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Food resource partitioning between bream (*Abramis brama*) and razor fish (*Pelecus cultratus*) in Lake Balaton (Hungary)

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Introduction

Food partitioning between coexisting fish species may exhibit a wide variation according to space and time in consequence of their interactions and competition (Lammens et al. 1985). Sharpening interspecific competition often results in interactive (niche) segregation especially when food is scarce, or due to size-selective predation (Nilsson 1978). Introduced exotic species, which are better adopted to exploit the available food resource (planktonic and/or benthic species), usually initiate niche shift between different fish taxa.

In the eutrophic, shallow Lake Balaton the dominant cyprinids exploit both open water and littoral food resources (plankton, benthos, periphytic invertebrates) in varying extent during different stages of development. Their interactions might have been intensified from the impacts of the introduced eel (*Anguilla anguilla*), a benthic feeder, and the hybrids of silver carp (*Hypophthalmichthys molitrix*) × bighead (*Aristichthys nobilis*), a phyto-zooplankton feeder.

In this study an attempt is made to show that the resource partitioning of bream (*Abramis brama* – mainly benthic) and razor fish (*Pelecus cultratus* – mainly pelagic) is largely affected by varying predation pressure on the abundant food organisms especially in their certain size classes.

Material and methods

Fish for food studies were collected from the commercial catch from the NE and SW-basins of the lake during different months (March–November) of 1982–84. After measuring the body sizes, their digestion tracts were prepared and fixed in 10% formalin. Gut contents were then washed out with distilled water and all the food species consumed were identified that were still sufficiently recognizable in the digested remains of prey animals under stereo- and light microscope. The food components were grouped into taxons and food spectra in different size and age groups of fish were constructed according to the frequency of occurrence during different months. For the quantitative analysis of food selectivity we used Ivlev's "electivity index" modified by Jacobs (1984).

Wet weight of food items consumed by individual fish were measured or assessed according to the length-weight relationships of food organisms. Data on the food species composition in the open water were used from Zánkai & Ponyi (1986). Data on mean lengths and weights of food organisms were obtained from the literature (see Biró et al. Ms.). Similarity of the food in the two basins of the lake during different months were evaluated according to Czekanowski (Růžicka 1958).

The food of altogether 377 bream specimens and 293 razor fish specimens were analysed in detail and reviewed in previous papers (Biró et al. Ms., Biró & Perényi Ms., Biró & Vörös 1990.).

Results

The diets and food consumption of two coexisting cyprinids showed many similarities in the shallow Lake Balaton. In percent of occurrence, zooplankton crustaceans dominated diets of both fish and dietary overlap between species was high during certain periods. Nevertheless, the relative importance of prey items differed between species. *A. brama* consumed mainly crustaceans (Cladocerea, Ostracoda, Copepoda) and benthic invertebrates (Chironomidae, Mollusca). However, *P. cultratus* fed a greater variety of prey items, with the dominance of cladocerans (*Daphnia galeata, Leptodora kindtii*), mysids (*Limnomysis benedeni*), dipteras, amphipods and fish.

Seasonal and size-dependent differences in the food spectra of bream were striking between the two outside basins of the lake. Based on the availability of food organisms, the gut content of bream in the NE-basin mainly consisted of cladocerans and copepods in nearly equal ratios (34.2–36.6%), then chironomids (21.5%) and molluscs (6.7%). However, 50% of the food consumed in the SW-basin consisted of cladocerans then copepods (28.5%) followed by chironomids (21.2%) (Fig. 1). Seasonal occurrence of the main food organisms showed wide variation and ac-

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cordingly plankton and benthos feeding periods of bream could be distinguished.

In the diet of razor fish originating from the NE and SW-basins, cladocerans predominated (90.5–94 %) and copepods were present in 8 and 6 %, respectively. The other food components were consumed in negligible ratios (Fig. 1).

According to the percent frequency of occurrence of the main food items, zooplankton (Cladocera) was preferred by both species (selectivity index for daphnids in bream was +0.56 and that in razor fish was +0.95) and the significant dietary overlap proves the resource partitioning in the lake. A dietary switch from zooplankton assemblage to benthic or littoral invertebrates occurred in both species parallel with increasing of their body sizes and during seasonal migration between open water areas and littoral zone of different trophic state.

Analysing the variation of food composition by size classes of bream it was clearly shown that 10–25 cm sized specimens mainly fed cladocerans during spring and summer months (May – August, even September) and after reaching 25–30 cm length they turned to benthos feeding when chironomids and molluscs dominated. However, razor fish proved to be an obligate planktivore all over the lake regardless to their sizes with some exception when they were caught at macrophyte-covered areas (August – November) consuming mainly mysids (*Limnomysis benedeni*).

