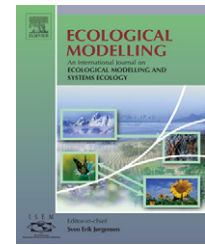


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Simulating cryptic movements of a mangrove crab: Recovery phenomena after small scale fishery

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ARTICLE INFO

Article history:

Received 19 June 2006

Received in revised form

29 January 2007

Accepted 1 February 2007

Published on line 26 March 2007

Keywords:

Ucides cordatus

Individual-based model

Field of neighbourhood

Pattern-oriented modelling

Competition

Movement

ABSTRACT

The semi-terrestrial burrowing crab *Ucides cordatus* is an important ecological component and economic resource of Brazilian mangrove forests. The crab population of the Caeté peninsula (the location of our study site) has been exploited for the last 40 years. Recovery of fished areas by crabs from non-fished areas under the roots of the mangrove tree *Rhizophora mangle* was hypothesized to be an important buffer mechanism against rapid overfishing. However, catch per unit effort decreased in recent years, suggesting that the sustainability of the crab fishery might become endangered. It is therefore important to better understand the movement behaviour of these crabs, even though it is hard to observe directly. Following the approach of pattern-oriented modelling, we developed an individual-based model to infer movement behaviour from patterns in density recovery that were observed in field experiments. Two alternative submodels simulating factors causing movement were contrasted: with and without local competition among crabs. To describe local competition, the field-of-neighbourhood (FON) approach was used, which was originally designed for sessile organisms. Without competition, unrealistically high movement frequencies were required to fit the observed linear recovery patterns. With competition included, better fits to the recovery patterns were obtained, and lower and thus more realistic movement frequencies were sufficient. This indicates that local competition between crabs is the main reason for them to move and change their burrows. Our work shows that the FON approach is suitable to describe local interactions not only among sessile organisms, but also among mobile organisms in conditions of competition for resources. The simulation results illustrate the importance of the non-fished rooted areas as buffers against rapid over-fishing. The IBU model presents a potential for future analysis of these buffer mechanisms and thus for a better understanding of the crab fishery and its management.

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1. Introduction

The semi-terrestrial crab *Ucides cordatus cordatus* (Linnaeus, 1763) (hereafter referred to as *U. cordatus*) is an important eco-

logical component (Branco, 1993; Blankenstejn et al., 1997; Wolff et al., 2000; Koch and Wolff, 2002; Schories et al., 2003; Nordhaus et al., 2006) and economic resource (Glaser, 2003) of Brazilian mangrove forests. Fisheries on this crab have been

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doi:10.1016/j.ecolmodel.2007.02.008

reported from many places of Brazil (e.g., Alcantara-Filho, 1978; Nordi, 1994a,b; Alves et al., 2005), and catches can reach very high values, up to $\sim 8.0 \text{ g m}^{-2} \text{ year}^{-1}$ in the Caeté peninsula, where our study was carried out (Diele, 2000; A.-R. Araujo, unpublished data). The Caeté peninsula is covered by 140 km^2 of mangroves and is located 200 km east-north-east of Belém. It was the focus area of a long-term interdisciplinary research project on sustainable coastal management (MADAM project; Berger et al., 1999) including work on the biology of *U. cordatus* (Diele, 2000; Nordhaus, 2004; Diele et al., 2005; Diele and Smith, 2006; Nordhaus et al., 2006).

The local crab population has been exploited for 40 years, but to date, crab collectors mainly employ non-destructive, artisanal capture techniques by using their bare arm or a hooked stick to pull the crabs out of their burrows (Glaser and Diele, 2004). Mainly mature large males are harvested, and crab collectors report recovery of fished areas in less than 2 weeks (Diele et al., 2005; C. Piou, pers. observation). So far, the traditional fishing techniques do not seem to have affected the biological sustainability of the Caeté crab population (Diele et al., 2005). However, 6 and 8% decreases in catch per unit effort occurred in 1999 and 2000, respectively (stable values thereafter) (Diele et al., 2005), suggesting that the economic and social sustainability of the crab fishery in this area might become endangered (Glaser and Diele, 2004).

The recovery of the fished areas is not yet fully understood and the factors influencing it at the individual level are not known. *U. cordatus* grows very slowly and reaches maturity after ~ 2.5 years and fishing size (usually $> 6.5 \text{ cm}$ carapace width) only after 7 years (Diele, 2000). This shows that the specimens that restock fished areas are not recently settled young recruits, as believed by crab collectors. The additional fact that large (i.e., old) and small (i.e., young) crabs are usually not found in same densities in the mangrove forest (e.g., Diele et al., 2005) indirectly indicates movement. Finally, one important buffer mechanism leading to recovery of fished areas is believed to be the movement of crabs from non-fished areas to fished ones. In *Rhizophora mangle* forests, the most important fishing grounds, non-fished areas are patches of dense roots, which are inaccessible to the fishermen (Diele et al., 2005). Forests dominated by *Avicennia germinans* and *Laguncularia racemosa* are less frequently fished because root carpets and/or sandy substrate hamper fishery. Both types, non-fished and less fished areas, might function as buffers at different spatial scales. However, in *A. germinans* forests, crab density and average size is much lower than in *R. mangle* dominated forests (Diele, 2000).

So far, only scarce information could be collected on individual movement behaviour. Crabs moving long distances and searching where to establish a new burrow were only very scarcely seen in a total of many dozens of full day observations. Nordhaus (2004) investigated the behaviour of *U. cordatus* near their burrows and found that most crabs remain quasi immobile in or nearby their burrow entrances. She quantified their short-distance movements around the burrows for foraging on mangrove leaf litter (during 0.3% of the time and with maximum distance of $\sim 1 \text{ m}$), but could not estimate how often crabs change burrows and to what distance new burrows are built or overtaken. Nevertheless, an impor-

tant conclusion made by Nordhaus et al. (2006) is that the *U. cordatus* population at the Caeté peninsula is food limited. This becomes obvious from the fact that *U. cordatus* usually completely depletes the leaf litter from the floor of *R. mangle* forests.

The purpose of this study was to understand the behaviour of *U. cordatus* crabs that promotes the recovery of fished areas on a small scales ($< 1 \text{ ha}$) in *R. mangle* forests. We tried to quantify this recovery pattern and the movement of crabs in the field. We developed an individual-based model of the crabs and their behaviour and followed the idea of pattern-oriented modelling (Grimm et al., 1996, 2005; Grimm and Berger, 2003; Wiegand et al., 2003) that patterns at the system level contain information about processes at the individual level. We thus formulated alternative sub-models, or theories (Grimm and Railsback, 2005), of movement behaviour and checked how well they were able to reproduce recovery patterns observed at the population level.

One of our main questions regarding the movement of crabs was to understand what forces them to give up a burrow in the first place and to establish themselves in a new area, e.g., a fished one. We tested whether competition among crabs for food as documented by Nordhaus et al. (2006) could be the trigger for crab movement. In the following, we describe the patterns observed in the field, the individual-based-*Ucides* (IBU) model and its submodels, and finally show the assumptions under which IBU best fits the observed recovery patterns.

2. Field experiments

2.1. Methods

To study the recovery of fished areas on a small scales ($< 1 \text{ ha}$), field experiments were conducted in a mangrove forest dominated by tall *R. mangle* trees in the northern part of the Caeté peninsula, close to the tidal channel, *Furo Grande* ($0^\circ 50' 15'' \text{ S}$ and $46^\circ 38' 30'' \text{ W}$). Although not according to the fishing method applied by local crab collectors, two experiments of complete exclusion of crabs from areas of high density of crabs ($> 4 \text{ m}^{-2}$) without roots were conducted in November–December 2003 and 2004. The proportions of closed burrows versus open burrows as well as occupied burrows versus non-occupied burrows were estimated before the experiments started. In the first year, one plot of 12.25 m^2 was fished entirely and the mud flattened to remove the signs of fishery and burrow entrances (hereafter referred to as experiment 1). In the second year, six plots of the same size were fished entirely but the burrow entrances and the holes created by the crab collector were left accessible for re-colonization (experiment 2). The numbers of active burrows, indicating the number of returning crabs, were determined for 50 days in experiment 1 and for only 15 days in experiment 2 because of a sampling hazard. The ratio of number of occupied burrows after fishery to the original number before fishery was taken as an indicator for re-colonization.

