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Interactions between developmental processes, growth, and food selection in the larvae and juveniles of *Rutilus rutilus* (L.) (Cyprinidae)

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Summary. The aim of this study was to assess the effects of developmental events, occurring in fish during the first weeks after hatching, on the quantity and quality of the ingested food and on growth. The investigation was carried out with the larvae and juveniles of *Rutilus rutilus,* the single cyprinid species occurring in an oligotrophic subalpine lake in Tirol, Austria. Comparison between availability of prey in the water and gut contents suggests that the selection of food by the young fish is strongly influenced by developmental processes. For example, the prevalence of indigestible phytoplankton in the gut of young larvae can be taken as a sign of the not yet fully developed sensory and locomotory capacities of the young fish (El-Fiky et al. 1987). Furthermore, quantitative and qualitative changes in the gut contents correlate strongly with changes in the form and relative length of the gut, but reflect only weakly the availability of prey in the water. In the Seefelder See population of *R. rutilus* the switch from a phytoplankton to a cladoceran dominated diet is accompanied by an increase in relative growth rate by nearly one order of magnitude (Wieser et al. 1988).

Key words: *Rutilus rutilus* – Growth – Diet composition – Food availability – Gut length – Cladocera

Food availability and competition are usually considered the major determinants of community structure. The size of the organisms involved is an important factor in this connection, affecting community structure via size-dependent resource utilization and size-dependent competition (Hutchinson 1959; Schoener 1974; Peters 1983). However, there is an *ontogenetic* aspect of species interactions in communities which is only just beginning to be appreciated in the literature. As far as aquatic communities are concerned we owe it to Werner (see Werner and Gilliam 1984) to have drawn attention to the fact that the pattern of an organism's resource use (thus its role in the community) changes as the organism increases in size from birth or hatching to its maximum (see also Lammens et al. 1985). This effect is particularly large in poikilothermic animals, for example in some fish which weight about 1 mg at hatching and may grow by three orders of magnitude within three months. But size is not the only ontogenetic variable affecting species interactions in natural communities. Apart from spectacular developmental processes, like metamorphosis and moulting, most animals pass through developmental steps, or "stanzas" (Ricker 1979), accompanied by structural and functional reorganizations which are likely to affect resource utilization as well as competitive abilities. In fish a number of larval stages have been recognized (Balon 1979) each characterized by changes involving one or several organ systems, like feeding apparatus, locomotor apparatus, gills, and sense organs (Blaxter 1986; El-Fiky et al. 1987; El-Fiky and Wieser 1988). Inasfar as these developmental events are reflected in specific nutritional requirements or specific abilities of food aquisition, synchronization with environmental events is necessary for fishes to survive this most sensitive phase of their life cycle (Wieser et al. 1988; Gadomski and Petersen 1988). The role of developmental processes in determining food selection and species interactions in aquatic communities has not yet received the attention it deserves.

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Material and methods

This study was carried out in Seefelder See, an oligotrophic subalpine lake situated at an altitude of 1210 m near Seefeld, about 30 km NW of Innsbruck. The hydrography of the lake has been described by Leutelt-Kipke (1934) and by Pechlaner et al. (1980). The fish fauna is restricted to roach (*Rutilus rutilus* L.), perch (*Perca fluviatilis* L.) and some pike (*Esox lucius* L.). Most of the lake is surrounded by a belt of Phragmites which serves as a spawning area for roach and as a shelter for the larvae. The lake is very shallow, its maximum depth not exceeding 5 m. Ice cover is present from about December to April/May. Spawning of roach takes place only once, in late May, and the larvae usually hatch in the first week of June. Due to the low temperature in the beginning of June (12–14° C) growth of *R. rutilus* is very slow at first, but with increasing temperature and food availability the specific rate of growth may increase from 3 to 30% fbw.d^{-1} within one week (Wieser et al. 1988). In 1985 larvae and juveniles of roach were sampled from June 12th to September 5th and their distribution in the lake as well as their gut contents and patterns of growth were studied. On most of the fish sampling days plankton samples were also taken in order to compare food

