

# Experimental evidence for interactive habitat segregation between roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) in a shallow eutrophic lake

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**Summary.** The competitive interactions between roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) were investigated in two habitats, the open water and the waterlily zone. The growth rates of both species in enclosures were lower when confined together than when alone, demonstrating interspecific competition. Allopatric roach had the highest growth rate in both habitats although the open water was preferred. The diets of both species were dominated by zooplankton in both the open water and waterlily zones. In laboratory experiments, roach had significantly higher feeding rates than rudd when fed *D. magna* and *Cyclops* sp. The impact of roach on the mean sizes and densities of zooplankton in the enclosures, together with the results from the laboratory study, indicate that roach were competitively superior in the open water. Because of high mortality in the sympatric waterlily enclosure, no conclusions about interspecific competition in this habitat could be drawn. The observed habitat segregation between roach and rudd was at least partly interactive.

**Key words:** Competition – Habitat segregation – Foraging efficiency

Observed segregation between species has often been attributed to competition, past or present, reflecting that species evolve in order to minimize competition (Schoener 1974; Roughgarden 1974, 1979). The role of competition as a structuring force in ecological communities has, however, been disputed (Connell 1980, 1983; Schoener 1982), primarily because competition is difficult to detect in natural communities. Failures to detect competition have often been explained by resource partitioning caused by past competition.

To evaluate the role of competition it must be distinguished between *selective* segregation, segregation due to genetically determined behaviors, and *interactive* segregation, segregation due to present interactions (Brian 1956; Nilsson 1960). Segregation between fish species, which has been studied by comparing resource utilization of species pairs in sympatry and allopatry, is mainly interactive (Andruzak and Northcote 1971; Nilsson 1960; 1965; Nilsson and Northcote 1981; Finger 1982). However, the evidence obtained is inconclusive without experimental verification. Experiments comparing the utilization efficiencies of preferred and unpreferred resources by both species, alone and together, must be included.

In many European lakes the cyprinid fishes roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) coexist. Rudd is a littoral species, found in or near the vegetation zone, whereas roach are far more abundant in the open water (Holcik 1967; Kennedy and Fitzmaurice 1974). Recent studies have suggested that the two species may compete but experimental evidence is lacking (Burrough et al. 1979).

The purpose of this study was to test if (1) the observed habitat differences between roach and rudd are due to selective or interactive segregation and (2) if the utilization efficiencies of the species are related to their distribution in lakes. The results from this study are based on both lake enclosure experiments and on laboratory studies of feeding behavior.

## Material and methods

### Study area

The field experiment was conducted in the eutrophic Lake Sövdeborg (maximum depth 3.5 m, mean depth 2.5 m, surface area 0.11 km<sup>2</sup>), situated in southern Sweden (55° 35' N, 13° 42' E). Studies on interactions between perch (*Perca fluviatilis*) and roach in the lake were previously conducted by Persson (1983c). A wide zone of waterlilies (*Nymphaea alba* and *Nuphar luteum*), covering one third of the surface area, occurred at depths between 0.5 and 2.5 m. Secchi disc transparency ranges from 0.8 to 1.2 m and chlorophyll *a* from 25 to 36 mg·m<sup>-3</sup> during the summer (Persson 1983a). The roach is the most abundant fish in the lake, while perch, pike (*Esox lucius*), rudd, crucian carp (*Carassius carassius*), tench (*Tinca tinca*), eel (*Anguilla anguilla*) and belica (*Leucaspis delineatus*) occur in smaller numbers.

### Laboratory experiments

*Daphnia magna* ( $\bar{x}$  = 1.87 mm, SE = 0.04 mm,  $n$  = 30) and *Cyclops* sp. ( $\bar{x}$  = 1.50 mm, SE = 0.03 mm,  $n$  = 45) were used as prey to estimate the foraging efficiencies of roach and rudd. Densities of *D. magna* and *Cyclops* sp. were 0.3, 0.6, 1, 2 and 4 prey·l<sup>-1</sup> and 2, 5, 10, 20 and 40 prey·l<sup>-1</sup>, respectively.

