Niche enlargement as a consequence of co-existence: a case study

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(With 4 figures)

Abstract

Spatio-temporal changes in the diet, niche breadth and niche overlap of two species of Characidium from three different sites along a Neotropical coastal stream were studied during a dry and rainy season. Seasonal changes were restricted to the occurrence of plant items in the stomach contents. The relative importance of food items in the diet of both species varied across sites, but Diptera, Ephemeroptera, Simuliidae, Trichoptera and Coleoptera larvae were always the main prey items. Contrary to the expected pattern, values of the niche breadth were higher at the site where Characidium species co-existed and niche overlapped at this site indicated 52% (p = 0.52) of feeding overlap.

Keywords: neotropical characidae, coastal stream, close related species.

1. Introduction

The idea that competition is an important mechanism in the organization of populations and communities has been considered the cornerstone of ecological and evolutionary theory. Since Hutchinson (1957) questioned the mechanisms that allow sympatric species to partition resources and co-exist, it has been noted that in highly diverse communities, realized niches and niche breadth are reduced as a consequence of competition (Mac-Arthur, 1972). As a result of these findings, it is thought that natural selection favours specialization through competition, thereby linking competition to specialization and a reduction of niche breadth among coexisting correlated species.

Across many animal groups, tropical communities support higher diversity than temperate ones, and according to the resource partitioning theory one would therefore expect a more specialist species. Many years of study have not resolved whether this is the case or not as various studies have shown that both trophic specialists (Vojtech et al., 2002) and trophic generalists (Dyer et al., 2007) predominate in the tropics.

The intensity of competition is traditionally estimated using some measure of similarity or overlap in the resources used by co-occurring species (Pusey and Bradshaw, 1996), but the observed patterns vary among environments and/or climatic regions (Zaret and Rand, 1971). The absence of competition in tropical regions has often been attributed to resource partitioning (e.g. Uieda et al., 1997; Esteves and Lobón-Cerviá, 2001; Deus and Petere-Junior, 2003; Fogaça et al., 2003; Barreto and Aranha, 2006) because of the high feeding plasticity (Gerking, 1994; Araújo-Lima et al.,...
1995; Kido, 2001) associated with the high diversity of food resources in these areas (Lowe-McConnell, 1979; Winemiller, 1989; Jepsen et al., 1997; Winemiller and Jepsen, 1998).

In the present work, we studied the spatio-temporal variation in the feeding habits of two close-related characins: Characidium interruptum (Pellegrin, 1909) and Characidium cf. vidali (Travassos, 1967) from a Neotropical stream. Following Mac-Arthur (1972), we hypothesized that for both Characidium species realized niche vary among sites and niche breadth is reduced in sites where the species co-exist. Thus, we focused on the potential differences in the feeding patterns, considering sites where species co-occurred and sites where they did not.

2. Methods

Mato Grosso is a 3rd order stream (22° 55' S and 42° 35' W) draining the east-facing watershed of the Serra do Mar mountains in Rio de Janeiro State, Brazil (Figure 1). Deforested areas predominate in the lowlands but there are still some areas where the secondary Atlantic rain forest dominates in the headwaters. Water level is solely regulated by rainfall and run-off, with abundant summer (December to March) rain. We took samples from three sites along the Mato Grosso stream-bed: Site 1 (headwater, only Characidium cf. vidali occurs), Site 2 (midstream, both Characidium occur) and Site 3 (downstream, only C. interruptum occurs). For the purpose of the present study, environmental parameters, of each sampling site, were quantified according to bathymetric maps based on transversal transects registered within an interval of 5 m long, from the lower to the upper section of the sampling site (Table 1).

