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ORIGINAL RESEARCH

Leaf Litter and Invertebrate Colonization: the Role of Macroconsumers in a Subtropical Wetland (Corrientes, Argentina)

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Abstract We studied the breakdown rates and the invertebrate abundance and biomass for the litter of five native aquatic plants (*Eichhornia crassipes*, *Eichhornia azurea*, *Thalia multiflora*, *Oxycaryum cubense* and *Hydrocotyle ranunculoides*) in a shallow rain-fed lake using litter bags. The diets of the prawn *Pseudopalaemon bouvieri* and the amphipod *Hyalella curvispina* were determined and classified into five food items. Litter breakdown was fast (>0.010 day^{-1}) for all species studied, although the breakdown rates were significantly affected by the litter species. The abundance of invertebrates colonizing the litter was significantly different among the species, but the biomass did not differ. The invertebrate taxa that colonized the litter of the different species were broadly similar, consisting primarily of oligochaetes, amphipods, prawns, ostracods, gastropods, water mites and several types of insect larvae (chironomids and mayflies). In terms of the number of individuals, naidid oligochaetes dominated the assemblages. In terms of biomass, *P. bouvieri* and *H. curvispina* reached 67.6 and 18.2 % of the total, respectively. Our results indicate that macroconsumers are involved in the breakdown process, since these species consume plant remains and detritus and highlight the importance of leaf litter composition on the abundance of invertebrates that colonize the litter.

Keywords Aquatic plants · Breakdown rates · *Pseudopalaemon bouvieri* · *Hyalella curvispina* · Shallow lakes

Introduction

Most food chains in wetlands are detrital, based on the high production of the vegetation (Mitsch and Gosselink 1993). Invertebrates are the link between primary producers and fish (and other vertebrates), for which they are prey. However, there is a paucity of detailed information about the roles that particular species play in the food webs in wetlands (Batzer et al. 1999).

Litter breakdown has been recognized as a complex process, and conceptual models have been formulated to describe this process in low-order streams in the context of the ecosystem as a whole (Graça et al. 2015). In forested streams, the abundant leaf litter subsidies from riparian trees are typically the major source of energy in food webs. The tropical and subtropical wetlands of South America have high productivity of aquatic plants, and year-round growth often leads to the development of large macrophyte standing stocks (Carignan and Neiff 1992; Melack and Forsberg 2001). Nevertheless, despite having high macrophyte diversity (Chambers et al. 2008; Neiff et al. 2011), the decomposition rates in South American wetlands are known only for the dominant aquatic plants (*Eichhornia crassipes*, *Eichhonia azurea*, *Paspalum repens*, *Polygonum* spp., *Panicum elephantipes* and *Typha latifolia*) in different types of riverine wetlands connected to large rivers (Bruquetas de Zozaya and Neiff 1991; Pagioro and Thomaz 1999; Poi de Neiff et al. 2006) and reservoirs (Stripari and Henry 2002; Bottino et al. 2013). Leaf breakdown processes are governed by intrinsic factors related to the chemical properties of the litter, such as secondary

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compounds and nutrient content, as well as extrinsic factors related to the environmental conditions where the process occurs (Webster and Benfield 1986). Many studies (see Webster and Benfield 1986) have provided indirect evidence for the importance of invertebrates in leaf breakdown, whereas others have suggested that invertebrates are not important in this process. A global analysis comparing six continents indicated that shredder density is 2.5 times higher in temperate streams than in tropical streams (Boyero et al. 2012). A paucity of shredding invertebrate detritivores and a high proportion of collectors or predators is a frequent characteristic of many tropical and subtropical wetland assemblages (Neiff and Poi de Neiff 1990; Dudgeon and Wu 1999; Stripari and Henry 2002; Mathuriau and Chauvet 2002; Capello et al. 2004; Gonçalves et al. 2006; Rueda-Delgado et al. 2006; Galizzi and Marchese 2007; Poi de Neiff et al. 2009). There are several possible explanations for this paucity that are not mutually exclusive (Boulton et al. 2008). One possibility is that the shredding taxa have been overlooked because some genera belong to a different functional feeding group in temperate rivers than those in tropical rivers. Other studies have suggested that the apparent lack of shredders in tropical systems reflects sampling deficiencies that exclude macroconsumers such as crabs (Wantzen et al. 2002; Dobson 2004), fish or shrimp (Rosemond et al. 1998). Shrimp play an important role in the food webs of tropical waters as grazers, predators and detritivores, but their ecological effects on food webs are strongly taxon-dependent (Jacobsen et al. 2008). Information is scarce about the functional feeding groups of aquatic invertebrates in South America, and studies generally follow classification from the Holarctic region (Merritt and Cummins 1996). Gut content analysis is needed to ascertain the function of invertebrates found in Afrotropical (Masese et al. 2014) and Neotropical (Tomanova et al. 2006) streams. A third explanation for the paucity of shredders in many wetlands, especially in those dominated by submerged and floating plants, is that the rapid breakdown of plant material by mechanical, microbial and chemical process precludes shredding (Wissinger 1999).

