



## Rudd (*Scardinius erythrophthalmus*) introduced to the Iberian peninsula: feeding ecology in Lake Banyoles

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### Abstract

The first data on the ecology of rudd (*Scardinius erythrophthalmus*) introduced to the Iberian peninsula are presented. The habitat and diet variation of rudd were studied in Lake Banyoles (Spain), an oligotrophic karstic lake dominated by exotic fish species. Rudd were strictly littoral and the diet was based on detritus and plant material. The most important animal prey were the cladocerans *Daphnia longispina* and *Scapholeberis rammneri*, amphipods and several late stages of nematoceran dipterans. Rudd were more zooplanktivorous in spring and autumn and less in summer. There was also a size-dependent diet shift, from microcrustaceans to macroinvertebrates. The diet of rudd was also distinguished by the importance of plant material and various small neustonic invertebrates, particularly *S. rammneri* and late stages of nematocerans, showing a strong resource partitioning with other fish species. The degree of herbivory in Lake Banyoles was lower than usual.

### Introduction

Rudd (*Scardinius erythrophthalmus*) are medium-sized cyprinid fish native to freshwaters of Europe and western Asia. In many European lakes, they are a littoral species, closely associated to vegetation (Holčík, 1967; Johansson, 1987; Haberlehner, 1988; Eklöv & Hamrin, 1989). The knowledge of their ecology is largely limited to ecophysiological aspects related to their high degree of herbivory (see Niederholzer & Hofer, 1980; Prejs, 1984 and references therein). Little is known about their habitat and diet in natural conditions besides some few studies on the behaviour (Haberlehner, 1988) and vulnerability to predation (Eklöv & Hamrin, 1989).

The interest in rudd ecology has been recently increased due to their potential impact as an exotic species. Rudd are not native to the Iberian peninsula, where they were introduced early in this century through Lake Banyoles (García-Berthou, 1994; García-Berthou & Moreno-Amich, 2000a). They were also introduced into the U.S.A. in late 19th century

or early 20th and since the 1980s are expanding their distribution (Burkhead & Williams, 1991), though their interactions with native species remain unknown (Easton et al., 1993).

We investigated the feeding ecology of the fish assemblage of Lake Banyoles, a Mediterranean lake dominated by exotic species, including rudd, roach (*Rutilus rutilus*), largemouth bass (*Micropterus salmoides*) and pumpkinseed sunfish (*Lepomis gibbosus*) (García-Berthou & Moreno-Amich, 2000a). The main purposes of this study are to report the first data on rudd ecology in the Iberian peninsula, and to describe the diet of rudd introduced into a Mediterranean lake.

### Materials and methods

#### Study area

Lake Banyoles, the second largest lake of the Iberian peninsula, 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 several basins with contrasting ecological features and containing bottom springs with suspended sediment (see bathymetric map in Moreno-Amich & García-Berthou, 1989). The mainly subterranean water sources and high calcium concentration restrict its productivity. Although usually considered oligotrophic because of the low nutrient concentration and phytoplankton biomass, it is rather mesotrophic according to its primary production and its benthic community. A number of detailed studies are available on its morphometry (Moreno-Amich & García-Berthou, 1989), hydrology (Roget et al., 1993), bacterioplankton (García-Gil et al., 1996), phytoplankton (Planas, 1973), zooplankton (Miracle, 1976) and non-littoral zoobenthos (Prat & Rieradevall, 1995). This paper is part of a comprehensive study on the feeding ecology of the entire fish assemblage (García-Berthou, 1994, 1999a, b; García-Berthou & Moreno-Amich, 2000b). The history of fish introductions in the lake and its current fish assemblage are described elsewhere (García-Berthou & Moreno-Amich, 2000a). The littoral of Lake Banyoles is dominated by the largemouth bass and pumpkinseed sunfish and the rest by roach and common carp (*Cyprinus carpio*). Other exotic fish species such as mosquitofish (*Gambusia holbrooki*) and perch (*Perca fluviatilis*) are also present, while freshwater blenny (*Salaria fluviatilis*) and chub (*Leuciscus cephalus*) are the most common among the remaining native species.

