Invertebrate associations with submersed aquatic plants in a prairie wetland

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Introduction

Diverse invertebrate communities exist among the submersed vegetation of ponds. The abundance of phytophilous invertebrates is probably related to a suite of factors, including plant morphology, surface texture, epiphytic algal growth and community composition, nutrient content of the plant tissues, and the presence of defensive chemicals (Downing and Cyr 1985). The aquatic plants provide the invertebrates with shelter from predators (Dvorak and Best 1982; Diehl 1992), act as spawning sites, and sites for attachment (Rooke 1984, 1986a,b). The invertebrates can consume part of the plant (Lodge 1991) or its associated periphyton (Rooke 1984, 1986a,b). In eutrophic waters, the grazing invertebrates may prevent algal blooms, thereby allowing submersed macrophytes to persist (Irvine *et al.* 1990).

Different submerged plants within a pond create various microhabitats which should result in different assemblages of invertebrates. Phytophilous invertebrates are not equally abundant on all plant species (Downing and Cyr 1985), and associations between invertebrates and specific aquatic plant species in lakes have frequently been examined (Quade 1969; Gerrish and Bristow 1979; Rooke 1986). Difonzo and Campbell (1988) found that relative abundance and composition of littoral cladoceran communities varied depending on the type of microhabitat (e.g., plant species, rocks, or water column). Some species may be specialized for certain microhabitats, allowing resource partitioning in the community. Other studies have shown associations between macrophytes and macroinvertebrates, particularly insects (Gerrish and Bristow 1979; Dvorak and Best 1982; Rooke 1984; Chilton 1990). The densities of organisms also varied depending on the type of plant, yet the invertebrate species composition was generally similar for all macrophytes (Gerrish and Bristow 1979).

The morphology of the plant may play an important role in determining invertebrate community composition and preferred associations. The abundance of invertebrates per unit macrophyte biomass may vary with plant species and the degree of leaf dissection (Krecker 1939; Rosine 1955; Gerking 1957; Gerrish and Bristow 1979; Dvorak and Best 1982; Rooke 1986a,b). Plants with finely dissected leaves may have higher invertebrate abundance per unit biomass or surface area than broad-leaved plants (Pardue and Webb 1985; Chilton 1990). Macrophytes with dissected leaves could provide more substratum for periphyton (Dvorak and Best 1982) or could trap FPOM and CPOM from the water column (Rooke 1984, 1986a,b), thereby enriching the food supply for plant-associated invertebrates. Despite strong support for this hypothesis, largely based on the premise that plant surface area increases with extent of leaf dissection, other studies have been equivocal. Complex-leaved macrophytes may act as better refuges from predation than finely dissected leaves on plants (Irvine *et al.* 1990). Although abundances of different taxa varied depending on plant species, macrophytes such as *Ceratophyllum demersum* and *Myriophyllum* spp. in general did not support more invertebrates per unit plant biomass than broad-leaved plants (Cyr and Downing 1988).

Most ecological research has focussed on open-water habitats rather than in the littoral zone of lakes and ponds. Littoral studies have been hampered by difficulties with quantitative sampling of the vegetational and sediment substrata (Lodge *et al.* 1988; Irvine *et al.* 1990). Sampling methods often give inaccurate, imprecise estimates of invertebrate abundance, and collection, processing, and counting can be laborious (Whiteside and Williams 1975; Downing and Cyr 1985). Various techniques have been used for sampling the phytophilous invertebrates: vacuum pumps (Campbell *et al.* 1982), activity traps (Whiteside 1974; Whiteside and Lindegaard 1980; Murkin *et al.* 1983), and plastic bags (DiFonzo and Campbell 1988). Many box-like samplers which clip the macrophytes and retain the sample have been devised (Macan 1949; Gerking 1957; McCauley 1975; Minto 1977). The Downing box sampler attempts to minimize habitat disturbance and the loss of invertebrates during collection (Downing 1984, 1986).

In this study, the associations between plants (macrophytes *Ceratophyllum demersum* and *Potamogeton zosteriformis* and the macroalga *Chara*) and invertebrates were examined in a prairie wetland pond. The objective was to determine if the structure and relative abundances of invertebrate communities associated with these aquatic plants differed among plant taxa.