Additionally, nine plots of 3 m^2 covering a more diverse type of habitat (in elevation and root density) as well as data from Diele (2000) and data from transect sampling (Piou et al.,

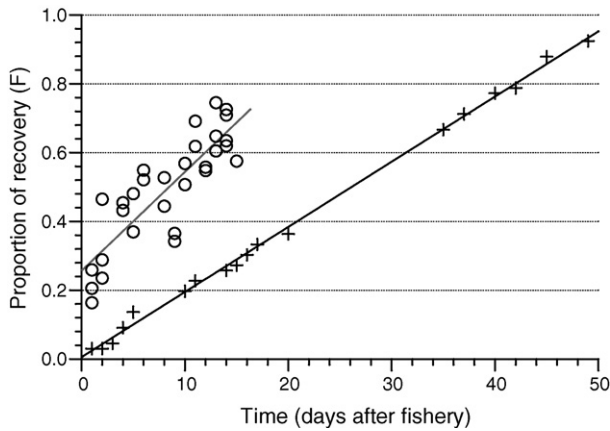


Fig. 1 – Proportion of occupied burrows through time after the fishing experiment, flattening the surface in 2003 (experiment 1: crosses) and leaving the holes in 2004 (experiment 2: circles) with respective regression lines.

unpublished data) were used to estimate proportions of burrow occupation and status (closed or open) and to estimate mean crab density and related size.

To enhance the knowledge on *U. cordatus* behaviour, we also observed individual specimens in the field. *U. cordatus* can spend several days in its burrow without coming out and blocks its entrance with a plug of mud. We followed the burrow status of >100 crabs during 2–5 weeks to obtain estimations on how often burrows were closed and for how long. In 2003 and 2004 several tagging-observation experiments were performed (in total 98 individuals tagged) to evaluate the frequency of burrow change and distances covered when crabs change their burrow. Tagging methods included radio-tracking, paint, or other visual marks fixed on the back of the carapace of individuals.

2.2. Results

For the areas of the two recovery experiments, mean burrow density before fishery was 5.29 ± 0.97 burrow m^{-2} . After fishery, recovery was faster when leaving holes on the ground surface (2004, experiment 2) than after flattening (2003, experiment 1) (Fig. 1). Comparing the first day after fishery in the two experiments, recovery was higher in experiment 2 because existing burrows could immediately be colonized. We found linear correlations between the proportion of occupied burrows found on the plot (F) and the number of days after fishery (t) for the two experiments:

$$F(t)_{2003} = 0.0056 + 0.0189t \quad \text{and} \quad F(t)_{2004} = 0.2568 + 0.0287t,$$

with R^2 of 0.99 and 0.71, respectively. These regression formulas were taken as the main patterns of linear recovery to be reproduced by the IBU model.

In general, in forests dominated by *R. mangle*, mean crab carapace size was 6.05 ± 0.9 cm with mean density of 3.16 crab m^{-2} . The proportion of closed burrows was measured as at least 60%, while the unoccupied burrow proportion was about 20%. Both proportions varied in space and depended on the tidal cycle.

None of the methods of following the crabs' movements in the field was entirely successful because crabs were generally not re-observed after release. We obtained rough estimates of the frequency of movement from >0 to 0.15 move/crab day and a mean walking distance between 0.2 and 50 m/day. Furthermore, our field observations showed that on average crabs closed their burrows once a week and that the burrows remained closed for a mean period of about 3 days.

3. The IBU model

3.1. Description

The following model description follows the ODD protocol (Overview, Design concepts and Details) for describing individual- and agent-based models (Grimm and Railsback, 2005; Grimm et al., 2006) and consists of seven elements. The first three elements provide an overview, the fourth element explains general concepts underlying the model's design, and the remaining three elements provide details.

3.2. Purpose

The main purpose of the IBU model was to reproduce the patterns of linear recovery of the crab population after fishery at small scales (<1 ha). It was tested whether local competition among neighbouring crabs is a reasonable explanation for the crabs' movement.

3.3. Structure, scales and states variables

The simulated area corresponded to a homogeneous mangrove mud flat of $15 \text{ m} \times 15 \text{ m}$ with a square fished area in the centre of 12.25 m^2 . The area had periodic boundaries (=Torus) so that the number of crabs was constant throughout the simulation. The temporal unit was 1 day.

The state variables of individual crabs were: identity number, position, carapace width (CW), angle of direction of movement, and identity number of occupied burrow. The burrows state variables were: identity number, position, hosted crab id (if any), open/close status and time without a crab (if not occupied, t_{empty}).

3.4. Process overview and scheduling

During each time step, the following sequence of processes was simulated: updating of parameters of the submodels that describe the interactions among the crabs, checking the status of all burrows with removing those that were empty for too long time (see submodels), and checking the status of all crabs in a random order. During this last process, individual crabs could accomplish one of the following actions: do nothing; change the open/close status of its burrow; or move, i.e., leave its burrow (if it was open) to take over or create a new one. The movement of a crab consisted of different sub-processes: reason for moving, walking behaviour and reason for stopping, which determined three modules described in the submodels section.

Table 1 – Parameters and initialization values for the IBU model

Parameter name	Description	Initial values	Assumptions	Source
D_c	Crab starting density (in./m ²)	3.16	Homogeneous area that does not consider habitat heterogeneity	(1)
$Prop_{Unoc}$	Proportion of unoccupied burrows at start	22%	Neap tide situation	(1)
$Prop_{closed}$	Proportion of closed burrows at start	60%	–	(1)
CW_{pop}	Mean carapace size of the simulated crab population (in cm)	6	Few fished-size crabs and more smaller ones	(1)
$S.D.CW_{pop}$	Standard deviation of the mean carapace size of the simulated crab population (in cm)	1	–	(1)
a and b	Constants for the interaction radius calculation (Eq. (1))	19 and 15 cm	For a crab of $CW = 1$ cm $R_{int} = 24.5$ cm, and above $CW = 9$ cm all crabs $R_{int} = 100$ cm	(2)
P_{c1}	Probability of taking over an occupied burrow	0.0	Impossible	(3)
P_{c2}	Probability of taking over a closed empty burrow	0.25	Possible if pass just on top	(3)
P_{c3}	Probability of taking over an open empty burrow	1.0	Would always prefer to stop if find an open empty burrow	(3)
$P_{closing}$	Probability that a crab closes its burrow at each time step	0.14	Close its burrow approx. once a week	(3)
$P_{opening}$	Once closed, probability of opening its burrow at each time step	0.33	Closing period of ~3 days	(3)

Sources: (1) compilation of data from Diele (2000) and additional measurements on population structure; (2) estimation from individual behaviour of Nordhaus (2004); (3) estimation from individual crab behaviour trials of experiments.

3.5. Design concepts

3.5.1. Emergence

Recovery of entirely fished areas emerges from the behaviour of the individual crabs and, in particular, from their interactions via local competition.

3.5.2. Interaction

For crabs in their burrows, two assumptions of competition interactions influencing their reason of movement were tested: no apparent interactions (null assumption); competition with neighbouring individuals for shared resources (field of neighbourhood or FON assumption). Food resources (mangrove leaves fallen from the trees) for which *U. cordatus* compete, are assumed as continuously renewed and homogeneous on the mangrove floor. However, the competition intensity for these leaves depends on their distance from the burrow entrance and, probably, on the size of the involved individuals. Thus, we adapted the field of neighbourhood (FON) approach to describe competition (Berger and Hildenbrandt, 2000, 2003). The FON approach assumes a circular intensity field around each crab representing its harvest area. Crabs were considered to interact if their fields overlapped. Distance and size of the neighbours determined the intensity of their FON effect on a given crab. The sum of the FON effects was assumed to influence the probability of leaving a burrow. Therefore, this approach implicitly assumed an effect of food limitation on the crabs' movement (Nordhaus et al., 2006).