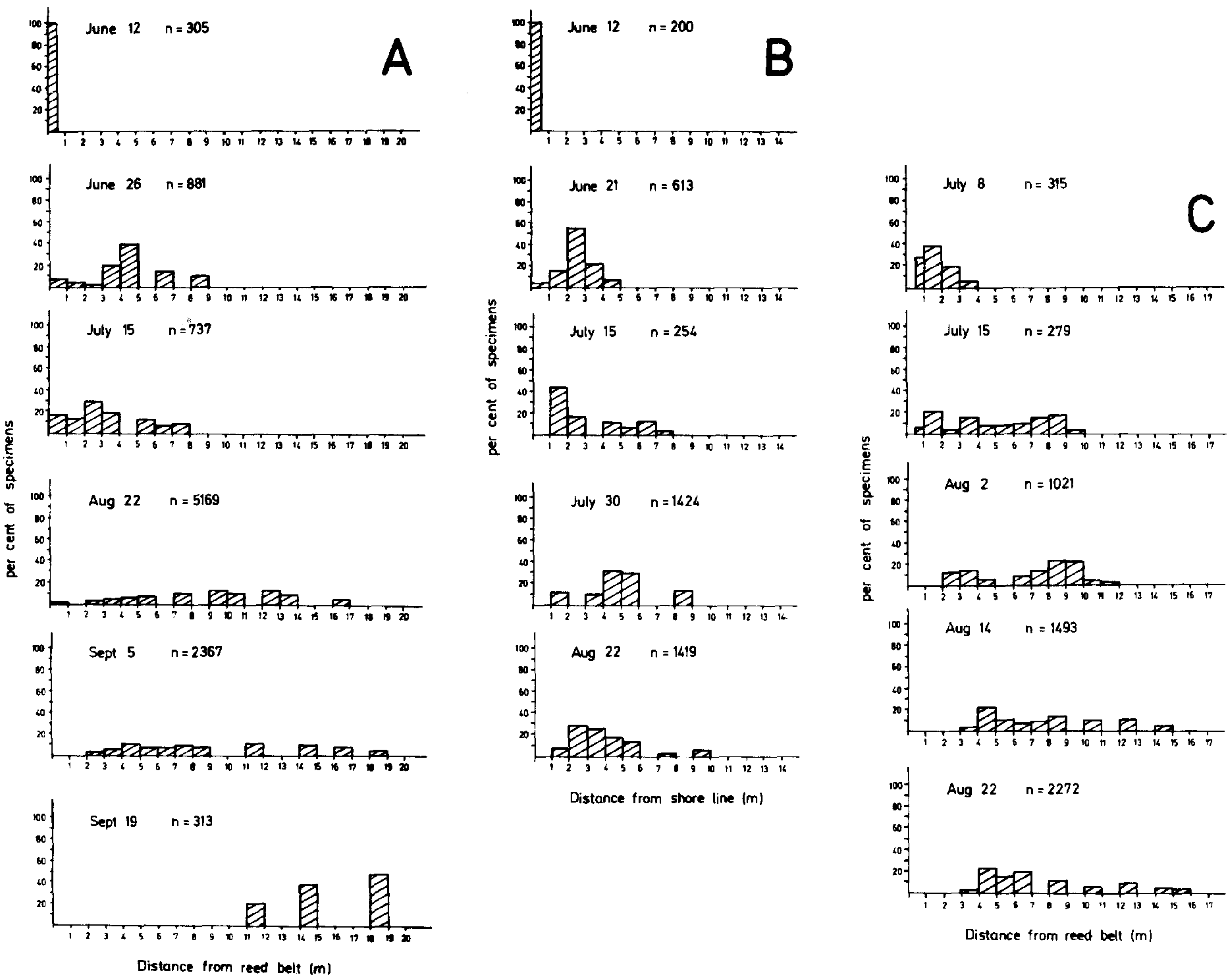

Fig. 1A–C. Horizontal distribution of *Rutilus rutilus* during approximately the first three months after hatching in Seefelder See, an oligotrophic subalpine lake in Tirol, Austria. The results of visual counts along three transects (**A, B, C**) are shown. Height of columns indicates relative abundance of fish swimming across submerged plexiglass plates. All specimens counted during one observation period = 100%. Abscissa: distance (in m) of observation point from shore line or edge of reed belt

availability in the water and food selection by the growing fish. However, due to technical problems this matching of samples was not always achieved (see Fig. 3).