Materials and Methods

Submersed vegetation and associated invertebrates were sampled from Crescent Pond, a shallow prairie wetland pond located at the University of Manitoba Field Station, Delta Marsh on three sampling dates in 1992: 18 June, 29 June, and 16 July. On 18 June, only *Ceratophyllum demersum* was abundant enough to permit sampling, whereas by 29 June, *Potamogeton zosteriformis* and *Chara vulgaris* were also sufficiently abundant to allow quantitative sampling.

The Downing box sampler, a transparent, rigid plastic enclosure (30 x 20 x 10 cm) with a capacity of six litres, was used to collect the invertebrates with the surrounding vegetation. Random samples were taken in Crescent Pond approximately one metre away from the *Typha* edge. Sampling was limited to monospecific beds of the particular macrophyte where possible. Areas where dense mats of floating filamentous algae occurred were also avoided. On each of the sampling dates, four box samples were taken in the *Ceratophyllum* beds, and two box samples from *Potamogeton* and *Chara*.

The Downing box was lowered carefully into the water. When submerged, the box was gently closed around the macrophyte, cutting its stems. The clasps on the box sampler were then locked and the box lifted to the surface. The contents of the box sampler were poured through a filter of 100 mesh to concentrate the invertebrates. The vegetation was removed from the box and placed into plastic bottles. Samples were kept cool during transport to the laboratory. To avoid captured invertebrate predators consuming other entrapped invertebrates, samples were processed as soon as possible. In the lab, the vegetation was sprayed with distilled water to dislodge any attached invertebrates. The vegetation was then placed in a oven, dried at 60°C for 24 hours, then weighed to determine biomass. The invertebrates were concentrated into 65 mL bottles then preserved in 10% formalin.

The plants were identified using keys in Fassett (1957). Edmondson (1959), Pennak (1978), Merritt and Cummins (1984), Wiggins (1977), and Brinkhurst (1986) were used to identify the invertebrates. The entire volume of the 65 mL bottles was examined under a dissecting microscope to determine the total number of macroinvertebrates in the samples. Due to their large abundance, subsampling was necessary for the Cladocera, Copepoda, Ostracoda, Chironomini, Rotifera, and *Chaetogaster*. The bottles were throughly shaken and successive 5 or 10 mL subsamples were taken using a wide bore syringe. Generally three subsamples were counted per bottle. Where rotifer numbers were very high, subsampling was modified to two samples of 2 mL.

Results

In general, the invertebrate species composition was similar for *Ceratophyllum demersum*, *Chara vulgaris*, and *Potamogeton zosteriformis* (Table 1). The most abundant taxonomic groups in the study were the Cladocera, Copepoda, Rotifera, Chironomidae, and the Ostracoda. These microinvertebrates occurred in similar abundance (numbers per gram dry weight of plant tissue) in association with *Ceratophyllum* and *Potamogeton*, but abundance was generally lowest with *Chara* (Fig. 1). Other numerically important taxa were *Chaetogaster, Hyalella azteca*, *Mesostoma*, Gastropoda, *Hydra*, and *Agraylea*. Numbers for macroinvertebrates such as the Ephemeroptera, Odonata, Dytiscidae, Corixidae, and Notonectidae were too low to permit quantitative comparisons among plants (Fig. 2). The Cladocera were the most diverse group with seventeen species found associated with the aquatic plants. The family Chydoridae predominated with ten species, of which *Chydorus* was most abundant.

On 18 June, the greatest abundance of Cladocera occurred in association with *Ceratophyllum* (Fig. 3). The mean number of organisms per gram of macrophyte biomass was at least two times greater than any subsequent value for other macrophytes on any sampling date. *Chydorus* spp. comprised about 75% of the total number of Cladocera. *Ceriodaphnia dubia*, the second most abundant cladoceran, made up only about 15%.

By 29 June, the cladoceran population had drastically decreased on *Ceratophyllum* to less than half the 18 June value (Fig. 3). Mean Cladocera numbers were slightly higher for *Potamogeton* than *Ceratophyllum* and *Chara*. Although *Chydorus* still predominated, *Ceriodaphnia dubia* and *Diaphanosoma birgei* contributed substantially to mean total cladoceran number. *Graptoleberis testudinaria*, *Camptocercus* sp., and *Eurycercus longirostris* were also more abundant on *Potamogeton* than *Ceratophyllum* and *Chara*. On 16 July, the mean total Cladocera numbers for *Ceratophyllum* and *Potamogeton* were very similar and somewhat higher than *Chara* (Fig. 3). Cladocera were least abundant on *Chara* compared to the other macrophytes over the sampling period.

