

Spatial heterogeneity in roach (*Rutilus rutilus*) diet among contrasting basins within a lake

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With 5 figures and 2 tables

Abstract: Habitat and diet variation of roach (*Rutilus rutilus*) were studied in Lake Banyoles (Spain), an oligotrophic karstic lake with strong spatial heterogeneity in food resources. In addition to seasonal variation in diet, roach displayed an ontogenetic shift from zooplanktivory (dominated by the cladoceran prey *Daphnia longispina*) to benthivory (based on detritus, plant debris, amphipods, algae, and other invertebrates). Strong patterns of spatial heterogeneity in roach diet were detected for this lake. Firstly, there was a winter aggregation of smaller fish in the deepest basin, where benthos was scarce but a patch of copepods had been previously described. These fish displayed a high condition and fed on zooplankton, particularly those copepods. Secondly, meiobenthos, mainly ostracods and other microcrustaceans, was more important in the diet in the shallowest basin. The ontogenetic diet shift was also mediated by spatial heterogeneity, because in basins where benthos was scarce, larger roach continued to feed on zooplankton.

Introduction

Spatial heterogeneity is a classical but difficult ecological subject (PINEL-ALLOUL 1995). In lake fish ecology, spatial heterogeneity has been generally addressed in littoral or bottom-dwelling habitats with a physically complex structure, basically in relation to prey abundance, spawning sites, or predation risk (BENSON & MAGNUSON 1992, PERSSON 1993, DIEHL & EKLÖV 1995). The implications of spatial heterogeneity not associated with a physical structure have been less well investigated. According to MIRACLE (1977) and URABE (1989), horizontal variation in zooplankton is less known than vertical or temporal variation, particularly in freshwater environments. While horizontal variation in zooplankton within the pelagic system is the rule (MIRACLE 1977,

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BETSILL & VAN DEN AVYLE 1994, PINEL-ALLOUL 1995), its effects on fish communities are largely ignored.

The effects of spatial heterogeneity in limnetic resources on roach (*Rutilus rutilus*) are largely unknown as well. Roach are cyprinid fish, dominant in many mesotrophic and eutrophic European lakes, and their ecology has been studied extensively (see PERSSON 1993, PERSSON & EKLÖV 1995, and references therein). I investigated the feeding ecology of the fish assemblage of Lake Banyoles, a Mediterranean lake dominated by exotic species including roach. This lake consists of several basins with contrasting physico-chemical features, mainly involving depth, subterranean water inflow, water circulation (holomixis/meromixis), and oxygen concentration (ROGET et al. 1993). These features produce strong spatial heterogeneity in ecological communities, which has already been well described for phototrophic bacterioplankton (GARCIA-GIL et al. 1996), zooplankton (MIRACLE 1975 and 1976), and sublittoral and profundal zoobenthos, including chironomids (PRAT & RIERADEVALL 1995) and oligochaetes (RIERADEVALL & REAL 1994). The purpose of my study is to assess the effects of this spatial heterogeneity on the feeding ecology of roach. Additionally, this exotic population of roach is one of the southernmost in Europe. Because the lake is monomictic (not ice-covered in winter), my study includes winter data in contrast to most previous studies.

Methods

Study area

Lake Banyoles is situated at 42° 7' N, 2° 45' E and 172 m above sea level in Catalonia (Spain). It is a lake of mixed tectonic-karstic origin, consisting of six basins and twelve bottom springs with suspended sediment (Fig. 1). The mainly subterranean water inflow and the high concentration of calcium constrain its productivity. It is usually considered to be oligotrophic because of the low nutrient concentration and phytoplankton biomass, though according to primary production and benthic community it is rather mesotrophic. Several detailed studies on its morphometry (MORENO-AMICH & GARCIA-BERTHOU 1989), hydrology (ROGET et al. 1993), bacterioplankton (GARCIA-GIL et al. 1996), phytoplankton (PLANAS 1973), zooplankton (MIRACLE 1976, MIRACLE & VICENTE 1983), and non-littoral zoobenthos (RIERADEVALL 1993, RIERADEVALL & REAL 1994, PRAT & RIERADEVALL 1995) are available (see Table 1 for selected features of the lake). This paper is part of the first comprehensive study of the fish assemblage that focuses on feeding ecology (GARCIA-BERTHOU 1994). An interesting feature of the lake is the contrasting limnology of the basins. Basins I and II are holomictic whereas basins III and IV are meromictic and anoxic in summer. Basin II is much deeper and basin IV shallower (Fig. 1). For this reason, basin II has almost no benthos all the year and in basins III and IV it disappears in summer. The hypolimnetic zooplankton community is also very different among basins.

