

Does diet overlap among larval and 0+ fish species decrease with ontogenetic development?

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Abstract. The aim of the study was to determine the degree of overlap in the feeding niches of early developmental stages of roach, *Rutilus rutilus* (L.), perch, *Perca fluviatilis* L., bleak, *Alburnus alburnus* (L.) and sunbleak, *Leucaspis delineatus* (Heckel). The hypotheses were that (i) larvae of different fish species of similar body sizes feed on similar food, and that (ii) smaller fish compete with larger ones for similar prey. The results of the analysis was to answer the question of whether the diet overlap of juvenile fish stages decreases with ontogenetic development. The study was conducted for two years (2001-2002) in two shallow, polymictic, eutrophic lakes. The diets of early developmental stages of fish species of similar body sizes differed. The few instances of diet overlap resulted from the abundance of food resources in the environment. However, fish of smaller body sizes exploited the same food resources as did individuals of the same species that belonged to different cohorts.

Keywords: diet overlap, juvenile fish, *Rutilus rutilus*, *Perca fluviatilis*, *Alburnus alburnus*, *Leucaspis delineatus*

Introduction

The co-occurrence of many fish species is often associated with the exploitation of the same food resources, and one result of this is highly similar diets

described as overlap in the exploitation of resources (Holbrook and Schmitt 1989). When food resources are limited, larval and juvenile fish compete with other similarly-sized developmental stages of other fish species, other cohorts of the same species (Garvey and Stein 1998), and with adult fish (Persson and Greenberg 1990, Olson et al. 1995). Diet overlap is often the greatest in the early larval period, when fish are likely less morphologically and behaviorally differentiated than in later periods of development (Garner 1996, Nunn et al. 2012).

Changes occurring in the diet structure of subsequent developmental stages of fish stem from the cumulative impact of many biotic factors such as the abundance and species composition of prey in the environment and their temporal and spatial distribution in lakes (Link 2004). These changes are also caused by fish body and gape size (González-Quirós and Anadón 2001, Nunn et al. 2007a). Once they begin to feed actively, larval fish grow rapidly, and their methods of locomotion and diet spectrum change. Relationships between the type and size of prey caught by early developmental stages of fish and the abundance of zooplankton in the environment have significant impacts on the growth and survival of larvae and 0+ fish (Schael et al. 1991). Temporally differentiated spawning periods of different fish species in lakes leads to differences in food consumption (Keast 1978). Juveniles of co-occurring fish species

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exploit food resources sequentially. Larval perch, *Perca fluviatilis* L., appear first (late April-early May), followed successively by other species including, among others, roach, *Rutilus rutilus* (L.), depending on water temperature. In the initial phases of life, perch feed on zooplankton and then benthic invertebrates under the impact of competition with 0+ roach (Persson 1987). Larval roach begin feeding on phytoplankton and small zooplankton-rotifers and smaller cladocerans (Mann et al. 1997, Hjelm et al. 2003, Bogacka-Kapusta and Kapusta 2007). As roach grow, their body height increases and so does their ability to maneuver, which is more suited for feeding on benthic organisms than for making the quick attacks required when preying on planktonic crustaceans (Hjelm et al. 2000). Although sunbleak, *Leucaspis delineatus* (Heckel), and bleak, *Alburnus alburnus* (L.), are very common in European lakes and rivers, little is known about their feeding ecology, the free niches they occupy, or their success when co-occurring with other species (Politou et al. 1993). In the first year of life, sunbleak and bleak food comprises small planktonic forms, then, as they grow, they begin consuming larger planktonic crustaceans and flying insects that fall onto the water surface and are readily available to them (Vinni et al. 2000, Pinder et al. 2005, Bogacka-Kapusta and Kapusta 2007).