The experiments were performed in four 90 l aquariums (95 × 30 × 30 cm) at a temperature of 18–19° C and a light/dark cycle of 14/10 h. Two aquariums were supplied with roach (four fish in each, averaging 95 mm TL (total length), range 85–104 mm) and two with rudd (four fish in each, averaging 96 mm TL, range 80–109 mm).

**Table 1.** Numbers, mean weight (g wet weight  $\pm 1$  SD) and metabolic units of the fish in the enclosures at the start of the experiment. Enclosures 1 and 4 contained roach, enclosures 2 and 5 contained rudd and enclosures 3 and 6 contained both species

Enclosure	Open water (1983)			Waterlilies (1984)		
	1	2	3	4	5	6
<b>Roach</b>						
no of fish	23		24	17		17
mean weight	6.3 $\pm$ 1.0		6.0 $\pm$ 1.3	2.8 $\pm$ 0.6		2.9 $\pm$ 0.5
metabolic units	100		101	39		40
<b>Rudd</b>						
no of fish		21	20		12	12
mean weight		4.1 $\pm$ 0.9	3.3 $\pm$ 0.8		4.4 $\pm$ 1.3	4.0 $\pm$ 1.0
metabolic units		64	53		39	36

The fish were acclimatized in the laboratory one week before the experiment began. During this period, the fish were fed commercial flake food in combination with the experimental prey species to obtain maximum feeding efficiency in the experiments (Werner et al. 1981). Before the experiment began, the fish were segregated behind partitions in the aquariums. The prey were introduced in the fish-free compartment (70 l) and were allowed to distribute for one minute. Two fish were then allowed to enter the compartment containing the prey, and the time required for one fish to consume a fixed number of prey was recorded. Prey depletion never exceeded 50% of the initial prey density, and the number of prey consumed per individual fish never exceeded 20, in order to avoid satiation effects (Werner 1974). The two fish were then allowed to eat the remaining food for 30 min or longer, depending on the prey density. The fish were returned to the compartment, and a similar procedure was carried out with the other fish. The fish were trained to this procedure during the week before the experiment.

The data were fitted to a modified Holling type II function using non-linear techniques (SAS statistical package);

$$y = \frac{ax}{1 + ahx} \quad (1)$$

where  $y$  is the number of prey consumed per unit time,  $x$  is the prey density,  $a$  is the attack coefficient and  $h$  is the handling time (in s).

The average swimming speed of roach and rudd while feeding on *D. magna* was estimated in a 400 l aquarium (100  $\times$  80  $\times$  50 cm). The feeding trials were recorded with a video camera, and the distance swam per unit time was measured.

#### Field experiment

The field experiment was conducted in the waterlily zone (May–October 1984) and in the open water zone (August–September 1983). Three enclosures (3 m deep in the waterlilies and 2.5 m in the open water), made from nylon-reinforced plastic, were placed in each habitat. The enclosures were pressed 20 cm into the lake bottom thus preventing fish and invertebrates from entering the enclosures. The diameters, which were 2.7 m in the open water enclosures and 3.0 m in the waterlily enclosures, were chosen so that the water volumes in all enclosures were equal (17 m<sup>3</sup>). One of the enclosures contained roach and rudd together with

a total density which is normal for cyprinids in South Swedish eutrophic lakes (Table 1, Persson 1983a, b). To study the effects of interspecific competition, the other two enclosures were stocked with roach and rudd alone with the same densities these species had in the sympatric enclosure. Thus, the experimental design simulated a removal experiment where the intraspecific competition was relatively constant (Werner and Hall 1977a).

Different numbers of fish were added to each waterlily enclosure in order to make the metabolic demands of the enclosures equal (Table 1). The metabolic demands were calculated using the formula

$$m = n \cdot w^{0.8}$$

where  $m$  is total metabolic demands,  $n$  is number of fish and  $w^{0.8}$  is the relationship between fish weight and metabolic demands (Winberg 1961).