Evaluating the food composition of both species by weight, quite another picture was obtained

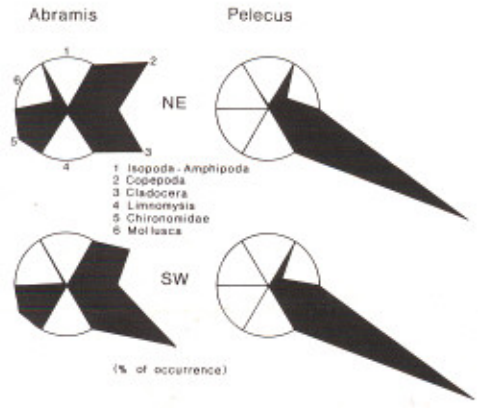

Fig. 1. Comparison of food composition in bream (May – November) and razor fish (March – October) in the NE and SW basins of Lake Balaton (the main food items are shown in % frequency of occurrence).

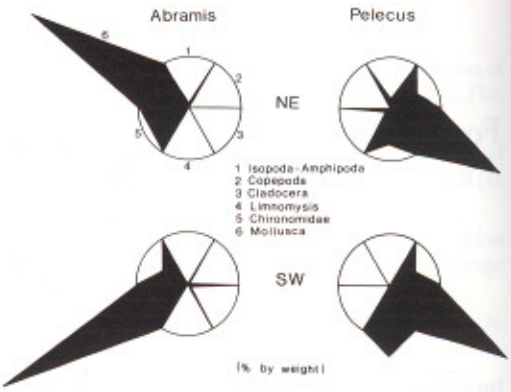

Fig. 2. Ratios of different food items by weight in the gut-contents of bream and razor fish in the two outside basins of Lake Balaton.

(Fig. 2). The overwhelming majority of the food of bream in the NE-basin consisted of molluscs (71.9 %) and chironomids (17 %), however, these groups were inversely related in the SW-basin amounting to 10.9 % and 82.9 % of the total food, respectively. The diet of *Pelecus cultratus* by weight showed a similar pattern as in Fig. 1 with the dominance of Cladocera in both basins (52.6–56.7 %), while the total weight of copepods ranged from 11.9 % (SW-basin) to 18.8 % (NE-basin). Chironomids (2.3 %) and isopods-amphipods (4.2 %) were present only in the gut contents of specimens originating from the NE-basin. Razor fish occasionally consumed insects and prayed upon fish (*Alburnus alburnus*) in less than 1 %.

Discussion

Contrary to earlier observations (Entz & Lukacsovics 1957) the food composition of bream in Lake Balaton has changed parallel with eutrophication. These changes were likely caused by an increased population density connected with the density-dependent growth, as well as the sharpened inter- and intraspecific competition among cyprinids and other species (Biró & Garádi 1974). Zooplankton members followed by benthic invertebrates consist the majority of food of bream (Biró et al. Ms.). Contrary to razor fish, bream do not select any of the zooplankton groups so sharply, however, seasonal changes in the food composition and selective consumption alternate

parallel with the trophic gradient along the longitudinal axis of the lake (Biró & Perényi Ms.).

Several studies show that overlaps in fish diet are highly variable: In periods of plentiful resources the overlap is considerable, but in lean periods overlaps are minimal. Grossman (1986) observed for a rocky intertidal fish assemblage that species which displayed the lowest amount of dietary overlap were those for which food limitation was probably most severe. Lammens et al. (1985) showed that overlaps between bream and eel in Tjeukemeer were highest when resources were abundant and condition of fish was good. A deterioration of condition and low availability of food resources was accompanied by niche shifts of bream and eel and a consequently smaller diet overlap. According to Nilsson (1978) resource partitioning in fishes is maximal in periods when food is scarce and niche shift, or interactive segregation has mainly been caused by size selective predation, as well as introduction of non-native species.

Comparing our data on the food composition of bream and razor fish in Lake Balaton by the % frequency of occurrence of the main food items, a clear evidence was shown for the zooplankton food resource partitioning between these sympatric cyprinids (Fig. 1). Their interspecific competition was especially pronounced during summer when the abundance of cladoceran species usually decreases (Zánkai & Ponyi 1986) and they (chiefly bream) showed size-related dietary changes. A quite another picture was obtained when the ratios of the main food items were compared by weight (Fig. 2), suggesting the interactive segregation of bream and razor fish. Although the food turnover of these species is more indicative for the rate of exploitation of the available food resources, contrary to bream, no sufficient data are available for the use of food energy by razor fish per unit of area. In Lake Balaton the bream, having a dense population, annually consumes $93-141\,kJ \cdot m^{-2} \cdot yr^{-1}$ of food energy (Biró & Vörös 1990.), however, no reliable census was made to estimate the stock density of razor fish.

Bream and razor fish partition their open water food resource weakly by consuming prey items in different proportions and sizes, and more strongly by utilizing the food resources within certain periods and size classes and at various areas in the littoral zone. The dietary overlap and interspecific competition between bream and razor fish may exhibit a high significance in the energy flux of the lake and needs further clarification in the context of other interspecific and environmental impacts.

The mechanism of resource partitioning is the most likely process responsible for assemblage organization because predators' competition for space and environmental disturbances do not seem to have a strong effect on this assemblage (Grossman 1986).

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