Food availability was estimated for the three study sites using a Surber (0.09 m² sampling area, 180 µm mesh net). We collected three samples of each substratum type (rock, sand and leaf litter) at each study site. Each sample was wrapped in a plastic bag and fixed in 80% ethanol. In the laboratory, samples were sieved (mesh 180 µm) and washed under running water and then screened. Then, macroinvertebrates and plant parts were separated from the substrate and counted. The macroinvertebrates were identified according to Mugnai et al. (2010). Densities of macroinvertebrates and plant parts were recorded as the number of individuals per m² (area of the Surber frame) (Table 2).

Fish were sampled by electrofishing (900 W, 2-3 A) during the rainy (January and March) and dry seasons (June and July) of 2007. Voucher specimens of

Table 1. Altitude (in meters); percentage of occurrence of the environmental descriptors splitted in three categories: i) water dynamics-pools, riffles and runs; ii) kind of substrata-mud, sand, gravel, rock and iii) riparian vegetation-canopy and marginal vegetation obtained from transects of 5 m apart during the four sampling periods (January, March, June and July of 2007) in the three sampling sites (S1-site 1, S2-site 2 and S3-site 3) of the Mato Grosso system. Distance = distance from the river mouth.

<table>
<thead>
<tr>
<th>Environmental descriptors</th>
<th>S1</th>
<th>S2</th>
<th>S3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude (m)</td>
<td>150</td>
<td>90</td>
<td>40</td>
</tr>
<tr>
<td>Pools</td>
<td>19.3</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
<td>Rifles</td>
<td>70.7</td>
<td>50.7</td>
<td>98.5</td>
</tr>
<tr>
<td>Runs</td>
<td>10</td>
<td>27.3</td>
<td>1.5</td>
</tr>
<tr>
<td>Mud</td>
<td>11</td>
<td>21.1</td>
<td>6.3</td>
</tr>
<tr>
<td>Sand</td>
<td>31.7</td>
<td>26.3</td>
<td>23.2</td>
</tr>
<tr>
<td>Gravel</td>
<td>52.3</td>
<td>51.4</td>
<td>59.2</td>
</tr>
<tr>
<td>Rock</td>
<td>5</td>
<td>1.2</td>
<td>11.3</td>
</tr>
<tr>
<td>Canopy</td>
<td>95</td>
<td>90</td>
<td>90</td>
</tr>
<tr>
<td>Marginal vegetation</td>
<td>5</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Distance (m)</td>
<td>15</td>
<td>13.5</td>
<td>3</td>
</tr>
<tr>
<td>Conductivity (µS.cm⁻¹)</td>
<td>83</td>
<td>105</td>
<td>100</td>
</tr>
</tbody>
</table>

Figure 1. Mato Grosso fluvial system showing the sample site (grey square).
Trophic ecology of two stream-dwelling Characidium

Table 2. Food items available (ind × m⁻²) and consumed (IAi) by Characidium species at the three study sites, of the Mato Grosso stream, Rio de Janeiro, Brazil. Arachnida = Aracnida and Araneae; Ephemeroperta nymph = Bætidae and Ephemeroperta; Coleoptera larvae = Cercopidae; Trichoptera larvae = Hydrobiosidae and Hydropsychoidea; other Diptera larvae = Ceratopogonidae, Chironomidae, Culicidae, Diptera, Dívidae, Dolichopodidae e Empididae.

<table>
<thead>
<tr>
<th>Items</th>
<th>Environmental availability</th>
<th>Characidium cf. vidali</th>
<th>Characidium interruptum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Site 1</td>
<td>Site 2</td>
<td>Site 3</td>
</tr>
<tr>
<td>Bivalve*</td>
<td>10</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>Arachnida*</td>
<td>6</td>
<td>11</td>
<td>7</td>
</tr>
<tr>
<td>Ephemeroperta nymph*</td>
<td>143</td>
<td>49</td>
<td>184</td>
</tr>
<tr>
<td>Odonata nymph*</td>
<td>14</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Coleoptera larvae*</td>
<td>49</td>
<td>13</td>
<td>23</td>
</tr>
<tr>
<td>Hymenoptera**</td>
<td>22</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Trichoptera larvae*</td>
<td>26</td>
<td>5</td>
<td>27</td>
</tr>
<tr>
<td>Lepidoptera larvae**</td>
<td>6</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Other Diptera larvae*</td>
<td>514</td>
<td>171</td>
<td>363</td>
</tr>
<tr>
<td>Simuliidae larvae*</td>
<td>71</td>
<td>32</td>
<td>31</td>
</tr>
<tr>
<td>Plant Matter *<em>+ Algae</em></td>
<td>300</td>
<td>297</td>
<td>323</td>
</tr>
</tbody>
</table>

