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Food niche partitioning between perch and ruffe: Combined use of a self-organising map and the IndVal index for analysing fish diet

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ABSTRACT

From June to August 2004, the available food base and the diet of 52 small perch and 38 ruffe specimens were investigated in a macrophyte habitat in the Warta lowland alluvial river, Poland, downstream from a large dam reservoir. The river bed was covered by large patches of *Potamogeton* spp. To recognise patterns in fish alimentary tracts' contents (ATCs), a Kohonen artificial neural network (i.e., a self-organising map, SOM) was used. The indicator value (IndVal) index was applied for the identification of food categories that were indicative of classes of ATCs distinguished by SOM. Among five SOM ATC classes (X_1, X_2, Y_1, Y_2 and Y_3), the first four contained alimentary tracts of one species (with no or few exceptions), and one class (Y_3) was heterogeneous in this respect. Thus, in general, the diet of perch and ruffe did not overlap, except for Y_3 (both species ate similar food because of the available rich food base composed mostly of epiphytic chironomids). The SOM ATC classes also differed in the sampling time. Moreover, significant IndVals (i.e., significant associations with any SOM ATC class) were recorded for 22 out of the 25 food categories studied, which clearly demonstrated that perch preferred to eat epiphytic chironomids, simuliids and *Daphnia*, while ruffe preferred to eat benthic chironomids and trichopterans and the remaining zooplankton. No food category was significantly associated with the overcrowded starving perch specimens assigned to X_1, for which the significantly lowest gut fullness coefficient was recorded. In summary, the combined use of SOM and IndVal, which have both previously been used in biocoenology, was an effective method for fish diet studies. Not only were homogenous alimentary tract groups distinguished but indicative food categories were identified as a result of the first application of both methods in an ecological analysis of diet. This study not only extends the use of SOM and IndVal to diet studies but also increases the credibility of the interpretation of the results obtained with both methods.

1. Introduction

An organisms' diet is a function of size-dependent morphological (e.g., gape size), physiological (e.g., vision, reactive distance, and digestion) and behavioural traits that change during ontogenesis (Borcherding et al., 2013). These ontogenetic diet shifts may be crucial for the condition and dynamics of a fish cohort or population, especially when resources are limited. Intra- and interspecific competition plays a key role in the persistence and life histories of populations, especially those belonging to the same trophic guild (i.e., that use similar food resources), because ecologically identical competitors cannot coexist (Bøhn et al., 2008). Ontogenetic shifts can strengthen or weaken competitive interactions, and this is why they may be critical for a populations' coexistence or for their elimination. However, competition only occurs when potential competitors use limited resources at the same time and place (Schulze et al., 2012). This is why the strength of competition may decrease with the sudden appearance of new habitats that are rich in food. Such a rich habitat in freshwater bodies, especially in large alluvial lotic ecosystems, are submerged aquatic macrophytes (SAM). The latter may serve as a substrate for periphyton and trap organic matter, thus, creating a space for fish that is rich in zooplankton, epiphytic fauna and benthic macroinvertebrates and that additionally provides shelter from predators (Grenouillet and Pont, 2001). To a small extent, SAM are also a direct food source (Tokeshi and Pinder, 1985; Pinder, 1992; Grzybkowska et al., 2003; Franklin et al., 2008; Kleeberg et al., 2010).

The untypical abundant development of SAM has been observed every year in the large lowland alluvial Warta River downstream of the Jeziorsko Reservoir as an effect of the low discharge in late

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spring and summer. Additionally, every year at the beginning of autumn, the SAM habitat disappeared as the result of water management, i.e., releases of large volumes of water from the reservoir. Thus, for a few months, fish may potentially exploit prey from three ecological formations, including zooplankton (mainly provided by the dam reservoir), epiphytic fauna (mainly composed of dipteran larvae (Chironomidae and Simuliidae)), and benthos, because submersed plants create favourable conditions for pelophilous forms, such as Oligochaeta and Chironomidae, by extensive particle trapping and the accumulation of a fine-grained, nutrient-enriched sediment (Grzybkowska et al., 2003; Dukowska et al., 2007, 2012). Rich fish assemblages were associated with SAM, and among them, two closely related percids were dominant: perch (*Perca fluviatilis* L.), a generalist, and ruffe (*Gymnocephalus cernuus* (L.)), classified either as a specialist (Gunderson et al., 1998; Tarvainen et al., 2005; Schleuter and Eckmann, 2006, 2008) or a generalist (Rösch et al., 1996). Generalists are considered to have a higher flexibility for niche partitioning than specialists. This is why Dukowska et al. (2012), with the use of conventional statistical methods, studied the diet overlap and the seasonal diet spectrum of these two species that coexist in the periodical macrophyte habitat of the Warta River in the tailwater of the Jeziorsko Reservoir.

However, on the one hand, data relating to alimentary tract contents are very noisy because many fragmented and/or digested elements cannot be identified. On the other hand, artificial neural networks (ANN) are resistant to the noise in data. This is why we decided to reanalyse the above problem (and respective data) with an application of an unsupervised ANN based on the Kohonen algorithm (also referred to as a self-organising map, SOM) (Kohonen, 1982) and, additionally, the indicator value (IndVal) index (Dufrêne and Legendre, 1997). These two methods, which are widely used in biocoenology, have not been previously applied in ecological studies to the diet of organisms. Thus, the aim of this study is the assessment of the efficiency of the combined use of the SOM method and the IndVal index for the analysis of data on fish feeding.