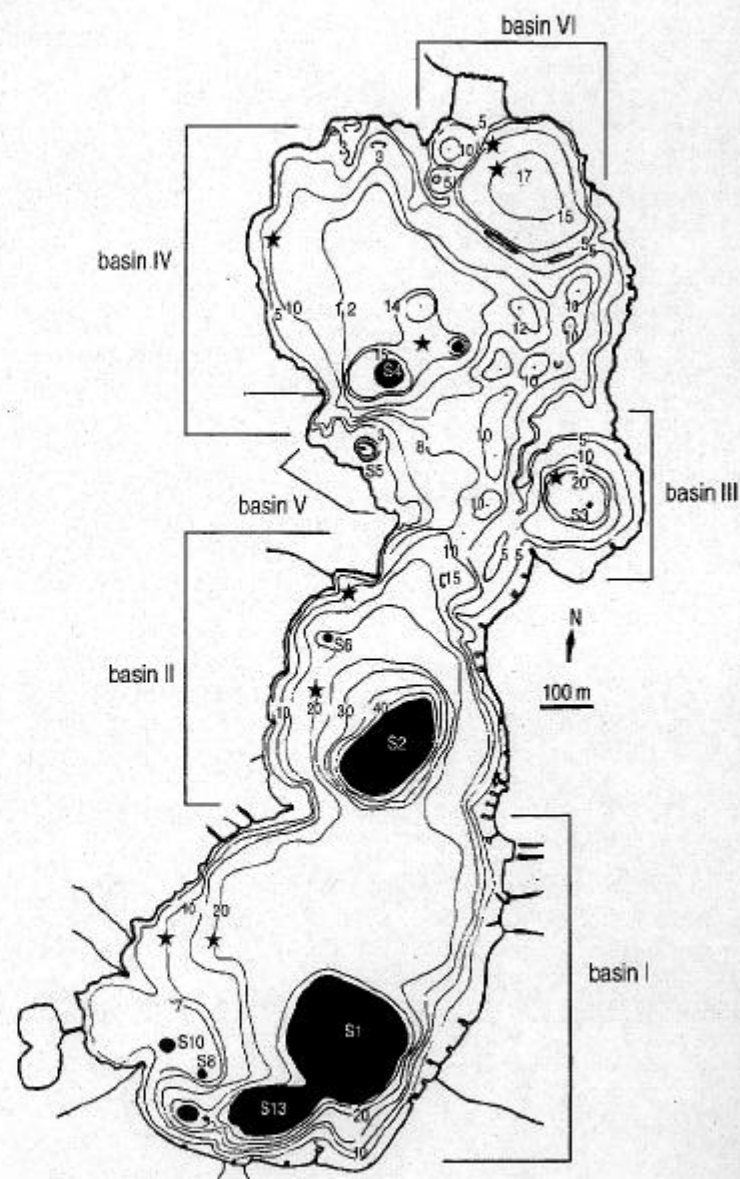


Fig. 1. Bathymetric map of Lake Banyoles (MORENO-AMICH & GARCIA-BERTHOU 1989), showing the different basins and bottom springs (S). ★ = sampling point with trammel nets (limnetic and bottom).

Table 1. Selected limnological features of Lake Banyoles (see e.g., MARGALEF 1983, GARCÍA-BERTHOU 1994).

Area	111.8	ha
Volume	16.1	hm ³
Mean depth	14.8	m
Temperature	7–26	°C
Conductivity	0.9–2	mS/cm
pH	6.8–8	
Total P	0.001	mg/l
Ca ²⁺	88–160	mg/l
SO ₄ ²⁻	512–835	mg/l
Phytoplankton biomass	1–4	mg chl-a/m ³
Phytoplankton production	81.8	g C m ⁻² year ⁻¹

Field and laboratory methods

Fish of Lake Banyoles were sampled in February, May, August, and November 1991 by boat electrofishing in the littoral and with trammel nets (stretched mesh size: inner net, 2 cm; outer, 12.5 cm). Trammel nets are less often used than gillnets but, for feeding studies, they have the advantage of being less size selective (HUBERT 1983), so a broader range of fish sizes is obtained. Trammel net size was 6×2 m in the littoral and 20×2.5 m in the rest of the lake. The sampling points for the latter (Fig. 1) were almost identical to those of a previous study of benthos (RIERADEVALL & REAL 1994, PRAT & RIERADEVALL 1995) and limnetic trammel nets were placed at 5, 10, and 15 m of depth and bottom trammel nets at 10 and 20 m, or 10 and 15 m for shallower basins (IV and VI). Nets were set for 24 h on six consecutive days. All basins except number V were sampled. Captured fish were immediately stored on ice and later frozen.