3.5.3. Stochasticity

Most elements of individual crab behaviour (such as closing/opening its burrow, taking over a burrow, and reason, direction or the stopping of movement for some submodels) and burrow disappearance were ruled by empirically deter-

mined probabilities (Table 1). Stochasticity was used for each of these probabilities. This accounted for individual variability and the fact that detailed lower level information on processes determining these behaviours is not available.

3.5.4. Observation

Information about crabs and burrows could be obtained at each time step with a graphical user interface including a map of burrows, crabs, fields of neighbourhoods, and movement paths (Fig. 2). This interface was used for model testing and visual debugging (Grimm, 2002). Numerical outputs were used for further analyses.

3.6. Initialization

IBU simulations were initialized by first creating the number of crabs given by the input density (D_c) together with their burrows in random position in the area; secondly by adding the proportion ($Prop_{Unoc}$) of unoccupied burrows at random positions. The open/closed status of all the burrows was determined randomly following a probability corresponding to expected proportion ($Prop_{closed}$). These last two proportions were given as input from the field observation at population level. Carapace size of individual crabs was randomly attributed according to a normal distribution with a given mean size (CW_{pop}) and standard deviation ($S.D.CW_{pop}$) for the simulated population (see Table 1 for all these parameters). After assigning these initial states, simulations were run for 10 days in order to establish a typical situation caused by the crabs' interactions. Tests showed that 10 days was sufficient for this. Then, fishing was simulated in the central fishing area by removing all crabs and also removing or not removing the burrows, to simulate the two field experiments, respectively (see description of experiments 1 and 2 above, and model analysis below).

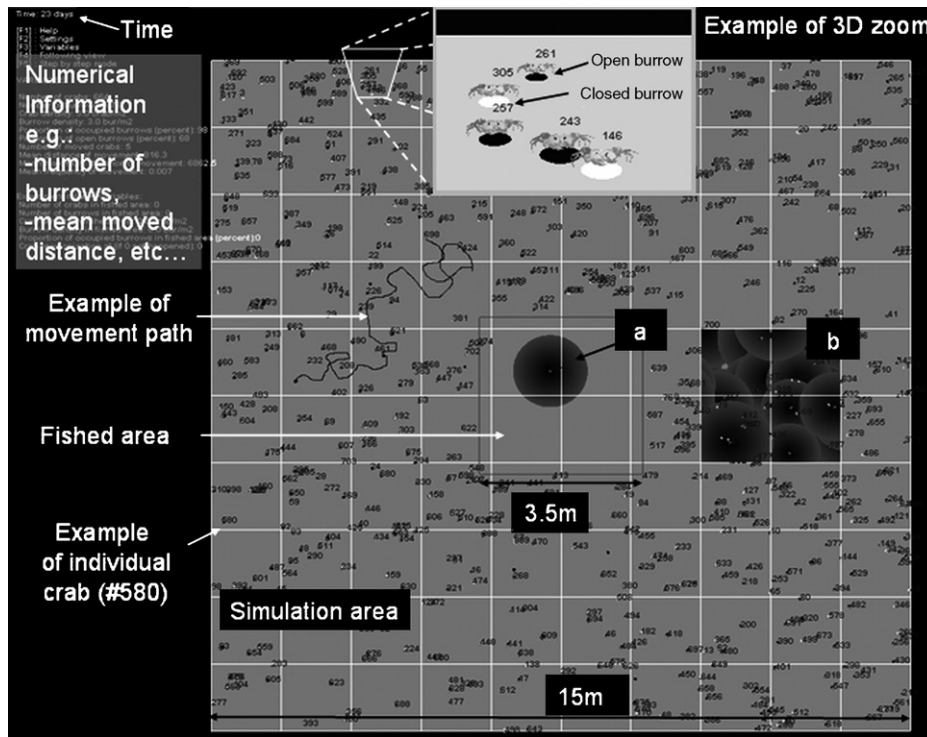


Fig. 2 – Snapshot of IBU model interface with examples of particular features related to the fishing experiment and the field of neighbourhood (FON) interaction submodel ((a) single crab FON area and (b) example of an area of interactions with visualization of FON areas of all crabs).

3.7. Input

Environmental conditions were assumed to remain constant during the simulation experiment, so no input was required after the initialization phase.

3.8. Submodels

Dispersal of crabs was described as a combination of three modules: reason for movement (RM), walking behaviour and

reason for stopping movement. The RM module had two submodels based on general assumptions of interactions among crabs (Null and FON). The two other modules had one submodel each. Additionally, IBU had a simple submodel describing the limited lifetime of unoccupied burrows.

3.9. Reason for movement

3.9.1. Random reason submodel (RM_r)

This submodel followed the Null assumption of no interaction among the crabs, which therefore had a constant probability

Table 2 – Descriptions and values of parameters tested with the two models, analyzing their effect on empirical pattern reproduction

Parameter name	Description	Values tested with the Null model	Values tested with the FON model
P_{move}	Probability of movement at each time step	0.01, 0.1, 0.2, 0.3	–
P_{base}	Base probability of movement at each time step (Eq. (3))	–	0.1, 0.2, 0.3
P_{stop}	Probability of stopping movement at each movement step	0.001, 0.002, 0.004, 0.008	0.002, 0.004, 0.008
C_{Rmove}	Constant for the radius calculation of crab's perception of burrows at end of movement-steps (Eq. (5))	1, 2, 3, 4	1
α_{dev}	Maximum deviation angle between each movement step (Eq. (4))	π , $\pi/2$, $\pi/4$, $\pi/20$	$\pi/4$
C_{disap}	Disappearing factor of burrows (Eq. (6))	0.15, 0.07, 0.02, 0.005	0.02
F_{A-max}	Maximum FON neighbors effect a crab could feel without increasing its probability to leave its burrow (Eq. (3))	–	0.1–1.9 with increment of 0.2

P_{move} (Table 2) of leaving their burrow (if it was open) at each time step.

3.9.2. Competition submodel (RM_{FON})

This submodel adapted the field of neighbourhood approach that was originally developed for trees and other sessile organisms (Berger and Hildenbrandt, 2000, 2003). The radius of interaction (R_{int}) was calculated for each crab at the start of the simulation with the following formula:

$$R_{\text{int}} = \min \left\{ a \times \left(\frac{CW}{2} \right) + b, R_{\text{max}} \right\} \quad (1)$$

where a and b were constants (Table 1) and R_{max} was a maximum radius assumed to be 100 cm. R_{int} reflected the radius of daily action (excluding burrow change) of crabs according to their size and was estimated from field observations (Nordhaus, 2004; C. Piou, pers. observation). The intensity of the FON at any point with distance r from a given crab was considered as (Berger and Hildenbrandt, 2000):

$$FON(r) = \begin{cases} 1 & \text{for } 0 \leq r < CW/2 \\ \exp \left(- \left(\frac{|\ln(F_{\text{min}})|}{R_{\text{int}} - (CW/2)} \right) \right) & \text{for } CW/2 \leq r \leq R_{\text{int}} \\ 0 & \text{for } r > R_{\text{int}} \end{cases} \quad (2)$$

where F_{min} was the minimum intensity (0.01) of the FON at R_{int} . The sum of the FON intensity of the neighbours over the FON area of a given crab was then divided by its own FON area. The resulting value F_A is used as a measure of competition intensity. Note that this measure takes into account size (carapace width) and distance away from the neighbouring crabs. F_A was calculated at the beginning of each time step for each crab. When the crabs were individually checked, F_A was used to determine the probability of leaving (P_{move}) an already open burrow:

$$P_{\text{move}} = P_{\text{base}} \times \frac{F_A}{F_{A\text{-max}}} \quad (3)$$

where $F_{A\text{-max}}$ was a constant to transform the competition intensity into probability of movement, and P_{base} was a base probability of changing of burrow at each time step (Table 2).