*Autochthonous; **allochthonous.

Characidium cf. vidali and Characidium interruptum were deposited in the Museu Nacional do Rio de Janeiro (MNRJ 29958, 29980 and MNRJ 29969, 29970, 29971, respectively). In order to access feeding habits, at each sampling occasion and study site, we randomly selected approximately 20 specimens of each species. Feeding habits were assessed using a sample of 295 specimens: 93 CV from Site 1; 51 CV and 63 CI from Site 2; and 88 CI from Site 3. Sampled fish were euthanized by a blow to the cranium, stomachs were removed and their contents preserved in 5% formalin.

Gut content analyses were performed under a stereoscopic microscope using the Volumetric (V) and Frequency of Occurrence (Fo) methods (Hynes, 1950; Hyslop, 1980). For each species, the relative importance of each consumed item was assessed by the Alimentary Index (IAi) proposed by Kawakami and Vazzoler (1980) and adapted by Hahn et al. (1997) (Equation 1):

$$IA_i = \frac{(F_i \times V_i)}{(F_i \times V_i)} \times 100$$

where $F_i$ and $V_i$ are the Frequency of Occurrence and Volume of each food item, respectively. Patterns in diet similarities among sites and seasons, as well as patterns in food availability were analyzed based on the food availability and IAi values (Table 2) using a cluster analysis based on the UPGMA method with Bray Curtis distances (McCune and Mefford, 1997).

The amplitude of trophic niche (diet amplitude) of each species was estimated for each species and study site using the Shannon’s Index of niche breadth (S). This index varies from 0 (the species eat only one kind of food) to 1 (the species use many kinds of food and each kind is equally consumed). Trophic niche overlap was estimated at site 2 according to Pianka’s Index of niche overlap (P) (Krebs, 1999). This index varies from 0 (no feeding overlap) to 1 (complete feeding overlap). Following Grossman (1986), the values of feeding overlap were considered: high (>0.60), medium (0.4-0.6) and low <0.4). Temporal and spatial differences in mean values of S were tested with a t-test (Zar, 1999). Spatio-temporal differences in food availability were also tested with a Kruskal-Wallis test (Zar, 1999).

3. Results

Environmental parameters were very similar for each sampling site (Table 1) and no significant differences (H = 1.91; p = 0.39) in prey availability were found between them (Table 2). Seasonal differences in feeding habits were only related to the relative consumption of plant and animal matter; both species consumed plant matter only during the dry season (Table 2). The cluster analysis (Figure 2) based on food consumption by both C. vidali and C. interruptum indicated a high similarity between the rainy and dry seasons for all study sites.

The diet of both species was based mainly on autochthonous insects, although some allochthonous items were also observed (Table 2). C. vidali consumed ten food items at Site 1 and five food items at Site 2. C. interruptum consumed nine food items at Site 2 and eight food items at Site 3. Niche breadth differed between sites and was larger at Site 2 but, with no significant interspecific differences ($t$-test; 1 df; $p = 0.18$) (Figure 3).