At the laboratory, fish were measured (fork length to the nearest mm) and weighed (to the nearest 0.1 g). The entire gut was preserved in 70% ethanol until analysis and eviscerated fish were weighed. Out of 323 roach captured, the whole gut contents of 261 individuals were examined under a dissecting microscope. First, I tried to identify all food categories present and especially to detect rare larger prey, which were separated. A subsample corresponding to about 10% (benthic food) or 25% (zooplankton) was then taken, after homogenisation, for more precise analysis. Prey were sorted with the highest possible taxonomic precision, usually to the species or genus level. Animal prey (i.e., excluding detritus, plant material and other uncountable material) were counted and all food categories weighed to the nearest 0.1 mg, after blotting the excess moisture. When available, four individuals of the cladoceran *Daphnia longispina* were measured (excluding caudal spine) with an ocular micrometer.

Data analyses

Although different sampling methods were used, the sampling effort was constant in different seasons and basins, and some general patterns of habitat use were clear considering the number of captured individuals. A hierarchical log-linear model was performed on this number, with depth, season, basin, and sampling method as categorical

factors, and impossible combinations of factors (e.g., electrofishing not at surface or non-existent depths of shallow basins) as structural zeros.

Percent number, percent biomass and frequency of occurrence were used to estimate the dietary importance of each food category. Percent number is the number of individuals of a prey type divided by the total number of individuals and expressed as a percentage, after pooling the gut contents of all fish. Percent biomass is the equivalent measure for biomass data. Frequency of occurrence is the percentage of guts in which a food category was present. To describe prey importance and feeding strategy, I used COSTELLO's (1990) graphical method, i.e. a plot of percent number (or biomass) versus frequency of occurrence. The most important prey are closer to the top right corner. The other diagonal corresponds to feeding strategy; prey with low occurrence but dominant by number or biomass correspond to some sort of specialisation and are closer to the top left corner.

Correspondence analysis (CA) was used to describe the main sources of diet variation, separately for number and biomass data. CA is an ordination technique generally better than principal component analysis for community ecology data (TER BRAAK 1987). This technique is better than the traditional procedure of a priori pooling food categories, which is usually based on taxonomic rather than on ecological criteria (GRAHAM & VRIJENHOEK 1988). Correlation analysis and an analysis of variance (ANOVA) design without interaction were used to interpret the dimensions in terms of the measured spatio-temporal coordinates of the fish samples.

Other variables (e.g., fish length and eviscerated weight) were analysed with analysis of covariance (ANCOVA). For instance, instead of computing a condition factor I analysed the variation in eviscerated weight of individuals (variable) among seasons and basins (factors) removing the effect of fish length (covariate) with ANCOVA (GARCÍA-BERTHOU & MORENO-AMICH 1993). Most variables were log-transformed because homoscedasticity and linearity were clearly improved. All factors (e.g., season, basin) of linear models were considered of fixed effects. All data analyses were performed with SPSS for Windows 6.0.

Results

Habitat use of roach

A hierarchical log-linear model on the number of fish captured showed that season × basin and depth × basin were the strongest two-way interactions ($P < 0.00005$), i.e. the seasonal and depth variation in the number of individuals captured depended mainly on basin, because there were two clear patterns of spatial heterogeneity (Fig. 2). First, most individuals captured at 0 m (electrofishing) during spring were from basins IV and II, which provide the best spawning grounds for roach due to the scarcity of vegetation along most of eastern shore. Second, out of 157 roach captured at 10 m: in winter, 16 were captured in basin II and 14 in the rest of basins; while for the rest of the year the respective counts were 10 and 117. This shows an aggregation in basin II

