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# Benthic macrofauna associated with decomposition of leaves in a mangrove forest in Ilhéus, State of Bahia, Brazil

ALEXANDRA BOMFIM DE OLIVEIRA[1], ALEXANDRA ELAINE RIZZO[2], ERMINDA DA CONCEIÇÃO[1] AND GUERREIRO COUTO[1]

[1]Universidade Estadual de Santa Cruz, Rodovia Ilhéus-Itabuna, km 16, 45662-900, Ilhéus, BA, Brazil, [2]Universidade do Estado do Rio de Janeiro, Instituto de Biologia Roberto Alcântara Gomes, Departamento de Zoologia, Rua São Francisco Xavier 524, 20550-013, Maracanã, Rio de Janeiro, RJ, Brazil

*We identified and quantified the benthic macrofauna associated with decomposing leaves of* Rhizophora mangle *and* Laguncularia racemosa*, to observe the differences in the abundance and composition of macrofauna between these mangrove species, and to examine whether the abundance and composition of organisms changed with different stations and collection times. Benthic macrofauna, mainly polychaetes and amphipods, were recorded from the fifth day after the installation of the experiment. Annelids including Oligochaeta and Polychaeta were the most numerous group. Crustacea were represented by peracarids (Amphipoda and Tanaidacea) and decapods. Of Hexapoda, only juvenile forms and pupae were present. The most abundant polychaete species was* Perinereis brevicirrata*, followed by* Capitella *cf.* capitata, Heteromastus filiformis *and* Neanthes succinea*. In one-way analysis of variance (ANOVA) there were no statistical differences between the macrofauna of mangrove species, seasons, or collection times, except among collection times for* R. mangle *litter bags. Two-way ANOVA showed homogeneity for macrofauna abundance between the groups of collection times for both mangrove species. The richness was similar for* R. mangle *litter bags, and showed a significant difference for* L. racemosa*. Abundance and richness were also similar between the mangrove species. The colonization of detritus by benthic invertebrates followed a successional sequence during the decomposition process. This suggests that the density of these organisms and their foraging behaviour affected the decomposition rates of leaves of* R. mangle *and* L. racemosa.

**Keywords:** Annelida, Crustacea, litter bag, succession, benthic macrofauna

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## INTRODUCTION

Estuaries, being transitional ecosystems among riparian, terrestrial, and marine environments, provide a diversity of habitats. In general, estuaries are characterized by unpredictable and widely varying hydrological and chemical conditions (Kanaya & Kikuchi, 2008). The benthic macrofauna is a key structural element of estuarine trophic webs, and plays an important role in the dynamics of these systems (Ysebaert *et al.*, 1998; Kanaya & Kikuchi, 2008). Mangroves located along estuaries are an important habitat and often support an abundant and diverse community of benthic invertebrates, which may serve as a source of food for resident and transient fauna (Kristensen *et al.*, 2008). A considerable number of species that live in or transit through this environment are commercially important for human consumption (Kristensen *et al.*, 2008).

The benthic macrofauna is classified as the group of organisms associated with the substrate that are visible to the eye, although they are usually only identifiable with the aid of a stereoscopic microscope. Benthic invertebrates from unconsolidated bottoms are represented primarily by species of Polychaeta, Mollusca and Crustacea, which alternate in dominance according to abiotic conditions (Paiva *et al.*, 2005). Other macrofaunal groups include Porifera, Nematoda, Sipuncula, Platyhelminthes and Urochordata (Elison, 2008). These animals pass all or part of their life cycles in the mangrove and depend on food (plankton and/or detritus) from this system. They also are primary consumers that incorporate organic matter from different sources into the system (Muniz & Venturini, 2001; Kanaya & Kikuchi, 2008).

The benthic macrofauna is a main element affecting the high rates of decomposition of detritus and efficient recycling of nutrients that generate the high productivity characteristic of mangroves (Odum & Heald, 1975; Bosire *et al.*, 2005; Kristensen *et al.*, 2008). Organic matter produced in mangroves forms the basis of a very complex detritivore food web. Newly fallen leaves first pass through the leaching process (Adaime, 1985) and are quickly attacked by microorganisms that decompose their structural components (Middleton & McKee, 2001). These form a thin film on the leaf surface, increasing its nutritional value and attracting benthic invertebrates. In addition to consuming the leaf material, the benthic fauna mechanically fragments it, accelerating the action of bacteria and fungi and consequently the

**Corresponding author:**
A.B. de Oliveira
Email: christambell@yahoo.com.br

process of decomposition (Odum & Heald, 1975; Ponte *et al.*, 1984). Detritus from vascular plants and the microorganisms associated with it are consumed by detritivorous invertebrates, which will serve as food for other, larger animals, thus establishing the complex food web characteristic of mangroves (Odum & Heald, 1975).

Benthic communities have proved to be important in programmes for environmental impact assessment. Therefore, ecological studies strive to understand the factors influencing the spatial and temporal distribution of these groups of organisms. Several studies have shown that benthic macrofauna associated with decomposition also plays an important role in, and is crucial to the conclusion of the decomposition process (Couto & Lima, 1997; Ashton *et al.*, 1999; Middleton & McKee, 2001; Kristensen *et al.*, 2008; Oliveira *et al.*, in press). Knowledge of these organisms and their food habits can provide information for better understanding of the leaf decomposition process. Few studies have explored this subject, and in most cases have evaluated only the macrofauna involved in the decomposition process or the action of crabs in the breakdown of detritus.

The purposes of this study were to: (1) identify and quantify the benthic macrofauna associated with leaf decomposition of *Rhizophora mangle* and *racemosa*; (2) check the differences in composition of the benthic macrofauna between the two mangrove species; and (3) examine whether the composition of organisms changes between the different stations and times of collection.