Sampling was done at monthly intervals. The fish in the open water enclosures were caught with a dip-net, anaesthetized with MS-222 and weighed to nearest 0.1 g. Because the dip-net could not be used in the waterlily zone, rudd were caught using hook and line. No mortality or wounds were observed from this method. Because of the small size of the roach I was unable to catch them in the waterlily enclosures; hence data on growth were only collected at the beginning and end of the experiment. Rudd captured in the waterlily enclosures were anaesthetized and weighed in the same way as fish captured in the open water enclosures. Four fish of each species, collected from each enclosure in both habitats, were killed and deep frozen for later diet analyses. These fish were replaced with four, fin-clipped individuals, which were collected for diet analysis on the next sampling occasion. With this technique, growth rate estimates were less biased. At the end of the experiment, all fish were killed with rotenone and deep frozen for later analysis.

On each sampling occasion, zooplankton were sampled from all enclosures using a tube sampler (diameter 40 mm), which extended from the surface to the bottom of the lake. Five l of water were sampled and filtered through a 45  $\mu$ m mesh. The zooplankton was preserved in 4% formaldehyde.

## Results

### Laboratory experiments

Roach were more efficient than rudd when feeding on *D. magna* (Fig. 1, ANOVA  $P < 0.0001$ , Table 2) and *Cyclops*

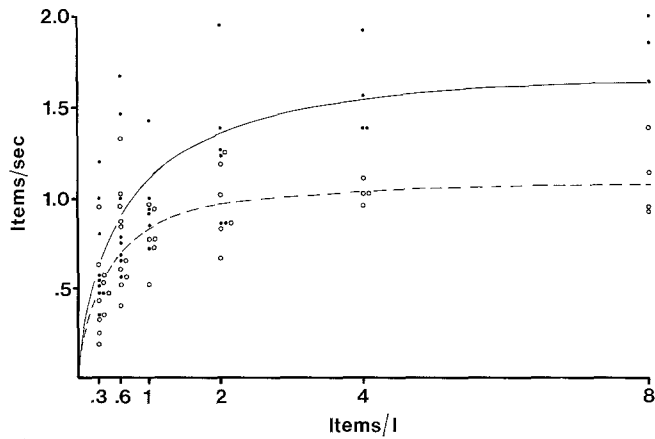


Fig. 1. Feeding rates of roach and rudd under laboratory conditions as a function of *D. magna* density. Dots roach, open circles rudd. The solid and dashed lines are the fitted Holling type II functions for roach and rudd, respectively

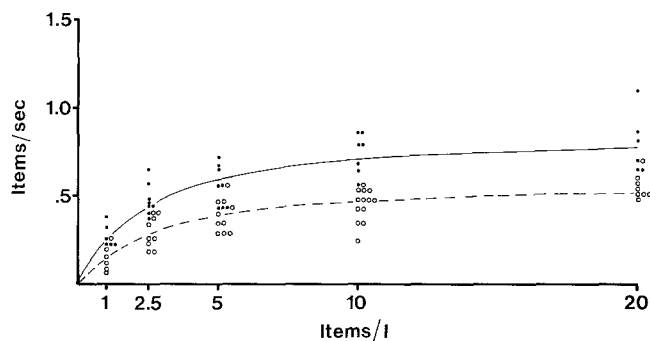


Fig. 2. Feeding rates of roach and rudd under laboratory conditions as a function of *Cyclops* sp. density. Symbols as in Fig. 1

Table 2. Two-way ANOVA on feeding rate of roach and rudd feeding on *Daphnia magna* and *Cyclops* sp. at different densities