The exploitation of limited resources by numerous individuals leads to reduced quantities of these resources that are available to all consumers, which results in food competition or the creation of equilibrium. This partitioning of resources permits long-term coexistence. This study attempts to test the hypotheses that (i) the larvae of different species with similar body sizes consume similar types of food, and (ii) smaller fish compete with larger ones for similar prey. The hypotheses were tested to determine the degree of feeding niche overlap in the early developmental stages of selected fish species. One of the elements that made it easier to test the hypotheses was the choice to study batch spawners (bleak and sunbleak), thanks to which specimens of the same body size belonging to successive cohorts occurred throughout the study.

Materials and methods

The study was conducted for two years (2001-2002) in two shallow, polymictic, eutrophic basins (Table 1). Lake Dołgie Wielkie (54°41'50"N, 17°11'24"E) is a coastal lake located between lakes Łebsko and Gardno (Słowiński National Park, northern Poland). Despite its location in a coastal zone, the lake has no direct connection with the Baltic Sea. The forested areas of the lake's drainage basin (73%) provide a natural shield for its ecosystem (Piotrowska 1997). Lake Dołgie Wielkie is a nature reserve, and, as a protected lake, there is no fisheries exploitation. Lake Gosławskie (52°17'8"N, 18°14'4"E) is a shallow, eutrophic, pond-type basin located in central Poland. Since 1969, the lake has been used as a cooling water and a post-cooling water reservoir for the Konin Power Plant (Socha and Zdanowski 2001). The litto-

Table 1
Morphological and limnological characteristics of lakes Dołgie Wielkie and Gosławskie

Characteristics	Lake Dołgie Wielkie	Lake Gosławskie
Area (ha)	156.4	454.5
Volume (thous. m ³)	2151.8	13485.3
Maximum depth (m)	2.9	5.3
Mean depth (m)	1.4	3.0
Direct catchment area (km ²)	7.1	153.9
Trophic type	eutrophic	eutrophic
Mictic type	polimictic	polimictic

ral zone is poorly developed, and only in the western part of it is the bottom overgrown with hydrophytes.

Larvae and 0+ fish were caught in shallow littoral zone habitats at six stations in Lake Dołgie Wielkie and at four in Lake Gosławskie monthly from April to August with a tulle trawl (mesh size 1 mm). In an effort to reduce the impact of daily differences in fish activity, hauls were always performed on sunny days at the same time (12:00-15:00). The fish caught were preserved in a 4% formaldehyde solution. In the laboratory, the species were identified

Table 2

Sample size, total length and body weight used in diet analysis for each fish species

Species	Total length		Body weight	
	mean	range	mean	range
Lake Dołgie Wielkie				
perch (n = 131)	29.45	14.00-39.07	0.538	0.049-1.197
roach (n = 141)	16.99	8.13-44.00	0.165	0.003-1.555
sunbleak (n = 620)	18.961	6.57-44.00	0.180	0.002-1.561
Lake Gosławskie				
perch (n = 86)	27.42	16.02-39.07	0.408	0.058-1.114
roach (n = 479)	23.98	7.82-43.34	0.335	0.001-1.547
bleak (n = 234)	16.76	7.84-35.92	0.077	0.002-0.624

(Koblickaya 1966, Mooij 1989, Pinder 2001), the fish were weighed and measured, and then they were classified into arbitrarily determined body length classes (5 mm intervals). The larvae and 0+ fish chosen for food composition analyses were from the most abundantly occurring species in the lake littoral zones (Table 2). The food composition analysis was based on the food contents found in the entire gastrointestinal tracts of ten specimens selected from each length class. In fish of such small size, the morphology of the mouth influences the composition of the diet and narrows the spectrum of potential prey, which is why, in an attempt to avoid generalizations in this study, taxonomic identification was made to the lowest possible systematic level since less detailed identification could suggest high diet overlap (Terlecki 1993). The prey were counted and their biomass was determined (Hillbricht-Ilkowska and Patalas 1967, Bottrell et al. 1976, Prejs and Colomine 1981, Ejsmont-Karabin 1998). The Schoener diet overlap index (Schoener 1970) was used to determine the diet overlap of the different fish species. The biologically significant food similarity coefficient (PS) was ≥ 60 (Lucena 2000, Jensen et al. 2004). The χ^2 test was applied to verify if the food overlap described by the PS coefficient was statistically significant. The overlap in food composition of the different species according to length class was analyzed using cluster analysis. The PS coefficient was used as the measure of distance when

