P < 0.05$ (*), $P < 0.00$ (***)

Flow	Between trees		Between days	
	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>
<i>MU</i>	2.286	(8, 48)*	12.002	(6, 48)***
<i>MD</i>	0.375	(8, 48)	497.082	(6, 48)***
<i>EU</i>	2.730	(8, 40)	335.090	(5, 40)***
<i>ED</i>	1.517	(8, 40)	27.223	(5, 40)***

Table 3 *Sesarma leptosoma*. Variability (expressed by the average SD) around their average times, of each of the migratory flows on the various observation days (*n* number of days). The only significant differences (Tukey test; $P < 95\%$) are $SD_{MD} > SD_{MU}$, $SD_{MD} > SD_{ED}$ and $SD_{EU} > SD_{ED}$

Flow	Av time (hrs)	Av SD (min)	<i>n</i>
<i>MU</i>	06:29	22.8	7
<i>MD</i>	08:56	43.7	7
<i>EU</i>	17:01	32.5	6
<i>ED</i>	17:48	17.3	6

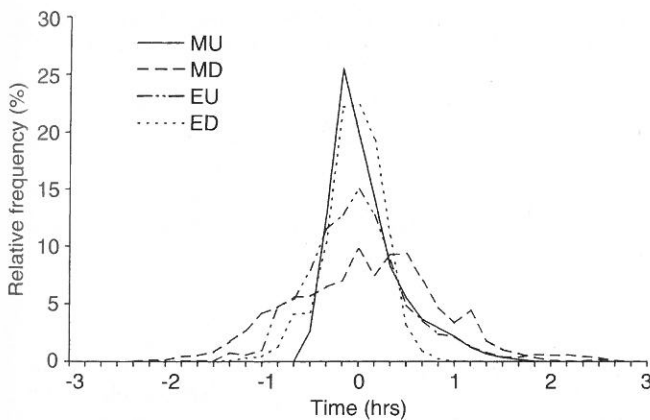


Fig. 3 *Sesarma leptosoma*. Average pattern of the seven morning and six evening migratory flows during the observation period (*MU* morning upward; *MD* morning downward; *EU* evening upward; *ED* evening downward flows)

Table 4 *Sesarma leptosoma*. Correlation between the average values of temperature (*T*), relative humidity (*RH*) and light in \log_e (lux) recorded during the time period shown in the right column and the average times of the four migratory flows (*ns* not significant)

Flow	T			RH			Light			Period (hrs)
	<i>r</i>	<i>df</i>	<i>P</i>	<i>r</i>	<i>df</i>	<i>P</i>	<i>r</i>	<i>df</i>	<i>P</i>	
<i>MU</i>	0.164	5	ns	0.584	5	ns	-0.803	5	<0.05	06:00–06:30
<i>MD</i>	-0.741	5	0.05	0.814	5	<0.02	-0.619	5	ns	07:00–07:30
<i>EU</i>	-0.086	4	ns	-0.014	4	ns	-0.411	4	ns	14:00–15:00
<i>ED</i>	-0.156	4	ns	-0.363	4	ns	0.485	4	ns	16:00–17:00

between the average times of *MU* and *MD* (crabs which did not have enough time to feed in the morning might climb earlier in the evening). However, none of these correlations proved to be significant (Table 5). On the other hand, the timing of *ED* is significantly correlated with that of *EU* (Table 5): crabs which climb earlier in the evening will also descend earlier.

Relationships between the times of the different migrations and the tide

Morning and evening migrations occurred without being affected by a change of tide, e.g. throughout low tides (Figs. 1E, F; 2D, F) or when the tree base was continually flooded (Figs. 1A; 2E, G). However, plotting the average water level versus the four average migration times, for the periods during which climatic parameters were recorded, shows that both *MU* and *MD* are

Table 5 *Sesarma leptosoma*. Correlation between the different average times of the migrations or the time difference between them, MU - MD, vs EU

Flow	<i>r</i>	<i>df</i>	<i>P</i>
MU vs EU	0.278	4	ns
MD vs EU	-0.055	4	ns
EU vs ED	0.984	4	<0.001
MU - MD vs EU	-0.076	4	ns

Table 6 *Sesarma leptosoma*. Correlation between the average tidal level during the periods indicated on the right and the average times of the four migratory flows

Flow	<i>r</i>	<i>df</i>	<i>P</i>	Period (hrs)
MU	-0.385	5	ns	06:00-06:30
MD	-0.494	5	ns	07:00-07:30
EU	-0.814	4	<0.05	14:00-15:00
ED	-0.960	4	<0.001	16:00-17:00

independent of the tide while EU and ED are related to it (Table 6): the higher the tide was in the early afternoon, the earlier the crab began both the EU and ED migrations.