Sampling of fish and plankton. Sampling was carried out from a small boat along three transects from the shore line to a distance of about 20 m offshore where the depth of the lake was still only about 1 m. Fish were sampled always at the same time in the morning to ensure constancy of the state of nutrition. A scoop net was used and the fish were immediately preserved in buffered 4% formaldehyde. Plankton was sampled with a Ruttner sampler holding a volume of about 5 L. Care was taken not to disturb the silty sediment of the bottom so that only the truly pelagic element of the plankton was collected quantitatively. The contents of the sampler were strained through a 47 μm mesh screen and the retained material preserved in formaldehyde. The density of the roach population at different sites along the transect was estimated by counting 4 to 5 times every 5 minutes the number of fish swimming across opalescent plexiglass plates (30 × 30 cm) that had been put down earlier (Rheinberger et al. 1987).

Preparation and analysis of gut contents. After determining total length and weight of a larva of juvenile the gut was removed under a dissecting microscope, measured, opened and the contents placed on a glass slide. Under a light microscope the food items were identified as near as possible to species, but in this paper only the most abundant species will be listed (see Table 5). Rarer species are collectively included in a higher taxon. The body length of the most undamaged food items was measured and average prey length was calculated. The volume of each type of prey was calculated as described by Ruttner-Kolisko (1977) for rotifers and by Edmondson and Winberg (1971) for crustaceans. For other groups simple assumptions were made as to the geometric shape of the organisms. Diet composition was expressed as the abundance, or volume, of a given food class in per cent of total food items, or total food volume, in the gut (see also Mark et al. 1987).

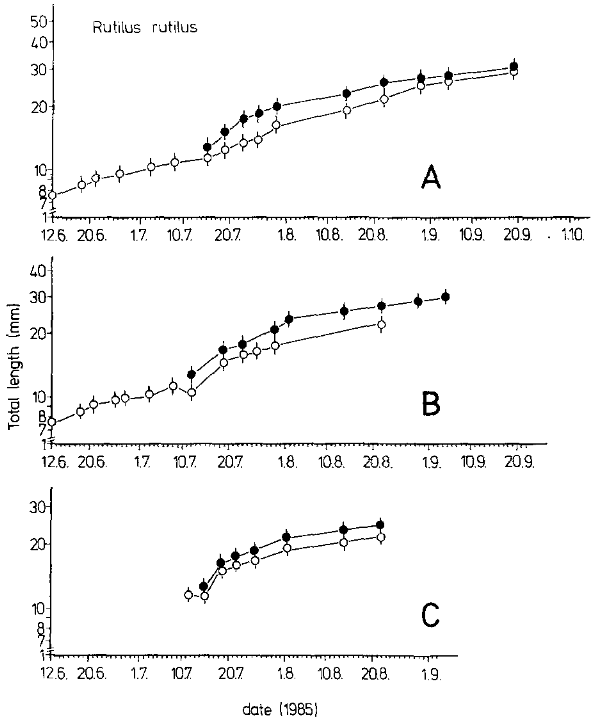

Fig. 2A–C. Total length of *Rutilus rutilus* at the three transects of Seefelder See. From about mid-July a distinction was made between specimens sampled close to the shore (*open circles*) and specimens sampled furthest offshore, as indicated in Fig. 1 (*closed circles*)

Results

Horizontal distribution and growth

The larvae hatched from eggs deposited within the belt of macrophytes around June 5th and on June 12th were still confined to this zone. In the second half of June the larvae began to move offshore as shown for the three transects in Fig. 1. Until the beginning of September the population appeared fairly spread out, with some specimens closer to the shore than others. It is interesting that from the beginning of July the more offshore members of the population were always significantly larger than the nearshore members (Fig. 2). Either the distribution was stationary and the offshore specimens found better nourishment, or the fish moved about horizontally and the larger and less vulnerable specimens dared further offshore than the smaller ones.

Prey selection

Prey availability in the open water based on plankton samples is summarized in Table 1. Since no differences were found between transects and between sites along one transect all samples have been pooled. Although the sampler contained benthic forms, particularly benthic cladocerans, their abundance in the sampler does not reflect their abundance at the bottom of the lake. In consequence, food selection by the fish can be given unambiguously only for the truly pelagic forms, i.e. pelagic rotifers, pelagic cladocerans and copepods. Amongst crustaceans only *Bosmina longirostris* and *Ceriodaphnia pulchella* were eaten with sufficiently high frequency (Table 2) to allow a comparison between food availability in the water and food selection by the fish. This comparison as set out in Fig. 3 shows that quantitative correspondence between food availability and gut contents holds for rotifers only, and only for the first month after hatching of the fish larvae. With regard to the two species of pelagic Cladocera the qualitative impression is that the juvenile fish started to select tham at a time when the prey had become less abundant in the water.