2. Materials and methods

2.1. Study area

The study site was established in the lowland alluvial Warta River, approximately 1.5 km downstream of the dam of the large Jeziorsko Reservoir, which has a maximum surface area of over 42 km^2 (Fig. 1). The Warta River rises 380 m a.s.l., is 795 km long and empties into the Oder River at 13 m a.s.l. Its catchment area is 54,519.6 km^2 (EMPHP, 2007) and its slope ranges from 2.0–1.0‰ in the upper course to 0.3–0.1‰ in the middle and lower courses. At the study site, the Warta River is approximately 60 m wide, with a maximum depth of 2.5 m in the erosion zone. As a result of water management during summer sampling in 2004, the discharge, similar to earlier years, was stabilised at a low level and resulted in the appearance of large patches of *Potamogeton pectinatus* L. and small patches of *Potamogeton lucens* L. in the transitional tailwater bed zone, which is located between the depositional area close to the banks and the mid river channel (Fig. 2) (Grzybkowska and Dukowska, 2002; Głowacki et al., 2011). The highest biomass of SAM, *P. pectinatus*, occurred in June (210 g m^{-2} d.w.); at that time, its leaves were covered with filaments of green algae, *Cladophora glomerata* (L.) Kutz (Fig. 2). SAM also favoured the accumulation of fine particulate organic matter on the river bottom; consequently, the highest abundance of fine particulate organic matter (FPOM) was recorded in late June, when the bed cover by macrophytes was the densest. The inorganic substratum was mainly fine and coarse sand and occasionally gravel (Dukowska et al., 2012). The riparian vegetation was mainly willows (*Salix* spp.) and occasionally *Alnus glutinosa* (L.) Gaertn. Detailed site descriptions can be

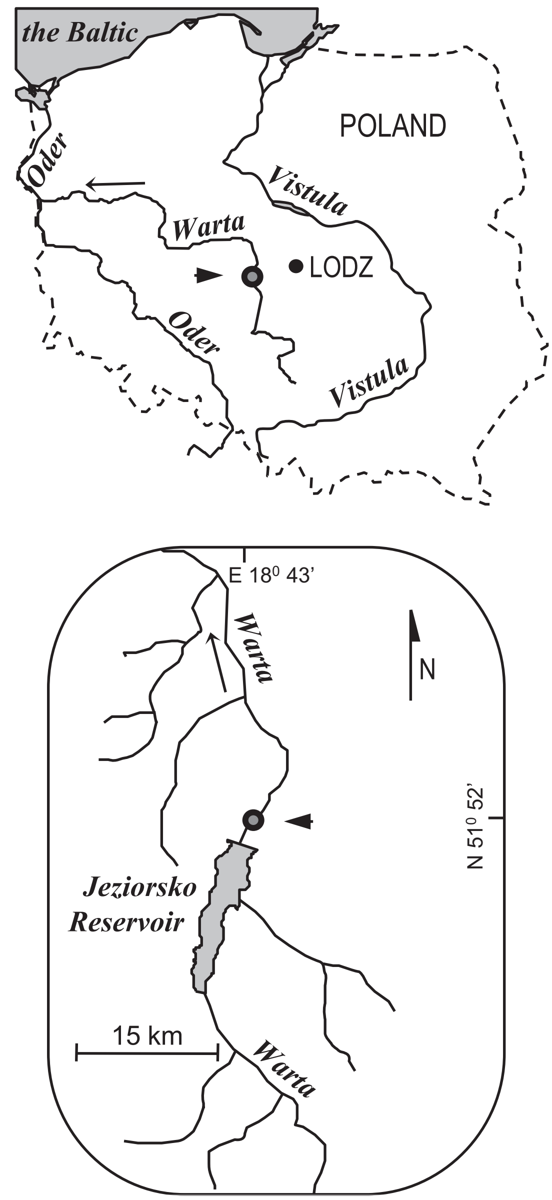

Fig. 1. The sampling site location in the Jeziorsko Reservoir tailwater.

found in Grzybkowska et al. (1990, 2003), Penczak et al. (1998) and Dukowska et al. (2009, 2012).

All materials were collected twice a month from June to August 2004.

Dukowska et al. (2012) provides the detailed description of the food base available for fish in the study area. Over the entire investigated period, Cladocera dominated in the water column, reaching 99% of the total zooplankton biomass, while Copepoda were less abundant (1%). The maximum values of cladoceran biomass were recorded in August due to, among others, the presence of a large-sized predator *Leptodora kindtii* (Focke). In addition, the most dominant species were the small-sized species, *Bosmina* spp. (19% of zooplankton biomass) and *Chydorus sphaericus* (O.F. Müller) (17% of zooplankton biomass), and larger-sized taxa, such as *Daphnia* spp. (9% of zooplankton biomass) (Fig. 2) (Dukowska et al., 2012).

During the study, dipterans, such as chironomids and simuliids, were dominant macroinvertebrates of epiphytic fauna (respectively 16% and 82% of the total epiphytic macroinvertebrate biomass); the maximum values for each of these groups was observed in late June. At the beginning of SAM persistence, *Hydra*