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NATURAL RECOVERY OF AMAZONIAN MANGROVE FOREST AS REVEALED BY BRACHYURAN CRAB FAUNA: PRELIMINARY DESCRIPTION

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AMAZONIA
MANGROVE FOREST RECOVERY
COASTAL DYNAMIC
BENTHIC FAUNA
CRUSTACEA
BIOTURBATION

ABSTRACT. – Due to the enormous influence of the Amazon River, accretion and erosion processes alternate in rapid succession on the North coast of South America. The shoreline is constantly redrawn and the mangrove forests progress, regress or decline accordingly. The coastline around the Kaw River estuary, French Guyana, was exposed to rapid and intense erosion, resulting in the elimination of a substantial portion of the littoral zone, and in the complete destruction of the mangrove forests. With the arrival and stabilization of a new mud bank, vegetation and fauna appeared. Natural recovery of the newly formed mangrove forest was monitored until habitat structure and species richness paralleled those of a neighboring mangrove forest, which remained unaffected and served as a reference site. Steps in the natural recovery of the newly formed mangrove forest are described herein from the carcinological viewpoint. In the mangroves, brachyuran crabs are the most abundant and species rich group of benthic megafauna. The following parameters were monitored for comparison between the two sites: tree height, crab species diversity, crab densities, crab biomass, and bioturbation by burrowing crabs. Mangrove forests under direct Amazonian influence are less diverse than typical Western Atlantic mangrove forests. It is apparent that full recovery of crab taxonomic diversity takes place faster than full recovery of crab density and ecosystem functioning (bioturbation).

AMAZONIE
RESTAURATION
FORÊT DE LA MANGROVE
DYNAMIQUE COTIÈRE
FAUNE BENTHIQUE
CRUSTACEA
BIOTURBATION

RÉSUMÉ. – En raison de l'influence énorme de l'Amazone, les processus d'accrétion et d'érosion alternent rapidement le long de la côte Nord de l'Amérique du Sud. La ligne de côtes est constamment redessinée et la mangrove progresse, régresse ou disparaît au fur et à mesure. La ligne de côte aux alentours de l'embouchure de la rivière de Kaw en Guyane Française est soumise à une érosion rapide et très intense qui a abouti à la disparition d'une portion importante de la zone littorale et à la destruction complète de la mangrove. Avec l'arrivée puis la stabilisation d'une nouvelle vase, la végétation et la faune sont apparues. La restauration naturelle d'une nouvelle mangrove a été suivie à partir de la structure des habitats, de la richesse spécifique en comparaison avec la mangrove ancienne dans le voisinage où elle n'avait pas été altérée. Cette mangrove a servi de site de référence pour cette étude. Les différentes étapes de la restauration naturelle de la nouvelle mangrove ont été suivies à partir de la faune carcinologique. Les Crabes Brachyours représentent le groupe le plus riche spécifiquement et le plus abondant de la mégafaune benthique des forêts de mangrove. Les paramètres suivants ont été mesurés afin de permettre la comparaison temporelle entre les deux sites étudiés: hauteur des arbres, diversité spécifique et densité des Crabes, et enfin bioturbation par les Crabes fouisseurs. Les forêts de mangrove sous influence directe de l'Amazone sont moins diversifiées que les mangroves typiques de l'Atlantique de l'Ouest. Il est évident que la restauration taxonomique de la diversité des Crabes est plus rapide que la restauration de leur densité et du fonctionnement de l'écosystème via la bioturbation.