This pattern suggests that food selection of the young fish was not only determined by the availability of prey but also by the schedule of developmental processes.

In those fish which had swallowed the highest number of a given prey class intensity of selection (=number of prey items in gut/number of prey items in one liter of water)

Table 1. Density of plankton in Seefelder See (Summer 1985). Figures are average numbers of animals per l of water. Averages are based on number of samples as indicated in column 4

date		T (°C)	no samples	rotif	Cladocera						Copepoda
day	month				B.l.	C.p.	D.spp	S.m.	S.c.	Pl.	
12	6	14.1	3	478	0.2	2.9	0.1	1.1	3.0	4.1	–
18	6	14.7	5	222	1.0	0.1	–	0.1	0.3	0.1	0.9
21	6	14.8	5	308	5.0	5.0	–	3.2	4.8	11.4	6.9
26	6	15.8	5	130	1.4	8.6	0.8	–	0.3	1.1	3.2
5	7	17.0	3	239	3.9	6.9	3.6	3.0	6.0	n.d.	3.9
12	7	17.8	6	232	1.3	2.4	1.2	0.9	2.0	5.0	0.1
15	7	18.9	5	368	0.3	0.2	2.1	0.2	–	0.8	1.0
19	7	n.d.	3	254	0.3	0.2	0.1	0.6	2.4	0.7	1.1
23	7	22.2	5	267	0.3	1.6	0.2	1.1	1.5	1.3	5.6
26	7	20.8	4	317	0.2	0.5	0.1	0.1	0.1	0.4	0.4
30	7	20.2	5	76	0.4	0.4	0.2	0.2	0.3	0.4	1.1
14	8	17.4	5	69	0.8	0.1	0.1	0.2	–	0.6	0.2
22	8	18.7	6	70	0.6	0.1	0.5	–	0.5	0.2	0.6
30	8	13.6	5	41	0.4	0.3	0.3	0.4	0.1	3.1	2.7
5	9	17.0	5	27	0.1	0.2	0.2	0.1	0.1	0.3	0.3

rotif rotifers; *B.l. Bosmina longirostris; C.p. Ceriodaphnia pulchella; D.spp Daphnia* spp.; *S.m. Scapholeberis mucronata; S.c. Sida crystallina; Pl. Pleuroxus* spp.

Table 2. Average number of food objects in gut of young roach. Number of fish examined listed in last column of Table 4. For higher taxa the figure given is the average of *all* fish examined; for the two species of Cladocera the figure given (in heavy print) is the average of only those fish in which the prey was present

date		phyto	rotif	Cladocera				cop	naup	allo	chiro	nema
day	month			bent	pel	*Bos*	*Cer*					
12	6	20.6	7.2	0.1	0.9	*3.0*	–	–	–	–	0.5	0.1
18	6	50.5	7.9	–	0.5	*1.0*	–	–	0.4	–	0.7	–
21	6	50.4	7.3	–	–	–	–	–	0.4	–	–	–
26	6	26.5	3.5	0.2	0.8	*1.3*	*6.5*	0.1	0.3	0.1	0.4	0.1
5	7	154.7	6.8	0.3	0.5	*1.0*	*1.5*	–	0.7	–	0.7	0.1
12	7	31.9	5.1	0.7	2.6	*6.7*	*1.7*	–	0.1	0.1	0.5	0.1
19	7	1.7	1.7	3.0	3.0	*2.7*	*2.6*	1.1	1.7	0.3	1.1	0.1
26	7	10.6	2.8	2.4	1.8	*2.0*	*2.0*	0.6	1.2	0.3	2.2	–
30	7	2.5	0.7	3.2	1.8	*5.5*	–	–	–	2.7	2.8	–
2	8	6.4	5.5	7.0	16.7	*18.7*	*9.0*	0.2	0.4	1.3	1.5	0.2
14	8	13.3	0.3	12.6	39.4	*44.0*	*2.6*	0.4	0.2	0.3	1.7	0.1
5	9	11.7	1.1	7.2	2.1	*3.0*	–	0.9	0.2	1.8	0.8	0.3

