NAT CONSERVACAO. 2014; **12(1)**:30-35

Natureza & Conservação
Brazilian Journal of Nature Conservation
Supported by O Boticário Foundation for Nature Protection

Research Letters

The invasive submerged macrophyte *Hydrilla verticillata* as a foraging habitat for small-sized fish

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ARTICLE INFO

Article history:
Received July 2013
Accepted April 2014

Keywords:
Foraging
Non-native macrophyte
Egeria najas
Paraná River

ABSTRACT

Several species of aquatic macrophytes have invaded ecosystems outside their ranges, producing a variety of impacts on native biota. In this study, we tested the role of the invasive macrophyte *Hydrilla verticillata* as a foraging habitat for small fish species. To achieve this goal, we assessed the feeding activity and diet composition of fish captured in patches of the invasive *H. verticillata* and of a similar native macrophyte (*Egeria najas*). Feeding activity did not differ significantly between *H. verticillata* and *E. najas*, indicating that foraging activity was not affected. However, differences in diet composition were significant in three out of five fish species and marginally significant in one species, suggesting that the invasive and native macrophytes provide different types of food resources for fish. Thus, although *H. verticillata* does not affect the foraging activity, it has the potential to affect the assemblages of small-sized fish through changes in the proportions of food resources.

Introduction

Aquatic ecosystems have been colonized by large numbers of exotic species in recent decades (Jenkins 2003), including macrophytes. This process has also occurred in Brazilian freshwater ecosystems, including the Paraná River Basin (Agostinho *et al.* 2004). Studies of the effects of invasive macrophytes on aquatic assemblages have produced contradictory results. For example, invasive macrophytes have shown both negative (Colon-Gaud *et al.* 2004; Stiers *et al.* 2011) and positive (Strayer *et al.* 2003; Hogsden *et al.* 2007) effects on the density of specific invertebrate taxa.

The floodplain located in the upper stretch of the Paraná river has suffered several anthropogenic changes, including water level regulation and increases in underwater light (Agostinho *et al.* 2004). These changes have facilitated the establishment of the submersed macrophyte *Hydrilla*

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DOI: 10.4322/natcon.2014.006

verticillata (L.f.) Royle. *H. verticillata* is an aggressive colonizer, native to Asia and Australia (Cook & Lüönd 1982), which competes effectively for light, displacing native aquatic plants (Langeland 1996). This macrophyte was first recorded in the Paraná River in 2005, and it has rapidly invaded the main river and its lateral channels (Sousa 2011).

The macrophyte *Egeria najas* Planch. is the dominant submersed native species colonizing the Upper Paraná River floodplain and it rarely co-occurs with *H. verticillata* (Sousa *et al.* 2010; Sousa 2011; Cunha *et al.* 2011). Both species have similar architectures and life forms (i.e., canopy forming) and thus, competitive interactions between them are expected (Sousa *et al.* 2010). Indeed, decreases in *E. najas* biomass following invasions by *H. verticillata* have been recorded in Paraná River habitats (Sousa 2011), and future scenarios that consider the replacement of *E. najas* by *H. verticillata* are a topic of concern.

In addition to its negative effects on native macrophytes, the spread of *H. verticillata* may have complex implications. For example, although it is morphologically similar to *E. najas*, *H. verticillata* may differ in terms of its associated organisms (e.g., microalgae and ostracods; Theel *et al.* 2008; Mormul *et al.* 2010a, b), which may serve as food resources for small sized-fish (Casatti *et al.* 2003; Pelicice & Agostinho 2006). Thus, since macroinvertebrates may be considered the primary link between plants and fish (Schultz & Dibble 2012), alterations of invertebrate assemblages following invasions by plants may produce cascade effects on fish assemblages.

In the Upper Paraná River floodplain, patches of native macrophytes (including *E. najas*) provide important habitats for small-sized fish (Dibble & Pelicice 2010; Cunha *et al.* 2011). Thus, given the high competitive ability of *H. verticillata*, other native macrophyte species may be excluded by this invasive plant, decreasing habitat heterogeneity and compromising the suitability of the habitat and the availability of food for fish.