3.10. Walking behaviour

The walking behaviour was defined as the type and order of actions a crab would execute when it left its burrow and looked for another one or created a new one. This behaviour was set as a repetition of three actions defining a movement step: (1) moving a short distance; (2) checking the surrounding area for a burrow to take over; (3) deciding whether to continue or not (described in the next module). The direction of movement was assumed to change between each movement step and was therefore calculated at the beginning of each step. A first random angle (α_0) was attributed to the crab at the beginning of its movement and the next ones (α_n) calculated as:

$$\alpha_n = \alpha_{n-1} + \text{Rnd}(\alpha_{\text{dev}}) \quad (4)$$

where α_{dev} was the “maximum deviation angle” and $\text{Rnd}(\alpha_{\text{dev}})$ was an angle randomly taken from the interval $[-\alpha_{\text{dev}}, \alpha_{\text{dev}}]$ (Table 2). The distance of a movement step was attributed randomly between 10 and 50 cm. On arriving at its new position the crab checked for all the burrows in a radius of perception, R_{move} , defined as:

$$R_{\text{move}} = c_{R_{\text{move}}} \times CW \quad (5)$$

where $c_{R_{\text{move}}}$ was a constant (Table 2). If no burrow was found in this area, the crab decided whether it should do another movement step or not (see next module). If burrows were found, the crab tried to take them over. This takeover was impossible if a burrow was occupied, and followed different probabilities of success in the other cases (parameters P_{c1} – P_{c3} , Table 1). The crab kept in memory the burrows that it had visited since the beginning of the walk. If a burrow had been previously checked, the probability of success of taking over was set to zero.

3.11. Reason for stopping movement

The first reason for stopping movement for a crab was whether it managed to take over another burrow. The crab position was then set to this burrow position. If no burrows were taken over at this step, the crab continued moving with probability $1 - P_{\text{stop}}$ (Table 2), or else created a new burrow at its actual position.

3.12. Burrow lifetime submodel

Empty burrows sooner or later disappear from mangrove floor because of tidal wash and bio-perturbation. To model this in a simple way, the probability of disappearance (P_{disap}) of the empty burrows was determined as:

$$P_{\text{disap}} = c_{\text{disap}} \times t_{\text{empty}} \quad (6)$$

where c_{disap} was a constant defined as the “disappearing factor of burrows” (Table 2) and t_{empty} was the number of days since a crab last occupied the focus burrow. Thus, the longer a burrow was without a crab, the higher the probability of its disappearing, until the burrow would disappear deterministically after the time $t_{\text{empty}} = 1/c_{\text{disap}}$.

3.13. Model analysis

Two different models were analyzed to find the parameterization that best fit the patterns observed in the field experiments. The first model used only the Null assumption of interaction between crabs (RM_r) (hereafter referred to as Null model). Five parameters (P_{move} , P_{stop} , $c_{R_{\text{move}}}$, α_{dev} , and c_{disap}) that were hard to estimate from field knowledge were considered to have a possible influence on the re-colonization patterns (Table 2). Four values were assigned for each of these parameters and all possible combinations of parameter values were tested. For each parameter set, two types of simulation experiments were performed, which correspond to the field experiments 1 and 2: removing of all burrows and crabs of a 12.25 m² area (experiment 1), and removing only the

crabs of an identical area but leaving the burrows (experiment 2). The simulations lasted 50 or 15 days, respectively after the initial phase of randomization/organisation of 10 days. Note, that both experiments mimic the field experiments carried out during this study. They do not imitate the traditional behaviour of crab collectors, who catch only big males and do not concentrate on a quadrat area. Thirty replicate simulations of each type of experiment were performed. To check the fit to the two linear patterns of re-colonization observed in the field (Fig. 1), an error of deviation from each pattern (ΔRec) was calculated with the formula of root mean square deviation (e.g., Jamieson et al., 1998; Wiegand et al., 1998):

$$\Delta\text{Rec} = \sqrt{\frac{\sum_{t=1}^{N_{\text{obs}}} (F(t) - \text{Sim}(t))^2}{N_{\text{obs}}}} \quad (7)$$

where N_{obs} was the number of days of observations (50 for the first experiment and 15 for the second), $F(t)$ was the regression describing the observed linear recovery of the percent of occupied burrows at time t after fishery and $\text{Sim}(t)$ was the corresponding simulated value. A total error estimation (Δtot) was calculated as:

$$\Delta\text{tot} = \sqrt{\Delta\text{Rec}_{\text{exp1}}^2 + \Delta\text{Rec}_{\text{exp2}}^2} \quad (8)$$

where $\Delta\text{Rec}_{\text{exp1}}$ and $\Delta\text{Rec}_{\text{exp2}}$ were the error of deviation for experiments 1 and 2, respectively (from Eq. (7)). Additionally, the proportion of crabs that moved per time step and the proportion of occupied burrows on the entire area were registered

and compared to field estimations. To understand the relative effects of parameters and their interaction on the total error (deviation between simulated and regressed dynamics of re-colonization), a general linear model (GLM) was computed as a large design ANOVA. Multiple comparisons among means of groups were based on Tukey's "honestly significantly different" tests in order to differentiate homogeneous groups of parameterizations that could be considered as having identical fit to the field patterns.

The second model included local competition among crabs using the FON approach in the reason for moving submodel (RM_{FON}) (hereafter referred to as FON model). Three base probabilities of movement and probabilities of stopping movement were tested, respectively (Table 2). For the parameter $F_{A\text{-max}}$ of calibration of the FON intensity, 10 values were tested (Table 2). With these 30 possibilities for P_{base} and $F_{A\text{-max}}$ combinations, we covered a large range of $P_{\text{base}}/F_{A\text{-max}}$ ratios as an index of transformation of FON intensity (F_A) into probability of leaving (Eq. (3), P_{move}). For each of the parameters c_{Rmove} , α_{dev} and c_{disap} a value was chosen based on the results from Null model (Table 2; a similar approach for parameterization is used by Mullon et al., 2003). Thirty replicates of each possible parameter's configuration were performed for both fishery experiments, 1 and 2. The deviations from the field patterns were calculated with the same estimations of error described above ($\Delta\text{Rec}_{\text{exp1}}$ and $\Delta\text{Rec}_{\text{exp2}}$ Eq. (7), and Δtot Eq. (8)). To be able to compare the two model versions (Null and FON), the results of the Null model with identical parameter set ($c_{\text{Rmove}} = 1$, $\alpha_{\text{dev}} = \text{Pi}/4$, $c_{\text{disap}} = 0.02$) were considered. The mean frequencies of movement of crabs were measured during the simulations.

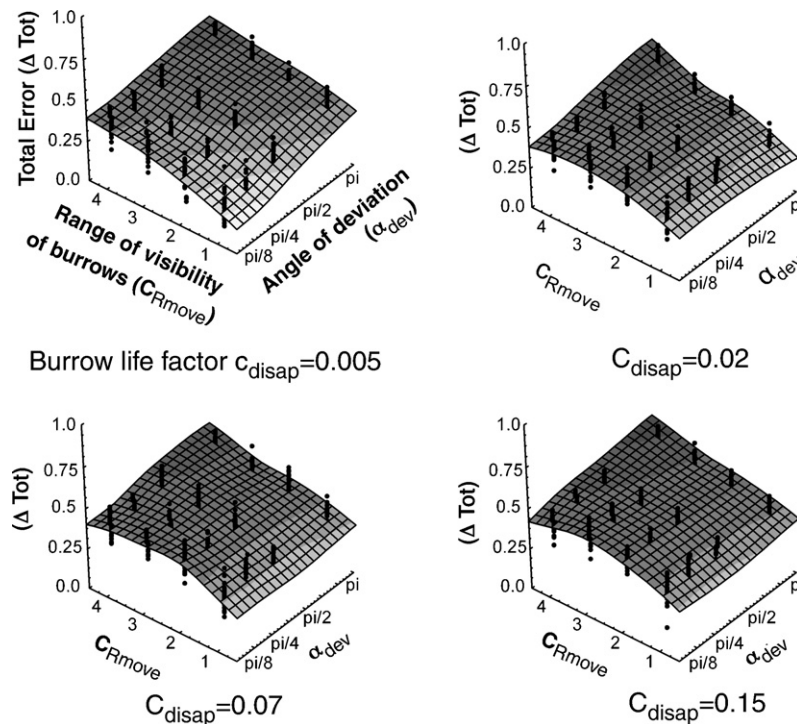


Fig. 3 – Effects of maximum deviation angle during movement (α_{dev}), range of crab's perception of burrows (c_{Rmove}) and disappearing factor of burrows (c_{disap}) on the reproduction of the recovery patterns (total error, Δtot). Data selected for this graph had all identical probability of movement ($P_{\text{move}} = 0.1$) and probability of stopping ($P_{\text{stop}} = 0.004$). Each point corresponds to one simulation result.