## MATERIALS AND METHODS

### Study area

The basin of the Cachoeira River empties into the Bay of Pontal, Ilhéus, State of Bahia. The mangroves of this estuary cover an area of approximately 248 ha (Martins, 2008), and are subject to accelerated eutrophication, mainly due to human activities (Souza, 2005; Santos, 2007; Silva, 2007). The tropical climate, Köppen Af, is always hot and humid, with no dry season. The annual mean temperature is 24°C, ranging from 17.0 to 30.5°C (Nacif *et al.*, 2004). The rainy season extends from May through to August, mainly June through to August, with a mean annual precipitation of 2179 mm, maximum 2628 mm, and minimum 1737 mm (SEPLANTEC, 1993).

The study area is located in the middle portion of the estuary (14°49′00″S 39°03′36″W 14°49′14″S 39°03′29″W), and is about 1 km long (Figure 1).

### Experiment

Four study stations, one permanently submerged subject to tidal currents and three with plots of 100 $m^2$ (10 × 10 m) each in the intertidal zone, were established along a transect perpendicular to the main channel. The sediment of the study stations intertidal can be considered as muddy because it presented a relative percentage of more than 50% silt and clay (Santos, 2009).

The litter-bag technique was used to estimate the process of leaf decomposition of *Rhizophora mangle* and *Laguncularia racemosa*. Yellowish senescent leaves from *R. mangle* and *L. racemosa* were collected, washed in running water, and separated into groups of 20 g (fresh weight), totalling 342 samples. Three replicates for each species were oven-dried to constant weight (at 60±/5°C, for 72 hours), and this was considered the initial dry weight. The remaining samples were packed in square nylon bags (2 mm mesh, 20 × 20 cm). A total of 14 groups of six litter bags (three for each species) were placed on the sediment surface and tied to *R. mangle* rhizophores, which were present in all the plots.

From June 2008 through to April 2009, 14 samples, each consisting of one set of litter bags, were collected to obtain the macrofauna associated with decomposing leaves. Table 1 shows the number of days after the installation of the experiment when each of the 14 samples was obtained.

The material in the litter bags was carefully washed over a sieve with a mesh opening of 0.5 mm, to retain the macrofauna. The organisms were fixed in 70% ethanol, and identified and counted with the aid of a stereomicroscope. The plant detritus was dried in an oven at 60°C, for 72 hours, until reaching constant weight.

### Data analysis

The abundance of benthic macrofauna at the stations during the study period was described and analysed. The four stations were grouped and the 14 collection times were divided

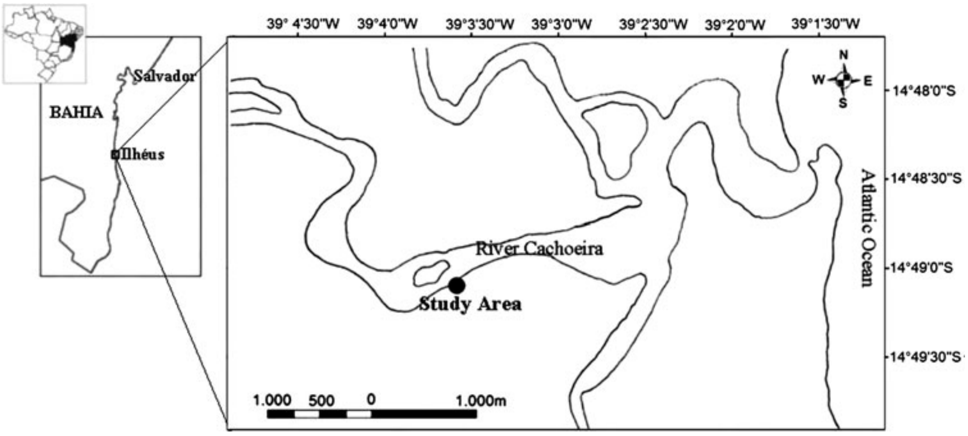

**Fig. 1.** Study area in the middle reach of the Cachoeira estuary (14°49′00″S/39°03′36″W 14°49′14″S/39°03′29″W).

**Table 1.** Collections and the respective number of days after the installation of the decomposition experiment (June 2008 – April 2009).

| Collection | Installation of experiment | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of days | 0 | 1 | 3 | 5 | 7 | 15 | 30 | 45 | 60 | 90 | 120 | 150 | 210 | 270 | 300 |

into: Beginning (collection times 1, 2, 3, 4 and 5), Intermediate (collection times 6, 7, 8, 9 and 10) and End (collection times 11, 12, 13 and 14) for the purpose of analysis.

Statistical differences ($P < 0.05$) were checked through one-way analysis of variance (ANOVA) (Statistica® 6.0) for the abundance and composition of organisms among stations and collection times for each mangrove species, and also between the mangrove species. Two-way ANOVA (Statistica® 6.0) was also used to check for statistical differences ($P < 0.05$) in the abundance and composition of organisms among groups of collection times for each mangrove species and between the mangrove species.

Multidimensional scaling (MDS) (PRIMER 5.0) was used to analyse the behaviour of the macrobenthic community along the three groups of collection times. The diversity of the community for each mangrove species was determined by the dominance curve (PRIMER 5.0). The analysis of similarity percentages (SIMPER®; PRIMER 5.0) determined the most important groups of organisms at the different stations and collection times; the data were transformed [log (x +1)].

The leaf decomposition analysis was performed by calculating the Olson constant and the two mangrove species showed similar decay patterns of leaf material among all stations (Oliveira *et al.* in press).

## RESULTS

The macrofauna associated with the process of leaf decomposition was recorded in litter bags in both mangrove species beginning with the third collection, i.e. day 5 of the experiment (Figure 2). Subsequently, macrofauna was found in at least one of the stations until the end of the experiment. Station I showed organisms until the sixth collection (day 30), and after this period, they reappeared at time 11 (day 150) for both mangrove species, and at collections 13 (day 270) and 14 (day 300) only for *L. racemosa*. Organisms were most regularly recorded at Stations II to IV, with peaks at collections 7 (day 45), 10 (day 120), and 11 (day 150) for *R. mangle*, and 6 (day 30), 7 (day 45), and 13 (day 270) for *L. racemosa*.

