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ORIGINAL PAPER

Invertebrate assemblages associated with root masses of *Eichhornia crassipes* (Mart.) Solms-Laubach 1883 in the Alvarado Lagoonal System, Veracruz, Mexico

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Abstract This paper describes the spatial and temporal variation of aquatic invertebrate assemblages associated with root masses of *Eichhornia crassipes* collected at 12 sites between July 2000 and June 2002 in the Alvarado Lagoonal System (ALS), Veracruz, Mexico. A total of 96 taxa were registered; acari showed the highest species richness with 15 taxa followed by decapods (14), mollusks (12), amphipods (9), and isopods (7). Freshwater organisms represented 44% of the total taxa, 53% belonged to estuarine taxa, and marine taxa 3%. The isopod *Munna* sp. was the dominant taxon throughout the entire study period, followed by Ephemeroptera, *Hyalella azteca*, *Chydorus* sp., *Physella* sp., *Podura aquatica*, and *Fossaria* sp. during the low salinity period (July–September 2001, 1.6–3.8 psu), and *Neritina virginea*, *Cassidinidea ovalis*, *Macrobrachium acanthurus* and *Melita longisetosa* during the high salinity period (March–May 2001 9.7–12.7 psu and April–May 2002, 8.2–8.9 psu). A spatial gradient of species richness and diversity was registered for the freshwater organisms. Additionally, the spatial and temporal patterns of invertebrate densities could be explained due to the movements of *Eichhornia crassipes* mats through the system, and the temporal variation of environmental variables such as salinity, dissolved oxygen, and turbidity.

Keywords Aquatic invertebrates · Coastal lagoon · *Eichhornia crassipes*

Introduction

The surface of aquatic plants is an ideal habitat for the colonization of epiphytic invertebrates (Sharitz and Batzer 1999). Water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach 1883, widgeon grass, *Ruppia maritima* Linnaeus 1753, wild celery, *Vallisneria americana* Linnaeus 1753, mermaid weed, *Potamogeton perfoliatus* Linnaeus 1753, and water-milfoil, *Myriophyllum spicatum* Linnaeus 1753 are examples of aquatic macrophytes that have been studied on this regard (Sharitz and Batzer 1999).

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Water hyacinth is a neotropical macrophyte native from the Amazon River basin, Brazil. This species possesses physiological characteristics and reproductive strategies that allow fast growth and expansion in several types of aquatic ecosystems in tropical and subtropical regions. Moreover, it is actually considered as the major invasive species for lakes and rivers in tropical as well as warm temperate areas throughout the world (Bartodziej and Leslie 1998). In Mexico, water hyacinth covers over 40,000 ha of lakes and channels (Gutiérrez et al. 1996). In the Alvarado Lagoonal System (ALS), the macrophyte arrives downstream when the flow of the Papaloapan River increases. Water hyacinth forms mats of variable size almost throughout the entire year with an increment in abundance during the rainy season, covering large areas of the ALS (Contreras and Castañeda 1995).

Water hyacinth roots accumulate sediment with high concentrations of organic matter from rivers where they originate (Poi de Neiff et al. 1994; Poi de Neiff and Carignan 1997), and they reduce water current velocity thus allowing microhabitat creation, which eventually can be occupied by a great variety of invertebrates (Bailey and Litterick 1993). However, high densities of water hyacinth reduce the photosynthetic rates and dissolved oxygen concentrations in the water column; both factors create physiological problems for invertebrates (Bechara and Andreani 1989).

There are several publications about invertebrate assemblages associated with water hyacinth root masses. The major issues that have been covered by these publications include: the specific composition of invertebrates assemblages, species–environment relationships, identification of functional groups and relations between plant decomposition, and invertebrates colonization (Bailey and Litterick 1993; Bartodziej 1992; Bartodziej and Leslie 1998; Masifwa et al. 2001; Montoya 2003). There have been few studies to examine the temporal and spatial patterns of invertebrates (Bechara and Andreani 1989; Poi de Neiff and Carignan 1997; De Marco et al. 2001). However most of the research has been done in freshwater systems and few studies have been conducted in coastal systems (Viljoen et al. 2001; Rocha et al. 2002; Toft et al. 2003).

To give further insights into the composition and relevance of invertebrate fauna associated with water hyacinth root masses, the aim of the present study was to describe the invertebrate assemblage structure, and to determine the relationship between invertebrate assemblages and the main environmental variables of the ALS.

Material and methods

Study Area

The ALS is located on the coastal plain of Veracruz State between 18°43′00″ and 18° 52′15″ N and between 95°42′20″ and 95°57′32 W (CONABIO 1998). The system comprises of three lagoons (Camaronera, Buen País and Alvarado) which are connected by channels (Fig. 1) with a total area of 6,200 ha (26 km long, 5 km wide). The climate is tropical and humid with a mean annual temperature between 22 and 26°C (García 1973). The mean water temperature oscillates between 25.6 and 26.1°C, and the mean annual precipitation is 2, 121 mm. Three seasons could be recognized in the ALS region: (1) a warm-dry season (March–May), (2) a warm-rainy season (June–September), and (3) a cold-dry season with strong winds from the north (“Nortes”) (October–February). The ALS is almost entirely surrounded by red mangrove (*Rhizophora mangle* Linnaeus 1753) and it is bordered by a landward zone of black (*Avicennia germinans* Linnaeus 1764) and white mangrove (*Laguncularia racemosa* Macbr. 1930). There are also palms and medium to high trees within the marshy forest. Submerged aquatic vegetation is dominated by widgeon grass (*Ruppia maritima*) with small zones of halophyte grasses.