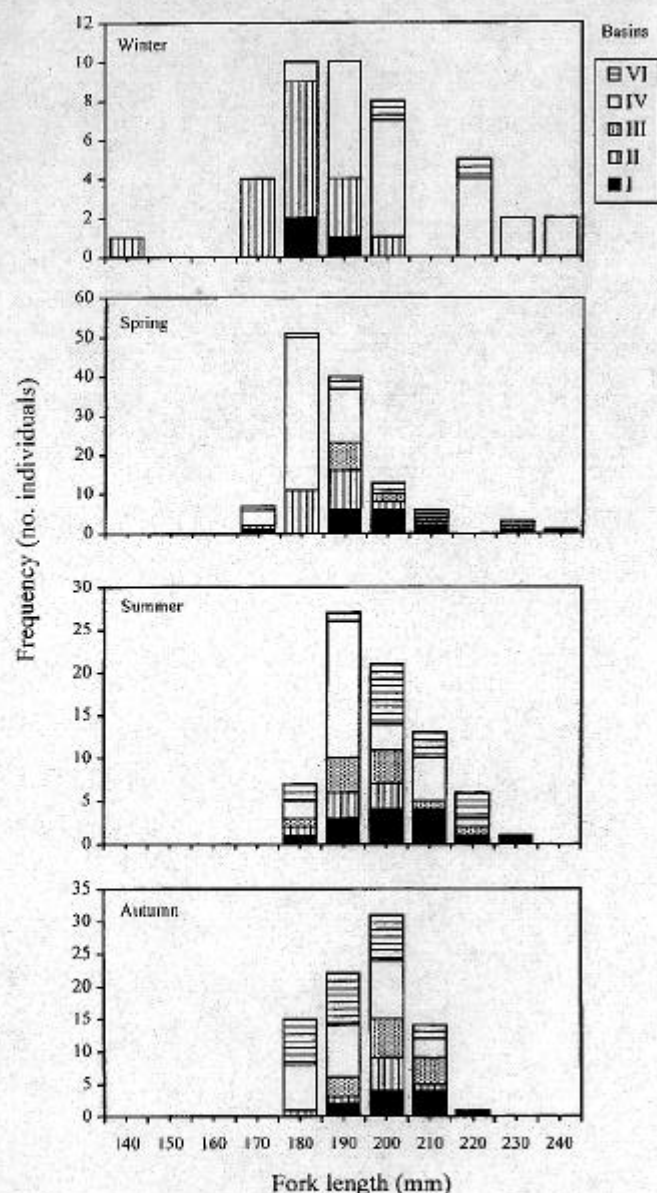


Fig. 2. Number of roach individuals captured by season, basin, and length class.

during winter that is consistent with the spatial heterogeneity of food resources (see Diet variation).

Moreover, there was ontogenetic variation in habitat use with a strong tendency of larger roach to use deeper zones (ANCOVA, $F_{1,294} = 39.2$, $P < 0.0005$). Season ($F_{3,294} = 2.9$, $P = 0.034$) and season-by-basin interaction ($F_{11,294} = 3.4$, $P < 0.0005$) were significant but basin was not ($F_{4,294} = 0.50$, $P = 0.74$). This is because roach were slightly smaller in spring (mean = 187.4 mm) than the rest of the year but this difference was highly dependent on basin (Fig. 2). The smallest mean size (178.8) corresponded to the aforementioned 16 winter fish of basin II (10 m); i.e., aggregation mainly involved smaller individuals.

Interestingly, eviscerated weight variation was significant for basin (ANCOVA, $F_{4,234} = 7.2$, $P < 0.0005$), nonsignificant for season ($F_{3,234} = 0.32$, $P = 0.81$), and significant for their interaction ($F_{11,234} = 2.3$, $P = 0.010$) and fish from basin II displayed the highest condition (mean of eviscerated weight, adjusted for length) in winter.

Roach diet

D. longispina was by far the most important animal prey for roach (Fig. 3, Table 2). Less notable prey were other planktonic cladocerans, like *C. reticulata* and *A. affinis*. There was also a strong benthic component, basically consisting

Table 2. Roach diet in Lake Banyoles: percent number, percent biomass, and frequency of occurrence of the main food components. Number of guts analysed = 261; total number of prey in the gut contents = 377,080; total biomass = 169.2 g. Note that the less important food categories have been pooled, in contrast to elsewhere in this paper.

Food category	Percent number	Percent biomass	Frequency of occurrence
Detritus	—	57.5	47.5
Algae	0.001	0.99	19.2
Plant debris	—	1.0	69.0
Plant leaves	—	0.18	1.9
Plant seeds	0.09	0.23	8.8
Digested material	—	29.4	60.2
<i>Ceriodaphnia reticulata</i>	6.3	1.4	8.8
<i>Daphnia longispina</i>	82.8	7.6	41.8
<i>Alona affinis</i>	2.2	0.26	4.6
<i>Candona</i> sp.	1.0	0.08	15.3
<i>Echinogammarus</i> sp.	1.0	0.28	21.1
Other Crustacea	3.9	0.25	30.3
Nematocera pupae	0.20	0.07	11.5
Nematocera exuviae	0.41	0.39	11.9
Other Insecta	1.7	0.47	35.2
Other invertebrates	0.29	0.003	8.8