4. Results

4.1. Null model

All tested parameters significantly influenced the total error of recovery pattern (GLM with all parameters as grouping variables and all cross interactions, all $p < 0.05$, Adjusted $R^2 = 0.836$). Smaller “maximum deviation angle” between movement steps reduced the total error (Fig. 3) by decreasing the erratic type of movement. Likewise, a smaller radius of the crab’s perception of burrows also decreased the total error (Fig. 3) by increasing the probability of finally creating a new burrow, and therefore increasing the probability of colonizing the fished area. The longer the lifetime of empty burrows (low c_{disap}), the better the simulations were at fitting the recovery patterns. This was particularly true for experiment 2, which could better reproduce the high recovery proportion at the beginning of recolonization with long-lasting burrows.

The probability of movement was seen as one of the most important parameters influencing the recovery patterns with higher frequency of movement leading to better fits (Fig. 4). However, the total error of simulations with $P_{move} = 0.3$ was not significantly lower than with $P_{move} = 0.2$ because with a too-high frequency of movement, simulations led to a very high recovery rate for experiment 1. The probability of stopping movement together with the maximum angle of deviation determined the distance walked by crabs. This altered the recovery pattern fit in cases of extremely short or extremely long walks. Too short led to no movement crossing the fished areas. Too long walks led to too high probability of finding an empty burrow somewhere else in case of experiment 1, therefore leading to slower recovery. The 81 best fitting parameterizations (lowest Δ_{tot}) were not found to be significantly different (Tukey HSD test; homogeneous groups, Between MS = 0.00343, d.f. = 29696). They were mainly follow-

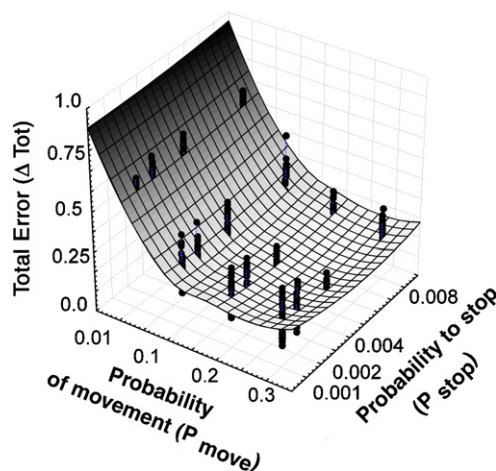


Fig. 4 – Effects of probability of movement (P_{move}) and probability to stop moving (P_{stop}) on the reproduction of the recovery patterns (total error, Δ_{tot}). Data selected for this graph had all identical maximum deviation angle ($\alpha_{dev} = \pi/4$), disappearing factor of burrows ($c_{disap} = 0.02$) and range of crab’s perception of burrows ($c_{Rmove} = 1$). Each point corresponds to one simulation result.

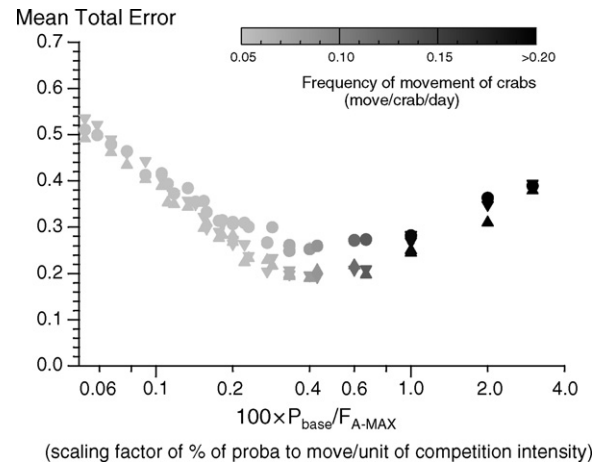


Fig. 5 – Effect of the scaling parameter to transform competition intensity to additional probability of movement ($100 \times P_{base}/F_{A-max}$, axis = $\log(x)$) on the mean total error of deviation from the field pattern of recovery with the second type of models. Circles: $P_{stop} = 0.002$; upward triangles: $P_{stop} = 0.004$; downward triangles: $P_{stop} = 0.008$. Gray intensity of markers represents the mean frequency of movement of crabs during simulations. Each point represent the mean of 30 replicates, variations of means were not presented here to facilitate reading (see Figs. 6 and 7).

ing the previously described trends: including high probability of movement, intermediate walking distance, small radius of burrow perception and long lifetime of empty burrows on the surface.

However, these parameterizations required probabilities of movement which led to high measured frequencies of movement to obtain the best fits. These frequencies of movement were much higher than the estimate of 15% of crabs per day leaving their burrows.

4.2. FON model

With the use of the FON submodel (RM_{FON}), the ratio of P_{base}/F_{A-max} determined the overall error (Δ_{tot}) and the measured frequency of movement of crabs during the simulations (Fig. 5). At intermediate P_{base}/F_{A-max} ratio (~ 0.003 to 0.007), the mean total error showed best fits to the field pattern of recovery (Fig. 5), indicating an optimal range of frequency of movement with the FON model. The probability of stopping movement also had an effect on these total errors, showing better fits with higher P_{stop} values (Fig. 5). But for the three P_{stop} values tested, similar patterns of effect of the P_{base}/F_{A-max} ratios on the total error were observed (Fig. 5). Among these parameterizations, the variance of total error was not identical, and assuming that a better parameterization would be the one reproducing the field pattern more often, the best parameterizations were believed to be the ones with smaller variance of total error.

Fig. 6 shows the mean total error of each parameterization using the FON model against their respective variance. Additionally the selected corresponding parameterizations of the

model using the Null interaction submodel were also plotted in Fig. 6. For this Null model, the parameterization leading to the lowest mean total error was not realistic in terms of measured frequency of movement (>0.20 move/crab day, parameterization α_1 in Fig. 6: $P_{\text{move}}=0.3$, $P_{\text{stop}}=0.004$). Considering a more realistic frequency of movement, the most realistic parameterization could be selected (β_1 in Fig. 6: $P_{\text{move}}=0.2$, $P_{\text{stop}}=0.004$) for this Null model. For the FON model, high frequency of movement led to high mean total error and high variance in the fit of the field patterns. Some parameterizations leading to very low mean total error were also observed with relatively high variance (e.g., the smallest mean total error given by parameterization α_2 in Fig. 6: $P_{\text{base}}=0.3$, $P_{\text{stop}}=0.008$ and $F_{A\text{-max}}=0.7$). We could select the best and most realistic parameterization considering a compromise between the goodness of fit, the low variance and the low frequency of movement (β_2 in Fig. 6: $P_{\text{base}}=0.3$, $P_{\text{stop}}=0.008$ and $F_{A\text{-max}}=0.9$).