Most chydorids occurred in much lower numbers than *Chydorus*. However, *Pleuroxus procurvus* appeared in moderate numbers on *Ceratophyllum*, was also well

Table 1. Aquatic invertebrate taxa collected in Crescent Pond, June-July 1992, in association with submersed plants.

Cladocera	Odonata
Alona sp.	*Lestes* sp.
Alonella excisa	Coleoptera
Bosmina longirostris	Dytiscidae
Camptocercus sp.	*Acilius* sp.
Ceriodaphnia dubia	*Dytiscus* sp.
Chydorus sp.	*Hydroporus* sp.
Daphnia magna	Haliplidae
Daphnia pulex/rosea	*Peltodytes* sp.
Diaphanosoma birgei	*Haliplus* sp.
Eurycercus longirostris	Hemiptera
Graptoleberis testudinaria	Corixidae
Pleuroxus aduncus	Notonectidae
Pleuroxus denticulatus	Diptera
Pleuroxus procurvus	Chironomidae
Pseudochydorus globosus	Chironomini
Scapholeberis kingi	Tanypodinae
Simocephalus vetulus	Tanytarsini
Copepoda	Orthocladiinae
Calanoida	Heleidae
Diaptomus nudus	(=Ceratopogonidae)
Cyclopoida	Annelida
Harpacticoida	Naididae
Rotifera	Stylaria lacustris
Ostracoda	*Chaetogaster* sp.
Conchostraca	Nematoda
Amphipoda	Mollusca
Hyalella azteca	Gastropoda
Hydracarina	Cnidaria
Trichoptera	*Hydra oligactis*
Agraylea sp.	Platyhelminthes
Ceraclea sp.	Turbellaria
Ephemeroptera	*Mesostoma* sp.
Caenis sp.	
Baetis sp.	

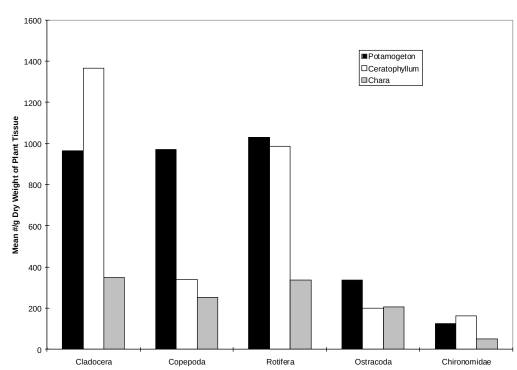

Figure 1. Abundance of microinvertebrates (mean number per gram dry weight of plant tissue) associated with submersed plants.

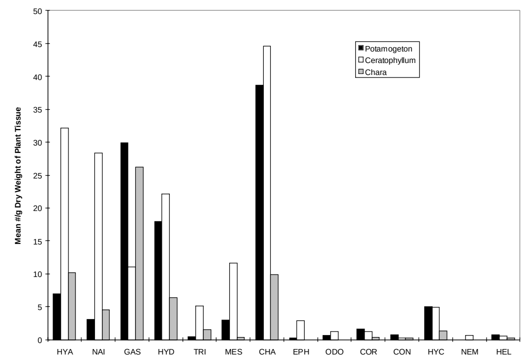

Figure 2. Abundance of macroinvertebrates (mean number per gram dry weight of plant tissue) associated with submersed plants. Macroinvertebrate taxa are identified as: HYA = Hyalella azteca (Amphipoda, Crustacea), NAI = Naididae (Oligochaeta, Annelida), GAS = Gastropoda (Mollusca), HYD = Hydra (Cnidaria), TRI = Trichoptera (Insecta), MES = Mesostoma (Turbellaria, Platyhelminthes), CHA = Chaetogaster (Oligochaeta, Annelida), EPH = Ephemeroptera (Insecta), ODO = Odonata (Insecta), COR = Corixidae (Insecta), CON = Conchostraca (Crustacea), HYC = Hydracarina (Arthropoda), NEM = Nematoda, HEL = Heleidae (Insecta).