INTRODUCTION

Mangrove forests are widespread in the circumtropical zone, totaling approximately 15 million hectares worldwide (Kjerfve & Macintosh

1997). In many regions of the world mangroves have been severely damaged as a result of anthropogenic pressure (Ellison & Farnsworth 1996, Walters 2000), but also by natural causes such as hurricanes, storms, floods, erosion and rapid accretion (e.g. Ellison 1998, Imbert *et al.*

1998, Panapitukkul *et al.* 1998). The most extensive mangrove forest stand surfaces occur on sedimentary shorelines (Ellison 1998) exposed to strong coastal dynamic processes such as erosion or heavy input of sediment. In South America, the Amazon River discharges $1,438,10^6$ tonnes y^{-1} of sediment into the Atlantic Ocean (Milliman & Meade 1983), part of which is transported northward by the North Equatorial Current to eventually reach the North coast of South America where it forms temporary mud banks (Guillobez 1980, Froidefond *et al.* 1988, Prost 1990). As a result, most of the North coast of South America (mainly North coast of Brazil, French Guyana, and Suriname) is bordered by these temporary mud banks, where *Avicennia germinans* (L.) L., mainly, dominate dense mangrove forests (Dodd *et al.* 1998). Because of the enormous influence of the Amazon River, accretion and erosion processes alternate in rapid succession on the North coast of South America. Here the shoreline is constantly redrawn (Augustinus 1978), and the mangrove forests progress, regress or decline accordingly (Blasco 1991, Prost 1990).

In 1991, the coastline around the Kaw River estuary, South of Cayenne, French Guyana (Fig. 1), was exposed to rapid and intense erosion. As a result, a substantial portion of the littoral zone was eliminated causing the southward displacement of the Kaw River estuary, and the complete destruction of mangroves along a shoreline of about 5 Km long and more than 1 Km wide. Intense erosion caused the exposure of Tertiary sediment basement in some places. Afterwards, a huge new mud bank was deposited in the area. At the beginning, the

freshly deposited mud slope consisted of extremely fluid and fine sediment, whitish brown in color, completely devoid of vegetation or benthic macro and megafauna. Later, with the stabilization of the mud bank, vegetation and fauna appeared.

While literature on mangrove reforestation is substantial (e.g. Walters 1977, 2000, Kaly & Jones 1998, Ellison 2000, Imbert *et al.* 2000), it is largely restricted to botanical aspects, and references to natural recovery of faunal species richness in the mangroves are extremely scarce. We monitored the natural recovery of the newly formed mangrove forest in the Kaw River estuary until habitat structure and species richness paralleled those of a neighboring pristine mangrove forest. Steps in the natural recovery of the newly formed mangrove forest are described herein from the carcinological viewpoint.

MATERIAL AND METHODS

Subsequent to the complete destruction of the Kaw mangrove forest and the subsequent deposition of a new mud bank from 1995 to 1998, field trips of about 15 days each were conducted in September 1998, January 1999, September 2000, and December 2001. On each occasion, surveys were conducted in the recovering Kaw mangrove forest and neighboring mangrove forest at Paul Emile, which served as a reference site. Aerial photographs and satellite images from the mud bank of Kaw were obtained in January 1999, February 2000, and November 2001 (Fig. 2A-C).