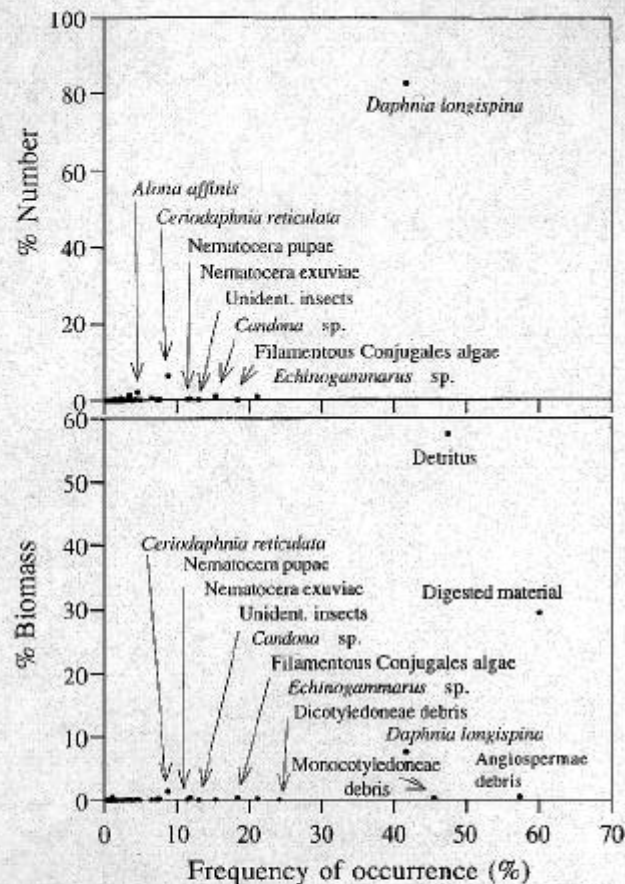


Fig. 3. Relationship among percent number, percent biomass, and frequency of occurrence of the main components of roach diet. Plots based on COSTELLO's (1990) method. Detailed food categories are the most important dietary items.

of detritus, which was dominant by occurrence and especially by biomass. Other important benthic food categories were plant debris, amphipods (*Echinogammarus* sp.), filamentous algae (Conjugales), and ostracods such as *Candona* sp.

The relationship between the three descriptors was different for zooplankton and benthic prey, the former being more important in number and biomass compared to their occurrence (Fig. 3). This is due to a greater specialisation of zooplanktivorous fish, i.e., when zooplankton is present in the gut contents it is dominant while the benthivorous fish diet is more diverse. Therefore, these simple plots suggest two alternative feeding strategies, as described below.

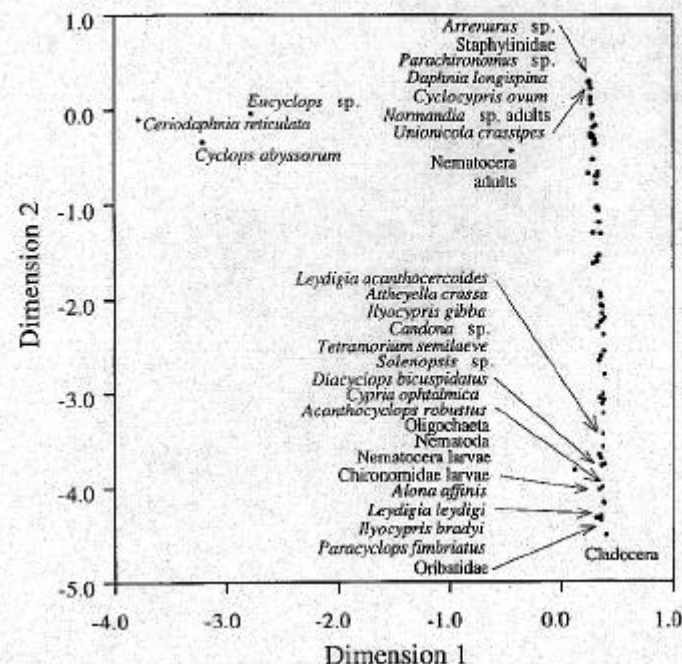


Fig. 4. Correspondence analysis of gut contents (prey number) of roach: food category scores for the first two dimensions.

Diet variation

For correspondence analysis of prey number, the first three dimensions explained 18% of the variation. The first dimension (hereafter *D1*) distinguished three zooplankton species from the rest of food categories: *C. reticulata* and two cyclopoid copepods, *C. abyssorum* and *Eucyclops* sp. (Fig. 4). *D1* fish scores were significantly correlated to fork length ($r = 0.39$, $n = 208$, $P < 0.0005$) and the 17 individuals with the lowest *D1* scores were less than 19 cm long. Furthermore, *D1* fish score showed seasonal (ANOVA: $F_{3,194} = 12.8$, $P < 0.0005$), among-basin ($F_{4,194} = 14.5$, $P < 0.0005$), and depth ($F_{6,194} = 3.4$, $P = 0.003$) variation because 14 out of the 17 individuals were captured in winter at a depth of 10 m in basin II; i.e., these fish correspond to the aforementioned aggregation. This food pattern agrees with the presence in basin II of an almost permanent population of adult *C. abyssorum* in contrast to the northern basins (MIRACLE 1975 and 1976). Therefore, *D1* showed the previously reported zooplankton patch, which induces aggregation of small roach.