The FON model in general needed lower mean frequency of movement of individual crabs to achieve better range of goodness of fit than the corresponding Null models (Fig. 6). This was also true for the two selected most realistic parameterizations of the respective two types of models (β_2 with 0.065 moves/crab day had lower mean total error than β_1 with 0.137 moves/crab day). These two selected most realistic

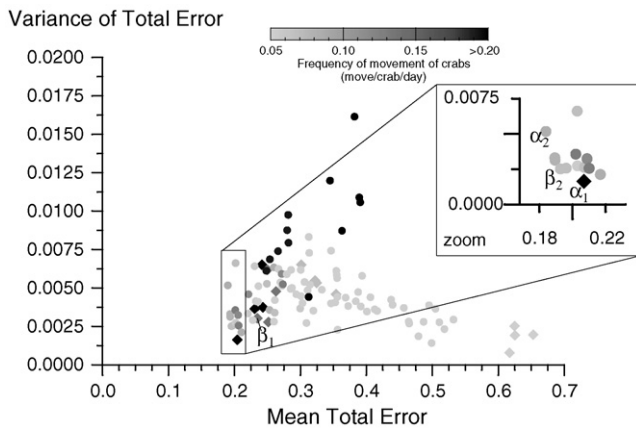


Fig. 6 – Mean total error against variance of total error in the reproduction of the recovery pattern for the parameterizations of the second model type (using the RM_{FON} submodel, circles markers) and selected parameterization of movement step behaviour ($c_{\text{Rmove}}=1$, $\alpha_{\text{dev}}=\text{Pi}/4$, $c_{\text{disap}}=0.02$) of the first model type (using the RM_{r} submodel, diamonds markers). Parameterizations on the lower left corner are the best and more reliable ones (zoomed part). Gray intensity of markers represent the mean frequency of movement of crabs during simulations (black markers are not realistic with a frequency higher than 0.20 move/crab day, i.e., $>20\%$ of the population move every day). Greek letters refers to best parameterizations following only the mean total error (α_1 and α_2 of respective model types) and selected best parameterizations according to a compromise between the mean total error, the variance and the frequency of movement (β_1 and β_2 of respective model types).

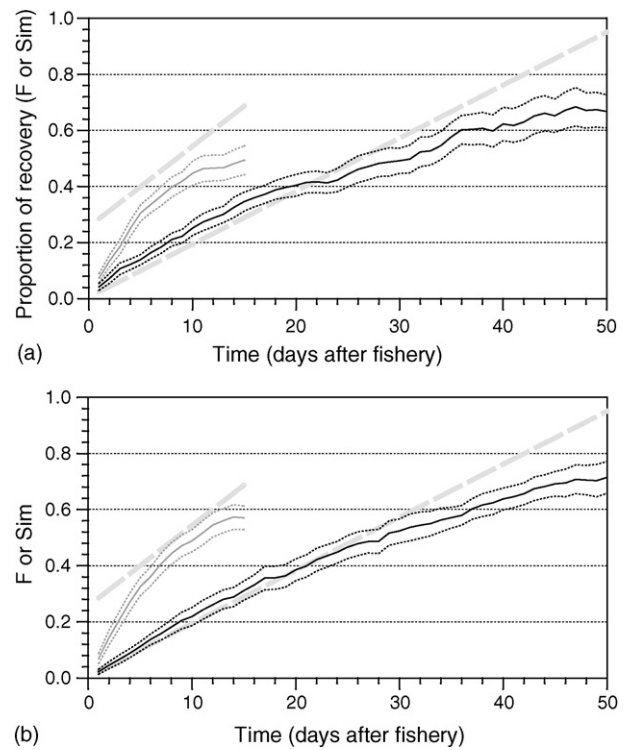


Fig. 7 – Recovery patterns of the most realistic and best fitting parameterizations for the two type of models: (a) using the no-interaction submodel (RM_{r}) (parameterization β_1 : $P_{\text{base}}=0.2$, $P_{\text{stop}}=0.004$, $c_{\text{Rmove}}=1$, $\alpha_{\text{dev}}=\text{Pi}/4$, and $c_{\text{disap}}=0.02$); (b) using the FON submodel of interaction (RM_{FON}) (parameterization β_2 : $P_{\text{base}}=0.3$, $P_{\text{stop}}=0.008$, and $F_{A\text{-max}}=0.9$) (solid black and grey lines: mean of proportion of recovery after fishing from 30 simulations experiment, with removing the burrows or leaving the burrows respectively; black and grey dashed lines: corresponding confidence interval; interrupted bold light grey lines: field patterns of recovery, c.f. Fig. 1).

parameterizations were distinct in their fit to the field patterns mainly because β_2 reproduced better the linear recolonization in experiment 1 and had a faster recovery in experiment 2 than with β_1 (Fig. 7). The reason for movement according to the intensity of competition (RM_{FON}) allowed therefore to have better fits and more realistic frequency of movement than assuming only a random reason for the crabs to change burrows (RM_{r}).

5. Discussion

Overall, our field experiments confirmed the statement of *U. cordatus* collectors that fished areas are recovered within 2 weeks. However, in our field experiments, we achieved a maximum recovery rate of about 80% during this time frame, which also confirms the results of Diele (2000). Several factors explain the small discrepancy between the statement of the crab collectors and the results of our experiments: crab collectors collect only large males while we removed crabs of all sizes during our field experiments. Furthermore, crab collectors do

not concentrate on a small area as we did, but walk around in the forest catching a crab here and there without probing every large burrow and thus never entirely depleting all large males along their path. Finally, their perception of recovery is not quantitative and what they call full recovery might not be 100%.

Nevertheless, the linear recovery phenomena are important population-level patterns since they demonstrate that *U. cordatus* indeed regularly moves from one burrow to another despite the fact that we found rather little evidence of this from direct behavioural observations in the field. This cryptic movement behaviour resulted in a high uncertainty of data regarding the frequency of crabs' movement. The maximum estimate of 15% of the crabs moving per day was considered as an extreme value because it would imply that crabs change their burrows every ~ 7 days on an average. Such a high turn-over of burrows does not seem compatible with the field observation that *U. cordatus* spends >90% of its time inside or inactive on top of its burrows (Nordhaus, 2004).

The field experiments further revealed that a fished area recovers much faster when holes are left on the sediment after the passage of the crab collector. *U. cordatus* obviously prefers to establish itself in an already created hole than to dig an entirely new one. This observation indicates that burrows are precious resources, energy-expensive to build and conserve. Thus, the question as to which factor forced a crab to change its burrow instead of staying where it was before arose. According to Nordhaus et al. (2006), the Caeté crab population is food limited, indicating competition among neighbouring crabs. Based on the information on individual behaviour and on recovery pattern on the plot level, simulation experiments were considered as most suitable to test whether crab movement triggered by local competition could explain the linear recovery patterns observed in the field.

By definition, local or neighbour competition occurs among individuals that interact with each other. Thus, we considered an individual-based, spatially explicit model as an adequate tool. Existing individual-based models implying competition among moving animals either explicitly describe resources use (e.g., Cuddington and Yodzis, 2000; Railsback and Harvey, 2002) or indirectly represent competition by assuming movement to be density-dependent (e.g., Taylor, 1981; Mogilner et al., 2003). Both of these approaches have their pros and cons: the direct approach is mechanistic, but requires detailed knowledge on behaviour and resource dynamics. The indirect approach does not represent feeding behaviour but the direct interactions among individuals (by proximity, fight or territoriality). It transforms distances of individuals into forces and direction of movement of the individuals for the analysis of animal aggregations (e.g., Mogilner et al., 2003). Thus, this second type of approach assumes interference competition (animals interact directly) and not exploitation competition (competition through the use of identical resources without direct interactions, definitions following Keddy, 1989). We needed both in our case.