#### *Field and laboratory methods*

Fish from Lake Banyoles were sampled quarterly from December 1990 to November 1991. Sampling was by boat electrofishing in the littoral and with trammel nets (stretched mesh size: inner net, 2 cm; outer, 12.5 cm) elsewhere. Trammel net size was 6 × 2 m in the littoral (i.e. set at 0–2 m deep) and 20 × 2.5 m in the rest of the lake. The latter sampling points are given elsewhere (García-Berthou, 1994, 1999a). Limnetic trammel nets were placed at 5, 10 and 15 m of depth and bottom trammel nets at 10 and 20 m or 15 m for shallower basins. Nets were set for 24 h on six consecutive days. All 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 the eviscerated fish were weighed. The gut contents of all captured rudd (56 individuals) were ex-

amined under a dissecting microscope. First, we tried to identify all food categories present and especially to detect rare larger prey, which were separated. A subsample corresponding to about a 10% (benthic food) or 25% (zooplankton) was then taken, after homogenisation, for more precise analysis. Prey were sorted usually to the species or genus level. Prey were counted and food categories weighed to the nearest 0.1 mg, after blotting the excess moisture.

#### *Data analyses*

Percent number, percent biomass, frequency of occurrence and mean biomass percentage 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. Mean biomass percentage is the biomass percentage of a prey type in the gut, averaged for all the fish. The graphical method of Costello (1990) was used to describe prey importance and feeding strategy.

Correspondence analysis (CA) was used to describe the main sources of diet variation, separately for number and biomass data. CA is an ordination technique that reduces a species × sample matrix to a few dimensions explaining most of the variation. For community ecology data, CA generally performs better than principal component analysis (Ter Braak, 1987). CA is better than the usual procedure of *a priori* pooling food categories, which is usually based on taxonomic rather than on ecological criteria (Graham & Vrijenhoek, 1988). Correlation analysis and analysis of variance (ANOVA) of the sample (fish) scores were used to interpret the dimensions in terms of fish length and season. All data analyses were performed with SPSS for Windows 6.0.

## **Results**

#### *Fish analysed*

Rudd were captured only at 0–2 m of depth (Figure 1). No rudd was captured with limnetic trammel nets (at 5 m or deeper), despite having the same mesh size than littoral nets. This contrasts with similarly-sized roach, which were dominant in the limnetic zone (Figure 1) and indicated that rudd were strictly littoral. Rudd was

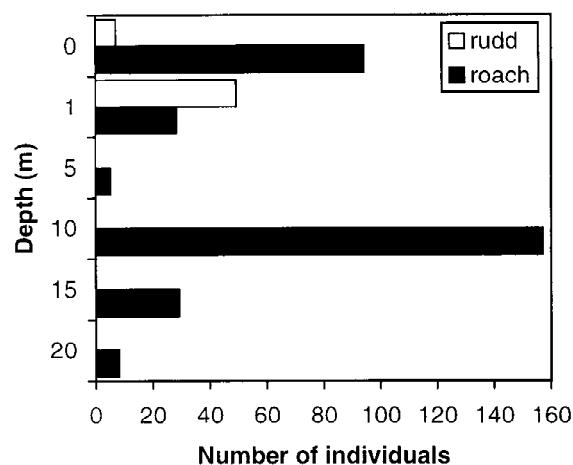


Figure 1. Number of rudd and roach captured by depth in Lake Banyoles.

Table 1. Diet of rudd in Lake Banyoles: percent number, percent biomass, frequency of occurrence and mean biomass percentage of the main food components. Number of guts analysed = 56; total number of prey in the gut contents = 31 058; total biomass = 66.6 g

| Food category                 | Percent number | Percent biomass | Frequency of occurrence | Mean biomass percentage |
|-------------------------------|----------------|-----------------|-------------------------|-------------------------|
| Detritus                      | –              | 36.4            | 39.3                    | 26.2                    |
| Algae                         | 0.0            | 12.3            | 37.5                    | 10.4                    |
| Plant debris                  | –              | 13.2            | 69.6                    | 10.0                    |
| Monocotyledoneae leaves       | –              | 6.0             | 7.1                     | 3.3                     |
| Plant seeds                   | 0.8            | 0.1             | 7.1                     | 0.1                     |
| Digested material             | –              | 30.3            | 57.1                    | 47.6                    |
| <i>Scapholeberis rammneri</i> | 55.1           | 0.3             | 5.4                     | 0.2                     |
| <i>Daphnia longispina</i>     | 28.0           | 0.6             | 14.3                    | 1.3                     |
| <i>Echinogammarus</i> sp.     | 1.6            | 0.3             | 16.1                    | 0.3                     |
| Other Crustacea               | 0.3            | 0.0             | 10.7                    | 0.0                     |
| Nematocera pupae              | 0.9            | 0.0             | 14.3                    | 0.0                     |
| Nematocera exuviae            | 5.0            | 0.3             | 12.5                    | 0.4                     |
| Nematocera adults             | 3.9            | 0.1             | 5.4                     | 0.1                     |
| Other Insecta                 | 3.5            | 0.1             | 39.3                    | 0.1                     |
| Other invertebrates           | 0.8            | 0.0             | 5.4                     | 0.0                     |
| Fish                          | 0.0            | 0.2             | 1.8                     | 0.1                     |