In several shallow lakes of the province of Corrientes, amphipods (*Hyalella curvispina* Shoemaker) and prawns (*Pseudopalaemon bouvieri* Sollaud) are frequent and abundant in vegetated areas (Poi and Galassi 2013). *P. bouvieri* is omnivorous, consuming a high proportion of algae and detritus (Carnevali et al. 2012).

The aim of this study was to evaluate how the diversity of litter species affects litter processing in a subtropical wetland. For this purpose, we compared leaf breakdown and the abundance and biomass of invertebrates that colonize the leaf litter of five aquatic plants in an in situ experiment with litter bags. To elucidate the importance of invertebrates in the leaf breakdown process, we also investigated the trophic spectrum of the dominant macroconsumers in the same wetland.

Our hypotheses are, first, that leaf litter of different species, which decompose at different rates, will support different invertebrate assemblages both in terms of abundance and biomass; second, that the biomass of prawns and amphipods dominate the invertebrates that colonize the litter and third, that macroconsumer omnivores contribute to litter breakdown by shredding leaf litter.

Methods

Study Area

The province of Corrientes is characterized by a subtropical climate with long, warm summers and short, not usually severe winters (Bruniard 1999). The average annual temperature ranges from 13 to 19.5 °C. During summer, the absolute maximum temperature ranges from 42.5 to 46.5 °C. In the northeastern region of the province, there are more than 100 subrounded, shallow, rain-fed lakes that have low salinity and electrical conductivity ranging between 25 and 150 $\mu S\ cm^{-1}$ (Poi and Galassi 2013). One such lake, which is located at 27°22’ S and 58°32’ W, was selected for this study. It has an area of 22 ha and a maximum depth of 4 m, and 25 % of its water surface is covered by different species of aquatic plants.

Experimental Design and Analysis

Leaf breakdown was measured by the litter bag method (Crossley and Hoglund 1962). Five macrophyte species, *Eichhornia crassipes* (Mart.) Solms, *Eichhornia azurea* (Sw.) Kunth, *Thalia multiflora* Horkel, *Oxycaryum cubense* (Poepp & Kunth) Lye, and *Hydrocotyle ranunculoides* (L. f.), were chosen on the basis of expected differences in nutrient (N and P) and lignin content. These species are native and very common in the wetlands of northeastern Argentina. *E. crassipes* and *H. ranunculoides* were distributed to several countries though the ornamental trade and are considered invasive species outside of their native range.

We collected recently senesced leaves of macrophytes in the study lake. Air-dried leaves (10 g) were placed into 20 × 20 cm nylon litter bags with 5 mm mesh. In November 2010, five replicate bags of leaf litter from each species were incubated on four sampling dates, for a total of 100 litter bags. Each set of bags was anchored to the bed of the wetland and was collected at random after 7, 14, 30 and 45 days. Each bag was packed into a separate plastic bag in the field and was returned to the laboratory. The leaf material was gently washed on a sieve (125 μm mesh) to remove silt, epiphytes and invertebrates. The remaining plant material was dried to a constant weight at 105 °C. When the mass loss was calculated, corrections were made for the moisture content of air-dried samples up to the constant dry weight (105 °C). The invertebrates were counted, separated by taxonomic group and, after identification, were dried to constant mass at 60 °C for 48 h and weighed to the nearest 0.01 g. Abundance was expressed as the number of invertebrates per litter bag. The total biomass (g per litter bag) was estimated as the sum of the dry weight of the dominant taxa (Naididae, Glossiphoniidae, Palaemonidae, Hyalellidae, Caenidae, Hydrachnidia, Libellulidae, Coenagrionidae, Gomphidae, Chironomidae and Ancylidae). The taxa of minor biomass were pooled, weighed and assessed as previously described.