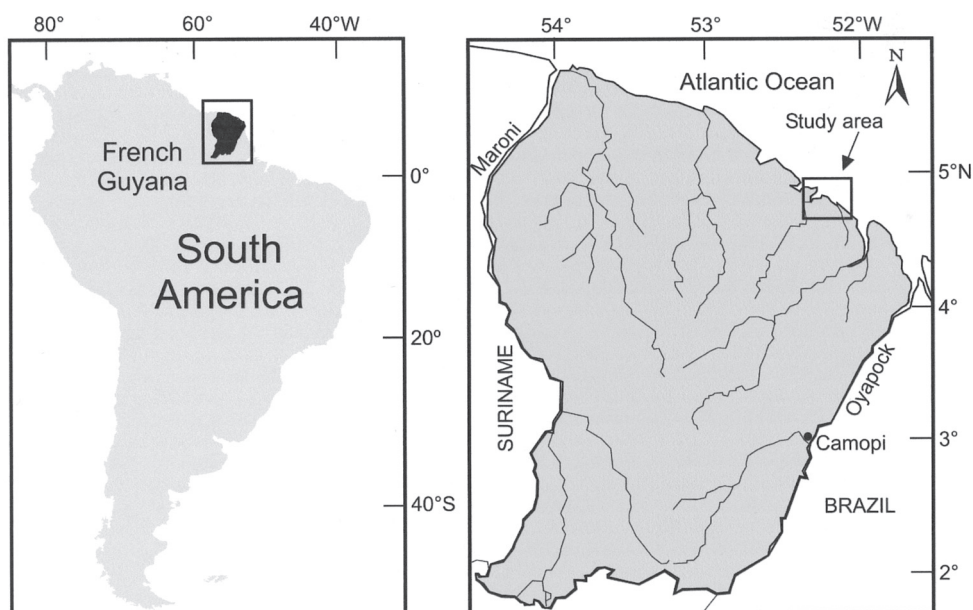


Fig. 1. – Study area. Kaw River estuary, South of Cayenne, French Guyana.