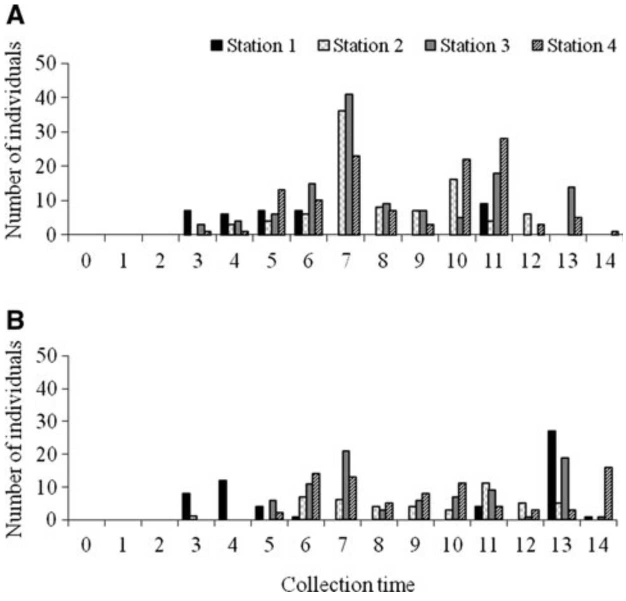

**Fig. 2.** Total abundance of the benthic macrofauna found in litter bags of *Rhizophora mangle* (A) and *Laguncularia racemosa* (B) for 4 stations and 14 collection times (June 2008 – April 2009).

The total number of individuals in the litter bags of *R. mangle* was higher (N = 364) than in the bags containing *L. racemosa* (N = 261). For both mangrove species, annelids were very abundant (Table 2), represented by Oligochaeta (188 individuals for *R. mangle* and 111 for *L. racemosa*) and Polychaeta (103 and 99 individuals respectively). Crustaceans were represented by Peracarida (Amphipoda and Tanaidacea) and decapods. For Hexapoda, only juvenile forms of insects and pupae were recorded, with Tabanidae as the most abundant group.

Polychaeta was the second most abundant group and was found most regularly in the collections, followed by crustaceans, mainly amphipods. Oligochaeta accounted for the peaks of macrofauna at collections 7 (day 45), 10 (day 120), and 11 (day 150) for *R. mangle*, and 6 (day 30), 7 (day 45), and 13 (day 270) for *L. racemosa*. At Station I, no oligochaetes or insect larvae were recorded during the study period, whereas at the other stations all the taxa observed were recorded. Arthropods showed a higher relative participation at the beginning of the experiment for the litter bags of both *R. mangle* and *L. racemosa* (Figure 3). After this period, annelids had the highest participation, with Oligochaeta dominating in the intermediate period and Polychaeta in the final period.

In one-way ANOVA the abundance and richness of benthic invertebrates for each mangrove species were homogeneous ($P > 0.05$) among stations. Among the collection times, the litter bags of *R. mangle* showed significant differences ($P < 0.05$) for both abundance and richness. For the litter bags of *L. racemosa*, abundance and richness were similar ($P > 0.05$) among the collection times.

In two-way ANOVA, abundance values among the groups of collection times were homogeneous ($P > 0.05$) for the litter bags of both mangrove species. Richness was similar among the groups of collection times for *R. mangle* and showed a significant difference ($P < 0.05$) between the intermediate and final periods for *L. racemosa*. Abundance and richness were

**Table 2.** Total numbers of individuals of benthic macrofauna associated with decomposing leaves of *Rhizophora mangle* and *Laguncularia racemosa* during the experiment (June 2008 – April 2009).

| Mangrove species | Benthic macrofauna | | | |
|---|---|---|---|---|
| | Crustacea | Hexapoda | Annelida | Total |
| *Rhizophora mangle* | 61 | 12 | 291 | 364 |
| *Laguncularia racemosa* | 34 | 17 | 210 | 261 |
| Total | 95 | 29 | 501 | 625 |

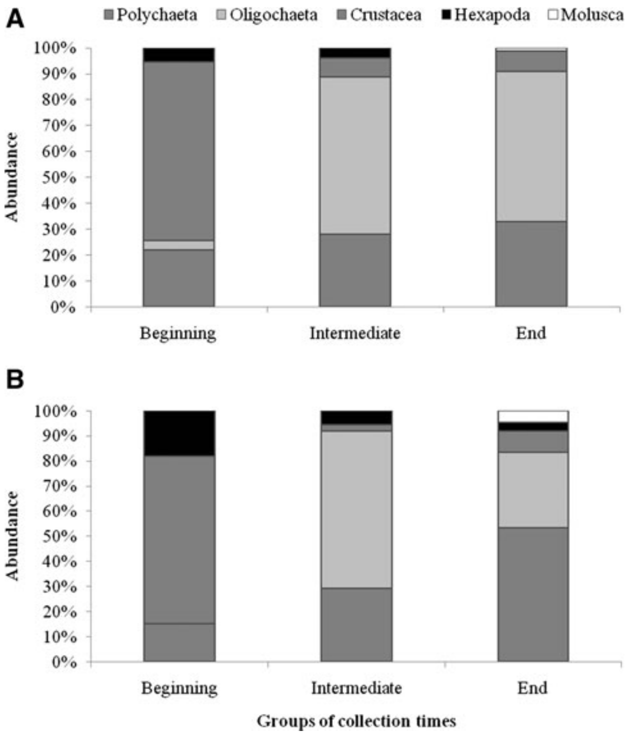

**Fig. 3.** Relative participation of taxonomic groups of benthic invertebrates found in litter bags of *Rhizophora mangle* (A) and *Laguncularia racemosa* (B) during the experimental period (June 2008 – April 2009); collection times are grouped.

also similar ($P > 0.05$) between the mangrove species in both ANOVAs (Figures 4 & 5).