<i>Daphnia magna</i>				
Source of variation	df	SS	MS	F
fish species	1	1.56	1.56	20.45***
<i>D. magna</i> density	5	5.90	1.18	15.51***
species × density	5	0.58	0.12	1.54
error	64	4.87	0.08	
total	75	12.91		
<i>Cyclops</i> sp.				
Source of variation	df	SS	MS	F
fish species	1	0.79	0.79	80.73***
<i>Cyclops</i> sp. density	4	1.99	0.50	50.93***
species × density	4	0.08	0.02	1.95
error	74	0.72	0.01	
total	83	3.38		

\*\*\* =  $P < 0.0001$

sp. (Fig. 2, ANOVA,  $P < 0.0001$ , Table 2). The attack coefficients were higher and the handling times lower for both fish species when feeding on *D. magna* compared to *Cyclops* sp. ( $t$ -test  $P < 0.001$  for the estimated  $h$ , Table 3). Handling times of roach were lower than those of rudd when feeding

Table 3. Values (means  $\pm$  95% CL) of the predicted attack coefficient,  $a$  and handling time,  $h$  (seconds) from the fitted Holling type II function and the estimated handling time for roach and rudd feeding on *Daphnia magna* and *Cyclops* sp. The estimated handling time is the reciprocal of the maximum feeding rate (Ware 1972)

	<i>D. magna</i>	<i>Cyclops</i> sp.
Roach		
predicted $a$	$2.92 \pm 1.19$	$0.36 \pm 0.11$
predicted $h$	$0.56 \pm 0.10$	$1.12 \pm 0.14$
estimated $h$	$0.55 \pm 0.15$	$1.30 \pm 0.36$
Rudd		
predicted $a$	$3.05 \pm 1.27$	$0.20 \pm 0.06$
predicted $h$	$0.87 \pm 0.13$	$1.62 \pm 0.21$
estimated $h$	$0.93 \pm 0.27$	$1.80 \pm 0.16$

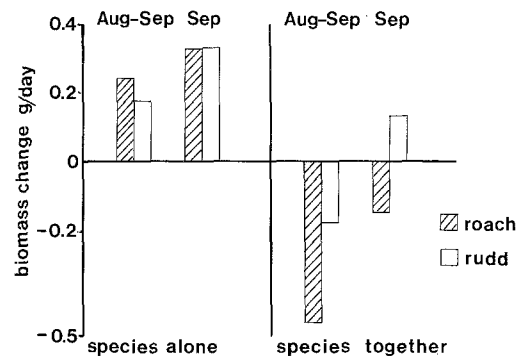


Fig. 3. Mean daily growth rate of roach and rudd from Aug 10 to Sep 7 and from Sep 7 to Sep 27 in the open water enclosures

on *D. magna* as well as *Cyclops* sp. ( $t$ -test  $P < 0.01$  for both prey types based on the estimated  $h$ , Table 3). Estimated handling time, calculated as the reciprocal of the maximum feeding rate (Ware 1972), were similar to that predicted by the model (Table 3). Roach had a higher attack coefficient than rudd when feeding on *Cyclops* sp., while there was no difference between the species when feeding on *D. magna* (Table 3).

At a density of one *D. magna* · l<sup>-1</sup> the swimming speed of roach was  $44 \pm 7$  cm · s<sup>-1</sup> (mean  $\pm$  1 SD) compared to  $32 \pm 4$  cm · s<sup>-1</sup> for rudd.

#### Field experiment

1. *Growth rate and mortality.* At least 86% of the fish (average 93%) were caught in the open water enclosures on every sampling date. In the waterlily enclosures, no roach but at least 44% (average 64%) of the rudd were caught on every sampling date.

In the open water enclosures, both species had similar growth rates in allopatry (Fig. 3). In the RO/RU enclosure, growth rates were lower than in allopatry and generally negative. In sympatry roach had lower growth rates than rudd (Fig. 3). In the waterlilies growth rates of roach were higher than those of rudd both in allopatry and sympatry (Figs. 4 and 5). In sympatry, both species growth rates were lower than in allopatry.

There was no mortality in any enclosure except in the RO/RU enclosure in the waterlilies. Here, mortality of roach was 41% ( $n = 7$ ) and that of rudd 25% ( $n = 3$ ).