Given the rapid spread of *H. verticillata* in the Upper Paraná basin, the invasion by this species may change other aquatic assemblages, influencing the availability of food to fish that use submersed macrophytes as feeding sites. Thus, in this investigation, we hypothesized that fish feeding activity and diet composition is affected by the invasive macrophyte *H. verticillata*. We predicted a change in the composition of food items eaten by small-sized fish, and that mean stomach fullness (SF) would be lower in *H. verticillata* than in *E. najas*. This prediction was based on the assumption that the two macrophytes differ in terms of organism composition (e.g., ostracods and epiphytic algae; Mormul *et al.* 2010a; Mormul *et al.* 2010b). To test our hypothesis, we compared the diet of fish species inhabiting monospecific patches of *H. verticillata* with the diet of fish inhabiting *E. najas*. The data for the fish inhabiting *E. najas* were considered to represent non-affected patches of habitat.

Methods

Sampling was performed on August 6 and 7, 2009 in a lateral channel (“Cortado” channel) of the Upper Paraná River (22° 47’ 30” S, 53° 24’ 37” W; see Cunha *et al.* 2011 for more details) located within a National Protected Area. The channel is shallow (<3 m), is approximately 2 km long x 0.03-0.09 km wide and has well-preserved riparian vegetation. In addition to our target species (*E. najas* and *H. verticillata*), this channel is colonized by other macrophytes, such as *Eichhornia crassipes* (Mart.) Solms, *Eichhornia azurea* (Sw.) Kunth, and *Polygonum* spp.

We selected three different sampling points (located a minimum of 500 m apart) in which both *E. najas* and *H. verticillata* form monospecific patches with similar biomasses (which was confirmed by our further analyses – see Results) and separated by approximately 15-30 m. Fish were sampled with transparent traps (Dibble & Pelicice 2010) within patches of each macrophyte. The traps were used in the top 30 cm of the water column, because both species of macrophytes concentrate their biomass in this layer (Cunha *et al.* 2011). A pair of traps was installed at 7:00 in each patch and checked at 11:00, 15:00, and 19:00. Fish caught in each pair of traps and at different times of the day were pooled for analysis, given that no differences in feeding activity and diet composition were expected for the time period during which the samples were collected (Carniatto *et al.* 2012). All fish were anesthetized with eugenol before being fixed for further analyses.

In addition, haphazardly in each macrophyte patch, we measured the temperature, oxygen content (YSI digital meters), pH, and conductivity (Digimed DM-2P and DM-3P) in the sub-surface stratum of the water column. We quantified the illuminated percentage of water column with a Secchi disk near the patches. Plant biomass was also collected in a volume of 0.5 x 0.5 x 0.3 m at the top of the water column and dried in an oven at approximately 80°C to a constant weight to test for differences in physical structure of the habitat between species of macrophytes.

We used 420 individuals belonging to five species: *Astyanax altiparanae* (Garutti & Britski, 2000) (standard length [SL] range = 20.2 - 46.1 mm); *Moenkhausia bonita* (Benine, Castro & Sabino, 2004) (SL = 9.0 - 37.5 mm); *Hyphessobrycon eques* (Steindachner, 1882; SL = 15.4 - 23.9 mm); *Pamphorichthys* sp. (SL= 10.3 - 24.4 mm); and *Serrapinnus notomelas* (Eigenmann, 1915; SL = 12.1 - 33.6 mm). Stomachs were visually assessed for the degree of SF using the following numerical scale: 0 = empty stomach; 1 = up to 25% SF; 2 = 25% to75% SF ; 3 ⊠ 75% SF. We assessed feeding activity using the value of mean SF: $mSF = (N_0 \times 0)+(N_1 \times 1)+(N_2 \times 2)+(N_3 \times 3)/N$, where N_0, N_1, N_2, and N_3 are the number of stomachs with SF values of 0, 1, 2, and 3, respectively, and N is the number of individuals (Santos 1978). For diet analysis, food items were identified and quantified with the volumetric method (Hyslop 1980).