Discussion and conclusions

Morning upward flow

The MU flow was very well concentrated around an average time (Table 3), was relatively constant in the number of crabs involved (Table 1), and its timing was independent of temperature, relative humidity and tide: the crabs climb trees only after the ambient light has reached a certain level. If the tide was rising while it was still too dark, the crabs would remain on the root and trunk surface, just above the water level, waiting for the light intensity at which they seem to be able to migrate (usually 25% of the crabs migrate between 06:00 and 06:30 hrs with a light level varying from virtually nil to 13 360 lux; see also Vannini et al. 1995).

Morning downward flow

The MD flow was variable in pattern (Table 3), very constant in the number of crabs involved, but much more variable than MU in its time of occurrence (Fig. 1). Its timing appears to be independent both of light and tide, but related to temperature and RH. Although the RH values were quite variable, a temperature threshold (24 °C) was found which optimises the relationship between temperature and the average MD flow time ($r = 0.958$, $df = 5$, $P < 0.001$; Fig. 4).

If the above mechanisms can explain the timing of both the MU and MD flows, one would expect the crabs to remain and feed on the canopy, from about 06:30 hrs

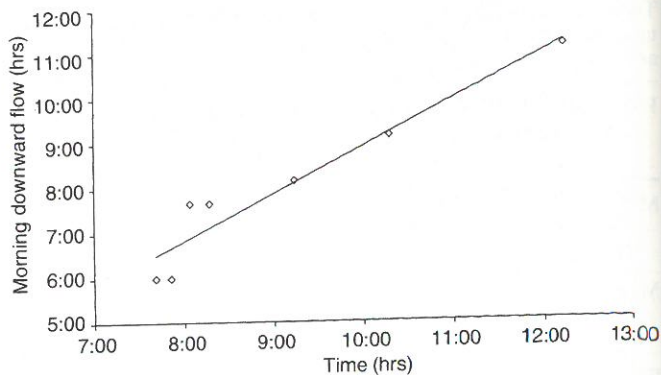


Fig. 4 *Sesarma leptosoma*. Relationship between the average time of the MD flow and the time in the morning at which the temperature exceeded 24 °C

(Table 1), for as long as they are able to withstand the local temperature and RH conditions; thus their available feeding time should be highly variable. In fact this is what happens and the crabs' morning stay in the canopy varies from about 1 h 30 min to more than 5 h (with an average of about 2 h 30 min) (Fig. 1B and D, respectively).

On the other hand, it would also be expected that the roots and the mud surface would offer the downward-migrating crabs considerably better microclimatic conditions than the canopy. Nevertheless, our measures showed that, when the canopy temperature varied within the range of 24 to 32 °C, the root offered a similar temperature, ranging from 24.0 to 32.1 °C. Moreover, when the canopy RH ranges within 40 to 70%, the root RH ranges from 44 to 73%, and this RH advantage of 3 to 4%, with no thermal advantage, seemed to be a poor reason for abandoning the canopy and migrating downwards.

Considering these data, a more important factor is surely the availability of free water which, in the canopy, the crabs could only extract from the leaf buds (Cannicci et al. 1996b) while, among the roots, they could take it from the sea itself, at high tide, or from the wet substratum (the mud or the red alga, *Bostrychia* sp., carpet covering the whole lower mangrove root system), at low tide.

Evening upward flow

The EU flow, which was very variable in duration (Table 3), timing and number of crabs (Table 1), does not seem to be strictly linked to any of the microclimatic variables examined, but is influenced only by the tidal cycle. Crabs climb mangrove trunks in coincidence with rising tides even when they face microclimatic conditions worse than those that they avoided by MD migration (cf. Fig. 2E; an EU peak at 15:20 hrs at a temperature of about 30.5 °C while on the same day, cf. Fig. 1E, the crabs had started to abandon the canopy around 10:00 hrs, with a maximum temperature of 26 °C, the whole MD migration being completed at a temperature < 30.5 °C). The explanation probably comes from the

fact that at 10:00 hrs the crabs were already stressed from being in the canopy for about 3 h, while crabs climbing at 15:20 hrs could have replenished themselves with water before leaving the roots and thus would have been more ready to withstand a potential hygro-thermal stress for the following 2 h.

When the tide does not affect the EU flow, crabs seem to climb at around 17:30 hrs (Fig. 2D, F). Data are too scarce to attempt explaining what triggers the EU flow in such conditions, but we are obliged to admit that some other exogenous or endogenous trigger must be involved.