Monthly samples were collected between July 2000 and June 2002 at 12 sites in the ALS (Fig. 1) with the exception of August 2000 and March 2002. At each station, two or three organisms of *E. crassipes* were collected by submerging a 20 l plastic container below the individuals to extract them from the water, and subsequently, the root

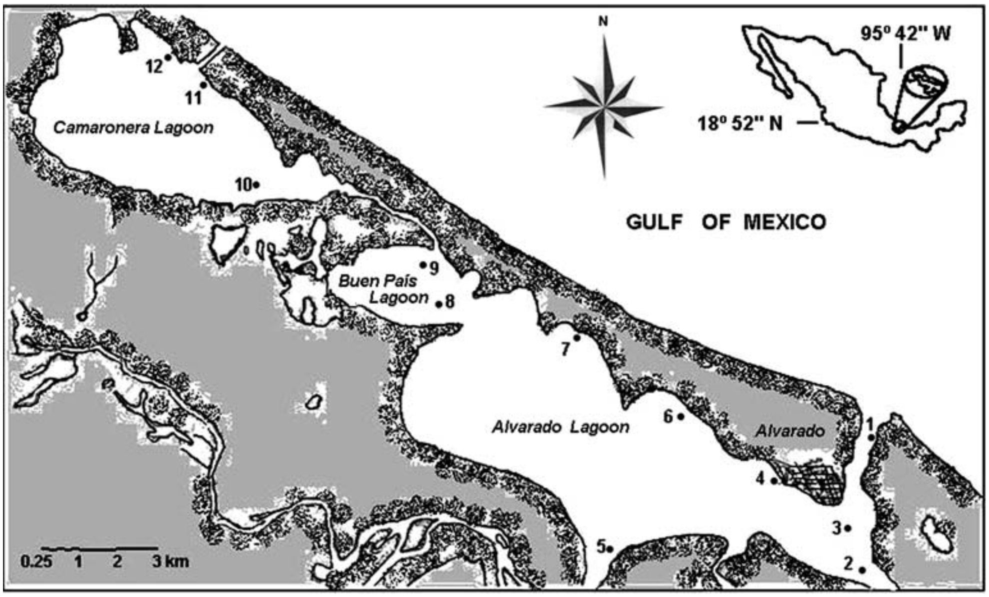


Fig. 1 Map of the ALS showing location of sampling sites: 1) Escollera, 2) Papaloapan I, 3) Papaloapan II, 4) Aneas, 5) Río Blanco, 6) Rastro, 7) Arbolillo, 8) Buen País II), 9) Buen País I, 10) Camaronera III, 11) Camaronera II, 12) Camaronera I

masses were manually separated from the rest of the plant to discard the presence of non-aquatic organisms. The water in the plastic container was filtered *in situ* through a 250μm mesh screen. The roots were washed to concentrate the organisms. Finally, the sample was preserved in 80% ethanol in plastic receptacles for further transportation to the laboratory. Simultaneously the following physicochemical variables were registered: salinity, water temperature, dissolved oxygen concentration, and turbidity. Individual plant roots were nominally classified according to the degree of decomposition as follows: no decomposition (1), low decomposition (2), and high decomposition (3). In the laboratory, root volume was calculated using the displacement method. Invertebrates were separated, counted, and identified according to criteria proposed by Williams (1984), Polhemus (1984), Burch and Cruz (1987), Kensley and Schotte (1989), Pennak (1991), Thorp and Covich (1991), and Rocha et al. (1996). Identification of taxa such as acari, cladocera and insects was carried out with the assistance of specialists (see acknowledgments). The density of organisms was standardized to org l^{-1} of plant roots.

The Shannon–Wiener Diversity index ($H' = -\sum_{i=1}^{S} p_i \log p_i$ decits/org) was calculated using a monthly density matrix. A graphical analysis was used to classify the taxa registered in a temporal criteria. This classification was carried out using the relation of the frequency percentage (per month and per site) and transformed density [log (density + 1)]. Two axes were established with the median values for both variables to differentiate four quadrats and the classification criteria were determined for the position of taxa in each quadrat, i.e., top right quadrat represents dominant taxa.

A Non Metric Multidimensional Scaling (NMDS) was performed using a Bray–Curtis similarity matrix from the monthly average values of registered environmental variables (salinity, temperature, DO, and turbidity) to determine the differences between months and define the climatic seasons. This test was performed using the software PRIMER v 5.2.8 (Plymouth Routine In Multivariate Ecological Research, Clarke and Warwick 1994). The variation in the dominant taxa registered was directly compared with the measured environmental variables by a Canonical Correspondence Analysis (CCA), focusing on the inter-species distance and using a biplot scaling. Simultaneously, a Monte-Carlo permutation test under a reduced model was conducted to obtain the significance of the ordination axes. This analysis was performed using the software CANOCO v 4.5 (Canonical Correspondence, ter Braak and Smilauer, 1997).

Results

The NMDS ordination plot (Fig. 2) of the environmental variables revealed conditions of temporality for the study zone. The stress value obtained (0.07) corresponds to a good ordination with no real prospect of a misleading interpretation (Clarke and Warwick 1994). In the diagram, it is possible to differentiate three groups. In general terms, each group includes those months reported by Contreras and Castañeda (1995) for each climatic season at this study site.

Freshwater contribution by rivers, principally the Papaloapan River, produced spatial and temporal shifts in the distribution of the water hyacinth, and thus, the invertebrates associated with the root masses. During the rainy season, a salinity gradient (limnetic to oligohaline) was found from Alvarado to Camaronera, changing from the beginning to the end of this season. During the "Nortes" season, the salinity of ALS was heterogeneous ranging from oligohaline conditions, near the river-discharge influenced zones, to mesohaline in the rest of the system. During the dry season, the gradient was oligohaline to mesohaline. Two maximum salinity values were registered during the study period (Fig. 3 III), at the Escollera site, the value was related to tidal flow, and at the Aneas site, which is influenced by a deep navigation channel.

Water hyacinth is transported to the ALS through its tributaries (Papaloapan, Acula and Blanco rivers), and it was registered during the entire study period although it differed in density. The highest water hyacinth frequency was recorded in both years during the rainy season and at the beginning of the "Nortes" season, whereas the lowest frequency was found during the dry season. The distribution pattern of water hyacinth was longitudinal with the frequency diminishing from Alvarado to Camaronera Lagoon. *E. crassipes* was collected at 124 (47%) of 264 possible records with a minimum frequency found in February 2002 and a maximum in September 2000 (Fig. 4). The degree of root decomposition followed the same pattern.