Differences in the physical and chemical characteristics of the habitat and in macrophyte biomass between *E. najas* and *H. verticillata* were tested with a one-way analysis of variance (ANOVA) using Statistica 7.0 (STATSOFT 2005). To test whether the feeding activity differed between *H. verticillata* and *E. najas*, we applied a Mann-Whitney non-parametric test to the mSF values. We used this test because our data did not have a normal distribution. *Pamphorichthys* sp. was not used in this analysis because this species does not have a clearly defined stomach. Mann-Whitney analyses were performed in Statistica 7.0 (STATSOFT 2005). To assess whether the fish diet composition differed between the two macrophytes, we employed a permutational multivariate analyses of variance

(PERMANOVA), using the Bray-Curtis dissimilarity of the log-transformed data matrix containing the volumes of food items; type III sums of squares were used to account for unbalanced statistical design (Quinn & Keough 2002). We used 9,999 permutations to assess the significance of the F statistic derived from the PERMANOVA. Multivariate analyses were performed in PRIMER 6.1.13 and in the PERMANOVA+ 1.0.3 add-on (Anderson *et al.* 2008; Clarke & Gorley 2001).

Results

The macrophyte patches varied from approximately 4 to 15 m². Patches of *H. verticillata* and *E. najas* did not differ in terms of temperature (*H. verticillata*: 22.3 ± 1.2, *E. najas*: 22.2 ± 1.1 °C), oxygen content (*H. verticillata*: 7.8 ± 1.2, *E. najas*: 7.7 ± 2.3 mg L^{-1}), pH (*H. verticillata*: 6.8 ± 0.4, *E. najas*: 6.6 ± 0.3), or conductivity (*H. verticillata*: 61.1 ± 3.6, *E. najas*: 59.2 ± 3.6 µS cm^{-1}) (all p-values > 0.05). The water column was completely illuminated at all sampling points (Secchi depth always reached the sediment), and the mean macrophyte biomass did not differ significantly ($p = 0.55$) between *H. verticillata* (281.78 ± 57.30 gDW m^{-3}) and *E. najas* (312.09 ± 57.77 gDW m^{-3}). In conjunction, these results indicate that the patches of both macrophytes provide similar habitats in terms of physico-chemistry and physical structure (as indicated by plant biomass) for fish.

Feeding activity was high for the four species analyzed (mSF > 2.1), indicating that the fish used both macrophytes as feeding sites. The differences in mSF between *H. verticillata* and *E. najas* were not significant (Table 1).

Table 1 - Mean stomach fullness (mSF) of the fish species caught in patches of *Hydrilla verticillata* (H) and *Egeria najas* (E) and values of the Mann-Whitney test. The numbers of stomachs analyzed are in parentheses.

	mSF		Mann-Whitney	
	H	E	U	p
Astyanax altiparanae	2.36 (7)	3.00 (4)	1.5	0.191
Moenkhausia bonita	2.66 (67)	2.36 (118)	1.0	0.121
Hyphessobrycon eques	2.32 (10)	2.11 (44)	3.5	0.650
Serrapinnus notomelas	2.41 (49)	2.56 (114)	2.0	0.275

With the exception of *Pamphorichthys* sp., the diet of the fish caught inside patches of *H. verticillata* differed from those caught inside patches of *E. najas*, although the difference was marginally significant for *M. bonita* ($p = 0.06$; Table 2). Higher plants and Ephemeroptera dominated the diet of *Astyanax altiparanae* in both macrophytes; however, Gastropoda, Trichoptera, and Diptera (adult) were exclusive in *H. verticillata*, and Diptera (larvae) and Aranae, in *E. najas* (Fig. 1a; Table S1, supplementary material online). The main items consumed by *Moenkhausia bonita* caught in *H. verticillata* were Ephemeroptera and Diptera (larvae), whereas in *E. najas*, the most abundant food items were Diptera (larvae), Ephemeroptera, and Hymenoptera (Fig. 1b; Table S1, supplementary material online). There were also differences between the macrophytes in the consumption of Cladocera, Lepidoptera, Hemiptera, and terrestrial Diptera.