Evening downward flow

The ED flow is well concentrated (Table 3) and quite stable in time, but extremely variable in the number of crabs involved (Table 1). Its time of occurrence appears to be related to both the tide and the time of occurrence of the previous EU flow (Table 5). The relationship with the tide appears quite contradictory: the descent is earlier when the tide is higher. Thus the tide versus ED correlation is probably a spurious one, i.e. the consequence of two other correlations, tide versus EU and EU versus ED.

The 18:30 hr threshold, which abruptly ends the ED flow, appears so well defined that it strongly suggests an analogy with the triggering system of the MU flow: MU only starts when the light intensity increases past a certain threshold, while ED ends when the light diminishes below another threshold. A comparison of the levels of light present when about 5% of the crabs in MU and 95% of those in ED have passed by, respectively, indicate that the "switching on" threshold (triggering the MU flow) is lower than the "switching off" threshold (triggering the ED flow): averages 1900 and 16 000 lux, respectively ($t = 3.052$, $df = 11$, $P < 0.02$).

Conclusions

Table 7 summarises the results of correlations between timing of migrations, microclimatic factors and tidal cycle. The onset of the four migratory flows appears to be triggered by a variety of factors (light, temperature,

Table 7 *Sesarma leptosoma*. Summary of the relationships between the timing of the four migratory flows and other factors (from Tables 4, 5, and 6) [+ , - indicate the sign of the correlation, the number of symbols (one, two or three) indicates its statistical significance at the 0.5, 0.2 or 0.1 levels, respectively; ~ indicates no significant correlation]

Flow	T	RH	Light	Other flows	Tide
MU	~	~	-	~	~
MD	-	++	~	~	~
EU	~	~	~	~	-
ED	~	~	-	+++	---

relative humidity, tide, and the other flows). Vannini et al. (1995) showed that the MU flow is induced solely by the light level. However, light also seems to play a role in ending the ED flow. Tide plays a role in ending the ED flow. Tide plays a role in triggering at least the EU flow. Temperature and/or RH, on the other hand, appear to induce the MD flow. Since temperature and RH are correlated with each other, only experimental tests under controlled conditions would reveal whether crabs react to one or both of these factors.

Comparisons with other decapod species will help little in the interpretation of the behaviour of *Sesarma leptosoma*. The only other comparable mangrove crab that has been extensively studied, *Aratus pisonii*, does not appear to perform rhythmical migrations (Warner 1967); and the few known tree crab species, which live on trees other than mangroves (Hartnoll 1965; von Hagen 1977; Diesel 1989), where they are subjected to entirely different ecological conditions, do not undergo periodical vertical migrations either.

Still, hypotheses on the adaptive value of *Sesarma leptosoma*'s migratory behaviour seem easy to formulate. In the morning, regardless of the tidal level, the crabs climb the trees only once suitable light is available, probably on account of a visibility problem. They have tremendous visual tasks to accomplish in orienting themselves among the tree branches and roots (Cannicci et al. 1996a, b). During the day, ambush predators such as *Metopograpsus thukuhar* and *Epixanthus dentatus* (Vannini et al. 1997; Cannicci et al. 1996b) are probably more easily avoided, among the mangrove roots, even at 2 m above the soil. Finally, frequent jumps from one leaf to another (Vannini personal observations) can probably be performed more safely in the day light. The same mechanisms may explain why crabs stop migrating around 18:30 hrs. MD flow is delayed as much as possible (increasing feeding opportunity) but is limited by dehydration. EU is triggered by the tide, and even if it pushes the crabs towards harsher climatic conditions, the crabs have had time to replenish their water supply among the tree roots. The ED drives the crabs that do not rest in the canopy, back to the roots and appears to be abruptly ended by lack of visibility.

A hypothesis on the general meaning of the whole migratory behaviour can also be formulated. By migrating towards the canopy, *Sesarma leptosoma* is avoiding predation and has access to unlimited food resources with no competitors. Its morphological and physiological adaptations, apart from relative dactylus shortening and carapace flattening (Vannini et al. 1997), are probably not very different from those of most ground-living sesarmids. Their success in invading the canopy is thus probably based on behavioural specialisation: oriented migrations driven by complex mechanisms telling the crabs where to go (Cannicci et al. 1996a, b) and when to go (the above microclimatic factors and tide).

The above hypotheses obviously require further testing, both in the field and in the laboratory, and the

possible role of a biological clock must be ascertained. A better understanding of the high variability among different days in the number of crabs descending before dusk instead of resting in the canopy is also needed.

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