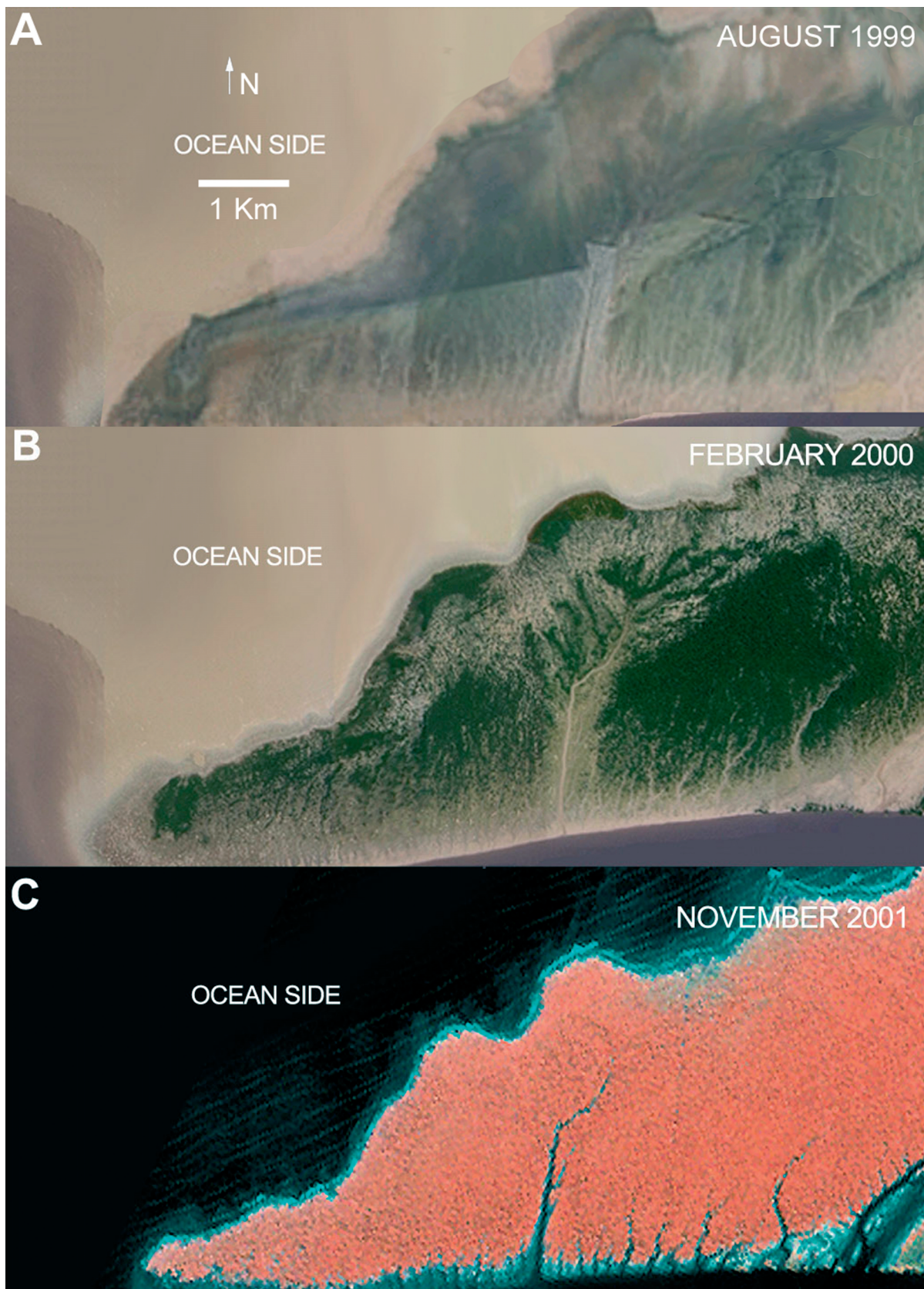


Fig. 2. – A-B, aerial photographs from the mud bank of Kaw taken in 1999 and 2000, respectively. C, satellite image taken in November 2001. Notice in A the dark patches of microphytobenthic diatoms and cyanobacteria and in B-C the progressive colonization by the mangrove forest.

In the Kaw mangrove forest, samples were obtained along two transects of about 800 and 1000 m long respectively, stretched across the mangroves from the river side to the open sea (Fig. 2A). In the Paul Emile mangrove forest a single transect of about 300 m long was monitored. Samples were obtained during low tides only.

Tree height was estimated visually in Paul Emile and by cutting down a few trees in the Kaw site. The crabs were actively sought during seven successive days in all habitats. Crab densities (individual numbers/m²) were estimated by the number of crab holes counted in a 1 m² quadrat, and thus refer to only the burrowing crabs, *Uca* spp. and *U. cordatus* (Warren 1990). Some quadrats were excavated to validate the method. At each sampling station along the transects, three replicates of the 1 m² quadrat were taken randomly and the active crab burrows counted (see Mouton & Felder 1996). In the Paul Emile reference site crab density was estimated only in 2000 and 2001. In order to estimate bioturbation, burrow architecture, burrow size, and burrow volume were assessed by filling the burrows with epoxy resin (Berkenbush & Rowden 2000, Thongtham & Kristensen 2003). Burrow casts allowed for the calculation of the following parameters: (i) the volume of sediment reworked during burrowing activities; (ii) the volume of sediment in the burrow plugs; (iii) the increment of surface area at the sediment-air-water interface created by burrowing activities. For calculation purposes, burrows were considered as cylinders. The volume of the burrow plug was estimated in 10% of the total volume of the burrow.

Crab holes from within a 1 m² quadrat were counted and grouped into one of the following categories (hole diameter/funnel depth): 1 cm/10 cm, 2 cm/20 cm, 3 cm/60 cm, 4 cm/60 cm, and 5 cm/70 cm. The relationship between hole diameter and funnel depth was inferred from measuring several castings of crab holes.

Table I. – Mangrove crabs recorded between 1999 and 2001 from the mangrove forests of Kaw and Paul Emile. (*) Ocypodidae. (**) Grapsidae.

Taxonomic richness	Mangrove crabs					
	Kaw			Paul Emile		
	1999	2000	2001	1999	2000	2001
<i>Uca maracoani</i> *	■	■	■			
<i>U. mordax</i> *	■		■	■		■
<i>U. vocator</i> *		■	■	■	■	■
<i>U. rapax</i> *		■	■			
<i>U. cumulenta</i> *		■	■			
<i>U. thayeri</i> *				■	■	
<i>U. burgersi</i> *		■				
<i>Ucides cordatus</i> *			■	■	■	■
<i>Goniopsis cruentata</i> **	■	■	■	■	■	■
<i>Pachygrapsus gracilis</i> **	■	■	■			■
<i>Aratus pisonii</i> **			■			■

The size and surface area of the recovering Kaw mangroves were calculated from field measurements coupled with satellite imaging. The measurements in the field were taken at the low tide (circa 2.90 meters), when the surface of the mud bank was fully exposed.