The physical and chemical water conditions were assessed on each collection date. The temperature and oxygen concentration were measured with a YSI 54A polarographic probe, and pH was measured with a WTW 330/SET-1 digital pH meter. The water samples were filtered within 1–2 h of collection using pre-washed Gelman DM-450 (0.45 mm-pore) membranes for the spectrophotometric analyses of NH_4^+ (indophenol blue method), NO_3^- + NO_2^- (called NO_3^-) by Cd reduction and total phosphorus (molybdenum blue method) with persulfate oxidation (APHA 1998). At the beginning of the experiment, the leaf subsamples from each litter type were dried at 60 °C to determine the nutrient content. The nitrogen (macro-Kjeldahl method), phosphorus (AOAC 1990), and fiber contents (Ankom Fiber Analyzer) were expressed as the percentage of dry weight.

The decomposition constant, *k* (Olson 1963), for the exponential model was calculated using the equation

$$W_t = W_0 e^{-kt}$$

where W_0 is the original amount of litter, W_t is the amount of litter remaining after time *t*, and *t* is the time in days.

The Macroconsumer Trophic Spectrum

Prawns (*Pseudopalaemon bouvieri*) and amphipods (*Hyalella curvispina*) were collected in the vegetated area of the lake during November and December, when the spring peak of their populations occurs, with a 35 cm diameter and 500 μm mesh net. The vegetation was rinsed into a white container, and the individuals were separated by hand. The diets of both macroconsumers were analyzed by removing their digestive tracts under a stereoscopic microscope. The stomach contents of *P. bouvieri* and the digestive tract of *H. curvispina* were mounted in 50 % glycerol. The contents of the digestive tract of *H. curvispina* were previously dyed with 0.004 % safranin for 24 h to facilitate the identification of the items consumed. We examined 44 *P. bouvieri* stomachs; the items consumed were sorted into taxonomic groups and counted under a compound microscope at 150× to 600×. The different taxonomic groups were identified to the lowest possible taxonomic level using the keys in Lopretto and Tell 1995; Merritt and Cummins 1996 and Domínguez and Fernández 2009.

A total of 32 *H. curvispina* individuals were analyzed, but only 20 had content in their digestive tracts. The material observed was classified into five food items: plant remains, algae, detritus, animal remains and indeterminate material. Twenty ocular fields were chosen randomly and photographed (400× magnification) with a digital camera mounted to the stereoscopic microscope (Leica ICC50 HD). The food items recorded in each ocular field were photographed, and their relative frequencies were calculated. To quantify the food items consumed, 10 ocular fields per individual were selected at random, and the percentage of the total area covered by each food item was estimated using the software ImageJ 1.44.

Statistical Analyses

Analysis of covariance (ANCOVA) was used to determine the differences in the decay coefficient (k day^{-1}) with species as the main factor. Tukey tests were used to identify significant differences among the mean breakdown rates of the litter species. The number and biomass of invertebrates per litter bag were compared among species using generalized linear mixed models (GLMMs) with species as the main factor and time as the repeated measure, and subsequent Fisher's LSD (alpha = 0.05) post hoc tests were used for comparisons among the means. ANOVA with Tukey's post hoc test was used to assess differences in the proportion of food items consumed by adults and juveniles of *P. bouvieri* between the sampling dates.

All statistical analyses were performed with INFOSTAT software (Di Rienzo et al. 2012). The data were log (x + 1) or arcsine transformed to reduce the heterogeneity of variances if necessary.

Results

Environmental Characteristics

During the experiment, the water temperature varied between 22.5 and 25 °C, the electrical conductivity varied between 55 and 72 μS cm^{-1}, and the pH varied between 7.3 and 7.7. High dissolved oxygen content was recorded in the surface layer (8.2 mg L^{-1}), decreasing to a minimum at the lake bottom (5.2 mg L^{-1}). The mean Secchi disk depth was 0.87 m. The water had a total nitrogen concentration of between 25 and 110 μg L^{-1} and a low total phosphorous concentration (<5 μg L^{-1}).

Leaf Litter Breakdown

The five species of aquatic vascular plants exhibited a wide range of initial litter nutrient concentrations, lignin contents and L:N ratios (Table 1). As expected, *H. ranunculoides*

Table 1 Concentration of Lignin (L) and Nitrogen (N) and Phosphorus (P) in the leaves of the five studied macrophytes

Litter types	L%	N%	P%	L:N	k day^{-1}	Adj.r^2	$t_{0.50}$ (days)
Eichhornia azurea	2.19	2.70	0.38	0.81	0.05205	0.955	13.31
Eichhornia crassipes	2.85	2.48	0.36	1.14	0.04047	0.9638	17.12
Hydrocotyle ranunculoides	1.04	3.70	0.23	0.28			
Oxycarium cubense	11.50	1.79	0.20	6.24	0.01771	0.917	39.13
Thalia multiflora	12.56	1.46	0.33	8.60	0 .01102	0.874	62.88

The decay coefficient (k day^{-1}), the model r^2 and the half live of the different leaf litter at the end of the incubation time (45 days)

exhibited low lignin content and high nutrient concentration. The initial lignin content of *T. multiflora* and *O. cubense* leaves was approximately 10 times greater than that of *H. ranunculoides* leaves.