The higher scores of the second dimension (hereafter *D2*) corresponded to zooplankton (*D. longispina*, *U. crassipes*, and *C. ovum*) and neuston such as

nematoceran and coleopteran (Staphylinidae and *Normandia* sp.) adults (Fig. 4). The lower $D2$ values corresponded to sublittoral and profundal prey, particularly meiobenthos (RIERADEVALL 1993), like chydorid cladocerans (*L. leydigi*, *L. acanthocercoides*, and *A. affinis*), ostracods (*Candona* sp., *C. ophthalmica*, and *I. bradyi*), nematodes, and cyclopoid copepods (*P. fimbriatus* and *D. bicuspidatus*). $D2$ was not significantly related to fork length ($r = -0.10$, $n = 208$, $P = 0.15$) but showed seasonal (ANOVA: $F_{3,194} = 8.6$, $P < 0.0005$), among-basin ($F_{4,194} = 7.9$, $P < 0.0005$) and depth ($F_{6,194} = 2.2$, $P = 0.045$) variation. Out of the 51 individuals with lowest $D1$ scores, most were from basin IV, captured at 10 m or more of depth, and only 2 in summer. These results agree with sublittoral and profundal benthos data because the meiobenthic prey, especially ostracods, are much more abundant in basin IV than in the remaining basins, and in that basin they decrease markedly in summer because of stronger anoxia (RIERADEVALL 1993). Therefore, $D2$ illustrates how spatial heterogeneity coupled with seasonal variation affects roach feeding.

Correspondence analysis of biomass data showed a similar pattern and the first two dimensions overall explained 31% of the variation. The second dimension was almost identical to the first one for number data. The first dimension ($D1$) was slightly similar to the second one for number data. However, the lower $D1$ scores differentiated zooplankton (*D. longispina*, *C. flavicans* larvae, *D. bicuspidatus*, and unidentified cyclopoids) or related food (digested material, diatoms, the chydorid *C. sphaericus*, *C. ovum*, *C. flavicans* pupae, and the cyclopoid *M. albidus*), neuston (floatoblasts of the bryozoan *P. repens*, cladoceran ephippia, *Normandia* sp. adults), and prey of terrestrial origin (ants). $D1$ was significantly related to fork length ($r = 0.17$, $n = 261$, $P = 0.005$) and thus showed an ontogenetic shift from zooplanktivory to a benthivorous diet. Moreover, $D1$ displayed seasonal (ANOVA, $F_{3,247} = 6.6$, $P < 0.0005$) and among-basin ($F_{4,247} = 5.1$, $P = 0.001$) variation but was nonsignificant for depth ($F_{6,247} = 1.5$, $P = 0.17$). Low $D1$ fish scores corresponded mainly to basin II; some corresponded in decreasing frequency order to III, IV, and VI, and few to I or the summer period. Therefore, zooplanktivory was much less common in summer, when cladocerans were not so available, and more common in basin III and especially II. This spatial heterogeneity in roach food is entirely consistent with benthos and limnological data: basin III is the most anoxic and hence its benthic community has the lowest biomass, completely dominated by the partially-planktonic (migratory) *C. flavicans* (RIERADEVALL 1993, RIERADEVALL & REAL 1994) while II is the deepest basin, with most of its bottom more than 20 m deep, where there is almost no benthos (RIERADEVALL 1993) or fish (MORENO-AMICH et al., unpubl. echosounding data). The availability of benthos for roach is much higher in basins IV, VI, and I.

A more traditional way of describing dietary data (Fig. 5) provided further explanation of these results. The dietary proportion of planktonic cladocerans