Table 3 lists the benthic macrofauna recorded. Polychaete annelids were identified to species level; *Perinereis brevicirrata* was most abundant, followed by *Capitella* cf. *capitata*, *Heteromastus filiformis* and *Neanthes succinea*. Crustaceans were represented by juvenile forms, except for amphipods, which were morphotyped; Brachyura was the most numerous group with 14 individuals. Among insect larvae and pupae, members of the family Tabanidae were prominent. Oligochaetes were abundant, but were not morphotyped and were classified only to major group.

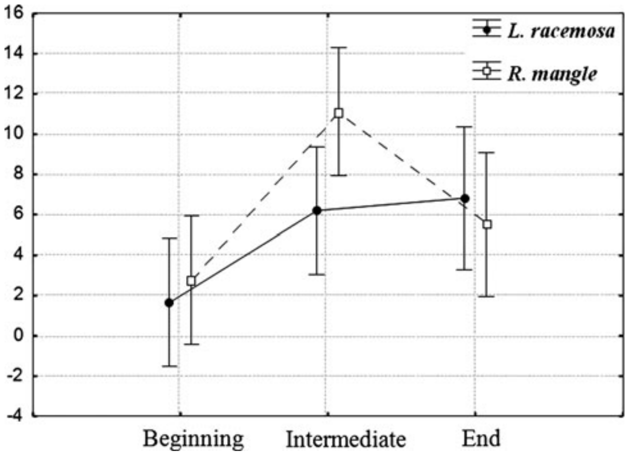

**Fig. 4.** Abundance of the benthic macrofauna found in litter bags of *Rhizophora mangle* and *Laguncularia racemosa* during the experimental period (June 2008 – April 2009); collection times are grouped.

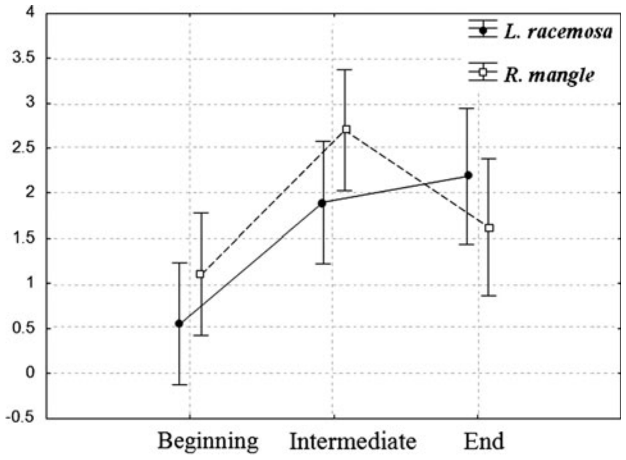

**Fig. 5.** Richness of the benthic macrofauna found in litter bags of *Rhizophora mangle* and *Laguncularia racemosa* during the experimental period (June 2008 – April 2009) collection times are grouped.

Annelids (polychaetes and oligochaetes), crustaceans (crabs and amphipods) and insect larvae were frequent in the litter bags of both mangrove species. Among arthropods, only grapsid crabs were notable, and tabanid pupae were not important in litter of *L. racemosa* (Table 4). The taxa appeared sequentially over time, and the benthic community in the litter bags became more complex and rich. Litter bags of *R. mangle*, in general, accumulated more taxa than those of *L. racemosa*. Collection 10 (day 120) of *R. mangle* showed the highest richness, with four taxonomic groups, while *L. racemosa* had three taxonomic groups, with the highest richness at collections 6 (day 30) and 13 (day 270) (Table 4).

The polychaete *Perinereis brevicirrata* was frequent from the early collections in litter bags of both mangrove species, as was the amphipod *Corophium* spp. in bags of *R. mangle*. Oligochaetes appeared at collections 5 (day 15) and 6 (day 30) for *R. mangle* and *L. racemosa* respectively, and remained frequent and abundant until the end of the experiment. Insect larvae were found only from collection 7 (day 45) for both mangrove species, but they disappeared at collection 9 (day 90) for *R. mangle* (Table 4).

Among the main groups in the litter bags of both mangrove species, Polychaeta and Oligochaeta were numerous in most collections, while Crustacea and Hexapoda were present in small numbers (Figure 6). Station I had a higher contribution of Polychaeta and Crustacea for both *R. mangle* and *L. racemosa* (Figure 7). For *R. mangle*, Stations II and III were represented by oligochaetes, polychaetes, and crustaceans, especially polychaetes at Station II and oligochaetes and polychaetes at Station III. For *L. racemosa*, Stations II and III had the highest contributions of oligochaetes and polychaetes, and oligochaetes were the dominant group at both stations. At Station IV, all four groups, especially oligochaetes, were present in litter bags of *R. mangle*; for *L. racemosa*, crustaceans were not numerous and oligochaetes and polychaetes were prominent.

The MDS analysis showed two distinct groups; the first was formed by samples from the beginning period, and was more uniform; and the second was formed by the other samples (Figure 8). The litter bags of *R. mangle* and *L. racemosa* showed similar dominance curves, indicating a general decrease in dominance and increase in richness during the course of the collections (Figure 9).