phyto phytoplankton (dominant taxa: *Microcystis* sp., *Coelosphaerium* sp., Dinophyta spp., *Botryococcus* sp., other Chlorophyceae); *rotif* rotifers (dominant species: *Lecane* sp., *Keratella* sp., *Trichocerca* sp.); *pel* pelagic; *Bos Bosmina longirostris; Cer Ceriodaphnia pulchella; cop* adult copepods; *naup* nauplii; *allo* allochthonous material (mainly aerial insects); *chiro* chironomid larvae; *nema* nematodes

Table 3. Average volumes of major groups of food organisms in gut of young roach. Figures are nl per fish. Number of fish examined listed in last column of Table 4

date		length (mm)	phyto	rotif	crust	insects	rest	total
day	month							
12	6	8.5	4.9	0.7	3.9	0.6	1.0	11.2
18	6	8.0–9.0	11.2	0.6	2.9	11.4	3.1	29.0
21	6	8.5–9.0	13.0	0.7	0.5	–	1.1	15.4
26	6	9.0–10.0	8.9	0.5	25.6	8.2	0.5	43.7
5	7	9.5–10.0	39.0	0.7	21.8	6.5	0.5	68.5
12	7	10.0–12.5	6.3	0.4	41.2	7.2	0.8	54.4
19	7	11.0–16.0	0.9	0.2	220.6	55.1	0.5	277.2
26	7	13.0–16.0	3.1	0.3	251.3	58.3	7.4	320.3
30	7	15.5–17.0	0.6	0.1	230.9	377.9	–	685.1
2	8	18.0–21.0	2.2	0.6	786.4	152.3	6.2	947.4
14	8	20.0–26.0	3.3	–	1255.7	72.2	2.7	1331.5
5	9	25.0–33.0	6.4	–	620.0	254.0	51.2	931.6

phyto phytoplankton; *rotif* rotifers; *crust* crustaceans; *insects* mainly chironomid larvae

was low for the Rotatoria, high for *Bosmina longirostris,* and intermediate for *Ceriodaphnia pulchella.*

Prey volume and gut contents

On the basis of volume determinations of the important prey items total volume of the different classes of food in the gut contents were determined. Table 3 shows that dramatic changes in total food volume as well as in the composition of the gut contents took place at least twice in the course of the investigation. Phytoplankton formed an important component of the gut contents until the larvae measured about 10 mm in body length. A short time later the volume of crustaceans and insects (the latter consisting mainly of chironomid larvae) in the gut increased, followed by yet another increase in the volume of crustaceans which at the beginning of August comprised 80 to 90% of the total gut contents. If one compares the occurrence of these three groups of food items in the gut with the relative length of the gut of the fish (= [length of gut/total length of body] · 100) (Fig. 4) it emerges that these changes in food content and food composition are correlated with a rather sudden change in the relative length and the form of the gut which probably also reflects functional changes in the digestive apparatus of the fish.

Further details of changes in the composition of the gut contents with development are summarized in Tables 4 and 5. Phytoplankton formed an important part of the gut contents until July 12th when the larvae measured 10–12.5 mm in length (Table 3). Although the smallest cladocerans, *Bosmina* and *Alona,* were occasionally swallowed by the smallest larvae, the bulk of the cladocerans began to comprise a significant portion of gut volume not until June 26, and it took another two weeks or so until the largest benthic form, *Pleuroxus laevis,* became the most prominent prey object in the gut. There was no corresponding increase in density of this cladoceran species in the water samples (Table 1). Adult copepods were never caught in