For these reasons, we chose an approach that is in between the direct and indirect approaches to modelling movement: interactions among crabs are modelled explicitly but without directly referring to feeding, resources or agonistic interac-

tions. This kind of modelling of local interactions has a long tradition in plant ecology (Czárán, 1998) but there is no reason why it should not be used for animal ecology as well. To our knowledge, there is only one previous attempt to model interactions among animals and among animals and plants in a similar way: the GECKO model (Booth, 1997) which is applied in microbial ecology (Kreft et al., 1999, 2001) and for arthropod food webs (Schmitz, 2001). In GECKO, individuals are assumed to have a circular zone-of-influence and zone overlaps are considered as interaction. Individuals are represented by spheres rather than the more dome-shaped field-of-neighbourhood, and the details of how interactions are implemented are different. Moreover, the mode of interaction of GECKO has never been analysed by itself or contrasted to other modes, including a Null model of no interaction at all. In contrast, the properties of the FON approach have been analysed in great detail (Bauer et al., 2002, 2004; Berger et al., 2002, 2004; Berger and Hildenbrandt, 2003).

Nevertheless, the applications of GECKO confirm our conclusion from using the FON approach for modelling local interactions among animals: the approach is conceptually simple and constitutes a good compromise between too-detailed and too-highly aggregated approaches. Berger et al. (2002) argue that the FON approach, or similar approaches, could be developed into a standard way of representing local interactions among plants. Here we would like to conclude that FON and similar approaches, which are based on the notion of a zone of influence, could and should also be developed into a standard approach for representing interactions among animals. Such standard building blocks are needed for developing individual-based models of communities and ecosystems (Grimm and Railsback, 2005).

We show that, at least if resources are distributed and replenished homogeneously, the FON approach is well suited for describing the competition intensity that each crab exerts on this resource. Since Nordhaus (2004) observed that *U. cordatus* generally stays close to its burrow and has a higher chance of obtaining leaves that land on the ground close to its burrow entrance, we considered that the highest competition intensity a crab exerts is at its burrow position, and this intensity should decrease with increasing distance from the burrow. The FON approach with an exponentially decreasing field was then believed to simulate the competition interaction among individual crabs well. A comparison with other approaches coming from plant interaction models such as fixed radius neighbourhood and zone of influence (ZOI) (e.g., Czárán, 1998, chapter 6.3, p. 218) could inform about the specific type of intra-specific competition but this could not be done within the scope of this study.

We also did not address differences between rooted and non-rooted areas. As mentioned above, crab collectors cannot fish underneath dense *R. mangle* roots. These areas are, therefore, considered as buffers against rapid over-fishing as they are likely to promote the recovery of fished areas. However, we do not yet have any information upon how the crabs' behaviour differs among habitat types. Thus, in the model we assumed the area surrounding the fished plot to be homogeneous. Since our experiments produced different crab densities, i.e., within and outside the fished area, we indirectly tested the relative importance of neighbour competition

depending on habitat quality but not the impact of habitat heterogeneity.

The Null version of the IBU model was used as an *a priori* test of the importance and range of movement parameters. Comparing simulation results with field data, a medium rate of burrow disappearance and an intermediary “maximum deviation angle” were selected as the most reliable parameters. In combination with an individual’s probability to stop and the radius of a crab’s burrow perception, these parameters were linked to the distance covered by the crabs and the probability that a crab settles inside a fished area. Not surprisingly, the probability of crab movement was the most important parameter affecting the recovery of fished areas for that model version. Highest movement frequencies fitted the linear recovery patterns observed in the field best. These frequencies exceeded, however, the maximum value observed in the field. The Null model version thus revealed that non-triggered movement cannot explain the observed linear recovery in the field because it requires unrealistically high movement frequencies.

In the second version of the IBU model, the frequency of movement is linked to the competition among crabs, and expressed by the overlap of their field-of-neighbourhoods (FONs). This description assumes an impact of food competition, suggested by Nordhaus et al. (2006) on the frequency of burrow change of *U. cordatus* in the study area. It resulted in a significant decrease of the movement frequency necessary to reproduce the linear recovery pattern. Crabs under high competition in the non-fished areas move more frequently than specimens under low competition, such as those already re-established in the fished area. These results imply that movement is triggered by competition for resources, and is therefore density-dependent. Perturbation of burrow entrances might also trigger crab movements (C. Piou *personal observations*). This factor should be investigated systematically in the field. However, such perturbations are likely to be random events and are thus indirectly considered by our Null model.

Density-dependent movement is a characteristic behaviour that has implications for the management of *U. cordatus* as a resource for human populations. In areas of *R. mangle* dominated forests that are easy to access, large males are frequently fished. The crabs hidden under the roots are not accessible to the crab collectors and probably replace the fished ones because of higher density (Piou et al., unpublished data) and therefore higher competition under the roots than on the accessible areas. Additionally, we observed with the different parameterizations of the IBU model that *U. cordatus* shall not walk too long distances for the linear recovery pattern to be reproduced. Thus, comparing the local non-fished areas of high root density to the peninsula level less-fished areas, the former are probably more important as a local buffer system for the recovery of artisanally fished areas. This argues in favour of keeping the traditional catching methods and not harvesting these local buffers by other techniques as observed in other places of Brazil (e.g., Nordi, 1994b). The peninsula level less-fished areas such as *A. germinans* dominated forests, or eventually the less-visited *R. mangle* forests, might not act as buffer within an identical time frame because they are further away.

However, as long as intraspecific competition of *U. cordatus* is high in these areas, they could function as large scale buffer system refilling the local scale buffers. The impact of fishing techniques allowing crab collectors to fish in these areas should be analyzed to conclude on their possible need of regulation. However, the capacity of both the local and the peninsula level buffer systems would depend ultimately on recruitment as under a hierarchal system. The relative importance of these buffer systems versus the recruitment processes is still to be investigated.

In the case of the Caeté peninsula which was not intensively exploited until the end of the 80’s (Diele et al., 2005), overall change of buffer capacity because of harvesting within all mangrove areas might explain the 6 and 8% drop in catch per unit effort in the late 90’s. If the hierarchy of buffer systems hypothesized above is correct, this would then suggest that the competition-induced local recovery rate that we observe today could have been much faster several decades ago when fishery was less intensive. This coincides with crab collectors’ statements (Senhor Manuel and Domingos de Araújo, *personal communications* to C. Piou) that fishery of large males could be done much faster several decades ago. Further study could investigate these aspects at multiple scales. Our IBU model could be used in the future to quantify the buffer capacity at local scale and to explore how it is indirectly related to recruitment. Larger-scale analysis might then inform how the buffer systems and the overall recruitment affect the rate of recovery and thereby help establish the sustainable yield that can be taken from the system.

Acknowledgements

We wish to thank Aldo deMelo, Senhor Manuel and Domingos de Araújo for their precious help and support during the field work, Martha Liliana Fontalvo Herazo and two anonymous reviewers for valuable comments on earlier versions of this manuscript, and Ana Rosa Araujo, Inga Nordhaus and Candy Feller for fruitful discussions on mangrove crab ecology. Amanda Stern-Pirlot verified the English language. This study was carried out as a part of the Brazilian-German Cooperation Project MADAM and was financed by the Brazilian National Research Council (CNPq) and the German Ministry for Education and Research (BMBF) under the code 03F0154A. This is MADAM-Contribution No. 110.

REFERENCES

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- Alcantara-Filho, P.D., 1978. Contribuição ao estudo da biologia e ecologia do caranguejo-uçá, *Ucides cordatus cordatus* (Linnaeus, 1763) (Crustacea, Decapoda, Brachyura), no manguezal do Rio Ceará (Brasil). Arquivos de ciências do mar 18, 1–41.
- Alves, R.R.N., Nishida, A.K., Hernandez, M.I.M., 2005. Environmental perception of gatherers of the crab ‘caranguejo-uçá’ (*Ucides cordatus*, Decapoda, Brachyura) affecting their collection attitudes. J. Ethnobiol. Ethnomed. 1.
- Bauer, S., Berger, U., Hildenbrandt, H., Grimm, V., 2002. Cyclic dynamics in simulated plant populations. In: Proceedings of the Royal Society of London B, vol. 269, pp. 2443–2450.