Estimates of biomass were calculated only for the burrowing crabs: *Uca maracoani*, *Uca* spp., and *U. cordatus*. Because *U. maracoani* is a much larger species in relation to its congeners it was treated separately. Crabs from the inside of the quadrats were taken to the laboratory to be identified, weighed, and measured (carapace length). The organic matter dry weight was obtained by difference between total dry weight (24 hours at 100°C) and ash weight (5 hours at 450°C).

The Paul Emile reference site: Paul Emile is a relatively pristine site, which remained unaffected by the strong erosion and sedimentation processes that heavily affected the Kaw site. Paul Emile is a mature mangrove forest bordered by a fringe of *Rhizophora* sp. about 10 m high. The *Rhizophora* sp. fringe extends for about 20 m towards the inner parts of the mangrove forest before it is replaced by stands dominated by *A. germinans*. In the Paul Emile forest full grown *Avicenia* may attain as high as 30 m. The Paul Emile forest is actually a mixture of young and senescent trees, with the soil abundantly covered by leaf-litter and dead woods.

RESULTS

The Kaw mangrove forest: recovery of habitats and taxonomic richness

In 1998 the freshly deposited mud bank of Kaw showed as an uniform, fine and somewhat fluid sediment, whitish brown in color, and completely devoid of vegetation or benthic macro and megafauna. By January 1999 Kaw was an irregular mudflat with a well developed net of water drains of different sizes and depths, covered with large patches of microphytobenthic diatoms and cyanobacteria (Fig. 2A). Scattered young shoots of *Avicennia germinans* (0.5 to 1 m high) were growing in its central part. Crab habitats were basically restricted to the poor plant root systems, water drains, river banks, and sea shore (Fig. 3A). Four species of brachyuran crabs were recorded in 1999 (Table I). Although found all over the mud bank, *Uca maracoani* was more common in the non vegetated mud flats exposed to direct sun light. *U. mordax* was found in the shaded areas, beneath or nearby the young shoots of *A. germinans*. The few individuals of *Goniopsis cruentata* encountered inhabited nearby the plant roots. Probably due to the scarcity of hard substrata in the newly formed mangrove, the single individual of *Pachygrapsus gracilis* was found in crevices of hardened mud, an unusual habitat for this species.

In September 2000 the *A. germinans* forest already attained 4 to 6 m high and covered most of