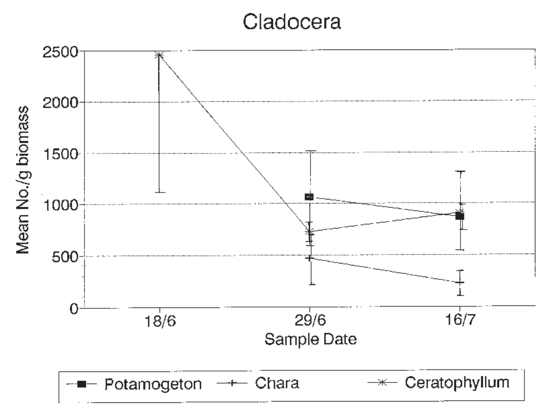

Figure 3. Cladocera abundance (number per gram dry biomass of plant tissue) associated with submersed plants on three sampling dates.

represented on *Potamogeton*, but numbers on *Chara* were lower. *Pleuroxus denticulatus* was collected only on *Chara* while *Pleuroxus aduncus* appeared equally abundant on all macrophytes. Another common species was *Graptoleberis testudinaria*, which was found mostly on *Ceratophyllum* and *Potamogeton* rather than *Chara*. On 18 June, *Camptocercus* numbers were quite high on *Ceratophyllum* but by 29 June more was collected on *Potamogeton* than *Ceratophyllum* and *Chara*. *Eurycercus longirostris* was most abundant on *Potamogeton. Alona* sp. occurred on *Ceratophyllum* and

Potamogeton to a larger extent than on *Chara*. *Alonella excisa* was collected only on *Ceratophyllum*.

Ceriodaphnia dubia was the second most numerous cladoceran. It had consistently high numbers on *Potamogeton* yet its greatest abundances occurred on *Ceratophyllum. Daphnia pulex/rosea* and *Scapholeberis kingi* were scarce throughout all sampling dates and on all macrophytes. *Diaphanosoma birgei* was found predominantly on *Potamogeton. Simocephalus vetulus* was abundant on *Ceratophyllum* on 18 June, otherwise, its presence in the study was low. Finally, *Bosmina longirostris* was collected only on *Chara*.

Besides the cladocerans, the rotifers formed an important and large part in the invertebrate communities of the submerged vegetation in Crescent Pond. An increasing trend in mean number of rotifers per gram plant biomass became apparent over the sampling period for all macrophytes (Fig. 4), but much less so for *Chara*. Cyclopoid copepods were the dominant suborder on all macrophytes. High numbers of copepods occurred on *Potamogeton* while both *Ceratophyllum* and *Chara* had smaller values (Fig. 5). The calanoid copepod *Diaptomus nudus* occurred in moderate numbers, chiefly on *Potamogeton*. The Ostracoda showed a substantial increasing trend in mean number per gram plant biomass on the three aquatic plants over the sampling period (Fig. 6). Ostracod abundance was also similar for all macrophytes.

The Chironominae were the principal insect larvae found in the study (Fig. 7). The Tanypodinae, Tanytarsini, and the Orthocladiinae had much less representation in the samples. The Chironomidae predominated on 18 June on the *Ceratophyllum* but their numbers drastically dropped by 29 June. The chironomids then were found on *Potamogeton* to a greater extent than *Ceratophyllum*.

Various other taxonomic groups comprised the remainder of the invertebrate communities within Crescent Pond. The oligochaete, *Chaetogaster*, was collected in large numbers on *Ceratophyllum* on 18 June. Although it remained moderately abundant on *Ceratophyllum*, its population on *Potamogeton* increased substantially by 16 July. It was found on *Chara* to a lesser extent. In the study, *Stylaria lacustris* occurred mainly on *Ceratophyllum* on 18 June. The amphipod, *Hyalella azteca*, predominated on *Ceratophyllum* over the entire sampling period. Its abundances on *Potamogeton* and *Chara* were similar and low.