After 45 days of incubation, the remaining dry weight varied between 4.4 and 58.6 % for all of the species (Fig. 1). The decay coefficients (k) estimated at the end of the incubation time ranged from 0.05205 to 0.01102 day^{-1}. Based on these k values, the estimated half-life of the litter was 13.31 days for *E. azurea* and 62.88 days for *T. multiflora* (Table 1). *H. ranunculoides* decomposed fairly rapidly, and the total loss of leaf litter through the 5 mm mesh occurred in the first 14 days. The half-life of *H. ranunculoides* litter could thus not be estimated, and this species was not included in the comparisons among the species.

The comparison of the decay coefficients (k) using ANCOVA showed that there was no interaction between the curves, and the slope of the regression differed significantly ($F = 38.69$, $p < 0.0001$) among the litter species. The mean leaf breakdown rate differed significantly between two pairs of species: *E. azurea*-*E. crassipes* and *O. cubense*-*T. multiflora* (Tukey's post hoc test, $p > 0.05$), but the rates of mass loss were similar between the species of each pair.

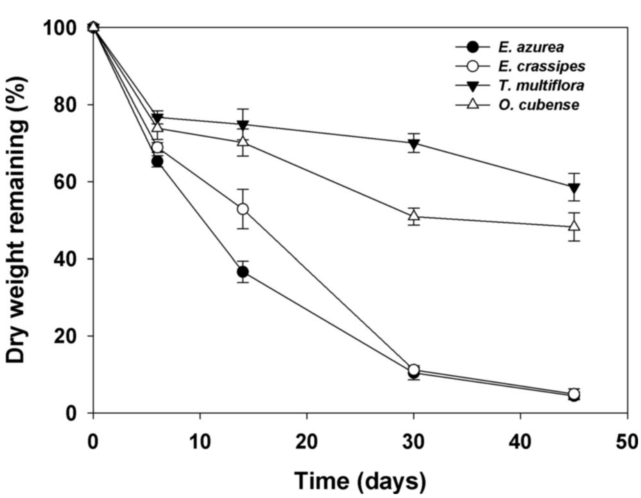

Fig. 1 Remaining litter dry weight for the different litter species. The errors bars represent ± 1 SD

Invertebrate Colonization

The leaves were rapidly colonized by macroinvertebrates, reaching 243 individuals per leaf bag for *O. cubense* (Fig. 2) after only 6 days of incubation. On this date, a mean abundance of 278 invertebrates was found for *H. ranunculoides*, but it was the only available information because the total mass loss occurred after 14 days. The number of invertebrates per bag peaked at 381 (Fig. 2) after 30 days of incubation for *E. azurea* leaf litter (469.3 invertebrates per g of remaining litter).

The differences in the number of invertebrates per litter bag were significant among the litter species (GLMMs, $F = 3.87$, $p = 0.0188$). The mean number of invertebrates colonizing *E. azurea* and *O. cubense* litter per litter bag was significantly different from the number colonizing the litter other plant species, as the abundance of invertebrates on *E. crassipes* and *T. multiflora* litter was similar (Fisher's LSD, $p = 0.05$).

E. azurea supported the highest macroinvertebrate biomass after 30 days of incubation (Fig. 3), peaking at 113.1 mg per litter bag. However, the biomass of invertebrates colonizing

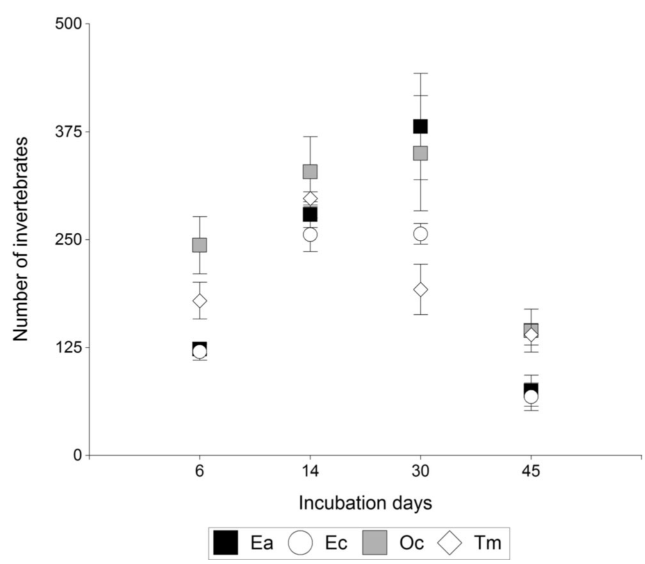

Fig. 2 Mean number (± S.E.) of invertebrates per litter bag for the different litter species during breakdown