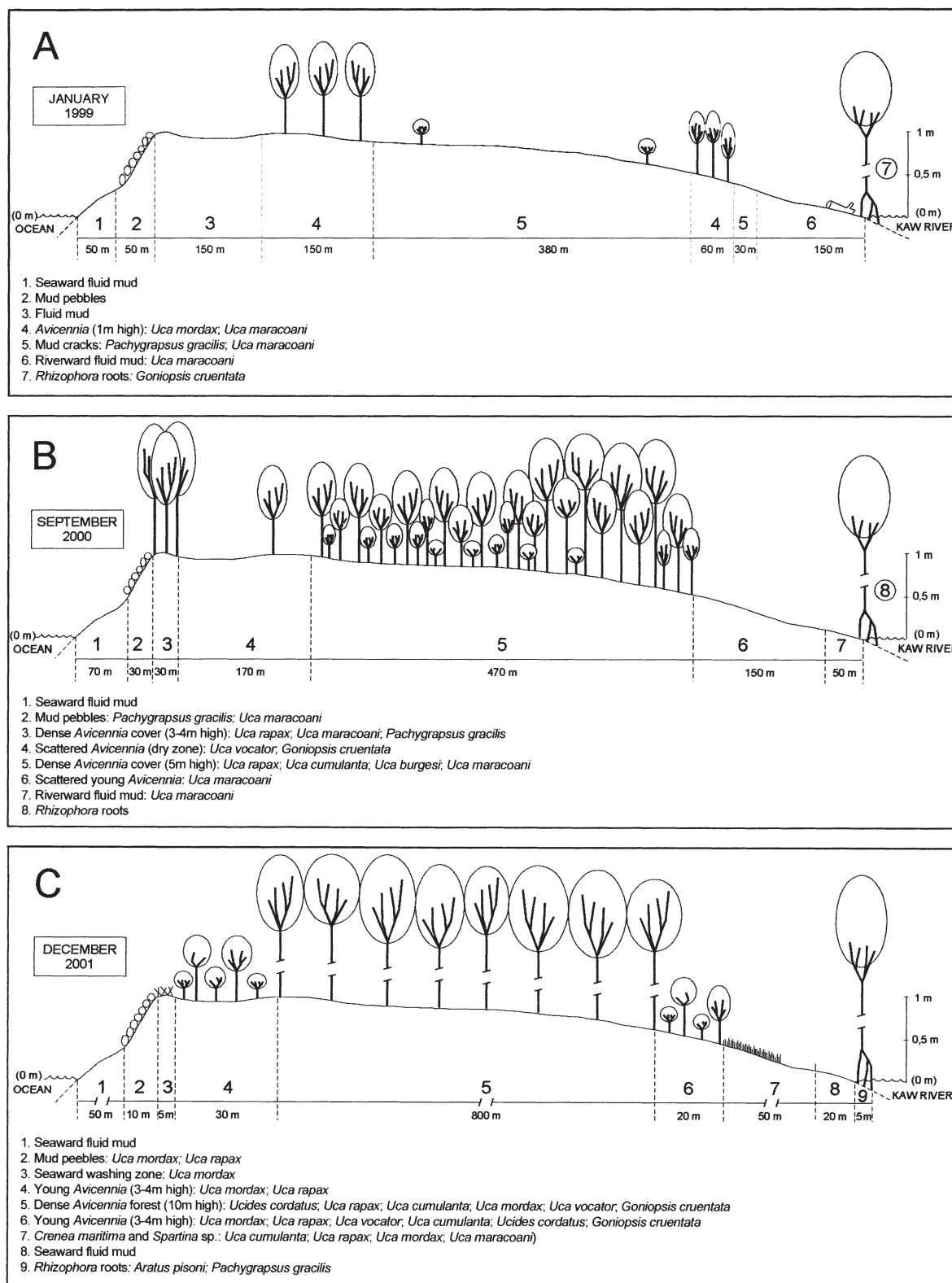


Fig. 3A-C. – Schematic profile of the mud bank of Kaw between 1999 and 2001. Notice the increase in crab habitats and crab species composition per habitat.

the surface of the mud bank providing a mosaic of sunny and shaded areas (Fig. 3B). A layer of leaf-litter developed under the shaded areas. The number of crab species almost doubled from 1999 to 2000 (Table I). All the species found in 1999, but *U. mordax*, were captured again in 2000; four new species colonized the area, all living in more or less shaded areas (Table I).

In December 2001 the mud bank was uniformly and densely covered by a quasi monospecific *A. germinans* forest, which then attained about 10 m high. The riverside margin was fringed by *Rhizophora* sp. and fields of *Spartina* sp. and *Crenea maritima* developed in the mudflats (Fig. 3C). As the *A. germinans* forest expanded, shaded areas with rich leaf-litter became the dominant crab habitat. Except for *U. burgersi*, all the other crab species found in 2000 were encountered again in 2001. *U. mordax* was absent in 2000 but reappeared in 2001. Altogether nine species were recorded in 2001 (Table I), two of which were new: *Ucides cordatus* and *Aratus pisonii*. *U. cordatus* prefers densely vegetated shaded areas (Tavares & Albuquerque 1989), particularly rich in leaf-litter (McIvor & Smith III 1995), a condition not available in the early stages of the Kaw mangrove forest. The tree crab *A. pisonii* is known to live on mangrove trees, *Rhizophora* and *Laguncularia* mostly (Warner 1967, Beever *et al.* 1979, Diaz & Conde 1988, Conde & Diaz 1989a, 1989b, Lacerda *et al.* 1991, MacIvor & Smith III 1995), and its presence in Kaw was obviously related with the colonization of the river banks by *Rhizophora* sp.