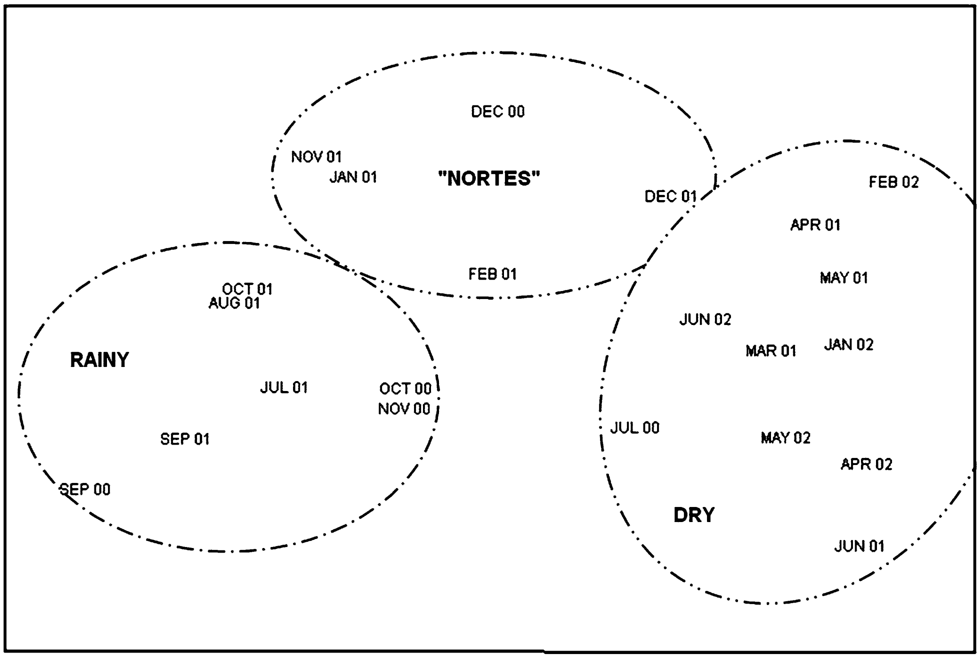


Fig. 2 NMDS ordination plot of the monthly average values of salinity, temperature, DO, and turbidity (months names are abbreviated and number indicates year)

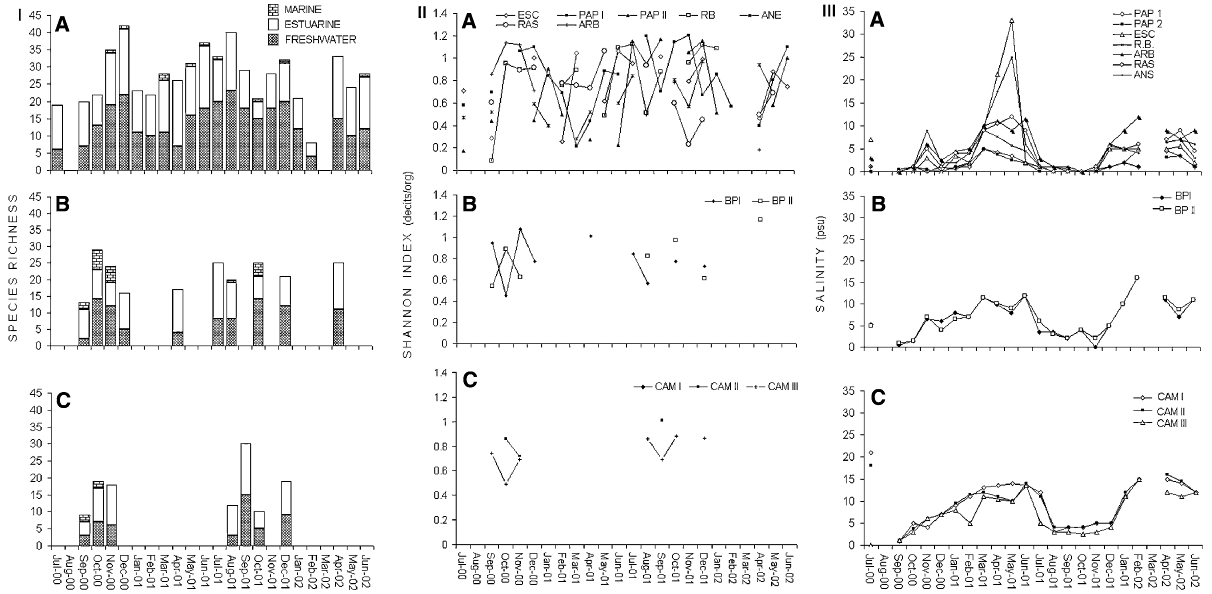
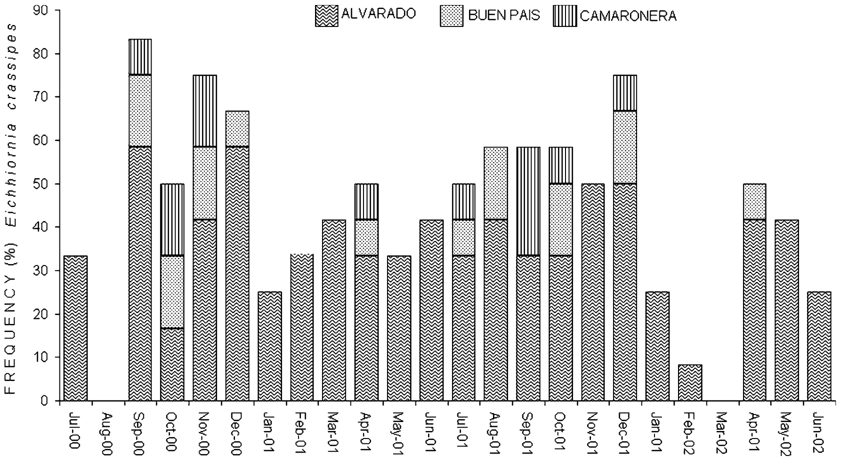