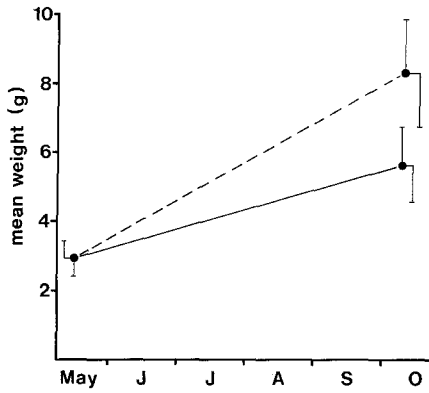


Fig. 4. Mean weight ( $\pm 1$  SD) of roach in the waterlily enclosures at the beginning and end of the experiment (----)=allopatric, (—)=sympatric

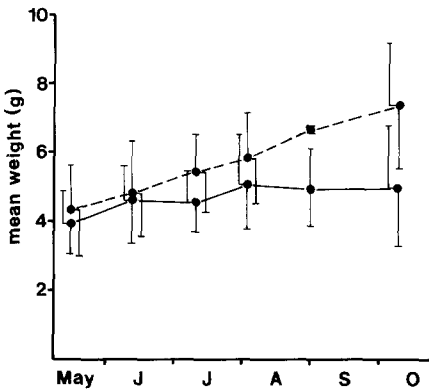


Fig. 5. Mean weight ( $\pm 1$  SD) of rudd in the waterlily enclosures from May to October. (----)=allopatric, (—)=sympatric

2. *Diet.* The diet of roach and rudd in the open water consisted mainly of zooplankton and plant food. Except for one enclosure in September, 30%–70% of the gut contents of both fish species consisted of zooplankton (Fig. 6). The zooplankton found in the guts of rudd were *Ceriodaphnia* sp. while roach had a more varied diet, consisting primarily of *Bosmina* sp. and *Ceriodaphnia* sp. (Fig. 6). Other important food items for roach were detritus and benthic cladocerans and for rudd, benthic cladocerans, filamentous algae, and chironomid larvae.

In the waterlily enclosures, zooplankton constituted a smaller portion of the diet than in the open water (Fig. 7). Benthic cladocerans and filamentous algae were important food items except in late August.

The diets of roach and rudd were different in sympatry and in allopatry as plant food constituted a greater part of the diet in sympatry. The plant food of roach consisted entirely of detritus, whereas rudd utilized mainly filamentous algae (Figs. 6 and 7).

Of the zooplankton species present in the enclosures only those consumed by the fishes (*Cyclops* sp., *Bosmina* sp., *Daphnia* sp., *Ceriodaphnia* sp., and *Diaphanosoma* sp.) are considered here. The total number of zooplankton was on the average two times higher in the RU enclosure than in either the RO or the RO/RU enclosures (Figs. 8 and 9). The patterns were similar in both habitats, indicating that the two species of fish affected the zooplankton populations differently. The experiments in the open water and in the waterlilies were conducted in two different years.