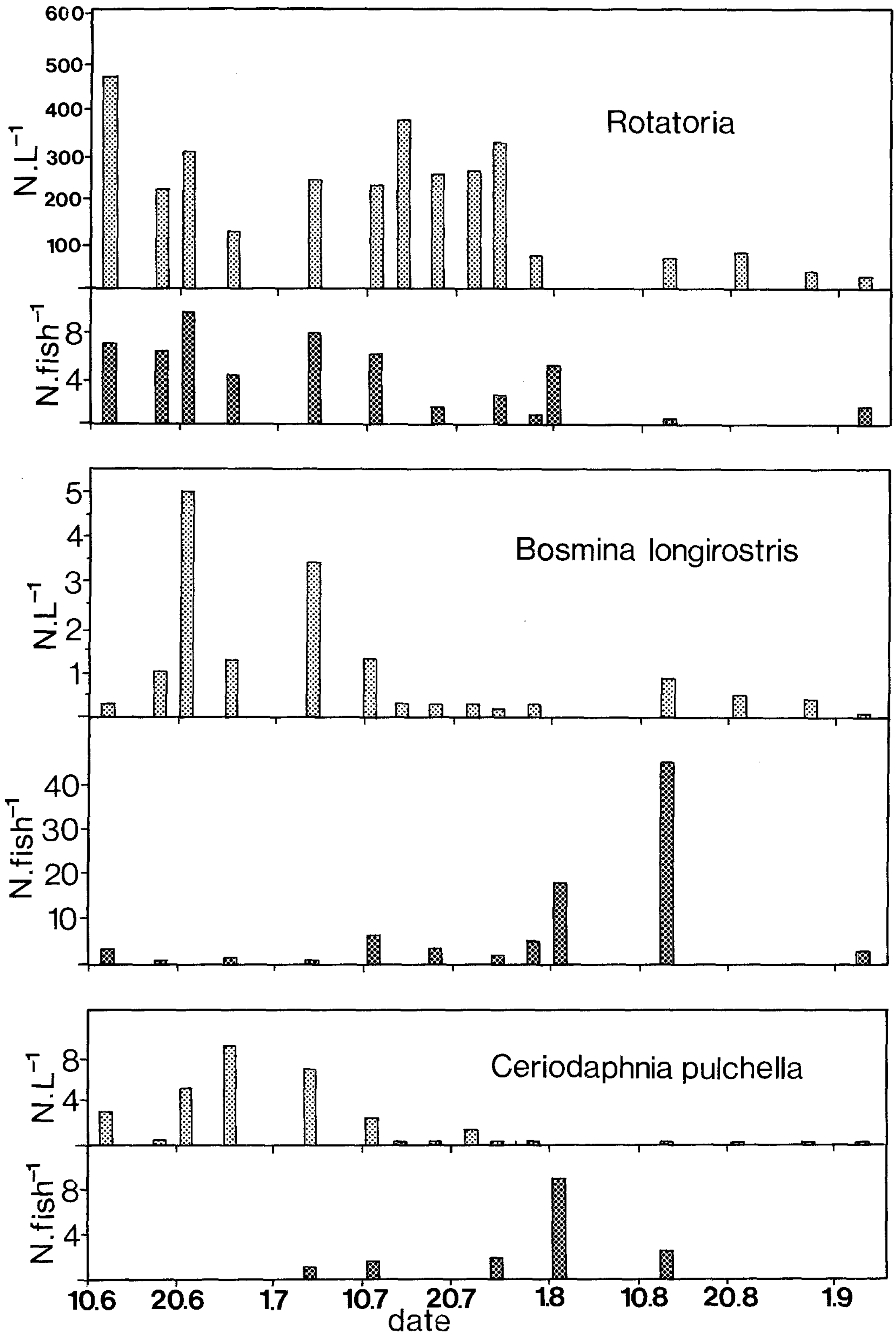

Fig. 3. Density of three types of pelagic prey in lake water (specimens per l) and in gut contents of young *Rutilus rutilus* (specimens per fish)

significant amounts by the young fish. On the other hand, large chironomids made up a substantial part of the gut volume even of some very small larvae. The most striking developmental change that occurred in these fish, however, is the increase in total food volume in two steps: first between July 12 and 17, second between July 26 and August 2 (Table 3). This *increase* in food uptake coincides with a general *decrease* in density of the lake fauna (Tables 1 and 6).

Discussion

After hatching in the littoral zone as larvae the juveniles of *R. rutilus* gradually move offshore into the open water.