Mesostoma numbers were large on *Ceratophyllum* on 18 June but then drastically dropped by 29 June. Numbers were scarce on other plants. On both *Potamogeton* and *Chara*, on 29 June, gastropod abundance was high when compared to *Ceratophyllum*. Their mean numbers had only been moderately high on

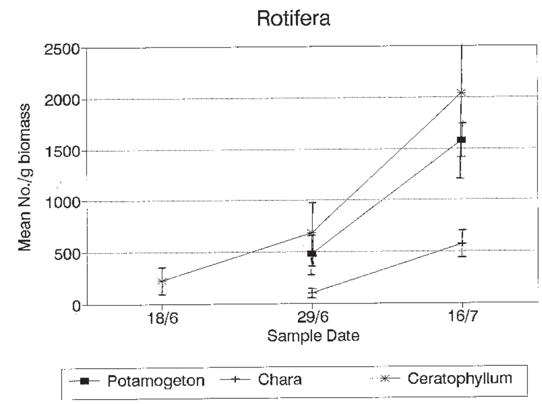

Figure 4. Rotifera abundance (number per gram dry biomass of plant tissue) associated with submersed plants on three sampling dates.

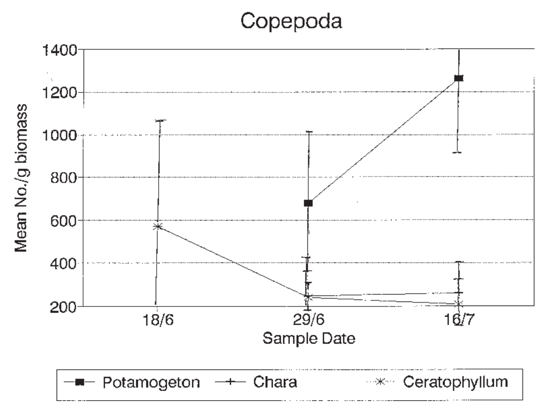

Figure 5. Copepoda abundance (number per gram dry biomass of plant tissue) associated with submersed plants on three sampling dates.

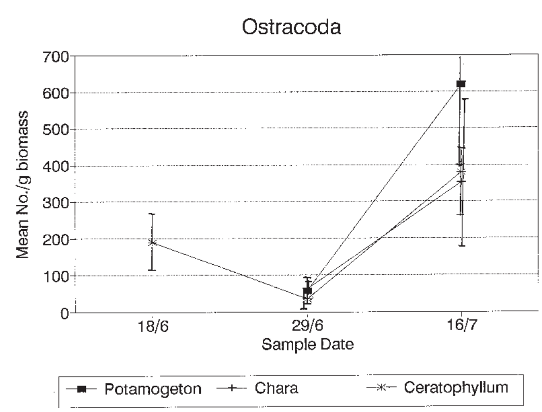

Figure 6. Ostracoda abundance (number per gram dry biomass of plant tissue) associated with submersed plants on three sampling dates.

Ceratophyllum on 18 June. In general, *Hydra* was found on *Potamogeton* and *Ceratophyllum* rather than *Chara*. Finally, *Agraylea*, the principal trichopteran, occurred abundantly only on *Ceratophyllum* on 18 June.

The Cladocera can be separated according to feeding mode into filter-feeders, typically ingesting phytoplankton from the water column, and scraper-grazers, feeding on epiphyton on the surfaces of submersed plants. Filterers occurred in highest abundance associated with *Ceratophyllum*, slightly lower numbers with *Potamogeton*, and substantially lower numbers with *Chara* (Fig. 8). Grazers occurred most abundantly on *Ceratophyllum*, lower numbers on *Potamogeton*, and somewhat lower abundance on *Chara*. Overall, numbers of filter-feeders were considerably lower than of grazers in association with submersed plants.

Macroinvertebrates can be similarly separated into trophic groups: predators and herbivore-detritivores. Predators would be expected to utilize the plants as surfaces only (e.g., “sit-and-wait predators”), whereas herbivore-detritivores would feed on epiphyton on the plant surfaces. As was observed for the cladoceran grazers, the herbivore-detritivores and predators occurred in highest abundance in association with *Ceratophyllum*, lower numbers with *Potamogeton*, and lowest with *Chara* (Fig. 9).

Discussion

Although the invertebrate species composition was generally similar in association with *Ceratophyllum demersum*, *Chara vulgaris*, and *Potamogeton zosteriformis*, differences in invertebrate abundance occurred for the taxonomic groups. Rooke (1984) showed that although each macrophyte does not appear to have a characteristic fauna associated with it, different submersed plants do provide a specific substatum or resource that can be utilized by different types of invertebrates.