Fig. 3 Monthly variation of species richness (I), Shannon–Wiener diversity index (II), and salinity (III) in the three lagoons of the ALS: Alvarado (A), Buen País (B), and Camaronera (C); and the 12 samplig sites: Escollera (ESC), Papaloapan I (PAP I), Papaloapan II (PAP II), Aneas (ANE), Río Blanco (RB), Rastro (RAS), Arbolillo (ARB), Buen País I (BP I), Buen País II (BP II), Camaronera I (CAM I), Camaronera II (CAM II), Camaronera III (CAM III)

Degrees 1 and 2 were frequent at the Papaloapan and Blanco rivers outlets (Alvarado Lagoon) while degree 3 was registered principally at the Aneas, Rastro, Buen País I, Buen País II and Camaronera III sites. The degrees of decomposition were also related to salinity values: lower decomposition stages were recorded at lower salinities (0–7 psu), while higher stages were found at salinities reaching 17 psu where the water hyacinth mats were found in an advanced stage of decomposition (degree 3).

A total of 96 invertebrate taxa were registered. The highest species richness was registered for the following groups (Appendix): acari (15 taxa), decapods (14), mollusks (12), amphipods (9), and isopods (7). Freshwater taxa represented the 53% of the total invertebrates collected whereas estuarine taxa represented 44%, and marine taxa 3%. Freshwater species richness increased during the rainy and “Nortes” seasons (Fig. 3 I), and it diminished during the dry season. Meanwhile, estuarine taxa had the highest species richness at

Fig. 4 Monthly frequency of *E. crassipes* mats collected at 124 of 264 possible records in the three lagoons of the ALS (*n* = 12 for each month)



Alvarado Lagoon during almost the entire study period with lower values in the other two lagoons. Marine species were of minor importance and their presence was sporadic. Only a few adults of the curculionid beetle (*Neochetina* sp.) were observed and not considered in this study.

In accordance with the data obtained, there is no evidence of a regular pattern of variation in invertebrate densities, in seasonal or temporal terms. The highest monthly overall densities were recorded in Alvarado Lagoon during the dry (86,939 org l^{-1}, April 2001) and ‘‘Nortes’’ seasons (131,576 org l^{-1}, November 2001). In spatial terms, the sites with highest densities belong to the same lagoon: Aneas (59,367 org l^{-1}) and Rastro (41,375 org l^{-1}) in November 2001, Río Blanco (33,558 org l^{-1}) in May 2001, Papaloapan I (19,030 org l^{-1}) in April 2002, and Papaloapan II (25,414 org l^{-1}) in April 2001. Nevertheless, a high invertebrate density value was registered during the rainy season (September 2001) at the Camaronera III site with 30,234 org l^{-1} (Fig. 5 I), which indicates the importance of water hyacinth movement trough the lagoonal system.

As well as species richness, the density of freshwater organisms was higher than the estuarine and marine taxa. A density gradient of freshwater organisms was recorded. The highest values were found at Alvarado Lagoon, with a maximum during the ‘‘Nortes’’ season (November 2001, 97,900 org l^{-1}), followed by Buen País Lagoon and the lowest densities at Camaronera Lagoon (Fig. 5 II). Estuarine taxa showed the highest densities at Buen País Lagoon with a maximum value during the rainy season. In the case of marine species, whose density values were not significant, organisms were registered in sites close to lagoon inlets.

The relative importance values were strongly influenced by freshwater species, mainly by the density of the isopod *Munna* sp. This taxon dominated in numerical terms throughout the study period with the exception of the 2001 rainy season. On the contrary, the Ostracod sp. 1 registered high importance values during the rainy season of both years, principally in September. Other taxa with high importance values, but considerably lower than *Munna* sp, were: Ephemeroptera, *Hyalella azteca* De Saussure, 1857, *Chydorus* sp., *Physella* sp., *Podura aquatica* (Linnaeus 1820) and *Fossaria* sp. (Fig. 6). Estuarine species with high importance values were *Neritina virginea* Linnaeus 1758, *Cassidinidea ovalis* Say 1818, *Macrobrachium acanthurus* Holthuis 1952, and *Melita longisetosa* Sheridan 1980.

The maximum Shannon–Wiener diversity values oscillated from 0.8 to 1.2 decits/org. and were registered during the 2000 and 2001 ‘‘Nortes’’ season as well as the 2001 rainy season at Alvarado lagoon. In contrast, minimum values for this lagoon were registered during the dry seasons. For the other two lagoons and during the ‘‘Nortes’’ seasons, diversity values were generally lower than 1 decit/org (Fig. 3 II). Diversity values per lagoon suggest the existence of a spatial pattern of diversity in ALS; maximum values were registered at Alvarado and gradually diminished to Buen País Lagoon and finally, the lowest values were found at Camaronera Lagoon. Diversity per site was significantly correlated with species richness ($r^2 = 0.71$; $P < 0.005$), although there was no relationship between diversity and density ($r^2 = 0.006$; $P > 0.05$).

The results of the CCA showed that the four environmental variables considered were explanatory variables for the species density, this was demonstrated with the low inflation factors of every variable. The first two CCA axes explained 79.6% of the relation species–environment (Table 1) and the 6.1% of the variation in species data (total inertia = 0.544). For the first CCA axis, salinity showed the highest correlation value with species density (0.5760) and was significant ($P = 0.002$, $F = 3.85$). Additionally, the Monte-Carlo test of significance of all canonical axes showed that they were significant ($P = 0.002$, $F = 2.428$). The CCA ordination biplot differentiated four groups of organisms (Fig. 7). A group of taxa correlated with salinity such as the amphipods Talitridae, *Cerapus benthophilus* Thomas & Heard 1979, *Gitanopsis laguna* McKinney 1978, *Grandidierella bonnieroides* Stephensen 1948, the isopod *C. ovalis*, and the crab *Sesarma reticulatum* (Say 1817). A second group correlated with DO with taxa such as amphipods *Apocorophium louisianum* (Shoemaker 1934), *M. longisetosa*, *H. azteca*, *Gammarus mucronatus* Say 1818, and the tanaid *Leptochelia savignyi* (Kroyer 1842).

