

Ontogenetic microhabitat shifts of 0+ rudd (*Scardinius erythrophthalmus* L.) in the littoral zone of a mesotrophic lake

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Introduction

The spatial heterogeneity of fish distribution varies in accordance with biological and physical factors such as habitat structure (BENSON & MAGNUSON 1992). For 0+ fish, microhabitat use constitutes a crucial aspect of their life histories, as they are closely linked to a selected littoral habitat providing food and shelter (COPP 1992). The study of ontogenetic microhabitat shifts is of crucial importance for the understanding of the population dynamics, as habitat use constitutes a key factor for the sustainability of a species which is particularly vulnerable to predation or lack of feeding resources during the first months of life. The saltatory theory of ontogeny proposed for fish by BALON (1985) purports that fish development occurs in a series of successive intervals with thresholds defined by the appearance of certain morphological and physiological structures which induce behavioural and probably habitat changes. On the basis of these observations, our aim was to investigate if there exists microhabitat shifts in the course of rudd ontogeny, and to define when they occur during the larval and juvenile development of rudd. Moreover, although rudd is a cyprinid species distributed throughout Europe, information about the larval and juvenile stages of its life is still limited.

Material and methods

The study was undertaken during summer 1997 in Lake Pareloup. This reservoir is located in the South West of France, near the city of Rodez. It covers an area of 1,350 ha and has a volume of about $168 \times 10^6 \text{ m}^3$. The maximum depth is 37 m and the average depth is 12.5 m. Lake Pareloup is a warm monomictic lake, which is submitted to summer thermal stratification with a low oxygen content below the thermocline (located at about 10 m from early June to mid-September) that prevents the fish from colonising deep water during this period. Fish sampling was performed weekly from the spawning (late June) to the juvenile period (late August) in the littoral zone of the lake. Point Abundance Sampling

by electrofishing (NELVA et al. 1979) modified for young fish (COPP 1989) was employed to evaluate the microhabitat shifts of 0+ rudd in the course of early development. Each week, 60 to 70 sampling points were investigated in the same area of the lake chosen for its topographical heterogeneity providing numerous kinds of habitats. For each of the 617 sampling points, nine habitat variables were taken into account: distance from the bank, depth, slope of the bank, flooded vegetation, percentage of boulders, pebbles, gravel, sand and mud. Collected fish were preserved in a 4% formaldehyde solution. In the laboratory, rudd were identified and numbered for each sampling point. The developmental stage of each of the 1,921 captured fish was defined according to CERNY (1977). A Canonical Correspondence Analysis (CCA) (TER BRAAK 1986) was used to define the microhabitat of each developmental stage of rudd and to visualise the microhabitat shifts. CCA was performed on the 119 samples containing rudd. Samples without rudd were removed from the statistical analysis, thus aiming to avoid an undue influence of nil values. Fish abundance data were log (n+1)-transformed in order to satisfy the assumptions of CCA.

Results and discussion

The microhabitat of 0+ rudd over the course of early ontogeny was characterised by three main microhabitat shifts, allowing us to establish four groups of developmental stages (Fig. 1a), including in each one several additional developmental steps defined by CERNY (1977).

The first group (Group 1) has three associate larval steps (L(I)1, L(I)2 and L(I)3) corresponding to the protopterygiolarval phase of rudd development (Fig. 1a), which start with the first uptake of exogenous feeding and terminate when the caudal fin begins its ossification. During this period, rudd-swimming capabilities are

reduced, rudd larvae are relatively immobile, and remain in the spawning area chosen by adults, inside the flooded vegetation (Fig. 1b). Free embryos were not found in the samples due to the fishing gear which did not provide sufficient current densities to capture fish smaller than five millimetres (COPP 1989). Rudd length at the beginning of the propterygiolarval phase was about six millimetres. Nevertheless, the almost nil swimming capabilities of free embryos led us to believe they were located in the same area as Group 1.

The second group (Group 2) was composed of the first three pterygiolarval steps (L(II)1, L(II)2 and L(II)3) (Fig. 1a). The most prominent characteristic of the beginning of the pterygiolarval stage was the advanced degree of differentiation of the finfolds at the sites of the future dorsal and anal fins, the end of the L(II)3 step was marked by the ossification of the first lepidotrichia in the pectoral and ventral fins. Group 2 was thus characterised by the presence of larval fins providing a limited swimming ability which permitted an active choice of microhabitat and coincided with changes in diet, as observed for roach (*Rutilus rutilus* L.), a closely related cyprinid species, by HARTMANN (1983).