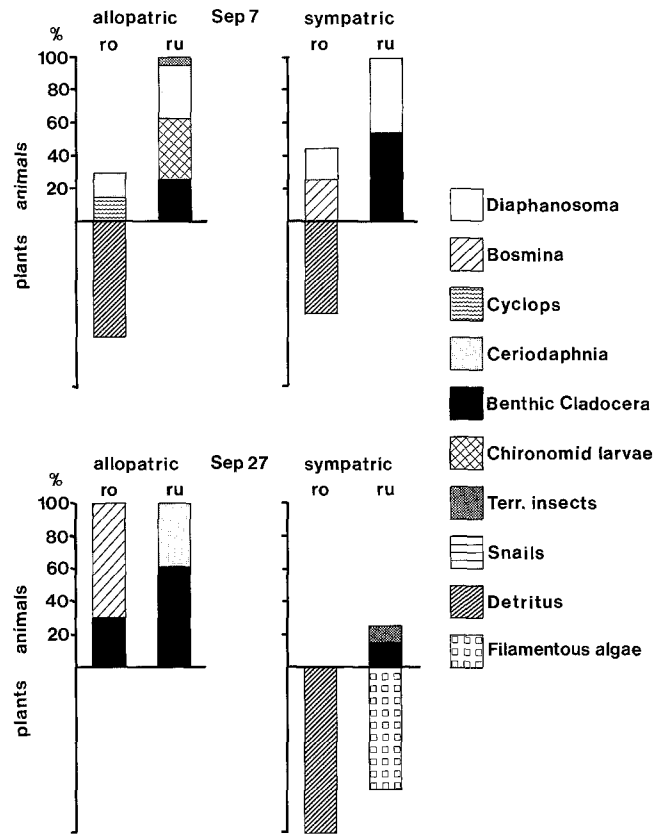


Fig. 6. Diets of roach and rudd in the open water enclosures on Sep 1 and Sep 27, 1983

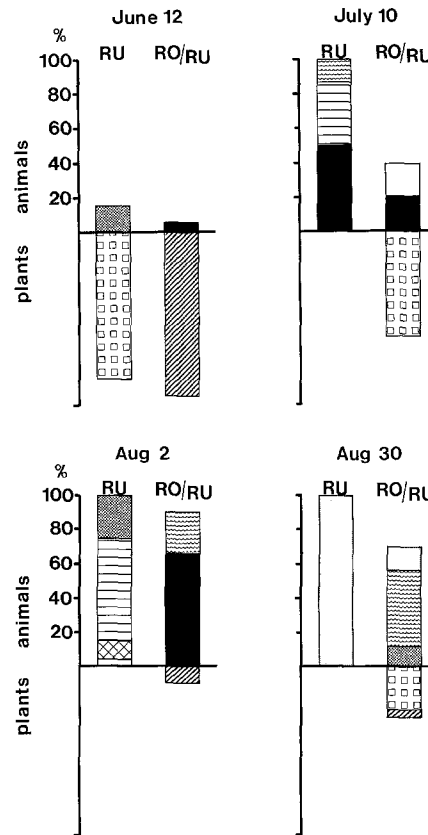


Fig. 7. Diets of rudd in the waterlily enclosures between June 12 and Aug 30, 1984. Roach were not collected in the waterlilies. The symbols are the same as in Fig. 6

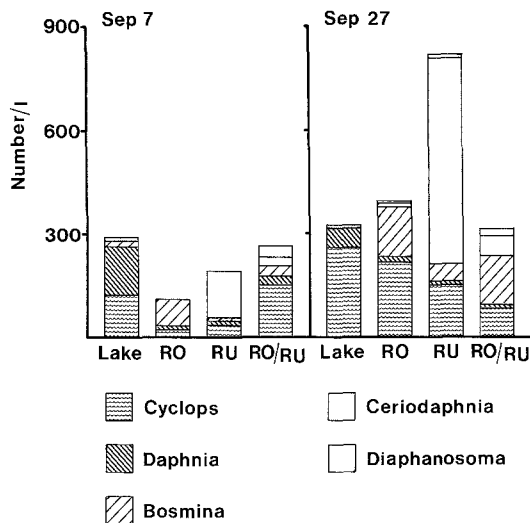


Fig. 8. Density of zooplankton in the open water region of the lake and in the enclosures located in the open water, 1983