**Table 3.** Abundance of benthic macrofauna recorded in litter bags of *Rhizophora mangle* and *Laguncularia racemosa* in the entire collection period (June 2008–April 2009).

| **Mangrove species** | ***Rhizophora mangle*** | | | | | | | | | | | | | ***Laguncularia racemosa*** | | | | | | | | | | | | | **Overall total** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Benthic macrofauna** | **T3** | **T4** | **T5** | **T6** | **T7** | **T8** | **T9** | **T10** | **T11** | **T12** | **T13** | **T14** | **Total** | **T3** | **T4** | **T5** | **T6** | **T7** | **T8** | **T9** | **T10** | **T11** | **T12** | **T13** | **T14** | **Total** | |
| Phylum Annelida | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Polychaeta | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Capitellidae | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Heteromastus filiformis* | | | | | | | | 1 | | 6 | | | 7 | | | | | | | | | | 2 | 25 | | 27 | 34 |
| *Capitella* cf. *capitata* | | | 2 | 7 | 1 | | 7 | 7 | 1 | | 1 | | 26 | | | | | | | 1 | 2 | 9 | 2 | | | 14 | 40 |
| Nereididae | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | 1 |
| *Perinereis brevicirrata* | 2 | 4 | 2 | 5 | 2 | 9 | 2 | 11 | 8 | | 1 | | 46 | 2 | | 1 | 8 | 1 | 8 | | 6 | 11 | | | | 37 | 83 |
| *Neanthes succinea* | | 1 | 1 | | 1 | 1 | | | 5 | | | | 9 | | | | 2 | | | | 2 | 2 | | 3 | | 9 | 18 |
| *Ceratonereis excisa* | | | | | | | | | 1 | | | | 1 | | | | | | | | | | | | | | 1 |
| Goniadidae | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Glycinde multidens* | | | | | | | | | 1 | | | | 1 | | | | | | | | | | | | | | 1 |
| Hesionidae | | | | | | | | | | | | | | 2 | | | | | | | | | | | | 2 | 2 |
| Dorvilleidae | | | | | | | | | | | | | | | | | | | | | | 1 | | | | 1 | 1 |
| Oligochaeta | | | 2 | 23 | 92 | | 6 | 14 | 34 | | 16 | 1 | 188 | | | | 21 | 35 | | 14 | 8 | 1 | | 17 | 15 | 111 | 299 |
| Phylum Arthropoda | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Subphylum Crustacea | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Decapoda | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Penaeidae | | | | | | | | | 1 | | | | 1 | | | | | | | | | | | | | | 1 |
| Caridea | | | 1 | | | | | | | | | | 1 | 1 | | | | | | | | | | | | 1 | 2 |
| Brachyura | | | | 1 | 1 | 1 | | 2 | | | | | 5 | | | | | | | | | | | | | | 5 |
| Grapsidae | | | | | | | | | 2 | 1 | | | 3 | | | | | | | | | | 3 | | 1 | 4 | 7 |
| *Pachygrapsus* spp. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Ocypodidae | | | | | | | | 2 | | | | | 2 | | | | | | | | | | | | | | 2 |
| Peracarida | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Amphipoda | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Corophium* spp. | | 6 | 3 | | | 1 | | 3 | 1 | | | | 14 | 1 | 1 | | | | | | | | | | | 2 | 16 |
| Amphipoda sp.1 | 1 | 1 | | 1 | | | | 1 | | | | | 4 | | | | | 1 | | | | | | | | 1 | 5 |
| Amphipoda sp.2 | | | 13 | | | | | | | | | | 13 | | | | | | | | | | | | | | 13 |
| Amphipoda sp.3 | | | | | | 2 | | | 1 | | | | 3 | | | 1 | | | | | | | | | | 1 | 4 |
| Amphipoda sp.4 | | | | | | 1 | | | | | | | 1 | | | | | | | | | 1 | | | | 1 | 2 |
| Amphipoda sp.5 | 6 | | 4 | | | | | | | | | | 10 | | 10 | 3 | | | | | | | | | | 13 | 23 |
| Amphipoda juveniles | | | | | | | | | | | | | | 1 | | 1 | | | | | | | | | | 2 | 2 |
| Isopoda | | | | | | 1 | | | | | | | 1 | | | | | | 1 | | | 1 | | | | 2 | 3 |
| Subphylum Hexapoda | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Odonata (Aesnidae CF) | | | | | | | | | | | | | | | | 5 | | | | | | | | | | 5 | 5 |
| Hemiptera CF | | | | | | | | 1 | | | | | 1 | | | | | | | | | | | | | | 1 |
| Halipidae (Coleoptera) | | | | | | | | | | | | | | | | | | 1 | | | | | | | | 1 | 1 |
| Amphizoidae | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Amphizoa* spp. | | 1 | | | | 1 | | | | | | | 2 | | | | | | | | | | | | | | 2 |
| Empididae | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | 1 |
| Diptera | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | 1 |
| Chironomidae | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | 1 |
| Tabanidae | | | | | 3 | 3 | 1 | | | | | | 7 | | | | | 1 | | | 2 | | 1 | 1 | 2 | 7 | 14 |
| Insecta not identified | | | 2 | | | | | | | | | | 2 | | | 1 | | | | | | | | | | 1 | 3 |
| Total | 9 | 13 | 30 | 37 | 100 | 20 | 16 | 42 | 55 | 7 | 18 | 1 | 348 | 7 | 11 | 12 | 31 | 39 | 11 | 16 | 20 | 26 | 8 | 47 | 18 | 246 | 594 |

**Table 4.** Most frequent and abundant benthic invertebrates found in litter bags of *Rhizophora mangle* and *Laguncularia racemosa* during the collection period (June 2008–April 2009).