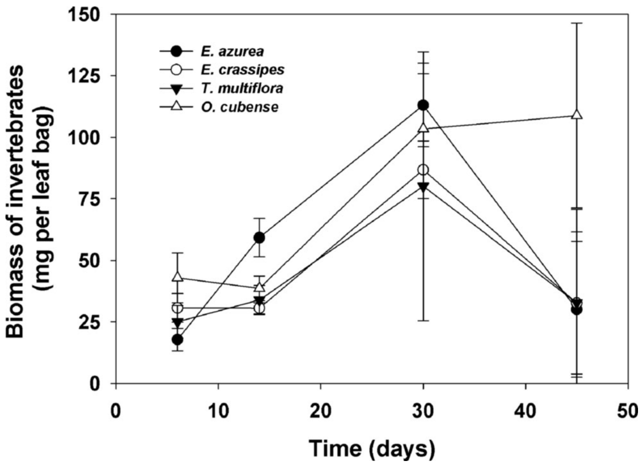

Fig. 3 Mean biomass (±SD) of invertebrates per litter bag for the different litter species during breakdown

the litter was not significantly different among the litter species (GLMMs, $F = 2.71$, $p = 0.06$).

The invertebrate assemblages that colonized the litter of each species were broadly similar, consisting primarily of oligochaetes, amphipods, prawns, ostracods (Limnocytheridae), gastropods (Ancylidae), water mites (Hydrachnidia) and several insect larvae, predominantly chironomids and mayflies. Naidid oligochaetes (mainly *Dero* spp. and *Pristina* spp.) were the most abundant taxa in all leaf litter, reaching 86.6 % of the total number of invertebrates (Fig. 4). Ostracods (*Cytheridella ilosvayi* Daday) were both frequent and abundant. Thus, collectors dominated the invertebrate assemblages on the studied litter of each species. Predatory water mites (*Piona* sp. and *Arrenurus* sp.) were more abundant at the beginning of the experiment than after 30 days of incubation (Fig. 4). The highest proportion of *Hyalella curvispina* was found on *O. cubense* and *E. azurea* litter (Fig. 4) after 6 incubation days. Prawns (*Pseudopalaemon bouvieri*) were recorded in low relative abundance after 30 incubation days. Several insect families, such as Pleidae (*Neoplea* sp.), Corixidae (*Tenagobia* sp.), Leptoceridae, Gomphidae, Libellulidae, Coenagrionidae, Staphylinidae and Pselaphidae, were found at low relative abundance (<1 %) and frequency.

When expressed in terms of biomass (Fig. 5), the proportion of Naididae did not exceed 56.4 %, and a significant portion of the total biomass was represented by leeches, prawns and amphipods. The Glossiphoniidae (*Helobdella* sp.) biomass (Fig. 5) was highly variable, ranging from 3.2 to 19.1 % of the total biomass. *Pseudopalaemon bouvieri* and *Hyalella curvispina* reached 67.6 % (*O. cubense*) and 18.2 % (*T. multiflora*), respectively (Fig. 5). Chironomidae larvae (*Dicrotendipes* sp., *Goeldichironomus* sp. and *Chironomus decorus* Johannsen) contributed up to 2.9 and 2.3 % of the total abundance and biomass (Figs. 4 and 5), respectively. The relative biomass of insect families with high individual dry weight such as Caenidae, Libellulidae, Coenagrionidae and Gomphidae (grouped as other taxa in Fig. 5) was highly variable. Mayfly (*Caenis* sp.) larvae were recorded at low abundance but accounted for 9.4 % of the total biomass in *O. cubense* and *E. crassipes* litter after 6 incubation days.

The Macroconsumer Trophic Spectrum

Adult prawns primarily consumed algae (both unicellular and filamentous), plant remains and detritus on both sampling dates (Fig. 6). Juveniles ate proportionally more animal remains (oligochaetes, copepods, cladocerans, midge larvae (Chironomidae), other insect larvae, protozoa and rotifers) than detritus. Animal remains were the item most consumed by juveniles in December (Fig. 6). The proportions of the food items consumed by juveniles differed significantly between the sampling dates (ANOVA, $F = 4.8$, $p = 0.04$), but the diet of adults did not differ (ANOVA, $F = 1.48$, $p = 0.2$).