not abundant (of the 1321 captured individuals of 11 fish species only 56 were rudd) and the sample was dominated by large individuals (fork length: range of 138–259 mm, mean = 200.9 mm, SE = 3.42 mm). There was no significant seasonal variation in mean length (ANOVA,  $F_{3,52} = 1.70$ ,  $P = 0.18$ ).

#### Rudd food

Due to the low abundance of rudd, only the clearest, general patterns of variation in diet are described. Detritus and plant material were the basis of rudd food

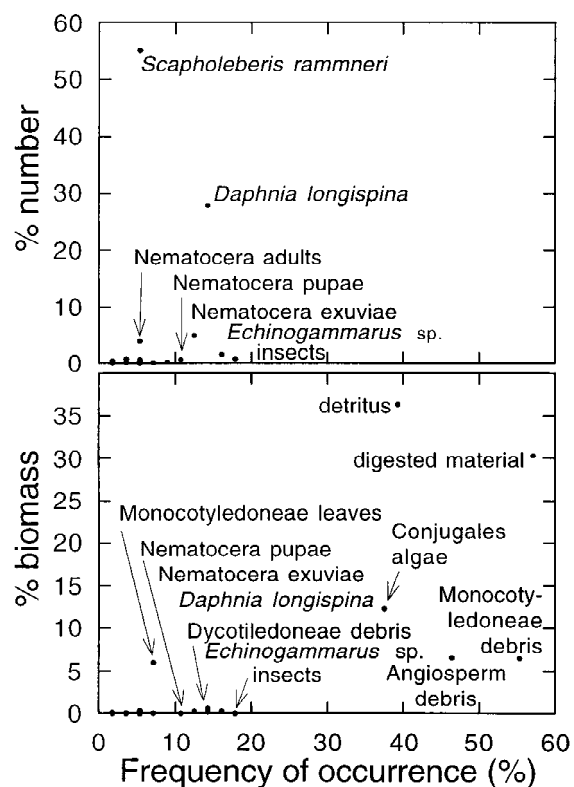


Figure 2. Relationship among percent number, percent biomass and frequency of occurrence of the main components of rudd diet. Plots based on Costello's method. Detailed food categories are the most important dietary items.

(Table 1). The most important animal prey were the cladocerans *Daphnia longispina* and *Scapholeberis rammneri*, amphipods (*Echinogammarus* sp.), and several late stages of nematoceran dipterans (exuviae, pupae and adults).

The relationship among dietary descriptors (Figure 2) pointed to some feeding variation, which was confirmed by correspondence analysis (see Diet variation, below). Firstly, some prey, such as *D. longispina* and particularly *S. rammneri*, were very important by number but very little by occurrence (i.e. consumed by very few individuals) and biomass (Figure 2). The same was observed for nematoceran exuviae and adults, in contrast to the rest of macroinvertebrates and even nematoceran pupae, pointing to obvious seasonal variation in availability of these resources.

The biomass-occurrence relationship distinguished fresh plant material (Conjugales algae and monocotyledon leaves) from plant debris and animal prey, indicating some specialised herbivorous fish.