| **Collection** | **Σ A. A.** | **T3** | | **T4** | | **T5** | | **T6** | | **T7** | | **T8** | | **T9** | | **T10** | | **T11** | | **T12** | | **T13** | | **T14** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** | **A. A.** | **%** |
| *Rhizophora mangle* | | | | | | | | | | | | | | | | | | | | | | | | | |
| Taxonomic group | | | | | | | | | | | | | | | | | | | | | | | | | |
| Oligochaeta | 59.6 | * | * | | | | | 5.8 | 84.2 | 30.7 | 88.7 | | | 2 | 35.0 | 4.7 | 29.9 | 8.5 | 30.0 | * | * | 8 | 100 | ** | ** |
| Polychaeta | 17.4 | | | 1 | 64.8 | 0.5 | 100 | 1.3 | 15.8 | 0.7 | 5.7 | 3 | 100 | 3 | 65.0 | 6 | 61.0 | 2 | 57.4 | | | | | | |
| *Perinereis brevicirrata* | 12.8 | * | * | 1 | 64.8 | 0.5 | 100 | 1.3 | 15.8 | 0.7 | 5.7 | 3 | 100 | 0.7 | 33.9 | 3.7 | 29.9 | 2 | 57.4 | * | * | | | | |
| *Capitella* cf. *capitata* | 4.7 | * | * | | | | | | | | | | | 2.3 | 31.2 | 2.3 | 31.2 | | | * | * | | | | |
| Crustacea | 2.7 | | | 1.5 | 35.2 | | | | | | | | | | | 0.7 | 9.1 | 0.5 | 12.6 | | | | | | |
| Ocypodidae | 0.7 | * | * | | | | | | | | | | | | | 0.7 | 9.1 | | | * | * | | | | |
| *Corophium* spp. | 1.5 | * | * | 1.5 | 35.2 | | | | | | | | | | | | | | | * | * | | | | |
| Grapsidae | 0.5 | * | * | | | | | | | | | | | | | | | 0.5 | 12.6 | * | * | | | | |
| Hexapoda | 1 | | | | | | | | | 1 | 5.65 | | | | | | | | | | | | | | |
| Tabanidae | 1 | * | * | | | | | | | 1 | 5.65 | | | | | | | | | * | * | | | | |
| Σ A. A. | | | | 2.5 | | 0.5 | | 7 | | 32.3 | | 3 | | 5 | | 11.3 | | 11 | | | | 8 | | | |
| Number of taxa | | | | 2 | | 1 | | 2 | | 3 | | 1 | | 3 | | 4 | | 3 | | | | 1 | | | |
| *Laguncularia racemosa* | | | | | | | | | | | | | | | | | | | | | | | | | |
| Oligochaeta | 33.5 | | | | | * | * | 5.3 | 72.7 | 11.7 | 100 | | | 4.67 | 100 | 2.7 | 65.2 | | | | | 4.3 | 42.1 | 5 | 100 |
| Polychaeta | 20.8 | 1 | 100 | | | | | 2.5 | 27.3 | | | 2.7 | 100 | | | 2 | 34.8 | 5 | 100 | 0.7 | 57.4 | 7 | 57.86 | | |
| *Perinereis brevicirrata* | 10.4 | 1 | 100 | | | * | * | 2 | 8.9 | | | 2.7 | 100 | | | 2 | 34.8 | 2.8 | 47.7 | | | | | | |
| *Heteromastus filiformis* | 6.9 | | | | | * | * | | | | | | | | | | | | | 0.7 | 57.4 | 6.3 | 32.9 | | |
| *Capitella* cf. *capitata* | 2.3 | | | | | * | * | | | | | | | | | | | 2.3 | 52.4 | | | | | | |
| *Neanthes succinea* | 1.3 | | | | | * | * | 0.5 | 18.4 | | | | | | | | | | | | | 0.8 | 25.0 | | |
| Crustacea | 1 | | | | | | | | | | | | | | | | | | | 1 | 42.6 | | | | |
| Grapsidae | 1 | | | | | * | * | | | | | | | | | | | | | 1 | 42.6 | | | | |
| *Corophium* spp. | | | | ** | ** | * | * | | | | | | | | | | | | | | | | | | |
| Amphipoda morphotype 5 | | | | ** | ** | * | * | | | | | | | | | | | | | | | | | | |
| Σ A. A. | | 1 | | | | | | 7.8 | | 11.7 | | 2.7 | | 4.7 | | 4.7 | | 5 | | 1.7 | | 11.3 | | 5 | |
| Number of taxa | | 1 | | | | | | 3 | | 1 | | 1 | | 1 | | 2 | | 2 | | 2 | | 3 | | 1 | |

*, all similarities are zero;
**, less than 2 samples in group;
A. A., absolute abundance.

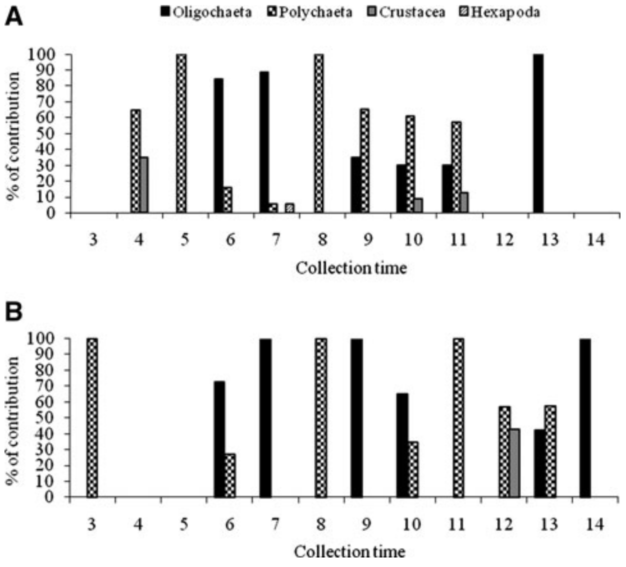

**Fig. 6.** Contribution of the main taxonomic groups of benthic invertebrates found in litter bags of *Rhizophora mangle* (A) and *Laguncularia racemosa* (B) (June 2008 – April 2009).

# DISCUSSION

The macrofauna recorded here, comprised the same taxonomic groups that usually appear in studies of decomposition in mangroves (Ponte *et al.*, 1984; Ashton *et al.*, 1999; Middleton & McKee, 2001; Bosire *et al.*, 2005; Aké-Castillo *et al.*, 2006). These organisms contribute to the decomposition process through the consumption of detritus, and especially by promoting fragmentation. The mechanical breakdown provided by shredder organisms apparently augments the degradability of litter by increasing the surface area accessible to microbial attack (Kristensen *et al.*, 2008).