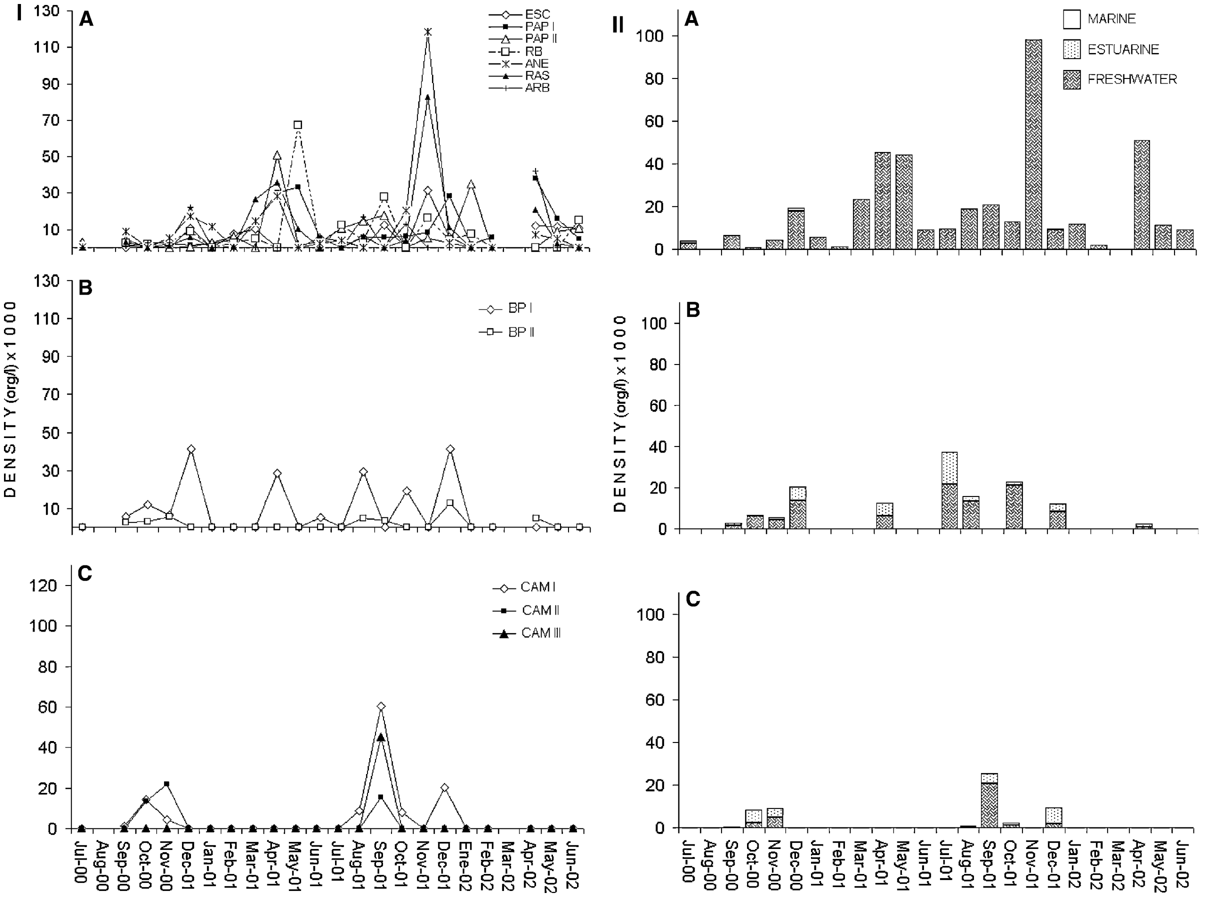


Fig. 5 Monthly variation of invertebrates density per sampling site (I) where: Escollera (ESC), Papaloapan I (PAP I), Papaloapan II (PAP II), Aneas (ANE), Río Blanco (RB), Rastro (RAS), Arbolillo (ARB), Buen País I (BP I), Buen País II (BP II), Camaronera I (CAM I), Camaronera II (CAM II), Camaronera III (CAM III); and density variation according to their origin (II) in the three lagoons of the ALS: Alvarado (A), Buen País (B), and Camaronera (C)

The third group correlated with turbidity with taxa such as cladocerans *A. cf davidi*, *Chydorus* sp., *Simocephalus mixtus* Sars 1903, the mollusks *Fossaria* sp., *Gyraulus* sp., among other taxa which are principally freshwater invertebrates. The fourth group of invertebrates includes those species that are not directly related with the measured environmental variables.

Discussion

Water hyacinth was present during the entire study period in ALS. In this way, root masses represented a complex habitat with spatial and temporal fluctuations as well as highly dynamic shifts in abundance, species richness, and diversity for a great variety of invertebrates. Compared with other studies, performed principally in freshwater systems, this paper registered higher species richness (Table 2). Thus, the importance of invertebrates associated with root masses in coastal systems is relevant due to the role of these organisms in ecological processes as well as commercial activities such as fisheries.