For the Cladocera, many genera did not indicate affinities. *Chydorus* spp. dominated the cladoceran communities of all the macrophytes. *Pleuroxus aduncus* also showed no preferences. In general, many species favoured both *Ceratophyllum* and *Potamogeton* but not *Chara*. This was unexpected as *Ceratophyllum* and *Chara* are more similar morphologically. However, the very low abundance of many species in association with *Chara* is perhaps attributable to the allelochemical properties of this macroalga. Preferences for certain macrophytes were found mainly for the species of Cladocera that occurred in lower numbers. *Eurycercus longirostris* and *Diaphanosoma birgei* appeared to favour *Potamogeton*, while *Pleuroxus denticulatus* was found only on *Chara*.

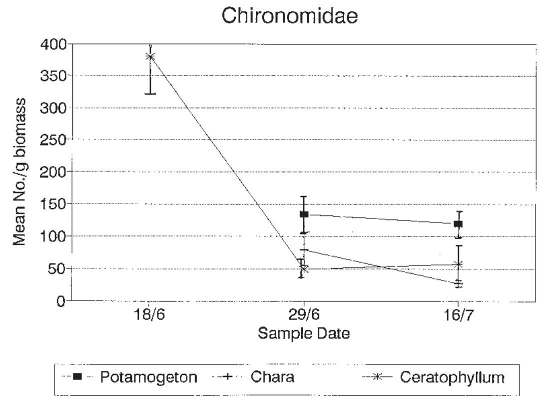

Figure 7. Chironomidae abundance (number per gram dry biomass of plant tissue) associated with submersed plants on three sampling dates.

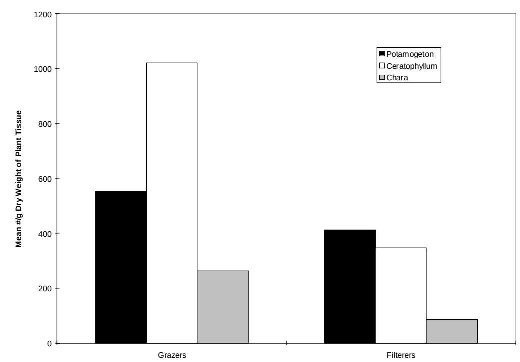

Figure 8. Microinvertebrate abundance (number per gram dry weight of plant tissue) separated by feeding method into grazers and filter-feeders associated with submersed plants.

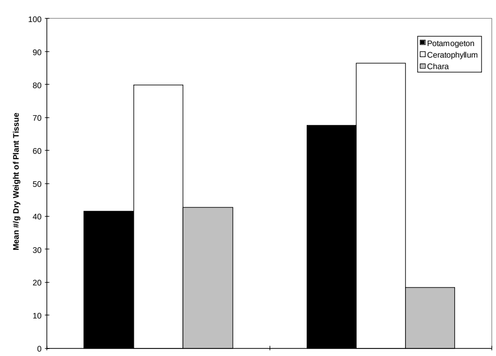

Figure 9. Macroinvertebrate abundance (number per gram dry weight of plant tissue) separated by feeding method into herbivores/detritivores and predators associated with submersed plants.

The Rotifera did not prefer any specific plant species. This was not surprising since they are mainly planktonic and not really dependent on any plant surface. The copepods, particularly *Diaptomus nudus*, appeared to favour *Potamogeton*. The copepods are also predominantly in the water column. Their abundance in proximity to *Potamogeton* may have resulted because *Potamogeton* beds were not as dense as those of other macrophytes.

Fewer planktonic organisms (e.g., daphniid cladocerans, copepods, rotifers) were associated with submersed vegetation, particularly dense beds of macrophytes which develop as the season progresses. Low concentrations of dissolved oxygen may occur in these weed beds, especially at night when plants are respiring, but physical conditions which are detrimental to the filtering and feeding activities of zooplankton may be of greater importance in restricting their distribution (Irvine *et al.* 1990).

For the Chironomidae, no preferences were suggested. *Chaetogaster* seemed to favour both *Ceratophyllum* and *Potamogeton* rather than *Chara*. *Hyalella azteca* clearly had a preference for *Ceratophyllum*. Chilton (1990) also found the highest densities of this amphipod on *Ceratophyllum*. This macrophyte, which occurs in dense beds, may protect the animal from predators or provide it with accumulated organic matter for food. Finally, preferences for a specific aquatic plant were not detected for other taxa such as *Mesostoma*, Gastropoda, *Hydra*, and *Agraylea*.

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