Most studies do not report the first record of the presence of macrofauna in litter bags. In a study on the decomposition of *Laguncularia racemosa* leaves at Sergipe in north-east Brazil, the benthic invertebrates appeared on the fourth day after the installation of the experiment (Couto & Lima, 1997), a similar period to that observed in our study. This suggests that even in early stages of decomposition, when

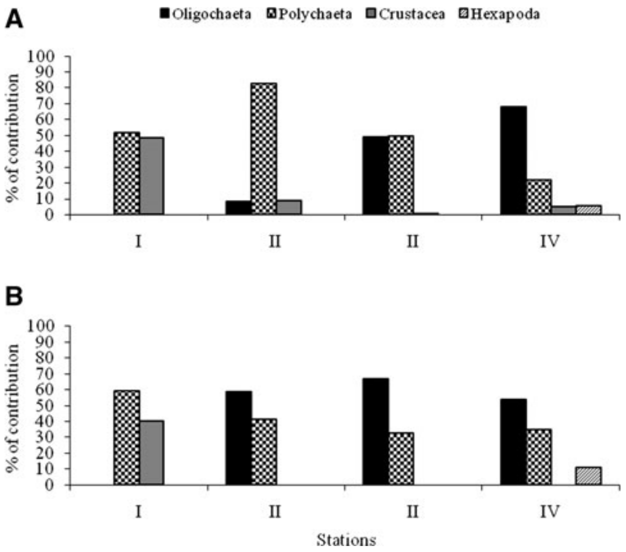

**Fig. 7.** Contributions of the main taxonomic groups of benthic invertebrates found in litter bags of *Rhizophora mangle* (A) and *Laguncularia racemosa* (B) at the four study stations (June 2008 – April 2009).

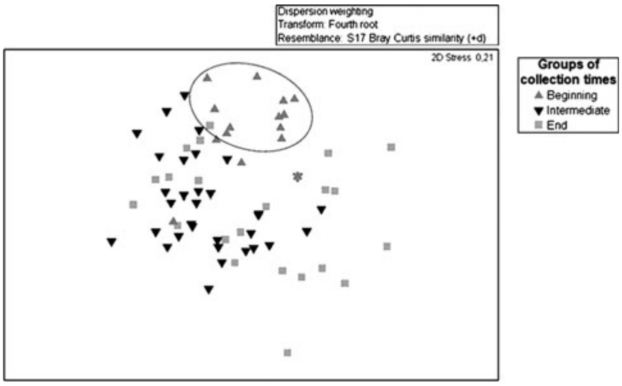

**Fig. 8.** Multidimensional scaling analysis for benthic invertebrates community found in litter bags of *Rhizophora mangle* and *Laguncularia racemosa* during the experimental period (June 2008 – April 2009); collection times are grouped.

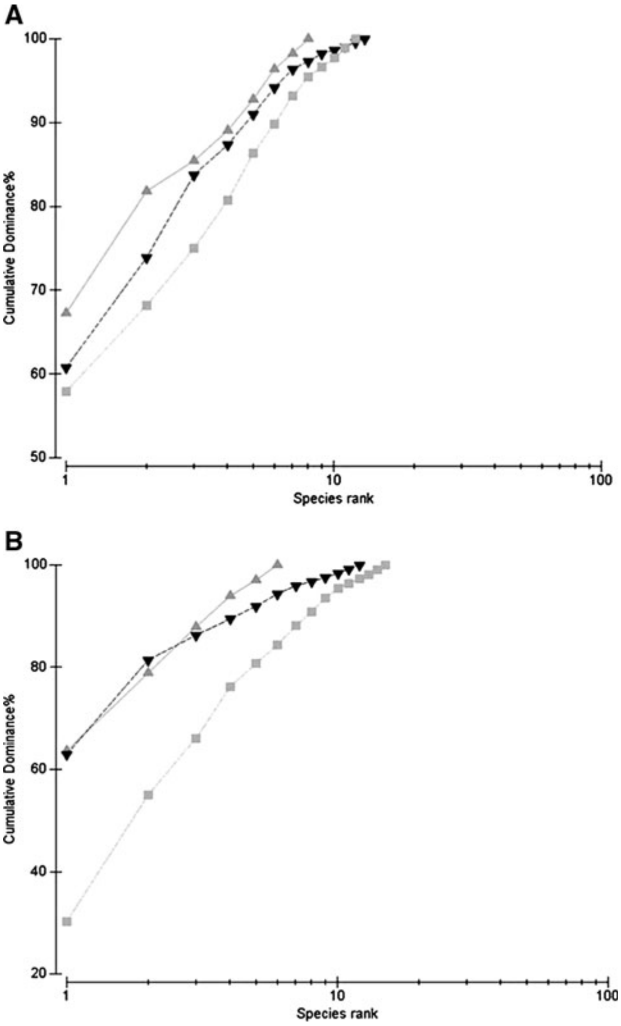

**Fig. 9.** Dominance curve for benthic invertebrates found in litter bags of *Rhizophora mangle* (A) and *Laguncularia racemosa* (B) during the experimental period (June 2008 – April 2009); collection times are grouped.

leaching and the action of bacteria and fungi predominate, the macrofauna can play an essential role (Oliveira *et al.*, in press), since in their absence, decomposition proceeds only to a certain point (Ashton *et al.*, 1999).

The study stations were not statistically different in abundance and composition of benthic macroinvertebrates, indicating that immersion time was not the most important factor. The small difference in topographic position between the stations and the extensive anastomosis of the area may have caused some homogeneity in the immersion time, reflected in the decomposition rate as well as in the composition of the benthic invertebrate fauna (Oliveira *et al.*, in press). Nevertheless, oligochaetes and insect larvae were absent from Station I, suggesting that factors at this site limit the presence of these organisms.