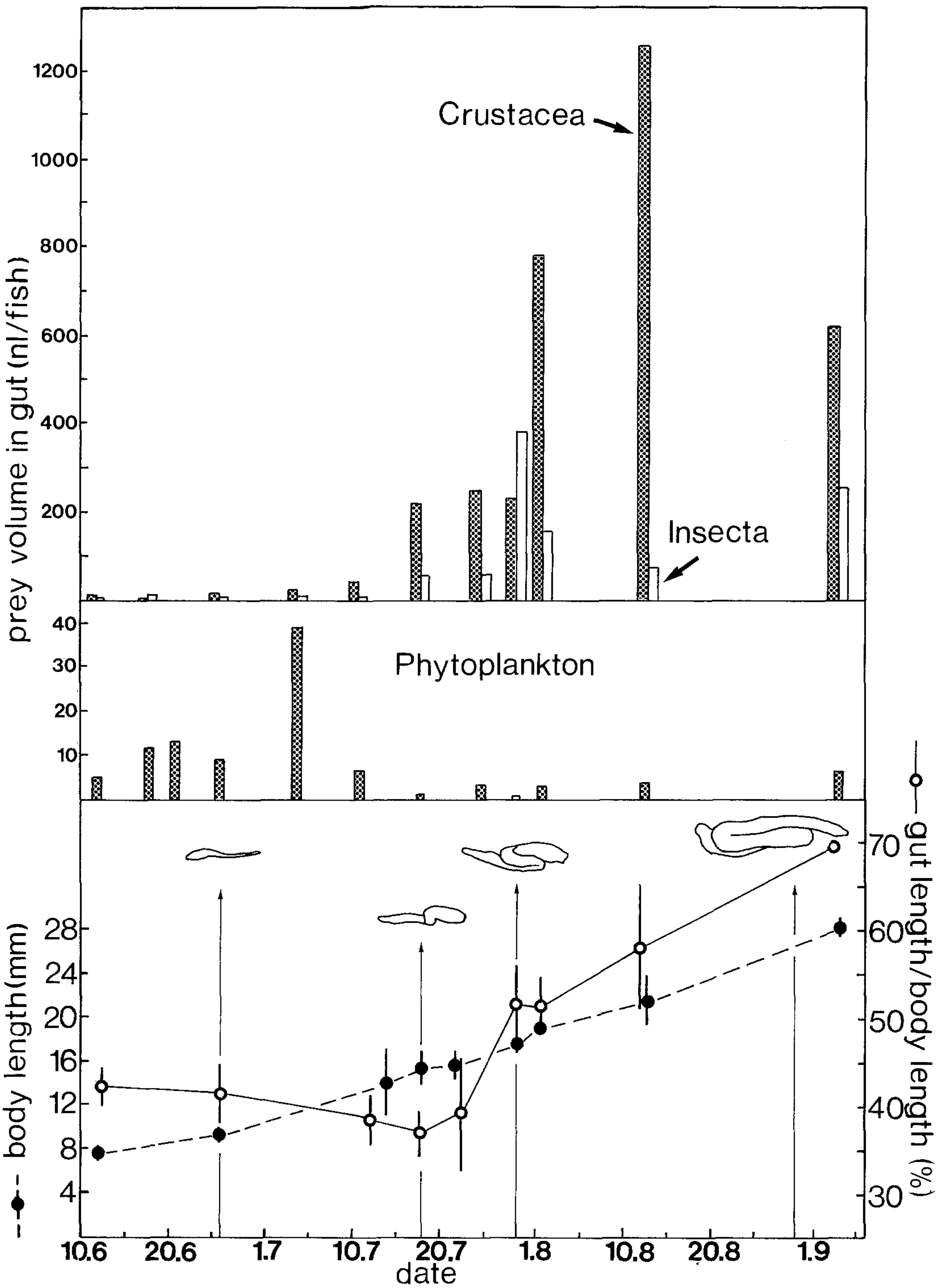

Fig. 4. Volume of the dominant types of prey in the gut of young *Rutilus rutilus* (*upper panel*), compared with total body length (*full circles*) and relative gut length (*open circles*) of fish sampled between June 12th and Sep 5th 1985, in Seefelder See (*lower panel*). Height of column represents prey volume in nl per fish. Four stages in the development of the gut are shown

This seems to be a genetically fixed behaviour since it has been observed in all populations of roach irrespective of whether the larvae of other cyprinid species occurred in the same habitat (Hammer 1985; Braband 1985; Rheinberger et al. 1987) or whether *R. rutilus* was the only cyprinid present in the lake (this investigation). In another subalpine lake, Piburger See, the horizontal movements of *R. rutilus* led to habitat separation between the juveniles of this species and those of the closely related rudd (*Scardinius erythrophthalmus*) and chub (*Leuciscus cephalus*) (Rheinberger et al. 1987).