The third group (Group 3) consisted of two stages, the last pterygiolarval stage (L(II)3) and the first juvenile stage (Fig. 1a). This group was characterised by fish which looked like small adults, but without scales (L(II)3) or with incomplete scales ossification (J1). These stages can be considered as a transition phase between larvae and real juvenile (sensu COPP & KOVAC 1996). The development of adult characteristics such as complete ossification of the fins rays and total resorption of the finfolds provides the fish with a better swimming ability, therefore enabling it to colonise a wider range of habitats located farther from the bank (Fig. 1b).

The last group (Group 4) was composed entirely of juveniles (Fig. 1a), characterised by a complete scale cover. That characteristic induces an improvement of rudd hydrodynamism (BURDAK 1986). Fish were located in the open waters, with muddy bottoms (Fig. 1b), located several meters from the vegetation.

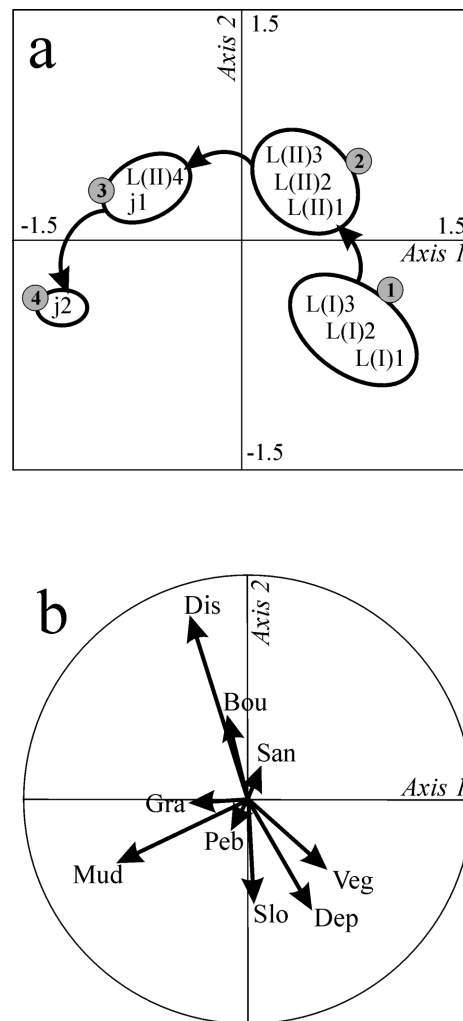


Fig. 1. Canonical correspondence analysis biplot, the nine rudd developmental steps and the nine environmental variables were represented on separate graphs for clarity. The first two canonical axis were represented; they accounted for 64 and 27% of the total inertia, respectively. (a) The nine rudd larval (L(I)1, L(I)2, L(I)3, L(II)1, L(II)2, L(II)3, L(II)4) and juvenile (J1, J2) developmental steps. Microhabitat shifts are represented by arrows and the four groups of developmental steps are surrounded by a black line and identified by the group number (Groups 1 to 4). (b) The nine environmental variables and the correlation circle. Dis, distance from the bank; Dep, depth; Slo, Bottom slope; Bou, % of boulders; Peb, % of pebbles; Gra, % of gravel; San, % of sand; Mud, % mud; Veg, % of cover by flooded vegetation.

Owing to their increased swimming ability, the juvenile rudd can minimise intraspecific competition pressure by the use of the open waters. Nevertheless, juvenile rudd remain vulnerable to predation (EKLÖV & HAMRIN 1989) and stay close to the flooded vegetation which constitute an efficient shelter.

From an ecological point of view, the correct choice of habitat is of crucial importance for individual survival (ROSENZWEIG 1991). Fish distribution permanently keeps a trade-off between available habitat and the necessity to accomplish vital functions such as feeding and predation avoidance. The ontogenetic microhabitat shifts of rudd were thus induced by a trade-off between fish mobility, feeding requirements and predation avoidance.

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