The abundance and composition of macrofauna did not differ significantly between the mangrove species. However, organisms were more abundant in litter bags of *Rhizophora mangle* (more than 100 individuals) than in those with *Laguncularia racemosa*. This was not expected, since the leaves of *R. mangle* are less palatable than those of *L. racemosa*, because of their chemical constituents. The organisms recorded within 15 days after the installation of the experiment were polychaetes and especially amphipods, which probably acted as shredders; the litter bags of *R. mangle* contained almost twice the number of amphipods during this period. The intense fragmentation caused by these organisms probably makes the detritus of both mangrove species equally attractive. Oligochaetes, which accounted for the higher total macrofaunal abundance in litter bags of *R. mangle*, appeared 15 and 30 days after the installation of the experiment for *R. mangle* and *L. racemosa* respectively. From that time, the debris was more palatable because of intense leaching, the action of bacteria and fungi, and fragmentation by amphipods, which facilitated the action of scavengers. This can be corroborated by analysing the decay constants of *R. mangle* and *L. racemosa* (Oliveira *et al.*, in press): 30 days after the installation of the experiment, the constants of both species showed an overlap, indicating that after a certain period, the decay rates of both mangrove species became similar (the constants of *R. mangle* showed variation between the stations of 0.017–0.022, and *L. racemosa* ranged between 0.021 and 0.030).

In a study from Kenya, amphipods were the dominant group in the process of leaf decomposition, suggesting their importance in the fragmentation of detritus (Bosire *et al.*, 2005). Middleton & McKee (2001) highlighted the presence of crabs and amphipods as the factor that tripled the speed of leaf fragmentation. Another study in the Gulf of Mexico emphasized the importance of gastropods in the decomposition process (Aké-Castillo *et al.*, 2006). In this study, the annelids were most prominent, with Oligochaeta and Polychaeta being the most abundant groups. Oligochaetes, despite the large number of individuals and prominence in the litter bags of both mangrove species, were recorded in seven collections but not continuously. Polychaetes, with the second-largest representation, were observed continuously in 11 and ten collections in bags with *R. mangle* and *L. racemosa*, respectively, and were represented mainly by nereidids and capitellids.

The species of Nereididae found were *Perinereis brevicirrata*, which was the most abundant polychaete species and was previously unrecorded in the State of Bahia; and also *Neanthes succinea* and *Ceratonereis excisa*. The family Nereididae is mostly omnivorous, and despite their impressive jaws, few species are considered carnivorous (Fauchald & Jumars, 1979). In general, they easily change their feeding mode according to the availability of food, and several species are capable of absorbing dissolved organic matter. *Perinereis brevicirrata* was recorded beginning five days after the installation of the experiment, and was present in eight and five collections for *R. mangle* and *L. racemosa*. Probably it acted as a shredder, since some species of *Perinereis* feed on microalgae and diatoms (Fauchald & Jumars, 1979). These microorganisms may have developed on the surface of the leaf detritus and attracted these polychaetes. In view of the feeding versatility of nereidids, this species may also have fed on decomposing material, as a detritivore. *Neanthes succinea* is considered a surface deposit feeder (Fauchald & Jumars, 1979), and was first observed seven days after the installation of the experiment, suggesting that the litter was consumed directly in that period.

Capitellids are classified as non-selective deposit feeders (Fauchald & Jumars, 1979). The species belonging to this family were *Capitella* cf. *capitata* and *Heteromastus filiformis*. The former, considered an indicator of organically enriched areas, was the second most abundant species among polychaetes, being recorded from day 15 of the installation of the experiment. It was probably feeding directly on the leaf detritus, since it has the capacity to absorb dissolved starch (Fauchald & Jumars, 1979). *Heteromastus filiformis*, as a deposit-feeder, possibly also fed directly on the detritus.

Insects were fewer in number and were represented by members of the family Tabanidae, mainly in the litter bags of *R. mangle*. Tabanid larvae are carnivorous, and appeared on the 45th day of the experiment. A small number of other carnivores were recorded, including *Glycinde multidens*, an unidentified species of Dorvilleidae, and larvae of Hemiptera and Odonata.

The observed sequence suggests that the detritus was first invaded by benthic macrofaunal shredders (amphipods and *Perinereis brevicirrata*). The shredding allowed greater colonization by microorganisms, making the leaves more attractive to detritivores, which appeared in the sequence represented by oligochaetes and polychaetes. Carnivores appeared 15 days after the experiment began, when prey were available in the litter bags.

The MDS analysis evidenced two distinct groups. The first consisted of samples that were less diverse and equitable, poor in taxa and individuals, and dominated by Arthropoda, represented by shredders. In the second group, representing the intermediate and end periods, assemblages of benthic invertebrates were richer, abundant, diverse and equitable, with annelids (considered to be decomposers) as the dominant group.

The succession of benthic invertebrates is even more evident when observing the dominance curves. Dominance was lower and richness was higher in the end period, indicating that the species were more numerous and equitable, and that the complexity of the macrobenthic community in litter bags increased during the leaf decomposition process.

The dominant role of mangrove detritus in the diet of primary consumers does not necessarily explain the high decomposition rates, since faunal consumption can have a very large effect on the dynamics of detritus, even when other inputs are the main food source (Kristensen *et al.*, 2008). The litter-bag method does not reflect the real action of the benthic macrofauna on the detritus, because leaves enclosed in nylon bags are more attractive since they provide a concentration of food and protection from predators. Some benthic invertebrates invade the mesh bags, but after they feed or escape from predators, the same mesh prevents them from leaving. These attraction and containment effects may mask the real action of organisms in leaf decomposition.

The data from this study demonstrate a succession of benthic macroinvertebrates during the process of leaf decomposition. This suggests that the density of these organisms and their foraging behaviour can influence the rate of leaf decomposition of *R. mangle* and *L. racemosa*, and that decomposition may have been accelerated by the large component of shredders and detritivores.

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**Correspondence should be addressed to:**
A.B. de Oliveira
Universidade Estadual de Santa Cruz
Rodovia Ilhéus-Itabuna, km 16, 45662-900, Ilhéus, BA, Brazil
email: christambell@yahoo.com.br