The relative importance (IAi) of each food item varied across sites for both species despite the fact that the availability of food items did not vary (Table 2; Figure 4). At Site 1, food items consumed by C. vidali were mainly Trichoptera and Simuliidae. At Site 2, where C. vidali and C. interruptum co-existed, food items were more diverse; both C. vidali and C. interruptum fed on the same items,
mainly Ephemeroptera, Trichoptera, Diptera and Simuliidae, but interspecific differences in the relative consumption of each food item were noted; *C. vidali* fed mainly upon Simuliidae and Trichoptera (IA$_i$ = 72.7 and 65.6, rainy and dry seasons, respectively) whereas *C. interruptum* fed mainly on Diptera and Ephemeroptera (IA$_i$ = 71.59 and 65.77, rainy and dry seasons, respectively). At Site 3 *C. interruptum* fed on Ephemeroptera with a low incidence of Simuliidae and Trichoptera. Pianka’s niche overlap index (P) indicated 52% of feeding overlap (P = 0.52) at Site 2, where the species coexisted.

4. Discussion

According to Ibañez et al. (2009) omnivorous are a species which consistently feed on substantial proportions of both plant and animal material and carnivorous/invertivorous are the species which feed on crustaceans, oligochaetes, mollusks and/or insects. Although the studied *Characidium* species presented both animal and vegetal items in their diet, the amount of consumed plant items were very low and rarely registered in stomachs (never exceeding 10% of IA$_i$) while larvae and nymphs of insects were the most important items. These results support the recurrent invertivorous classification used for many different *Characidium* species (e.g. Godoy, 1975; Costa, 1987; Sabino and Castro, 1990; Castro and Casatti, 1997; Uieda et al., 1997; Aranha et al., 2000; Araújo et al., 2005; Barreto and Aranha, 2006; Ferreira, 2007; Gomiero and Braga, 2008) but raises the question about changes in the consumption of food items and feeding plasticity of fish species.

In the study area, apart from the seasonal changes in water temperature and photoperiod, the occurrence of summer spates are probably the most typical environmental factor affecting resources as food availability (Suárez, 2008; Mazzoni and Rezende, 2009; Mazzoni et al., 2010a; Mazzoni et al., 2010b). The presence of plant matter was the only seasonal difference in the diet of both *Characidium* species and probably resulted from changes in plant availability owing to environmental changes associated with seasonality. Plant matter was a food item during the dry season when stream volume and water velocity were at their minimum (Mazzoni and Lobón-Cerviá, 2000), reducing the availability of aquatic insect fauna (Pinto and Uieda, 2007) and giving rise to conditions conducive to the proliferation of in-stream marginal vegetation and periphyton, making it more available as a food resource for fish fauna (Carvalho and Uieda, 2010).

During the dry season (= lower temperature in southeast Brazil), insect densities decline in streams (i.e. Prejs and
Prejs, 1987; Goulding et al., 1988; Casatti et al., 2001) making it reasonable to expect that during this period the feeding spectrum would be enlarged as fish change from preferred food items to the available ones (Zaret and Rand, 1971; Matthews, 1998). In fact, it was noticed that the IAi’s values of preferred food items (Simulidae, Trichoptera and Ephemeroptera) tended to be smaller during the dry season. Taking this into account, the occurrence of algae and plant items in the diet of both Characidium species could be interpreted as an opportunistic circumstance resulting from environmental conditions related to this season.

In fact the most significant variation of C. vidali and C. interruptum feeding habits were related to changes in the abundance of consumed prey within the insects, agreeing with the conclusions of Barreto and Aranha (2006) about the importance of environmental alterations, such as floods as the main cause for diet shifts of four characins from an Atlantic Rain Forest stream in Brazil. In addition, the feeding behaviour of Characidium species, described in Leitão et al. (2007), could help to explain these opportunistic and/or seasonal shifts in food consumption. Although the “sit-and-wait” foraging tactic used by Characidium species (e.g. Sazima, 1986; Aranha et al., 1998) supports the invertivore classification adopted in the present study, the opportunistic/circumstantial use of plant parts and algae could be explained by the findings of Leitão et al. (2007) about the “nuclear-follower association” feeding behaviour registered for a Characidium species from an Atlantic rain forest from southeast of Brazil. According to Leitão et al. (2007) this feeding behaviour involving one Characidium species was characterized by the presence of a nuclear species, in this case a Loracaridae catfish species, which causes some kind of disturbance on the bottom while foraging, and a follower species, in the case of a Characidium, which feeds on the dislodged sediment, algae and (possibly) small animals. Considering that two species of Loracaridae catfish co-exist with our C. vidali and C. interruptum (unpublished data), we can explain the observed pattern of feeding behavior during the dry season.