determining diet overlap. The reciprocal positions among new clusters were determined with the Ward method, and the results obtained are presented as dendrograms (Stanisz 1998). The clusters were identified by interpreting the dendrograms based on the diet similarity coefficient values of the analyzed fish species. The groupings formed by diets that overlapped at a level of $PS \geq 60\%$ were described as trophic guilds.

Results

Hierarchical classification permitted designating three trophic guilds in Lake Dołgie Wielkie (Fig. 1) and four in Lake Gosławskie (Fig. 2). However, among the 27 combinations pairs of reciprocal links for which the PS similarity coefficient was higher than 60%, statistically significant overlap in the food structure was only confirmed in Lake Dołgie Wielkie in seven instances (test χ^2 , $P < 0.05$) and in Lake Gosławskie among eight combination pairs only in one instance (test χ^2 , $P < 0.05$). The diet of 0+ perch in both lakes differed in comparison to those of the other fish species so a separate branch of the dendrogram was created during the classification analysis. Perch food overlap ($>60\%$) was determined in three length classes (26-30, 31-35, 36-40 mm) in Lake Dołgie Wielkie and also in a smaller length class (21-25 mm) in Lake Gosławskie. The food

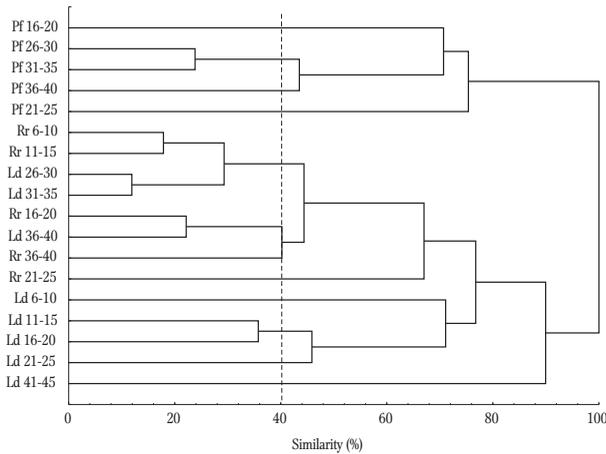


Figure 1. Cluster analysis illustrating similarity in diet composition between different size classes of perch (Pf), roach (Rr), and sunbleak (Ld) from Lake Dołgie Wielkie. Each sample represents an body length classes (mm) of each fish species.

composition overlap of perch larvae determined for the length classes in Lake Dołgie Wielkie was associated with the occurrence in the diet of the crustacean: copepodites *Thermocyclops crassus* (Fischer) and *Daphnia cucullata* Sars, while in Lake Gosławskie it was associated with the cladoceran *Sida crystallina* (O.F. Müller) and juvenile stages of the copepod *Eucyclops serrulatus* (Fischer). The second guild identified in Lake Dołgie Wielkie comprised roach (16-20 and 36-40 mm) and sunbleak with body lengths of 26 to 40 mm. These fish were placed in a separate group because of the high share in their diets of cladocerans: *Chydorus sphaericus* (O.F. Müller), *D. cucullata*, and *Bosmina coregoni* Baird, and within these groups two sub-groups were identified that exploited the same food resources. The highest diet overlap (90%) was noted for sunbleak from the two body length classes of 26-30 and 31-35 mm. The diets of roach (16-20, 36-40 mm) and sunbleak (36-40 mm) had high shares of the planktonic cladocerans *D. cucullata* and *B. coregoni*. The third guild comprised sunbleak larvae and early juvenile with body lengths of 11-25 mm. The high food overlap (70%) between these length classes of sunbleak was associated with the large shares of rotifers of the genus *Lecane*, which did not occur in the food of the other fish species.