The overall densities of invertebrates were higher at Alvarado Lagoon throughout all seasons. Freshwater isopod *Munna* sp. dominated invertebrate assemblages reaching up to 75% of invertebrate total densities during the dry and

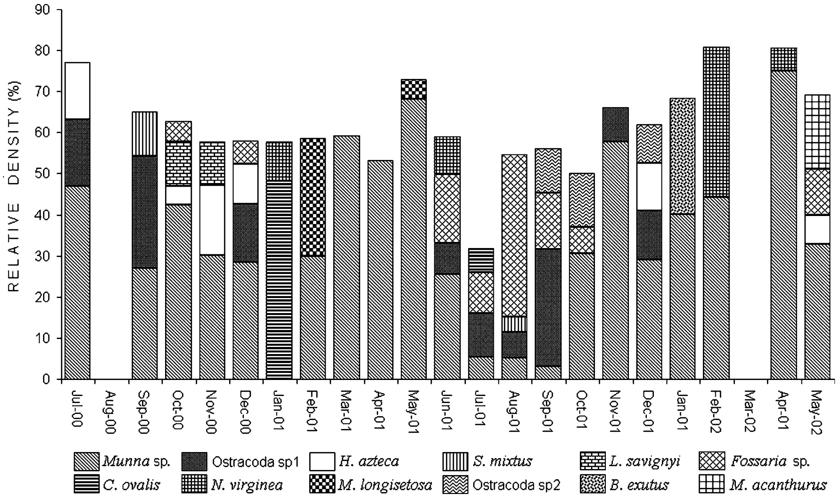


Fig. 6 Relative density values for principal invertebrates taxa

''Nortes'' seasons. The specimens collected were juveniles, adult males and females as well as ovigerous, and post ovigerous females. This suggests that this species is a permanent resident of water hyacinth roots, with a high tolerance to brackish conditions. This taxon was registered at the Papaloapan River basin, (locality: Tlacotalpan, 18°36′37.60″N, 95°38′57.67″W) where it also was a dominant component of invertebrate assemblages of water hyacinth roots (A. Ramírez-Rojas unpub. data). However, previous reports of the invertebrates of the ALS system (García 1988, Winfield 1999) did not mention this isopod, but A. Ramírez-Rojas (unpub. data) found this species associated with widgeon grass beds. This suggests that this organism could be an invasive species transported from the Papaloapan River basin that has taken advantage of this microhabitat.

In aquatic ecosystems, the temporal patterns of invertebrate densities are principally defined by reproductive pulses (Levin et al. 2001). Moreover, in estuarine systems, invertebrate assemblages associated with aquatic macrophytes are directly related to salinity tolerance limits more than any other environmental variable. In general terms, species composition and distribution could be controlled first by substrate availability, and second, by osmoregulatory stress effects (Verschuren et al. 2000; Weatherhead and James 2001).

The species–environment relationships showed by the CCA suggested that the environmental variables registered had different effects. Species such as *Ischadium recurvum* (Rafinesque 1820) and *Sesarma ricordi* Milne Edwards 1853 were highly correlated with temperature. For most of the freshwater species, the turbidity (used as a proxy for water current, which in turn carries out freshwater organisms) was the principal factor correlated with density; taxa such as Talitridae, *C. benthophilus* and *S. reticulatum* were positively correlated with salinity, and finally, dissolved oxygen was positively correlated with the density of species such as *A. louisianum*, *L. savignyi* and *M. longisetosa*. In this regard, Toft et al. (2003) registered the highest invertebrate densities in

Table 1 Results of the CCA for the first four ordination axes

Axis	1	2	3	4
Eigenvalues	0.280	0.153	0.071	0.040
Species–environment correlations	0.694	0.645	0.464	0.410
Cumulative percentage variance				
of species data	4.0	6.1	7.1	7.7
of species–environment relation	51.5	79.6	92.7	100.0
Sum of all eigenvalues (Total inertia)				7.057
Sum of all canonical eigenvalues				0.544

low dissolved oxygen levels in sediment; De Marco et al. (2001) found the highest densities with elevated values of temperature, conductivity, and pH. Poi de Neiff and Carignan (1997) positively related density with dissolved oxygen concentration and negatively with turbidity, and Poi de Neiff and Neiff (1980) negatively related density with mechanical swell action.

A large number of organisms use macrophytes for reproduction, protection against predators, and as a food resource during part of or for the entire life cycle (Bailey and Litterick 1993). Kornijow (1989) considered that macroinvertebrate associations with macrophyte roots are not due to trophic relations, but to the substrate provided. However, it is possible to consider water hyacinth roots not only as a substrate (Hamilton et al. 1990; Bartodziej 1992; Evans et al. 1999), according to Stripari and Henry (2002), alterations of the chemical composition of detritus during decomposition of *Eichhornia azurea* Kunth 1842 had an important ecological significance. They observed, during the first days of decomposition, a high reduction of polyphenols from detritus, which caused an increase in the palatability of roots. In the present study, *Eichhornia crassipes* roots with the highest degree of decomposition were registered in the northern section of the ALS, associated with high densities of detritivorous and omnivorous taxa such as *G. mucronatus, L. savingyi* and *N. virginea*. Thus, occupation of roots could be due to trophic relationships.

According to Montoya (2003), a minimum fraction of invertebrates found in root mats actually feeds on the plant, although *Macrobrachium* has been reported to consume water hyacinth roots. Invertebrates associated with root mats in