The analysis of the digestive tract contents of *H. curvispina* showed that detritus and plant remains were the food items that covered the greatest percentage of the total covered area, followed by algae and indeterminate material, in both males and females (Fig. 7). The lowest proportion of the total area was covered by animal remains (0.2 %). Detritus (fine particulate organic matter) was the most frequently occurring item (87.3 %) followed by plant remains (72.3 %), algae (mostly Chlorophytes, 24.7 %), indeterminate material (18.8 %) and

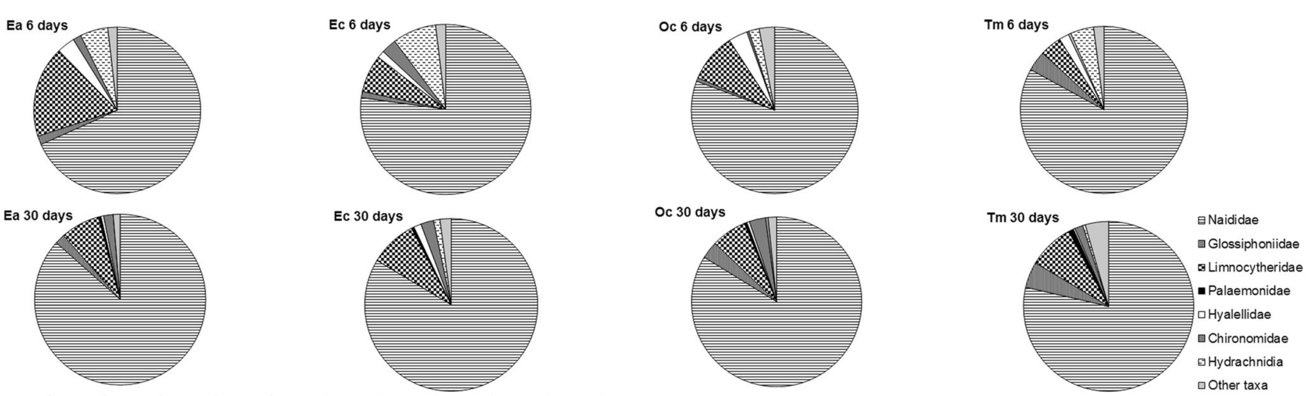

Fig. 4 Relative abundances of the main taxa found in the leaf litter after 6 and 30 incubation days

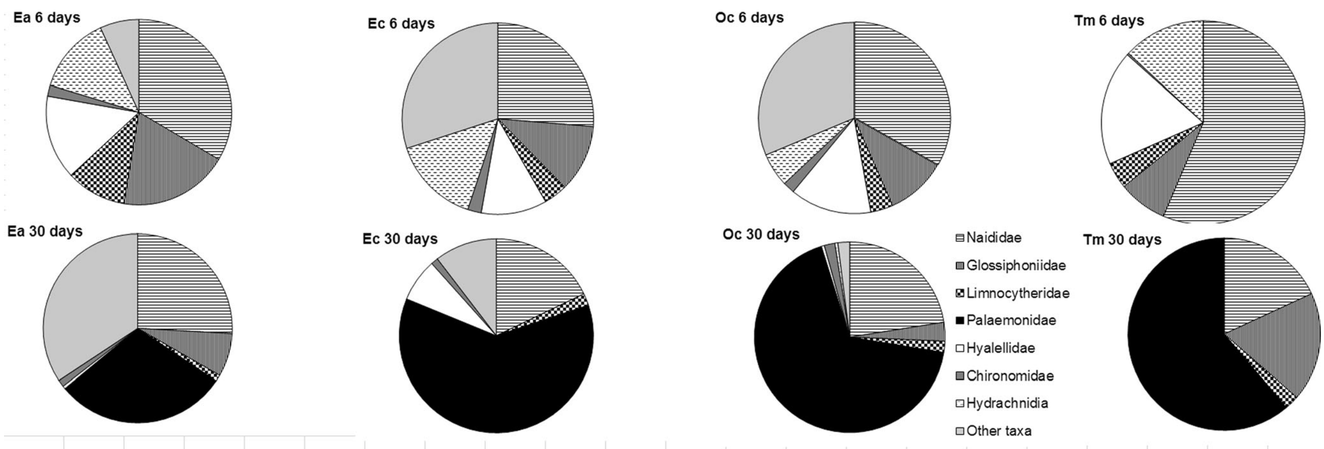

Fig. 5 Relative biomass of the main taxa found in the leaf litter after 6 and 30 incubation days

animal remains (2.5 %). Additionally, we found calcium oxalate crystals and fungal spores at frequencies of 5 and 0.5 %, respectively, and these items occupied a low percentage of the total covered area (0.1 %).