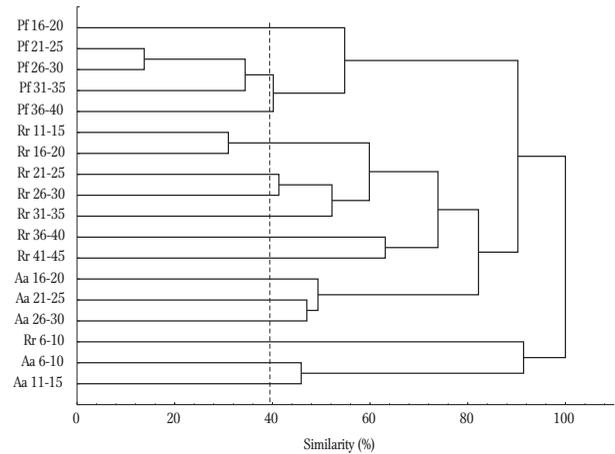


Figure 2. Cluster analysis illustrating similarity in diet composition between different size classes of perch (Pf), roach (Rr), and bleak (Aa) from Lake Gosławskie. Each sample represents an body length classes (mm) of each fish species.

In Lake Gosławskie, the food composition of the fish of the smallest body size, which were larval roach (6-10 mm) and bleak (6-15 mm), differed definitely from that of the other length classes of the fish analyzed. Larval roach (11-15 and 16-20 mm) were grouped on a separate branch of the classification tree. Within this group, the food overlap was 73% and was linked with the occurrence in the diets of the cladocerans *B. coregoni* and *Leptodora kindti* (Focke). Early juvenile roach from the subsequent length classes (21-25 and 26-30 mm) were the third guild. The value of the Schoener coefficient for this group was 64%. The food composition overlap in both size classes of roach was linked with the occurrence in them of larval Chironomidae and the large planktonic cladocerans *Alona affinis* (Leydig), *Eurycercus lammellatus* (O.F. Müller), and *L. kindti*. The fourth guild included larval bleak with body lengths of 6 to 15 mm and with a diet composition that differed distinctly from that of the other fish species. It was grouped, along with larval roach measuring from 6 to 10 mm, in a separate branch of the classification tree. Intra-group food overlap among bleak size classes (6-10 and 11-15 mm) was 60% and stemmed from the domination in the diet of juvenile and naupli copepod stages and a smaller share of the rotifer *Keratella cochlearis* f. *tecta* (Gosse).

Discussion

Larvae and early juvenile fish often compete for limited food resources with the same developmental stages of other species, with other cohorts of the same species (Garvey and Stein 1998, Nunn et al. 2012), and with adult fish (Persson and Greenberg 1990, Olson et al. 1995). Consequently, growth rates decrease, which leads to increased mortality from starvation (Letcher et al. 1996) or predation (Brabrand 2001). The periods during which the different larval species occur or in which their abundance fluctuates can intensify interactions among them. Larval assemblages with the same trophic requirements form large shoals that are characterized by high diet overlap. Differences in feeding behavior and defensive reactions to predators are probably the main factors influencing the division of the different species and the reasons why they occupy separate niches (Schoener 1983). The feed composition of 0+ perch from both lakes differed decidedly from that of the other fish species examined. Perch feeding pressure was directed at other types of prey, namely copepodites of the copepod *T. crassus* (Lake Dołgie Wielkie) and *E. serrulatus* (Lake Gosławskie), which could confirm that low diet overlap is an indication of interspecific segregation in the exploitation of available prey (Okun et al. 2005). The high diet overlap of early juvenile perch suggests that this species exploit similar food resources. In both lakes, only perch from the 16-20 mm length class was characterized by a decidedly different diet. Although diet overlap among cyprinid fish in the two lakes presented a different pattern, it did possibly suggest a certain general rule. Roach and bleak exhibited very low diet overlap, while with roach and sunbleak in Lake Dołgie Wielkie there was often considerable overlap in diet composition. However, in both instances it can be concluded that diet specialization appeared at the start of ontogenetic development. Higher diet overlap in roach and sunbleak could occur with high prey density, especially of *D. cucullata*, in the environment (Bogacka 2005). These observations are contrary to those of Garner (1996), who reports high diet