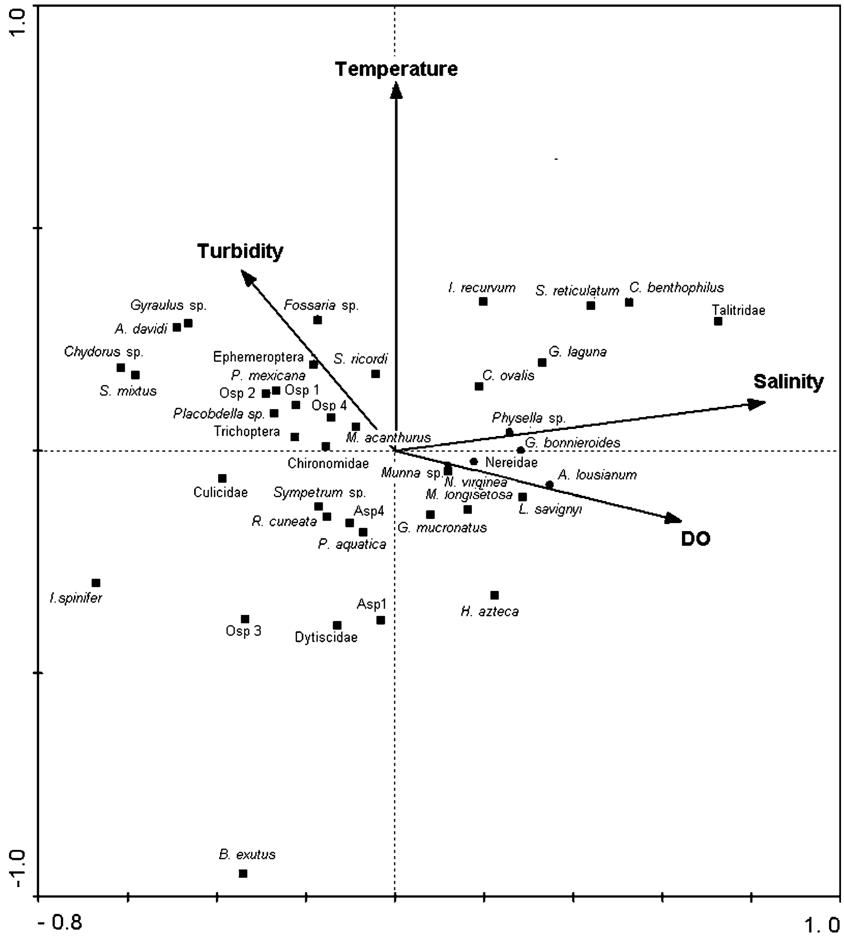


Fig. 7 CCA biplot of environmental variables and the dominant taxa

Table 2 Comparison of the dominant groups and localities of the invertebrates associated with *E. crassipes* root masses

Source	Locality	Number of taxa reported	Dominant groups
Poi de Neiff and Neiff, 1980	Paraná River, Argentina	84	Nematoda, Oligochaeta and Cladocera
Paporello de Amsler, 1983	Correntoso River, Argentina	82	Copepoda and Oligochaeta
Paporello de Amsler, 1987	Paraná River, Argentina	72	Ephemeroptera and Chironomidae
Poi de Neiff and Carignan, 1997	Paraná River, Argentina	64	Ostracoda, Conchostraca and Chironomidae
Bailey and Litterick, 1993	Nilo River, Sudán	78	Coleoptera, Odonata and Gastropoda
Bartodziej and Leslie, 1998	St. Marcos River, Florida, USA	55	Chironomidae, Trichoptera and Ephemeroptera
Toft et al., 2003	Sacramento Delta River, USA	30	Amphipoda and Isopoda
Viljoen et al. 2001	Lake Cubhu	55	Decapoda, Amphipoda and Chironomidae
	and Lake Nsezi KwaZulu-Natal, Sudafrica	54	Cladocera, Copeda and Gastropoda
Rocha et al., 2002	Coyuca Lagoon, Pacific coast, México	21	Amphipoda and Isopoda
Present study	SLA, México. Gulf of Mexico coast	96	Isopoda, Amphipoda and Cladocera

ALS have different feeding mechanisms (Appendix), such as detritivores, limnivores: *N. virginea, N. reclivata* Say 1822, *Rangia cuneata* (Gray 1831), *I. recurvum*, *Brachidontes exutus* Linnaeus 1758, filter feeders: *G. bonnieroides*, Chironomidae, and omnivores: *G. mucronatus* Say 1818, *Discapseudes holthuisi* (Basescu and Gutu 1975), *M. acanthurus, S. ricordi, Callinectes rathbunae* Contreras 1930. In addition, water hyacinth mat movements in the ALS are not constant. There were periods where mats were stable in shallow zones and during these periods, epibenthic invertebrates are able to occupy the radicular system of the plant. In a study carried out in the ALS, A. Ramírez-Rojas (unpub. data) found habitat segregation in tanaids (*L. savignii* and *D. holthuisi*). Adults were present in the sediment whereas juveniles were found on *R. maritima* leaves and this last stage was recorded in water hyacinth roots. Similar mechanisms can explain the presence of estuarine taxa on root assemblages. Macintosh et al. (1999) found that mangrove leaves and algae are used as temporal substrates during larval recruitment and dispersion of megalopae and juveniles of brachyuran crustaceans. Other authors, such as Tankersley et al. (2002), suggest that passive transport of organisms within estuaries is related to the presence of floating aquatic vegetation.

In the ALS, the movements of water hyacinth along the lagoonal surface due to the action of wind and currents allow the plant to act as a passive transport, favoring dispersion of associated organisms (*sensu* Peterson and Peterson 2004). According to Viljoen et al. (2001), the spatial distribution pattern of invertebrates within water hyacinth might be related to mobility. Moreover, temporal and spatial fluctuations of the environmental variables registered, principally salinity, dissolved oxygen, and turbidity are related with invertebrate densities. In this way, particular groups of invertebrates are temporally correlated with specific variables, as is the case of freshwater organisms with the turbidity. In addition to mat mobility, the salinity gradient of the ALS produces a spatial gradient of species richness and diversity from the continentally influenced zone to the northern section of the system.