Table 2 -Results of a permutational multivariate analysis of variance (PERMANOVA) applied to data on the diets of fish species caught in patches of *Hydrilla verticillata* and *Egeria najas.*

Species	PERMANOVA
A. altiparanae	pseudo-$F_{1,9} = 1.96$; $p = 0.03$
M. bonita	pseudo-$F_{1,74} = 1.87$; $p = 0.06$
H. eques	pseudo-$F_{1,50} = 4.12$; $p < 0.001$
Pamphorichthys sp.	pseudo-$F_{1,23} = 0.96$; $p = 0.44$
S. notomelas	pseudo-$F_{1,154} = 8.81$; $p < 0.001$

The diet of *Hyphessobrycon eques* consisted primarily of Ephemeroptera in *H. verticillata* and of Diptera (larvae) and Ephemeroptera in *E. najas* (Fig. 1c; Table S1, supplementary material online). *Pamphorichthys* sp. primarily consumed detritus in both macrophytes, and its diet did not differ between the macrophyte species (Fig. 1d; Table S1, supplementary material online). *Serrapinnus notomelas* primarily ate algae (mainly Cyanophyceae) in both *H. verticillata* and *E. najas*; however, in certain instances, such as the algae Oedogoniophyceae, Diptera (larvae) and higher plants were consumed in different proportions between macrophytes (Fig. 1e; Table S1, supplementary material online).

Discussion

The information regarding feeding activity obtained by this study indicates that macrophyte species did not influence the foraging activity of fish, suggesting that *H. verticillata* provides food resources that are quantitatively comparable to those furnished by the native *E. najas*. The lack of differences in fish feeding activity between invasive and native macrophytes might have occurred because both plants have similar physical complexity and occupy the same stratum of the water column (Cunha *et al.* 2011). Because *H. verticillata* and *E. najas* have similar morphology, they most likely support similar densities of invertebrates, resulting in similar amounts of food to fish. Indeed, previous investigations in the Upper Paraná floodplain showed that the densities of some invertebrate groups did not differ between *H. verticillata* and *E. najas* (Mormul *et al.* 2010a). A lack of differences in invertebrate abundance, biomass, and species richness has also been found by a comparison of monospecific patches of *H. verticillata* with multispecific patches of macrophytes in ponds in the southern USA (Theel *et al.* 2008). From such evidence, together with our findings, we infer that *H. verticillata* provides a suitable amount of food resources to the small-sized fish that inhabit its patches. However, this interpretation should be considered in the light of our sampling strategy, since we chose patches of macrophytes where *H. verticillata* and *E. najas* attained similar