overlap among early larval stages of roach and bleak and decreases in it among the older larvae and early juveniles of these species. These differences could stem from different levels of precision in identifications, since Garner only identified the organisms in fish gastrointestinal tracts to the level of genus or family (Cladocera). This also suggests that small differences stemming from morphological and behavioral differences among related zooplankton species play significant roles in the feeding of fish larvae and juveniles. Because the diets of roach and sunbleak included, in addition to the common cladoceran *D. cucullata*, *Ch. sphaericus* and *B. coregoni*, which occurred in the lake at low abundances, the question arises of whether this is reflected in the competition between these two species. The diet overlap of roach larvae and early juveniles and sunbleak juveniles described with the Schoener coefficient was high. However, substantial niche overlap does not necessarily indicate a competitive dependence among species. It is possible that species exploit resources precisely when they are abundant.

Ontogenetic changes in diet that occur as fish larvae grow are also associated with predator avoidance and the effectiveness of feeding on various types of food (Graeb et al. 2004, Nunn et al. 2012). The increased abundance of prey influences higher diet overlap (Keast 1977, Nunn et al. 2007b), but the occurrence in the food of prey that is not a significant component of the zooplankton could be an indication of competition among these species. Small resources of potential prey occurring with high abundances of fish assemblages suggests limited access to food sources, which is reflected in the lack of diet overlap (Terlecki 1993). This situation occurred in Lake Gosławski, where zooplankton resources were relatively low in comparison to those in Lake Dołgie Wielkie (Bogacka 2005), and the diet overlap of the species compared was lower. Additionally, the diets of fish from Lake Gosławskie contained a substantial share of macroinvertebrates (Bogacka-Kapusta and Kapusta 2007), which could indicate limited access to zooplankton. The low diet overlap of the fish species analyzed in this lake suggests considerable food specialization. The slight overlap in diet composition

could have resulted from partitioning food resources or competition for food (Xie et al. 2000, Declerck et al. 2002). During ontogenetic development food specialization increases probably as a result of morphological and behavioral differentiation (Balon 1985, Nunn et al. 2007b). Specialization leads to decreased competition among species (Brabrand 1995) and increased effectiveness of feeding on less accessible prey (Scott 1987).

The results of the analysis of food composition based on the Schoener diet overlap index indicates that similarly sized early juvenile of different species most frequently feed on different prey. The few instances of significant diet overlap (roach and sunbleak 36-40 mm) was the effect of simultaneously abundant food resources. Fish of smaller sizes partially exploited the same resources as individuals of the same species belonging to another cohort (sunbleak) or of larger body sizes (perch, roach, bleak). In Lake Gośląskie, the greatest diet overlap was confirmed in perch (body length from 21 to 40 mm) and roach (11-15 and 16-20 mm and 21-25 and 26-30 mm) and larval sunbleak (6-10 and 11-15 mm). However, in Lake Dołgie diet overlap in the species analyzed was slightly higher than that in Lake Gośląskie. This permitted identifying three distinctly different guilds. The differences confirmed in the two lakes probably stem from different bases. The high diet overlap among specimens in some length classes of certain species in Lake Dołgie Wielkie was associated with the high abundance of the food base; whereas the few instances of high diet overlap of the early juveniles of various species from Lake Gośląskie that were examined probably reflects the effects of competition when food resource availability is low.

Conclusions

1. Feeding specialization in roach, bleak, and sunbleak begins in the initial period of larval development. Within species, larvae and early juveniles of different body sizes exploit the same food resources.
2. Early juveniles of different species with similar body sizes were characterized by different diet composition. The few instances of substantial similarity in diet composition were associated with abundantly available prey.

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