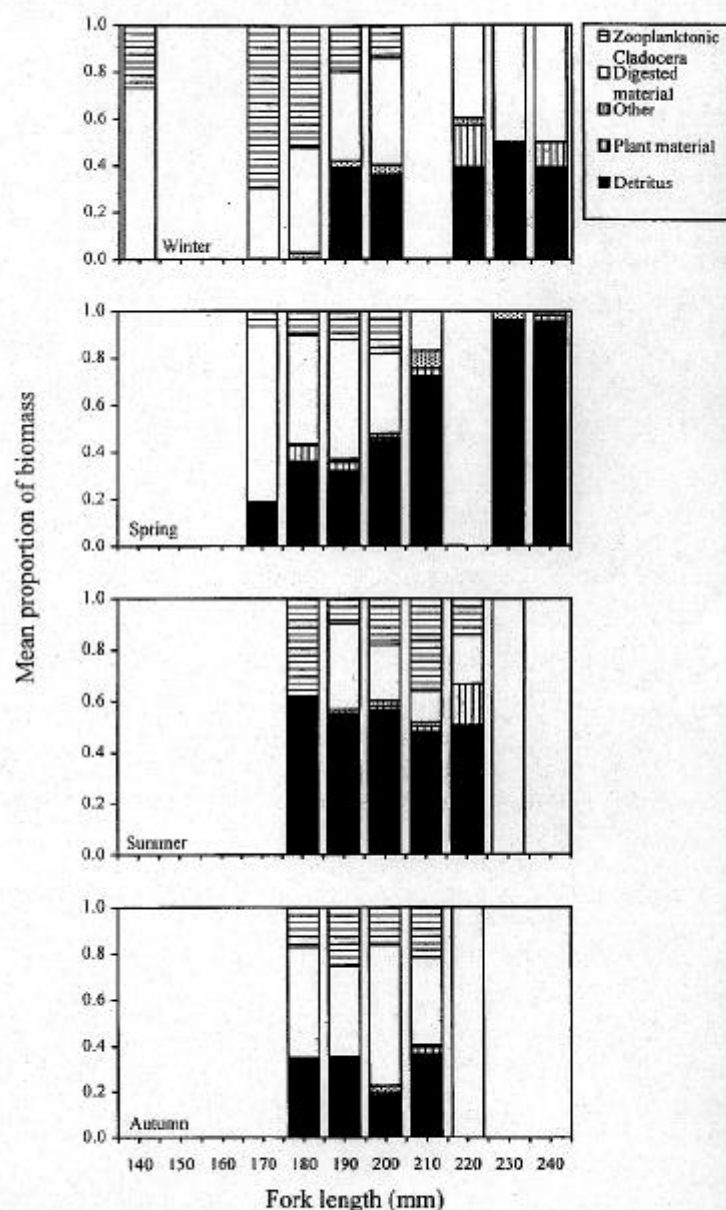


Fig. 5. Ontogenetic and seasonal variation in the main food categories in roach diet. Data are the proportion of gut biomass for each category, averaged for 10 mm length classes of roach.

decreased with roach size (ANCOVA, $F_{1,253} = 4.8$, $P = 0.030$), but the slope varied seasonally ($F_{3,253} = 3.2$, $P = 0.024$). Zooplankton was less important in spring and more in winter ($F_{3,253} = 3.7$, $P = 0.013$), when strong ontogenetic variation was evident. Most other food categories provided similar statistical results but with positive slopes. Detritus was more important in spring and summer, and the ontogenetic increase stronger in spring and winter. Plant material, less important, also increased with size, especially in winter, and was less common in autumn. On the other hand, there was no ontogenetic variation in size-selectivity of *D. longispina* (relationship between *D. longispina* body length and roach fork length: $r = -0.09$, $n = 97$, $P = 0.38$).

Discussion

Roach diet and resource availability

A zooplanktivorous diet based on cladocerans has been reported previously for many other lake populations of roach (PERSSON 1983, CRYER et al. 1986, PERSSON & GREENBERG 1990). The lesser importance of copepods is general in fish, including roach (GILES et al. 1990, JAMET et al. 1990, GLIWICZ & JACHNER 1992). Experimental studies with roach and rudd have shown that feeding rates are higher and handling times lower when feeding on *Daphnia magna* than on *Cyclops* sp. (JOHANSSON 1987) and that *Cyclops vicinus* displays a fast escape behaviour which reduces the attack efficiency of roach to less than 20% (WINFIELD et al. 1983). I detected six different species of cyclopoid copepods in roach diet but not the calanoid copepod dominant in the lake (*Arctodiaptomus salinus*), probably because calanoids are even more difficult to capture than cyclopoids due to their higher escape ability (HURLBERT & MULLA 1981).

However, roach are omnivorous and other food categories, like detritus (very important in Lake Banyoles), macrophytes, zoobenthos, and even planktonic Cyanophyceae can account for up to 70% of diet, depending on availability (NIEDERHOLZER & HOFER 1980, PERSSON 1983, VØLLESTAD 1985, L'ABÉE-LUND & VØLLESTAD 1987, MARTYNIK et al. 1991). The consumption of plant material in my study (overall, 2.4% of biomass) was lower than for many other populations (PREJS 1973 and 1984, PREJS & JACKOWSKA 1978, PREJS et al. 1990, MARTYNIK et al. 1991), because submerged macrophytes were not abundant in Lake Banyoles due to low productivity and a peculiar bathymetry with scarcity of shallow bottoms. The use of food of plant origin depends basically on the relative availability (PREJS 1978, NIEDERHOLZER & HOFER 1980). In two close British lakes, diet was zooplanktivorous (*Daphnia hyalina*) or herbivorous (Conjugales algae: *Spirogyra* sp.) depending on availability (GILES et al. 1990).

The seasonal variation in diet, with eventually increased use of benthos, is common when there is a season with lower zooplankton availability (VØLLESTAD 1985, MARTYNIK et al. 1991). In many temperate lakes, there is more use of non-animal food by roach in summer, as in Lake Banyoles, due to increased resource limitation (PERSSON 1983, PERSSON & GREENBERG 1990).