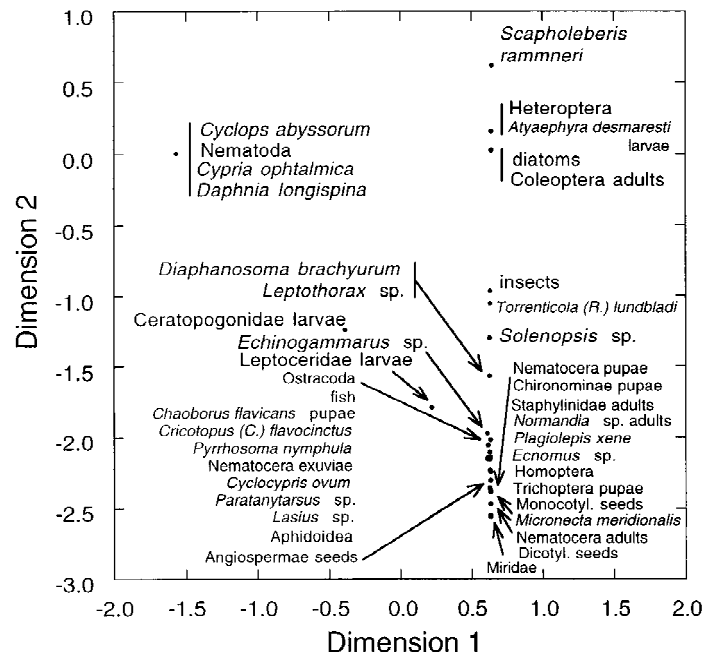


Figure 3. Correspondence analysis of gut contents (prey number) of rudd: food category scores for the first and second dimension.

#### Diet variation

For correspondence analysis (CA) of prey number, the first two dimensions explained 22% of the variance. The first dimension (hereafter, *D1*) distinguished two zooplankters (*D. longispina* and *Cyclops abyssorum*) and two small prey (nematodes and *Cypria ophthalmica*) (Figure 3). *D1* scores were not significantly correlated with fish length ( $r = 0.32$ ;  $n = 32$ ;  $p = 0.07$ ) but showed significant seasonal variation (ANOVA,  $F_{3,22} = 3.4$ ;  $P = 0.03$ ). Most fish with least *D1* scores were from spring or autumn, while most fish with larger *D1* scores were from summer. Therefore, *D1* distinguished fish captured in spring and autumn with a zooplanktivorous diet.

The second dimension (*D2*) differentiated, among the prey with high *D1*, several neustonic prey, namely *S. rammneri*, unidentified heteropterans, unidentified coleopteran adults, and ants (*Solenopsis* sp. and *Leptothorax* sp.) (Figure 3). The other extreme of *D2* had a higher proportion of benthic, larger prey, with amphipods dominating in diet. In contrast to *D1*, *D2* was correlated significantly with fish length ( $r = -0.37$ ,  $n = 32$ ,  $P = 0.04$ ) while it was not significant for season ( $F_{3,22} = 0.54$ ,  $P = 0.67$ ). Therefore, *D2* corresponded to size-dependent variation, with large rudd preying on macroinvertebrates, mostly benthic, and smaller fish

feeding on microcrustaceans such as *S. rammneri* or *D. longispina*.

The CA of biomass data was slightly different, with the first two dimensions explaining a higher percentage of variance (40%). The first dimension was equivalent to that of the CA for number data. *D2* differentiated algae (Conjugales and diatoms) and angiosperm debris. *D2* was not correlated with fish length ( $r = 0.05$ ,  $n = 56$ ,  $P = 0.72$ ) and was significant for season (ANOVA,  $F_{3,46} = 3.8$ ,  $P = 0.02$ ). The fish with highest *D2* were from spring or winter, while those with lowest *D2* were from summer. Therefore, *D2* differentiated benthivorous rudd captured in spring or winter, which consumed more algae and plant debris, especially compared to other fish captured in summer.

## Discussion

#### Diet and habitat of rudd

The distribution of captures and the diet of rudd indicate that it was strictly littoral in Lake Banyoles, in contrast to other cyprinids such as roach and common carp. In many European lakes where rudd and roach coexist, the former is littoral, associated to vegetation, whereas roach is more common in open habitats

(Holčík, 1967; Johansson, 1987; Haberlehner, 1988; Eklöv & Hamrin, 1989). This habitat segregation is, at least partially, interactive, i.e. produced by present interactions between the two species and not only by genetically-determined behaviour and is due to the fact that rudd is less efficient and has lower growth rates than roach when exploiting zooplankton (Johansson, 1987). Moreover, rudd displays less capacity of adaptation to different kind of food than roach (Hofer, 1979a, b; Niederholzer & Hofer, 1980).