- Bauer, S., Wyszomirski, T., Berger, U., Hildenbrandt, H., Grimm, V., 2004. Asymmetric competition as a natural outcome of neighbour interactions among plants: results from the field-of-neighbourhood modelling approach. *Plant Ecol.* 170, 135–145.
- Berger, U., Hildenbrandt, H., 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. *Ecol. Model.*, 287–302.
- Berger, U., Hildenbrandt, H., 2003. The strength of competition among individual trees and the biomass-density trajectories of the cohort. *Plant Ecol.* 167, 89–96.
- Berger, U., Hildenbrandt, H., Grimm, V., 2002. Towards a standard for the individual based modeling of plant simulations: self-thinning and the field of neighborhood approach. *Nat. Res. Model.*, 15.
- Berger, U., Hildenbrandt, H., Grimm, V., 2004. Age-related decline in forest productivity: modelling the effects of growth limitation, neighbourhood competition and self-thinning. *J. Ecol.* 92, 846–853.
- Berger, U., Glaser, M., Koch, B., Krause, G., Ruben, L., Saint-Paul, U., Schories, D., Wolff, M., 1999. An integrated approach to mangrove dynamics and management. *J. Coast. Conserv.* 5, 125–134.
- Blankensteyn, A., Cunha Filho, D., and Santarosa Freire, A., 1997. Distribuição estoques pesqueiros e conteúdo protéico do caranguejo do mangue *Ucides cordatus* (L. 1763) (Brachyura: Ocypodidae) nos manguezais da baía das laranjeiras e adjacências, Paraná, Brasil. *Arquivos de biologia e tecnologia* 40, 331–349.
- Booth, G., 1997. Gecko: a continuous 2-D world for ecological modeling. *Artif. Life J.* 3, 147–163.
- Branco, J.O. 1993. Aspectos bioecológicos do caranguejo *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Decapoda) do manguezal do Itacorubi, Santa Catarina, Brazil. *Arquivos de biologia e tecnologia* 36, 133–148.
- Cuddington, K.M., Yodzis, P., 2000. Diffusion-limited predator-prey dynamics in euclidean environments: an allometric individual-based model. *Theor. Populat. Biol.* 58, 259–278.
- Czárán, T., 1998. *Spatiotemporal Models of Population and Community Dynamics*. Chapman & Hall, London, 284 pp.
- Diele, K., 2000. Life history and population structure of the exploited mangrove crab *Ucides cordatus cordatus* (L.) (Decapoda: Brachyura) in the Caeté estuary, North Brazil. Ph.D. Thesis, ZMT Contribution 9, Bremen, Germany.
- Diele, K., Koch, V., Saint-Paul, U., 2005. Population structure, catch composition and CPUE of the artisanally harvested mangrove crab *Ucides cordatus* (Ocypodidae) in the Caeté estuary, North Brazil: indications for overfishing? *Aquat. Liv. Resour.* 18, 169–178.
- Diele, K., Simith, D., 2006. Salinity tolerance of northern Brazilian mangrove crab larvae, *Ucides cordatus* (Ocypodidae): necessity for larval export? *Estuar. Coast. Shelf Sci.* 68, 600–608.
- Glaser, M., 2003. Interrelations between mangrove ecosystem, local economy and social sustainability in Caeté Estuary, North Brazil. *Wetlands Ecol. Manage.* 11, 265–272.
- Glaser, M., Diele, K., 2004. Asymmetric outcomes: assessing central aspects of the biological, economic and social sustainability of a mangrove crab fishery, *Ucides cordatus* (Ocypodidae), in North Brazil. *Ecol. Econ.* 49, 361–373.
- Grimm, V., 2002. Visual debugging: a way of analyzing, understanding and communicating bottom-up simulation models in ecology. *Nat. Resour. Model.* 15, 23–38.
- Grimm, V., Berger, U., 2003. Seeing the wood for the trees, and vice versa: pattern-oriented ecological modelling. In: Seuront, L., Strutton, P.G. (Eds.), *Handbook of Scaling Methods in Aquatic Ecology: Measurement, Analysis, Simulation*. CRC Press, Boca Raton, pp. 411–428.
- Grimm, V., Railsback, S.F., 2005. *Individual-Based Modeling and Ecology*. Princetown University Press, Princeton, NJ, 480 pp.
- Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J., Wissel, C., 1996. Pattern-oriented modelling in population ecology. *Sci. Tot. Environ.* 183, 151–166.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310, 987–991.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jorgensen, C., Mooij, W.M., Mueller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rügen, N., Strand, E., Souissi, S., Stillman, R.A., Vabo, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. *Ecol. Model.* 198, 115–126.
- Jamieson, P.D., Porter, J.R., Goudriaan, J., Ritchie, J.T., van Keulen, H., Stol, W., 1998. A comparison of the models AFRCWHEAT2, CERES-Wheat, Sirius, SUCROS2 and SWHEAT with measurements from wheat groan under drought. *Field Crops Res.* 55, 23–44.
- Keddy, P.A., 1989. *Competition*. Chapman & Hall, London, 202 pp.
- Koch, V., Wolff, M., 2002. Energy budget and ecological role of mangrove epibenthos in the Caté estuary, North Brazil. *Marine Ecol. Progr. Series* 228, 119–130.
- Kreft, J.-U., Booth, G., Wimpenny, J.W.T., 1999. Applications of individual-based modelling in microbial ecology. In: Bell, C.R., Brylinsky, M., Johnson-Green, P. (Eds.), *Microbial Biosystems: New Frontiers* (Proceedings of the Eighth international symposium on microbial ecology). Atlantic Canada Society for Microbial Ecology, Halifax.
- Kreft, J.-U., Picioreanu, C., Wimpenny, J.W.T., van Loosdrecht, M.C.M., 2001. Individual-based modeling of biofilms. *Microbiology* 147, 2897–2912.
- Mogilner, A., Edelstein-Keshet, L., Bent, L., Spiros, A., 2003. Mutual interactions, potentials, and individual distance in a social aggregation. *J. Mathe. Biol.* 47, 353–389.
- Mullon, C., Fréon, P., Parada, C., van der Linden, C., Huggett, J., 2003. From particles to individuals: modelling the early stages of anchovy in the Southern Benguela. *Fish. Oceanogr.* 12, 396–406.
- Nordhaus, I., 2004. Feeding ecology of the semi-terrestrial crab *Ucides cordatus cordatus* (Decapoda: Brachyura) in a mangrove forest in northern Brazil. Ph.D. Thesis, ZMT contribution 18, Bremen, Germany.
- Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. *Estuarine. Coast. Shelf Sci.* 67, 239–250.
- Nordi, N., 1994a. A captura do caranguejo-uçá (*Ucides cordatus*) durante o evento reprodutivo da espécie: O ponto de vista dos caranguejeiros. *Revista Nordestina de Biologia* 9, 41–47.
- Nordi, N., 1994b. A produção dos catadores de caranguejo-uçá (*Ucides cordatus*) na região de várzea nova, Paraíba, Brasil. *Revista Nordestina de Biologia* 9, 71–77.
- Railsback, S.F., Harvey, B.C., 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* 83, 1817–1830.
- Schmitz, O.J., 2001. From interesting details to dynamical relevance: toward more effective use of empirical insights in theory construction. *Oikos*, 94.
- Schories, D., Barletta-Bergan, A., Barletta, M., Krumme, U., Mehling, U., Rademaker, V., 2003. The keystone role of leaf-removing crabs in mangrove forests of North Brazil. *Wetlands Ecol. Manage.* 11, 243–255.

- Taylor, R.A.J., 1981. The behavioral basis of redistribution. I. the Δ -model concept. *J. Anim. Ecol.* 50, 573–586.
- Wiegand, T., Naves, J., Stephan, T., Fernandez, A., 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecol. Monogr.* 68, 539–570.
- Wiegand, T., Jeltsch, F., Hanski, I., Grimm, V., 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos* 100, 209–222.
- Wolff, M., Koch, V., Isaac, V., 2000. A trophic flow model of the Caeté mangrove estuary (North Brazil) with considerations for the sustainable use of its resources. *Estuarine. Coast. Shelf Sci.* 50, 789–803.