Similarly, though roach are considered one of the most efficient molluscivores among European cyprinids (WINFIELD & WINFIELD 1992), the consumption of molluscs in Lake Banyoles was negligible (overall, 0.03% of biomass) compared to other studies (RASK 1989, PREJS et al. 1990, MARTYNIK et al. 1991). Molluscs were not consumed simply because they are rare in Lake Banyoles due to the scarcity of submerged macrophytes. The same was observed in another notable molluscivorous fish, the pumpkinseed sunfish (*Lepomis gibbosus*), which has also been introduced into the lake (GARCÍA-BERTHOU 1994).

Winter aggregation of roach in basin II of Lake Banyoles

This study (*D1* for prey number) has detected a winter aggregation of smaller roach, with high condition, exploiting a zooplankton patch in the deep limnetic water of basin II. The spatial heterogeneity of zooplankton had been documented previously for this lake. Copepods, especially *A. salinus* and *C. abyssorum*, are the most segregated among different basins because they are the largest and most mobile (MIRACLE 1975). The southern basins (I and II) have a permanent population of these two copepod species, in contrast to the northern basins (III, IV and VI) where they decrease markedly in winter (MIRACLE 1976). Although the mechanism generating these differences is largely unknown, it seems that in the southern basins, which are deeper, there is enough phytoplankton production in winter to maintain *A. salinus* and its predator *C. abyssorum*. Recently, a hydrological feature has been described that might be related to this zooplankton patch. During the mixing period (autumn and winter), there is a strong bottom current from the northern to the southern basins, due to differential heating and depth (ROGET et al. 1993). This baroclinic current may enhance phytoplankton or zooplankton production and explain the spatial heterogeneity. Unfortunately, though an annual cycle of phyto- and zooplankton of the lake was thoroughly studied in 1970–1971, there are no further comprehensive data on its trophic state and plankton community.

There are few references reporting a link between horizontal heterogeneity of zooplankton and fish migration within a lake. The larvae of a zooplanktivorous cyprinid in Lake Kinneret (Israel) aggregated near inflowing streams, where prey (rotifers) were more abundant (LANDAU et al. 1988). A more common pattern is migration from the lake to a tributary, which L'ABÉE-LUND &

VØLLESTAD (1987) described for a roach population due to feeding and reproductive reasons.

I believe this kind of aggregation has been neglected in the literature, in part due to the rare use of correspondence analysis (CA) or other multivariate techniques in feeding studies. The traditional procedure for analysing dietary data consists of pooling food categories a priori into some broad groups and simply representing percentages of use of these groups by season or size, and ignoring other factors. In this study, CA detected a relatively small group of fish that had a homogeneous, peculiar diet, which contrasted with the rest of the individuals and was distinguished by particular food categories (not all zooplankton taxa). The advantage of CA over the traditional procedure is that in CA: a) similar food categories are identified by the method according to common occurrence, and not subjectively pooled a priori by the researcher (often by taxonomic rather than ecological criteria), and b) relevant factors (e.g., fish size, season) are not selected a priori but emerge from similarity of samples. The virtues of multivariate ordination methods and particularly CA and related techniques are well appreciated and documented in "pure" community ecology. Unfortunately, the use of ordination methods is still rare in feeding ecology though it would benefit from the same advantages.

Spatial heterogeneity and ontogenetic variation in diet

The ontogenetic shift to a more benthivorous diet by roach in Lake Banyoles has already been reported in many other populations (BERGSTRAND 1990, JAMET et al. 1990, MARTYNIAK et al. 1991), especially in relation to an increased consumption of plant material (MANN 1973, PREJS 1978, NIEDERHOLZER & HOFER 1980, JAMET et al. 1990). Though ontogenetic food variation is almost universal among fish (WERNER & GILLIAM 1984), it is more pronounced in species attaining a larger size, like perch (*Perca fluviatilis*) or largemouth bass (*Micropterus salmoides*). Ontogenetic variation has been shown experimentally to depend on interspecific competition, e.g., an increase in roach density induces the shift by perch from zooplanktivory to benthivory (PERSSON & GREENBERG 1990). It has also been demonstrated to interact with predation risk and the structural complexity of the littoral, i.e., macrophyte abundance (PERSSON & EKLÖV 1995).

The results of this study (*D1* for biomass data) showed ontogenetic variation interacting with spatial heterogeneity, i.e., the shift from zooplanktivory to benthivory depends on the contrasting availability of resources in different basins. In basins II and III, where benthos is scarce, larger roach continued to feed on zooplankton in contrast to the other basins, where there was the usual ontogenetic niche shift to benthic prey. As far as I know, this feature has not been documented before, probably because less is known about fish interac-

tions in the open water compared to the littoral, where most fish experiments have been made. The same pattern should be expected in reservoirs, where there is often strong spatial heterogeneity (URABE 1989, BETSILL & VAN DEN AVYLE 1994).

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