Discussion

Leaf Litter Breakdown

According to the three groups of decay rates (fast, medium and slow) proposed by Petersen and Cummins (1974), litter breakdown was fast (>0.010 days^{-1}) for all of the species studied. The water conditions in the studied wetland (good dissolved oxygen availability, neutral pH and temperature above 22.5 °C) favor rapid decomposition, even in marsh plants with high lignin content such as *O. cubense* and *T. multiflora*. The half-life of *E. crassipes* was within the range recorded in wetlands connected to the Paraná River at similar latitudes (10.3–34.6 days) (Poi de Neiff et al. 2006). The decay rate found for *E. azurea* leaf litter was faster than the rate obtained by Pagioro and Thomaz (1999) in the Upper Paraná River (0.0047 day^{-1}) using leaf packs and that obtained by Stripari and Henry (2002) and Bottino et al. (2013) in two Neotropical reservoirs using leaves and petioles in litter bags.

The effect of litter species on breakdown rates may be due to differences in the initial chemical composition of the leaves of the studied species. Many studies have found that under uniform environmental conditions, decomposition rates were explained by internal factors related to litter quality, such as nitrogen, carbon and lignin content or the ratios of C:N and L:N (Webster and Benfield 1986; Richardson et al. 2004; Leroy and Marks 2006; Poi de Neiff et al. 2006). Due to the limited number of species and the variation in leaf quality in our study, we did not test the relationship between breakdown rates and the initial chemical composition of the litter.

The litter bag methods that have been used in decomposition studies vary greatly in both the amount of material placed in the litter bags and the mesh size used (Abelho 2001),

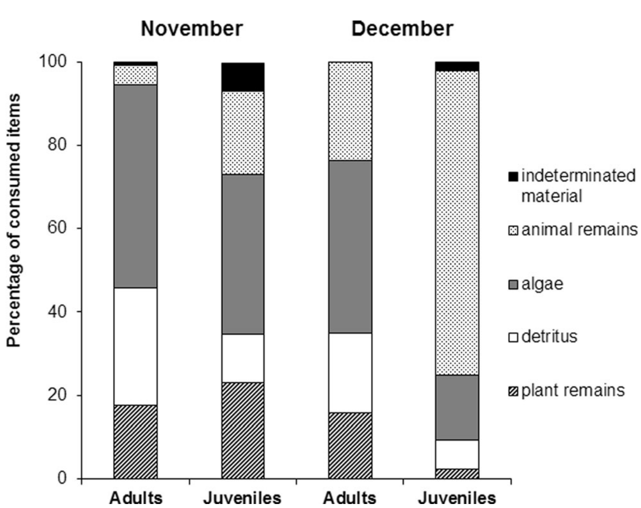

Fig. 6 Proportions of the food items consumed by *Pseudopalaemon bouvieri* in the lake during November and December

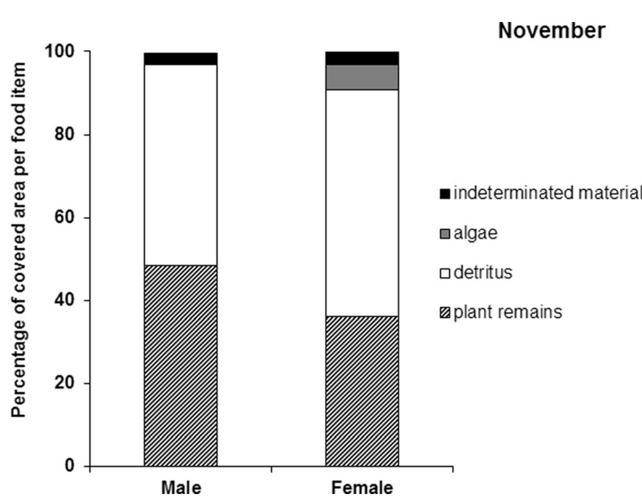

Fig. 7 Percentage of the total area covered by each food item in the lake during November

although a mesh size of 5 mm was proposed by Wantzen et al. (2008) as a standard methodology for studies of leaf decomposition in streams. However, a great loss of leaf fragments in the 5 mm mesh occurred in aquatic plants that are structurally very weak (such as *H. ranunculoides*), for which leaves decompose soon after death. The fast disappearance of *H. ranunculoides* may be due to the mesh size used in our experiment, but more studies are needed regarding this topic in Neotropical wetlands.