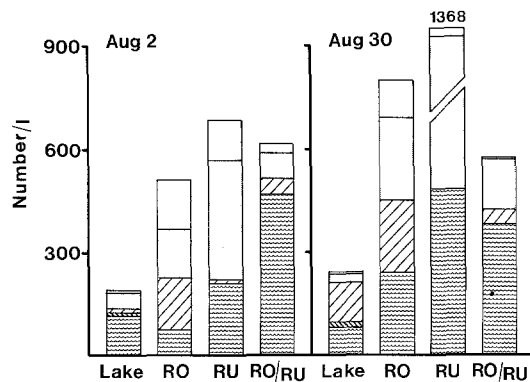
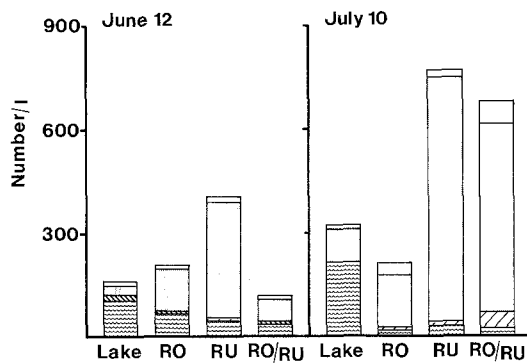


Fig. 9. Density of zooplankton in the waterlily zone in the lake and in the enclosures located in the waterlily zone, 1984. The symbols are the same as in Fig. 8

The fact that the zooplankton populations were affected similarly in the two habitats indicated that the observed patterns were real treatment effects and not due to demonic or nondemonic intrusions (Hurlbert 1984). The abundances of zooplankton in the lake were similar or lower than those in the RO and RO/RU enclosures, indicating that the density of fish in the enclosures was similar or lower than in the lake. About 70% of the zooplankton in all RU enclosures consisted of *Ceriodaphnia* sp. In the waterlilies *Cerio-*

Table 4. Differences in the mean sizes (student's *t*-test) of two zooplankton species in enclosures containing roach (RO), rudd (RU) and roach and rudd together (RO/RU)

		Waterlilies		
		RO-RU	RU-RO/RU	RO-RO/RU
June 12	<i>Ceriodaphnia</i> sp.	NS	NS	NS
	<i>Cyclops</i> sp.	*	NS	NS
July 7	<i>Ceriodaphnia</i> sp.	***	***	NS
	<i>Cyclops</i> sp.	NS	NS	NS
Aug 2	<i>Ceriodaphnia</i> sp.	*	NS	*
	<i>Cyclops</i> sp.	NS	NS	NS
Aug 30	<i>Ceriodaphnia</i> sp.	NS	NS	NS
	<i>Cyclops</i> sp.	NS	NS	NS
		Open water		
		RO-RU	RU-RO/RU	RO-RO/RU
Sep 7	<i>Ceriodaphnia</i> sp.	NS	NS	NS
	<i>Cyclops</i> sp.	**	NS	NS
Sep 27	<i>Ceriodaphnia</i> sp.	NS	NS	NS
	<i>Cyclops</i> sp.	NS	NS	NS

\* =  $P < 0.05$ , \*\* =  $P < 0.01$  and \*\*\* =  $P < 0.001$

*daphnia* sp. was abundant in the RO and RO/RU enclosures (48% and 44% in RO and RO/RU enclosures respectively), while in the open water enclosures, *Cyclops* sp. and *Bosmina* sp. constituted most of the zooplankton (Figs. 8 and 9). In some samples, *Cyclops* sp. and *Ceriodaphnia* sp. were smaller in size in the RO and RO/RU enclosures than in the RU enclosures (Table 4). This was observed in both habitats, again suggesting that the observed patterns were treatment effects.

## Discussion

### Feeding efficiencies of roach and rudd

Vertebrate predators generally have a Holling type III functional response (Hassel 1978). However, no such response was found in this study; instead the functional responses of roach and rudd were of type II when feeding on *D. magna* and *Cyclops* sp. (Figs. 1 and 2). The same was found by Persson (1986) on roach and perch fed *Chaoborus*. For type III functional responses the attack coefficients and handling times depend on prey density (Hassel 1978). In simple environments such as the open water, fish are not likely to increase their attack coefficient by developing a search image. It is also unlikely that the handling time and capture success for fish feeding on relatively small zooplankton are affected by prey density. Thus, in simple environments with small prey type II rather than type III functional responses are more likely to occur. Turbidity and low light intensity decrease the reaction distance (Vinyard and O'Brien 1976; Confer et al. 1978; Gardner 1981). Therefore, under low light conditions, encounter rate and consequently feeding rate depend more on the swimming speed of the fish than on the reaction distance. This favors roach since they swim more rapidly than rudd when feeding

on zooplankton. Thus, the difference in feeding rate between roach and rudd in the laboratory study is probably accentuated in the lake due to high turbidity and low light intensities.