Biotic factors, such as predation and competition and abiotic factors, such as stream order and width, current velocity, degree of vegetal cover and substrate diversity have been reported to influence local fish assemblage (Tejerina-Garro et al., 2005; Ibáñez et al., 2009) and food availability (Rezende and Mazzoni, 2006a, b; Pinto and Uieda, 2007). These factors differ along spatial and temporal scales inducing general patterns of trophic organization and specific local responses (Uieda and Motta, 2007). Stream-dwelling fish predators are generalist and feed upon organisms from many different origins such as allochthonous invertebrates, including those present in the water surface and those that fall from the riparian vegetation, as well as autochthonous invertebrates such as immature forms of aquatic and terrestrial insects, crustaceans, oligochaetes and mollusks (Rezende et al., 2011). Such a feeding plasticity is responsible for temporal and spatial variations in feeding patterns of stream-dwelling fishes.

Spatial patterns in feeding habits were the most notable differences in the present study; no seasonal variation on feeding habits were registered. Although food availability was similar at all studied sites, niche breadth was smaller at sites where both C. vidali and C. interruptum did not co-exist, but were larger at Site 2 where both species were present. At the site of co-existence, C. vidali and C. interruptum consumed an almost identical array of prey items and presented a medium to high value of niche overlap. In contrast, in the site where they did not co-occur, both C. vidali and C. interruptum diets were based on completely distinct food items, although prey availability was the same in these sites. These results are contradictory to the expectations of the niche theory (Mac-Arthur, 1972), which predicts feeding segregation between closely-related species in response to a limited amount of resources. Although the theory is largely based on the idea that natural selection tends to lessen competition among closely-related species by making them consume different food items and favouring specialists (Cunha et al., 1951), there are still some contradictory opinions about

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**Figure 4.** Dendrogram of similarity (Bray Curtis distance) based on available and consumed food items. Food items availability at site 1 (Avail S1), site 2 (Avail S2) and site 3 (Avail S3) and consumed food items by Characidium cf. vidali from site 1 (Use Cv – S1) and site 2 (Use Cv – S2) and Characidium interruptum from site 2 (Use Ci – S2) and site 3 (Use Ci – S3), from Mato Grosso stream, Rio de Janeiro, Brazil.
the importance of specialists versus generalists in tropical communities (Wilson and Yoshimura, 1994), with many examples of both generalists and specialists (Vojtech et al., 2002; Dyer et al., 2007). Although the enlargement of niche breadth among coexisting species is paradigmatically counter to the niche theory, the statement postulated by Cunha et al. (1951), that feeding plasticity is an important strategy to maintain different populations could explain our results.

Contrary to current ecological expectations about coexisting species, we demonstrated that the two studied congeneric species tended to specialize feeding behaviour when living alone in a given site and to generalise behaviour when co-occurring in the same site. Considering that congeneric species tend to have similar environmental and/or trophical requirements (Gerking, 1994) we can suppose that some other characters (e.g. Chase and Leibold, 2003), which were not measured in the present study, could explain the observed patterns of distribution and coexistence of the Characidium species from the Mato Grosso stream. In fact, many other behavioural and morphological traits (e.g. Casatti and Castro, 2006; Nunes and Hartz, 2006) have been indicated as being responsible for species coexistence in stream-dwelling fish communities from the Neotropical region.

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References