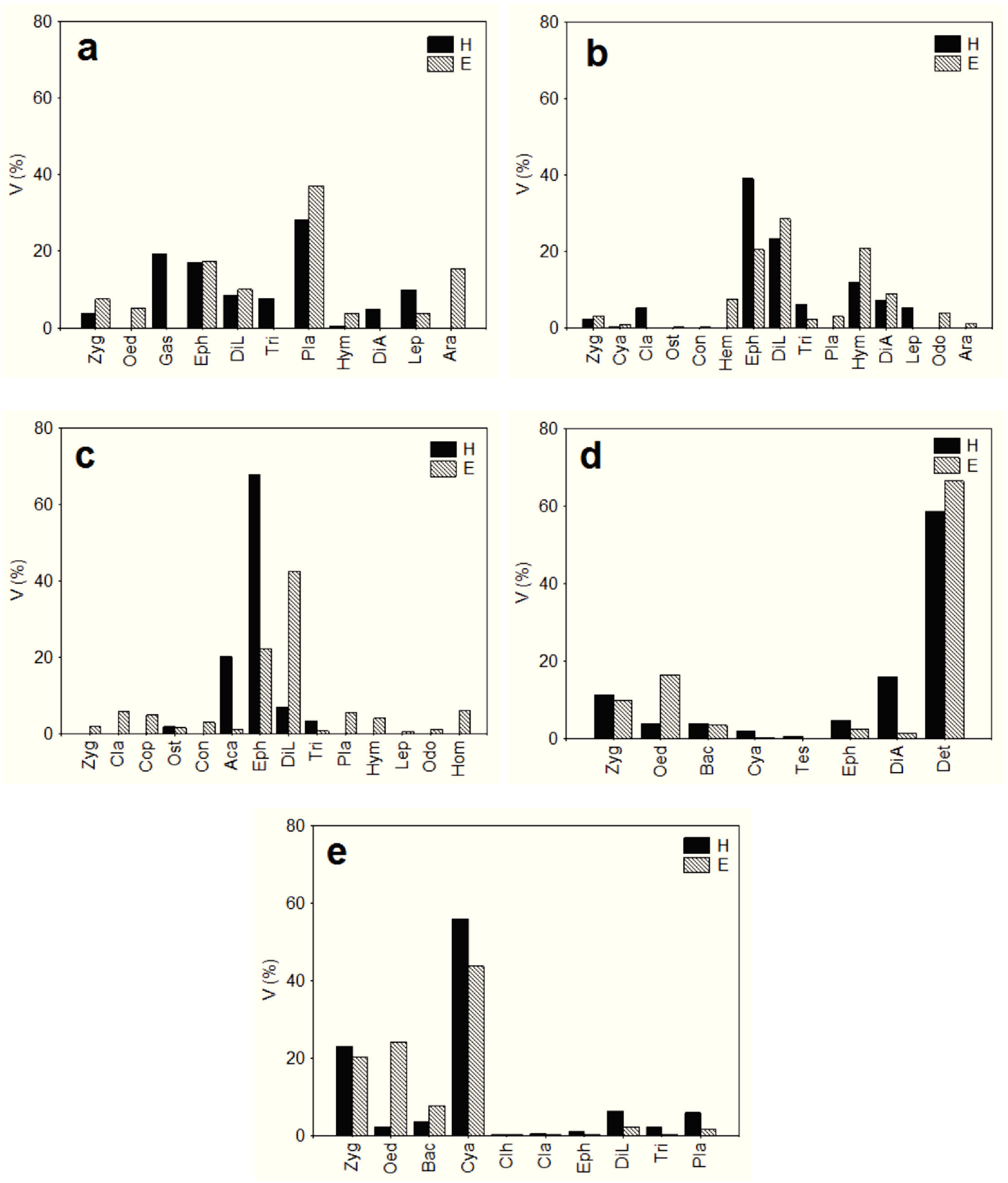

Fig. 1 – Percentage of volume of food items composing the diet of fish caught in patches of *Hydrilla verticillata* (H) and *Egeria najas* (E). a = *Astyanax altiparanae*; b = *Moenkhausia bonita*; c = *Hyphessobrycon eques*; d = *Pamphorichthys* sp.; e = *Serrapinus notomelas*. Zyg = Zygnemaphyceae; Oed = Oedogoniophyceae; Bac = Bacillarophyceae; Cya = Cyanophyceae; Clh = Chlorophyceae; Tes = Testacea; Gas = Gastropoda; Cla = Cladocera; Cop = Copepoda; Ost = Ostracoda; Con = Conchostraca; Aca = Acarina; Hem = Hemiptera; Eph = Ephemeroptera; DiL = Diptera (larvae); Tri = Trichoptera; Det = Detritus/sediment; Pla = Higher plants; Hym = Hymenoptera; DiA = Diptera (Adult); Lep = Lepidoptera; Odo = Odonata; Hom = Homoptera; Ara = Araneae.

biomasses. In this respect, it is difficult to predict whether differences in feeding activity might appear if the biomass of *H. verticillata* is greater than that of *E. najas*, as observed in other habitats (Sousa *et al.* 2010). Thus, this scenario involving biomass differences remains to be tested before any general inferences can be drawn.