#### *Habitat utilization efficiency of roach and rudd*

The growth data indicated similar utilization efficiencies for roach and rudd in the open water. However, since roach had a higher mean weight than rudd (Table 1), the growth rates must be compensated by the different metabolic costs of roach and rudd. This correction resulted in an increased difference between the species allopatric growth rates, favouring roach, and a decreased difference between their sympatric growth rates. As the optimal size of a predator generally decreases with decreasing resource availability (Schoener 1969; Case 1979), small size should be competitively superior (Persson 1985). In sympatry, with lower resource availability, the growth rate comparisons are thus also biased by the smaller sizes of rudd. Taking this into consideration, my results indicate that roach have a higher utilization efficiency than rudd in the open water.

Metabolic costs were similar for roach and rudd in the waterlily enclosures; hence the growth rates can be directly compared. The results in allopatry demonstrate that both species can utilize the waterlily zone profitably. However, the mortality in sympatry was high, indicating resource limitation due to interspecific competition. The apparent growth of the fishes in sympatry may be due to selective mortality of the smallest fish. Thus, it is not possible to draw any conclusions about the relative utilization efficiencies of the two species in the waterlily zone under interspecific competition.

The food resources in the open water and in the waterlily zone in Lake Sövdeborg consist mainly of zooplankton and detritus (Persson 1983a). Roach and rudd fed more on plant material when they were sympatric, which supports the hypothesis that omnivorous fish forage on less valuable food types when competition intensity is high (Persson 1983b). The higher utilization efficiency of roach in the open water is probably due to their higher feeding rates on zooplankton. The laboratory experiments confirm this conclusion and it is further supported by the profound effect that roach had on the zooplankton within the enclosures.

Schoener (1974) proposed that segregation by the habitat was the most common niche difference for terrestrial animals. Werner (1977) and Werner and Hall (1976, 1977b, 1979) showed that the habitat dimension was also important for fish (but see Werner 1985). The disappearance of submerged macrophytes following severe eutrophication resulted in a decreased population of rudd (Burroughs et al. 1979; Peirson et al. 1985), suggesting that rudd require a well developed vegetation zone to coexist with roach. This hypothesis is supported by laboratory studies which showed that the feeding rate of roach decreases with increasing vegetation density while rudd increases its feeding rate when vegetation density is increased to a maximum of 200 stems  $\cdot$  m<sup>-2</sup> (Peirson et al. 1985). The waterlily zone where the field experiment was carried out is probably not dense enough (maximum 25 stems  $\cdot$  m<sup>-2</sup>) to reduce roach feeding rate. The laboratory results of Peirson et al. (1985) suggest that rudd is dependent on the denser vegetation along the shore for coexistence with roach.

#### *Interactive versus selective segregation*

Studies of resource utilization by fish species in sympatry and allopatry have indicated that observed segregation is mainly interactive (Nilsson 1960, 1965; Andruzak and Northcote 1971; Finger 1982). However, it is not possible from observational data alone to understand the reasons for this segregation. Werner and Hall (1979) experimentally demonstrated that sunfishes in sympatry had different habitat preferences than in allopatry. This was due to a differential ranking of the habitats under interspecific competition. The results from my field experiment suggest that the segregation between roach and rudd is partly interactive as both species showed positive growth rates in both habitats and were negatively affected by interspecific competition in these habitats. Roach are, however, better adapted to feeding on zooplankton in the open water which is in accordance with the observed habitat preferences of the fishes (Holcik 1967; Kennedy and Fitzmaurice 1974).

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