Invertebrate Colonization

The number of invertebrates per litter bag was significantly affected by the litter species, but we did not find consistent differences in invertebrate biomass. The absence of differences was most likely due to the large variability in biomass among replicate bags caused by the sporadic presence of species with high individual dry weight, such as members of Libellulidae, Coenagrionidae and Gomphidae. The total invertebrate abundance in our study was higher than has been reported for *E. azurea* and *E. crassipes* in other Neotropical wetlands (Stripari and Henry 2002; Poi de Neiff et al. 2009).

Our results show that leaf litter from the different species supported different abundances of invertebrates in the wetland studied. Many studies, primarily those that have been conducted in streams, have found that invertebrate densities are high for leaf litter with rapid decomposition rates (Webster and Benfield 1986). We found high abundances of invertebrates in the litter of both *E. azurea* and *O. cubense*, for which leaf litter decomposes at different rates. However, the lowest abundance was found in the litter with the slowest breakdown rate (*T. multiflora*). According to Stripari and Henry (2002), *E. azurea* has high polyphenol content, although during the decomposition process, a decrease in its concentration was observed after 14 incubation days. We did not measure polyphenol content, but it is clear from the high abundance and biomass of invertebrates that none of the aquatic plants studied produced deterrent substances that would prevent invertebrate colonization.

Naidid oligochaetes (mainly collector-gatherers) are the largest invertebrate group in terms of the number of individuals, but the proportion of this group decreased when biomass is included in the analysis. The importance of oligochaetes in litter breakdown was described by Chauvet et al. (1993) in the Garonne River, where naidids represented up to 73 % of the total number of invertebrates. The most frequent insect families associated with leaf breakdown in our study were Caenidae and Chironomidae. The larvae of *Caenis* spp., which are typical of lentic condition, are closely associated with macrophyte stands in different wetlands (Batzer et al. 1999).

The taxonomic composition of these invertebrate assemblages were different than those reported in previous decomposition studies carried out with aquatic plants in the Paraná River floodplain (Poi de Neiff et al. 2009). In these floodplain wetlands, macroconsumers are often rare or absent. This paucity could be related to the extreme variation in limnological conditions: turbidity at rising water and oxygen depletion in falling water (Poi de Neiff and Carignan 1997). Conversely, in rain-fed oligohaline lakes of Corrientes with high water transparency and good dissolved oxygen availability, the *P. bouvieri* population reached 1,411 individuals per m^2 (Carnevali et al. 2012).

Our results suggest that the biomass of a single species of prawn and a single species of amphipod dominate the invertebrates that colonize the litter. In a similar way, the biomass of crabs in tropical African streams often comprise at least 70 % of the total benthic invertebrate biomass (Dobson et al. 2007).

The Macroconsumer Trophic Spectrum

Pseudopalaemon bouvieri adults and juveniles are omnivorous and feed at different trophic levels, and this coincides with previously published evidence from 6 lakes in the same area of study (Carnevali et al. 2012). The food items found in the digestive tracts of *H. curvispina* corroborate the findings of Saigo et al. (2009) in a previous study of individuals collected in lakes of the Paraná River floodplain. *Hyalella curvispina* acts as collector-gatherer and shredder, consuming detritus (the item with greatest proportion and frequency) and vegetal tissue.

In the floodplain lakes located near the studied site, herbivory by invertebrates on the above-water line parts of *E. crassipes* floating meadows varied between 13 and 26 % of the leaf biomass (Franceschini et al. 2010). Therefore, when a large fraction of the biomass remains available as detritus and the litter decomposes quickly, it is not surprising that collector-gatherers dominate invertebrate assemblages in terms of the number of individuals. However, macroconsumers become important when invertebrate biomass is considered in breakdown studies.

Our results indicate that macroconsumers are involved in the processing of detritus in the wetland studied, as these species consume both plant remains and detritus. Our findings are supported by previous studies of tropical streams, where shrimp have been shown to significantly influence on ecosystem function (Cross et al. 2008) by regulating leaf litter breakdown (Crowl et al. 2006).

The results of this study contribute to elucidating the role of invertebrate omnivores on litter breakdown processes in subtropical rain-fed wetlands and highlight the importance of leaf litter composition on the abundance of invertebrates that colonize the litter. We suggest that future studies evaluate both the abundance and biomass of invertebrates (most published data refer to the former), which would allow amphipods and prawns to be considered as integral components of these assemblages.

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