The most frequently consumed items are organisms associated with macrophytes (e.g., epiphytic Oedogoniophyceae and Cyanophyceae, Acarina, Ephemeroptera, and Diptera larvae). The use of organisms associated with macrophytes, together with the results of feeding activity, indicate that the small-sized fish use patches of both species of macrophytes as feeding sites. Although fish could move from one macrophyte patch to the other in the field, our conclusion that fish use both plants as feeding sites is re-enforced by experiments showing that fish exposed to both plants in isolation had high and similar feeding activity (N. Carniatto, unpublished).

Despite the similarities in feeding activity that we found, diet composition differed in three species and marginally differed in one species of fish between *H. verticillata* and *E. najas* patches, indicating that the invasive macrophyte does not provide the same proportion of food items as the native plant. In addition, this pattern appears to be even stronger for species that consume aquatic invertebrates. Because both macrophytes have the same architecture, we infer that differences in invertebrate assemblages may be associated with foliar texture, growth and senescence rates, and allelopathic compounds, which may affect invertebrate colonization (Taniguchi *et al.* 2003; Vieira *et al.* 2007).

Aquatic invertebrates (primarily insects) were the main items consumed by *A. altiparanae*, *M. bonita*, and *H. eques* in both macrophytes sampled. Differences in the consumption amount among these items, together with others that were less abundant, produced the observed differences in the composition of the diet. These findings should mirror the real differences between the types of available items provided by each species of macrophyte. For example, Ephemeroptera and Trichoptera were more important in the diet of the fish colonizing *H. verticillata*, whereas aquatic Diptera were more important in the fish colonizing *E. najas*. Several items with less predominance in the diet also differed: Gastropoda were found only in the fish colonizing *H. verticillata*, whereas Copepoda, Conchostraca, Hemiptera, and Homoptera were found only in the fish colonizing *E. najas*. These results indicate that *H. verticillata* provides invertebrates other than those found in *E. najas*. Indeed, in a manipulative experiment in the Upper Paraná River, these two plants differed in terms of ostracod assemblages (Mormul *et al.* 2010a), corroborating our findings for the fish stomachs analyzed in the current study.

Microalgae were the dominant item in the diet of *S. notomelas* in both macrophytes; however, there was a higher consumption of Oedogoniophyceae in *E. najas*. Given the significant results for the diet composition for this species, these results may also reflect differences in the algal species available in these two macrophytes, as the two plant species show distinct patterns of colonization by epiphytic algae (Mormul *et al.* 2010b). *Pamphorichthys* sp., which was the sole species of fish that clearly showed no differences in diet composition between the macrophyte species, has a restricted diet consisting of detritus and sediment. Detritivory is one of the most specialized feeding habits in fish (Gerking 1994); what may explain the lack of difference in the diet between the habitats used by *Pamphorichthys* sp.

In summary, our results indicate that *H. verticillata* did not influence the foraging activity of small-sized fish, but it affected their diet composition. We suggest that these differences are results of the availability of food items, such as invertebrates and microalgae, which most likely tend to colonize each species of macrophyte in different ways. Whether the differences in diet composition found in this work are sufficient to influence the composition of assemblages of small-sized fish and to produce cascade effects are questions for further investigation. Although similar foraging activity was found in the two plant species, we continue to view *H. verticillata* with concern, since fish movement and feeding are limited in sites with high plant densities (Dibble *et al.* 1996; Harrel & Dibble 2001) and *H. verticillata* has the potential to grow much more rapidly (Bianchini Jr. *et al.* 2010) and achieve a higher biomass than native macrophytes (Sousa *et al.* 2010; Sousa 2011). We suggest that future investigations should test the effects of a gradient of *H. verticillata* biomass on fish feeding activity and diet composition.

Acknowledgments

We thank RR Ota for fish identification, and we thank JC Oliveira and CF de Souza for helping with the stomach contents. N Carniatto acknowledges the Brazilian Council of Research (CNPq) for providing grants, and SM Thomaz also thanks CNPq for continuous funding through a Research Productivity Grant. This study was supported by CAPES, a Brazilian organization focused on the development of human resources.

Supplementary material

Supplementary material associated with this article can be found, in the online version, at www.naturezaeconservacao.com.br.

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