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Diet overlap between two cyprinids: eurytopic roach and rheophilic dace in tailwater submersed macrophyte patches

Małgorzata Dukowska, Andrzej Kruk *, Maria Grzybkowska

Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, University of Łódź, 12/16 Banacha Str., Łódź 90-237, Poland

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ABSTRACT

From May to August 2004, the available food base and diet of two cyprinid species, eurytopic roach, represented by 75 small specimens, and rheophilic dace, represented by 37 small specimens, were investigated in seasonal patches of submersed aquatic macrophytes (SAM) in the impounded lowland Warta River, Poland. The aim of the study was to recognize spatial and temporal patterns in the feeding of both species in relation to available resources, and to evaluate their food niche overlap. To distinguish homogenous classes of fish alimentary tracts on the basis of their contents, a Kohonen artificial neural network (i.e., a self-organizing map, SOM) was used. Indicator food categories were identified using the IndVal index. Roach and dace partitioned the food niche, which was demonstrated in this study by 1) insignificant values of the Schoener's interspecific diet overlap index on particular sampling occasions, and two SOM sub-clusters (homogenous diet classes) with alimentary tracts almost exclusively of roach (axis of resources), 2) zero or low percentage of specimens of both fish species coming from the same sampling occasions and assigned to any of the remaining homogenous diet classes (axis of time), and 3) absence of roach in May and dace in August in the SAM patches, i.e., on almost half of the sampling occasions (axis of space). The diet overlap was highest when the SAM patches and food base were most developed, which is congruent with the niche overlap hypothesis saying that maximal tolerable niche overlap can be higher in less intensely competitive situations.

We recommend the combined application of SOM and IndVal index, which have both previously been used in biocoenology, to the analyses of animal diets. They effectively allowed getting insight into the complex trophic relationships.

1. Introduction

Aquatic macrophytes growing on river bottom may be divided into three groups: 1) emergent aquatic macrophytes, 2) floating-leaved aquatic macrophytes, and 3) submersed aquatic macrophytes (SAM), which complete their life cycle under the water surface. The SAM habitats are complex and important, because they are splendid hiding and feeding habitats of riverine young fish. For example, they produce more stable prey–predator relations between fry and piscivorous fish (de Nie, 1987; Dukowska et al., 2013; Grenouillet and Pont, 2001). Also, they constitute a place for the development of invertebrates on which fish may prey, such as epiphytic fauna (mainly dipterans, such as Chironomidae and Simuliidae, and highly mobile taxa, such as Ephemeroptera), zooplankton, and taxa living on or within the bed sediment. In particular, SAM create favourable conditions for pelophilous forms, like Oligochaeta and Chironomidae, by extensive particle trapping and the accumulation of a fine-grained, nutrient enriched sediment (Franklin et al., 2008; Głowacki et al., 2011; Grzybkowska et al., 2003; Kleeberg et al., 2010; Köhler et al., 2010; Tokeshi and Pinder, 1985). All the above factors make a river bed covered with such vegetation more productive than macrophyte-free patches (Grzybkowska and Dukowska, 2002).

Untypical, but abundant development of SAM has been observed every year in the large lowland alluvial Warta River downstream of the artificial Jeziorsko Reservoir due to low water levels in late spring and summer for over 20 years now. The low water level results from low river discharge through the dam of the reservoir, which is caused by water management there. In every early autumn an opposite process takes place: the discharge is much increased and large volumes of water, released from the reservoir, destroy the SAM habitat, because its macrophytes are torn out of the bottom or get covered with bottom substrate (Głowacki et al., 2011; Grzybkowska et al., 2003).

The two studied fish species have a number of similar and a number of dissimilar traits. Roach (*Rutilus rutilus* (L.)), a eurytopic (generalist) cyprinid (Schiemer and Wieser, 1992), belongs to the dominant species in lowland temperate rivers. This applies particularly to human-

* Corresponding author. Tel.: +48 42 635 44 33; fax: +48 42 66 55 817.
E-mail addresses: mdukow@biol.uni.lodz.pl (M. Dukowska), a.kruk@biol.uni.lodz.pl (A. Kruk), mariagrz@biol.uni.lodz.pl (M. Grzybkowska).

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impacted reaches, including inflows of coal mine waters (Grzybkowska, 1988; Kruk, 2007) and regulated and/or navigable river fragments (Pinder et al., 1997; Wolter and Vilcinskas, 2000; Wolter et al., 2000). Dace (*Leuciscus leuciscus* (L.)), also a cyprinid, resembles roach in size, but is slimmer and thus more effectively swims in fast moving water. It is a rheophil (i.e., riverine specialist), usually suffering from human-induced changes in aquatic environments and thus considered a good bioindicator (Kruk, 2007; Penczak and Kruk, 2000; Raat, 2001). Both species show trophic ontogenetic shifts during juvenile stages (Nunn et al., 2007; Persson et al., 2000). Due to the different vulnerability of these two species to human pressure, roach population has significantly increased, while the abundance of dace significantly declined in the Warta River since the Jeziorsko Reservoir was created in 1986; these changes were observed to a much greater extent in the tailwater than in the backwater because the latter maintained a quite natural hydrologic regime (Kruk and Penczak, 2003; Penczak and Kruk, 2000).

The SAM patches in the tailwater of Jeziorsko Reservoir are inhabited mainly by eurytopic roach and percids (perch, ruffe). Unexpectedly, this habitat (characterized by considerably reduced water speed) is also exploited by rheophilic dace (Dukowska et al., 2013), which is rather classified as a dweller of mid-river channel, avoiding both the emergent and submersed water plants (Kucharczyk et al., 2008; Tadajewska, 2000). Its occurrence in the SAM patches results in interspecific competition for food between roach and dace. The competition plays a key role in the persistence and life histories of populations, because ecologically complete competitors cannot coexist (Hardin, 1960). In other words, coexistence of species requires niche partitioning between them at minimum one of the following niche axes: resources, predators, space and time (Schulze et al., 2012).