This habitat segregation implies a resource partitioning, clear in Lake Banyoles, where rudd consumed a higher proportion of neustonic prey than the rest of fish species. Several important prey of rudd were typically neustonic, such as *S. rammneri*, and late stages of nematocera. Many other were from terrestrial origin and thus mostly captured at the water surface, such as ants (*Lasius* sp., *Solenopsis* sp., *Plagiolepis xene*, *Leptothorax* sp.), unidentified homopterans and Aphidoidea, Miridae heteropterans and adults of coleopterans (unidentified and Staphylinidae). Other prey were aquatic but dependent on the water surface, such as the heteropteran *Micronecta meridionalis* and adults of the coleopteran *Normandia* sp. In addition to nematocera, many food items were related to the emergence of insects, e.g. the pupae of trichopterans, the dipteran *Chaoborus flavicans*, and chironomid Chironomina. Contrastingly, most chironomid larvae dominating both non-littoral benthos (Prat & Rieradevall, 1995) and the diets of roach (García-Berthou, 1999a) and common carp (García-Berthou, 1994) were lacking in rudd diet.

This resource partitioning was also linked to the high consumption by rudd of very small invertebrates, such as nematodes, larvae of a freshwater shrimp (*Atyaephyra desmaresti*), larvae of small, littoral chironomids (*Paratanytarsus* sp. and *Cricotopus flavocinctus*), and particularly microcrustaceans, such as ostracods (unidentified, *C. ophthalmica*, *Cyclocypris ovum*), *C. abyssorum* and cladocerans (*Diaphanosoma brachyurum*, *S. rammneri*, *D. longispina*). On the other hand, abundant littoral macroinvertebrates, dominating diets of other littoral fish (pumpkinseed sunfish and largemouth bass), were not present in rudd guts, such as nymphs of ephemeropterans and odonates (except some few *Pyrrosoma nymphula*), and particularly *A. desmaresti*.

As in Lake Banyoles, seasonal variation in rudd diet was also detected in an Italian lake (Ravera & Jamet, 1991) but was not in a dimictic Tyrolean lake (Niederholzer & Hofer, 1980) and in *Scardinius*

*acarnanicus*, an endemic from Greece recently differentiated from *S. erythrophthalmus* (Iliadou, 1990).

#### *Herbivory of rudd*

In Lake Banyoles, detritus were not as important in rudd diet as in roach (% biomass = 57.5) and carp (% biomass = 50.4), likely because rudd feeding is less benthic. Rudd was the fish in Lake Banyoles with highest consumption of plant material (% biomass = 31.6, pooling fresh material and debris), followed by chub (17.5%) and common carp (10.0%) (García-Berthou, 1994). Moreover, fresh plant material was especially important in rudd, particularly algae (mostly Conjugales algae) and Monocotyledon leaves, which were not so important in any other fish species. Although most fish species of European lakes consume plant material to some extent, this consumption is only important in rudd, roach and ide (*Leuciscus idus*) (Niederholzer & Hofer, 1980; Prejs, 1984). Herbivory is much more common in fish of tropical or subtropical systems (Okeyo, 1989) but rudd adults are often almost totally herbivores, consuming plants and algae (Holčík, 1967; Prokes & Rebickova, 1987; Ravera & Jamet, 1991). *S. acarnanicus* is also herbivore, with juveniles feeding on phytoplankton, and adults on macrophytes (Iliadou, 1990). However, the use of plant material by rudd in our study was lower than usual (80–95% of biomass in young fish and up to 99% in adults; Prejs, 1978; Prejs & Jackowska, 1978). The same pattern was observed for roach (García-Berthou, 1999a) probably due to low availability (Niederholzer & Hofer, 1980; Prejs, 1984). Moreover, macrophytes usually dominate among plant food of rudd (% biomass = 65–95; Prejs, 1984) but they did not in Lake Banyoles.

The extraordinary herbivory of rudd suggests that it may be particularly successful as an exotic species. Lake Banyoles was the first site of the Iberian peninsula where rudd was introduced. Rudd is nowadays expanding its distribution, which presently includes most Catalan watersheds and the Ebro river delta. In Lake Banyoles, the consumption of plant material was lower than usual although there is some evidence that it was higher during the beginning of its introduction (Vidal, 1925) and produced the decline of macrophytes and the consequent local extinction of the three-spined stickleback *Gasterosteus aculeatus* (Nadal, 1983, unpublished report).

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