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Appendix

Invertebrate taxa associated with *E. crassipes* root masses in ALS (July 2000–June 2002)

		Origin	Trophic guild	Habitat	Stage
Nematoda	*Actynolaimus* sp.	Fresh			
Nemertea	Nemertea				
Annelida	Nereidae				
	Oligochaeta	Fresh			
	Placobdella hollensis (Whitman 1892)	Fresh			
	Placobdella sp.	Fresh			
Mollusca	*Neritina virginea* Linnaeus 1758	Est	Limnivore microfague	Epibenthic grasses	Juvenile
	Neritina reclivata Say 1822	Est	Limnivore microfague	Epibenthic grasses	Juvenile
	Physella sp.	Fresh			Juvenile Adult
	Gyraulus sp.	Fresh			
	Fossaria sp.	Fresh			
	Laevapex sp.	Fresh			
	Rangia cuneata (Gray 1831)	Est	Limnivore saprofague	Infaunal mud	Juvenile
	Pyrgophorus sp.	Fresh			
	Biomphalaria sp.	Fresh			
	Ischadium recurvum (Rafinesque 1820)	Est	Limnivore filtrator	Epibenthic Mangrove roots	Juvenile
	Brachidontes exutus Linnaeus 1758	Est	Limnivore filtrator		Juvenile
	Helisoma sp.	Fresh			
Acari	Oribatida sp1				
	Uropodidae				
	Piona sp.				
	Oribatida sp2				
	Mamersellides sp.				
	Arrenurus sp.				
	Koenikea sp.				
	Halacaridae	Mar			
	Copidograthus sp.				
	Halacarus sp.				
	Acari sp9				
	Acari sp10				
	Sperchontidae				
	Acari sp12				
	Acari sp13				
	Acari sp14				
	Acari sp 15				
Ostracoda	Ostracoda sp 1				Adult
	Ostracoda sp 2				Adult
	Ostracoda sp 3				Adult
	Ostracoda sp 4				Adult

Appendix continued

		Origin	Trophic guild	Habitat	Stage
Cladocera	*Chydorus* sp.	Fresh		Planktonic	Adult
	Ilyiocryptus spinifer (Brady 1886)	Fresh		Planktonic	Adult
	Alona cf davidi	Fresh		Planktonic	Adult
	Sarsilatona serricauda Sars 1901	Fresh		Planktonic	Adult
	Simocephalus mixtus Sars 1903	Fresh		Planktonic	Adult
	Latonopsis australis Sars 1888	Fresh		Planktonic	Adult
Cirripedia	*Balanus* sp.	Est		Epibenthic several sustrates	Juvenile
	Artemia sp.	Est		Planktonic	Adult
Amphipoda	*Cerapus benthophilus* Thomas & Heard 1979	Est		Epibenthic several sustrates	Adult Juvenile
	Gammarus mucronatus Say 1818	Est	Omnivore	Epibenthic several sustrates	Adult Juvenile
	Melita longisetosa Sheridan 1979	Est		Epibenthic several sustrates	Adult Juvenile
	Gitanopsis laguna McKinney 1978	Est		Epibenthic several sustrates	Adult Juvenile
	Apocorophium louisianum (Shoemaker 1934)	Est		Epibenthic several sustrates	Adult Juvenile
	Grandidierella bonnieroides Stephensen 1948	Est	Tubicole filtrator	Epibenthic several sustrates	Adult Juvenile
	Hyalella azteca De Saussure 1857	Fresh	Limnivore	Epibenthic several sustrates	Adult
	Gammaridae				Adult
	Talitridae				Adult
Isopoda	*Munna* sp.	Fresh			Adult Juvenile
	Cassidinidea ovalis Say 1818	Est	Detritivore	Epibenthic	Adult
	Caecidotea sp.	Fresh			Adult
	Cirolanidae	Mar	Omnivore	Sand fund	Adult
	Sphaeroma terebrans Bate1866	Est	Barrenadora	Mangrove roots	Adult
	Dynamenella quadrilirata Kensley 1984	Est			Adult
	Ancinus sp.				
Tanaidacea	*Leptochelia savignyi* (Kroyer 1842)	Est	Detritivore	Epibenthic mud	Juvenile
	Discapseudes holthuisi (Basescu y Gutu 1975)	Est	Omnivore	Epibenthic mud	Juvenile
Decapoda	*Potimirim mexicana* (De Saussure 1857)	Fresh	Limnivore	Epibenthic vegetation	Juvenile
	Penaeus (Litopenaeus) setiferus (Linnaeus 1767)	Est	Omnivore	Planktonic	Postlarva
	Macrobrachium acanthurus Holthuis 1952	Est	Omnivore	Epibenthic	Juvevile
	Sesarma ricordi Milne Edwards 1853	Est	Omnivore	Planktonic benthic	Megalopae Juvenile
	Sesarma (Sesarma) reticulatum (Say 1817)	Est		Planktonic benthic	Megalopae Juvenile
	Sesarma (Chiromantes) cinereum Bosc 1802	Est		Benthic	Juvenile
	Panopeus lacustris Desbonne 1867	Est		Benthic	Juvenile
	Eurypanopeus depressus (Smith 1869)	Est	Omnivore	Benthic	Juvenile
	Panopeus bermudensis Benedict & Rathbun 1891	Est		Benthic	Juvenile
	Pachygrapsus gracilis De Saussure 1858	Est		Benthic	Juvenile
	Uca marguerita Thurman 1981	Est		Benthic	Juvenile
	Uca (Minuca)vocator (Herbst 1804)	Est		Planktonic Benthic	Megalopae Juvenile
	Dyspanopeus texanus (Stimpson 1859)	Est	Depredator	Benthic	Juvenile
	Callinectes rathbunae Contreras 1930	Est	Omnivore	Planktonic	Megalopae
Collembolla	*Podura aquatica* (Linnaeus 1820)	Fresh			Larva

Appendix continued

		Origin	Trophic guild	Habitat	Stage
Diptera	Chironomidae	Fresh	Filtrator		Larva
	Culicidae	Fresh			Larva
Coleoptera	Hydrophilidae	Fresh			Adult
	Dytiscidae	Fresh			Larva
	Laccophilus sp.	Fresh			
	Desmopachria sp.	Fresh			
	Hidrovatus sp.	Fresh			
Ephemeroptera	Baetidae	Fresh			Larva
	Tricorrythidae	Fresh			
	Heptageniidae				
	Caenidae				
Trichoptera	Polycetropodidae	Fresh			Larva
	Hydrospsychidae	Fresh			
Hemiptera	Belostomatiodae	Fresh			
	Corixoidea	Fresh			Larva
Odonata	*Sympetrum* sp.	Fresh			Larva

Fresh = Freshwater; Est = Estuarine; Mar = Marine

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