Because dace foraging in SAM patches in the Warta River became a competitor for a closely related roach, the aim of the study is to recognize patterns in feeding of these two species in order to evaluate the niche overlap as concerns resources, space and time. Because data obtained from alimentary tracts are noisy (many fragmented and/or digested food items cannot be identified) we decided to realize the aim of the study with a Kohonen artificial neural network (i.e., a self-organizing map, SOM) (Kohonen, 1982) as it is resistant to the noise in data (Lek and Guégan, 1999; Park et al., 2006b; Zhang et al., 2011). We also applied the indicator value (IndVal) index (Dufrêne and Legendre, 1997) in order to identify indicator food categories. These two methods, which are widely used in biocoenology, have been previously only once (Dukowska et al., 2013) applied in ecological studies to the diet of organisms. Thus the additional aim of the study is the confirmation of efficiency of the combined use of the SOM method and the IndVal index for the analysis of data on fish feeding.

2. Material and methods

2.1. Study area

The lowland alluvial Warta River is 795 km long and its catchment area is 54,519.6 km^2 (EMPHP, 2007). The river rises at 380 m a.s.l., empties into the Oder River at 13 m a.s.l., and its slope range is 2.0–1.0‰ in the upper course and 0.3–0.1‰ in the middle and lower courses. In 1986 the Warta was impounded in kilometre 306 (EMPHP, 2007) of its course. The then created large Jeziorsko Reservoir, with a total surface area of 42.3 km^2, was completely emptied because of construction errors in 1986, and refilled in 1988. Next, in 1994, a 5 MW hydroelectric power plant was put into operation, which considerably increased short-term amplitudes of water discharge (Penczak and Kruk, 2000, 2005). Several years after the final filling intensive changes in the tailwater fish community were observed, which were followed by its moderate stabilization in the first decade of the 21st century (Penczak and Kruk, 2005; Penczak et al., 2012).

The study site was established in the Warta River, approximately 1.5 km downstream of the reservoir's dam (Fig. 1). At the study site, the river is approximately 60 m wide, with a maximum depth of 2.5 m in the erosion zone. During sampling the discharge in the tailwater, similar to earlier years, was stabilized at a low level as a result of river discharge management. This allowed large patches of *Potamogeton pectinatus* L. and small patches of *Potamogeton lucens* L. to appear in the transitional bed zone, which is located between the depositional area close to the banks and the mid river channel. *Cladophora glomerata* (L.) Kutz filaments covered SAM, especially in June (Głowacki et al., 2011; Grzybkowska and Dukowska, 2002). It should be noted that the place of SAM development is quite untypical. In the studied tailwater, the transitional bed zone is much more stable than the depositional zones where the riverbed is often exposed. In consequence, also SAM patches developing in the transitional bed zone are most stable despite the fact that in large alluvial natural rivers the depositional zones are typical for the development of SAM. Further details of this sampling site were given by Grzybkowska and Dukowska (2002) and Grzybkowska et al. (2003).

2.2. Food resource sampling

Sampling was conducted in 2004, i.e., 18 years after the reservoir started functioning and 10 years after the construction of a hydroelectric power plant. We sampled a majority of the most stable SAM patches developed in the sampling site. In the SAM habitat the water depth, current speed, percentage of river bottom covered by macrophytes, as well as temperature were measured twice a month, from late May through August 2004. At the same time, macroinvertebrates, benthic particulate matter and fish were sampled.

Each sample of benthic invertebrates consisted of 10 subsamples of 10 cm^2 each (i.e., in total 100 cm^2 of stream-bed area) taken with a tubular sampler in the SAM habitat. The invertebrates were sorted from the detritus by hand and preserved in 10% formalin. All macroinvertebrates from these quantitative samples were counted and their wet weight (w.w.) was assessed; these data were used to estimate density and biomass in the habitat sampled. Chironomids were identified to the species level when possible, while other macroinvertebrates were classified to the lowest taxonomic level. Because exact identification on the basis of chironomid larvae was often impossible, we reared their immature stages in the laboratory, from additional qualitative samples taken on each sampling occasion, in order to obtain larval and pupal skins and imagines.

The same samples were used to estimate the coarseness of benthic inorganic substrate. The composition of benthic particulate inorganic matter was analysed according to Cummins (1962). This method divides the dry sediments into size classes that have been shown to be of ecological significance. Field data on particle size distribution were transformed into the single substrate index (SI) by summing the midpoint values of size classes weighted by their percentage mass (Quinn and Hickey, 1990). The same field samples were also used to determine the organic matter content in the bottom sediment. For this purpose a 1 mm sieve was used to separate benthic particulate organic matter (BPOM) into two fractions: particles with a diameter > 1 mm (coarse BPOM—BCPOM) and particles with a diameter < 1 mm (fine BPOM—BFPOM) (Petersen et al., 1989). Next, the benthic organic matter was dried at 60 °C for two days, weighed, ashed at 600 °C for 2 h and reweighed. A more detailed description of these methods can be found in Grzybkowska and Dukowska (2002) and Grzybkowska et al. (2003).

In order to estimate the amount of plants growing in the study site a special frame (0.5 × 0.7 m) was placed on the riverine bottom and all *Potamogeton* plants within the frame were collected. This procedure was repeated three times on each sampling occasion. In the laboratory, the pondweeds were dried for 24 h at 65 °C to estimate their dry weight (d.w.).