In the early stages species richness was comparable between Kaw and Paul Emile, but from 2000 throughout 2001, Kaw presented a richer crab fauna. The fiddler crabs genus *Uca* were the main component of the mangrove crab fauna in both sites (Table I). There were only minor differences in taxonomic composition between Kaw and Paul Emile, *Uca rapax* and *U. cumulanta* were never recorded from Paul Emile, while *U. thayeri* never occurred in Kaw (Table I).

Density, biomass and bioturbation

In 1999 Kaw harbored only two burrowing species, while in 2000 five burrowing species were recorded causing the mean crab density to increase twice as much (Tables I, II). In relation to 2000 mean crab density increased more than fourfold in 2001, whereas the number of burrowing species was only slightly higher (Tables I, II). In contrast, crab density in Paul Emile was much higher doubling from 2000 to 2001 (Table II), probably as a result of the recruitment of *Uca mordax* in 2001 (Table I), a species commonly found in high densities.

In the mangrove of Kaw both crab biomass and bioturbation (and consequently the increment in sediment-air-water surface, see Aller & Yngst 1978, Aller & Aller 1988, Ferro *et al.* 2003), decreased from 1999 to 2000, to increase dramatically from 2000 to 2001 (Table II). These fluctuations are related to both, reduction in area of the mudflats (Fig. 2A-C, 3A-C), the preferred habitat of *U. maracoani* (Tavares & Albuquerque 1989), and the recruitment of *Ucides cordatus* in 2001. These are by far the two largest crab species in the area. Both crab biomass and bioturbation, and increment of surface area at the sediment-air-water interface created by burrowing activities, were much higher in Paul Emile than in Kaw and increased from 2000 to 2001, probably as result of the recruitment of *U. mordax* in 2001 (Tables I, II).

DISCUSSION

Recovery of mangrove forests after destruction has been described to take as long as 20 years (Lugo 1980, Lugo & Snedaker 1974, Roth 1992). This contrasts dramatically with the extremely rapid recovery observed in Kaw. Roth (1992) pointed out that dead woods (slash) left behind by

Table II. – Burrowing crabs density and biomass, and sediment transportation and surface increment in the air-water-sediment interface between 1999 and 2001 as a result of crab burrowing. PE, Paul Emile.

	Kaw 1999	Kaw 2000	Kaw 2001	PE 2000	PE 2001
Density of burrowing crabs (ind/m ²)	3.6	7.1	31.5	61.0	122.0
Biomass (g A.F.D.W.O.M./m ²)	2.36	1.56	12.0	25.0	30.0
Bioturbation: sediment transport (cm ³ /m ²)	358	245	1767	2750	3750
Bioturbation: water/sediment interface (m ² /m ²)	0.06	0.05	0.259	0.40	0.60
Total number of crabs	57.5.10 ⁵	113.6.10 ⁵	508.10 ⁵	508.10 ⁵	610.10 ⁵
Total surface wall of burrows in the area (m ²)	167.10 ³	134.10 ³	195.10 ³	195.10 ³	400.10 ³
Total volume of burrows in the area (m ³)	1200	800	2800		3200
Total volume of burrow's plugs in the area (m ³)	120	80	280		320

storms and hurricanes constitute an obstacle for seed dispersion and destroy young shoots by mechanical action during high tide. The strong coastal dynamic processes so characteristic of the North Coast of South America (Guillobez 1980, Milliman & Meade 1983, Froidefond *et al.* 1988, Prost 1990), may well have played a role in the fast recovery process observed in Kaw. What was not washed away by the extremely strong erosion processes was deeply buried with the arrival of the next mud bank. Only very few dead wood remained exposed. During the accretion process we observed buried dead wood being exposed locally as a result of a brief new erosion cycle.

In the mangroves, brachyuran crabs are the most abundant and species rich group of benthic megafauna (Golley 1962, Malley 1977). Mangrove crabs are closely associated with both sediment texture and mangrove plants (Miller 1961, Crane 1975, Icely & Jones 1978, Warren & Underwood 1986, Lee 1989, Snelgrove & Butman 1994). Monotonous soil texture and poor plant species composition result in less diversified crab habitats. Besides, the short period of stability between successive processes of erosion and accretion leave perhaps not enough time for more sensitive species to establish (Connell 1978). These may well be the reasons behind the rather impoverished crab fauna of Kaw, compared to other Western Atlantic mangrove forests growing far from Amazonian influence. Indeed, a number of crab families, genera, and species are missing from both Kaw and Paul Emile, in spite of being known from many localities north and south of it (e.g. *Cardisoma guanhumi* Latreille, 1828; *Sesarma rectum* Randall, 1840; *Armases* spp.; *Eurytium lymosum* (Say, 1818); *Panopeus* spp.; *Pinnixa* spp.; as well as a number of species of *Uca*). Vergara Filho *et al.* (1997), for instance, recorded as much as 18 brachyuran crab species from the highly impacted mangrove forest of Guanabara Bay, Rio de Janeiro (23°S).

Bioturbation is a major component of mangrove functioning being relevant to creation of new surface areas at the sediment-air-water interface (Aller & Yngst 1978, Aller & Aller 1988), to soil aeration through destabilization of mud cohesion (Botto & Iribarne 2000, Deckere *et al.* 2001), to stimulation of mangrove vegetation growth (Mouton and Felder 1996), to modification of the microtopography (Warren & Underwood 1986), and to changes in the abundance and distribution of the meiofauna (Hiffman *et al.* 1984, Olafsson & Ndaró 1997). In both, Kaw and Paul Emile, the burrowing crabs *Ucides cordatus* and *Uca* spp. are by far the largest mangrove crab species and the most important bioturbators. While density of *U. cordatus* in Kaw and Paul Emile are equivalent, sediment reworking in Kaw was smaller than in Paul Emile (Table II), as the Kaw population is younger (mean of 37 mm of carapace length, in-

stead of 47 mm as in Paul Emile) and was recruited in 2001 only.

Despite the evidence accumulated showing that forest plantation in upland tropical and subtropical degraded areas can foster the recovery of species richness (e.g. Lugo 1992), recent findings suggest that such might not be always the case (Walters 2000). In the Philippine mangrove forests, in plantations of *Rhizophora mucronata* and *R. stylosa* up to 50 or 60 years old, recruitment of other non planted mangrove species proved to be almost negligible (Walters 2000): "... if you want diverse mangrove forests, you have to plant diverse mangrove forests". Whether or not the benthic macro and megafauna of planted mangrove forests parallel that of natural mangrove forests is unknown.

Traditionally the field of restoration ecology has attracted attention from botanists mainly (Ellison 2000, Young 2000, Longcore 2003). Patterns of recovery of species richness of benthic fauna in planted mangroves remain uncovered.

Concluding remarks

The strong and fast coastal dynamic processes in the North coast of South America greatly influenced both mangrove forest structure and crab taxonomic composition. Our findings suggest that mangrove forests under direct Amazonian influence are less diverse sedimentologically, floristically, and faunistically, than typical southwestern Atlantic mangroves. Their comparatively lower diversity may well be the main reason behind fast natural recovery.

As revealed by the brachyuran crab fauna, full faunal taxonomic diversity takes place faster than full recovery of faunal density and ecosystem functioning (bioturbation). These findings suggest that mangrove restoration projects should take into consideration that taxonomic diversity alone is an insufficient criteria for determining whether or not a given restoration process has been completed, and ecosystem functioning must be addressed.

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