Our data confirm the role of the roach as one of the most versatile generalists in European lakes. Despite this feature the composition of the diet during the first weeks after hatching is not only determined by availability of food in the habitat but by developmental events. The most general of these is, of course, the increase in size of the fish which correlates with an increase in the average size of the food objects swallowed (Werner and Gilliam 1984). Up to a total body length of about 10 mm the gut contents of roach larvae consisted mainly of the smallest pelagic objects, phytoplankton, rotifers and the smallest cladocerans, particularly *Bosmina longirostris*, the most vulnerable species of cladocerans (Bohl 1982). The prevalence of phy-

Table 4. Relative volumes of major groups of food organisms in gut of young roach. Figures are average per cent of total food volume; number of fish examined indicated in last column

date		phyto	rotif	Cladocera		cop	chironomids		allo	detri	no sample	no fish
day	month			bent	pel		small	large				
12	6	39.8	6.6	9.0	22.6	–	13.5	–	–	8.2	1	17
18	6	32.6	2.0	–	5.5	–	2.5	46.2	–	10.1	2	15
21	6	84.7	4.5	–	–	–	–	–	–	7.4	1	7
26	6	27.0	1.7	21.6	19.6	4.2	2.4	18.6	3.9	–	3	22
5	7	52.0	0.9	12.3	15.7	–	1.9	16.0	–	–	1	10
12	7	15.0	1.0	38.5	26.8	–	2.3	15.5	–	–	3	17
19	7	0.1	0.1	37.1	37.1	11.5	0.5	10.2	10.9	–	2	10
26	7	1.3	0.2	27.5	24.6	9.8	2.8	14.4	7.2	–	2	12
30	7	0.1	–	14.8	1.3	–	1.5	7.3	74.9	–	1	6
2	8	0.3	0.1	48.3	27.1	1.3	0.6	2.5	19.1	–	2	10
14	8	0.4	–	71.6	17.8	2.2	2.7	3.8	1.6	–	3	16
5	9	0.4	–	62.8	1.0	4.9	0.2	5.3	20.0	6.1	2	14

phyto phytoplankton; *rotif* rotifers; *bent* benthic; *pel* pelagic; *cop* copepods; *allo* allochthonous material (mainly aerial insects); *detri* detritus; *chironomids* larvae <2 mm long (small), >2 mm long (large)

Table 5. Relative volumes of crustaceans found in gut of roach. Details as in Table 4

date		Acr	Al	Alla	Gr	Per	Pl	Bos	Cer	Diaptomus	
day	month									cop	ad
12	6	–	9.0	–	–	–	–	22.6	–	–	–
18	6	–	–	–	–	–	–	5.5	–	–	–
21	6	–	–	–	–	–	–	–	–	–	–
26	6	10.5	9.9	0.9	–	–	–	3.6	16.0	4.2	–
5	7	–	2.5	–	–	–	9.8	0.8	14.8	–	–
12	7	–	5.3	0.3	3.2	–	29.7	10.4	16.4	–	–
19	7	3.8	2.8	0.3	–	0.9	18.0	1.1	26.3	11.5	–
26	7	–	1.8	0.2	6.5	4.7	25.8	0.8	23.9	9.8	–
30	7	1.7	9.0	0.1	–	3.1	26.2	1.3	–	–	–
2	8	1.4	7.7	0.1	1.5	0.4	13.5	6.4	20.8	0.5	0.7
14	8	0.6	5.5	0.1	–	5.8	57.0	13.1	4.7	2.3	0.6
5	0	–	15.4	0.1	–	1.5	43.4	1.0	–	1.9	3.0

Acr Acroperus harpae (Baird 1835); *Al Alona* spp.; *Alla Alonella nana* (Baird 1843); *Gr Graptoleberis testudinaria* (Fischer 1848); *Per Peracantha truncata* (O.F. Müller 1785); *Pl Pleuroxus laevis* (Sars 1862); *Bos Bosmina longirostris* (O.F. Müller 1785); *Cer Ceriodaphnia pulchella* (Sars 1862); *cop* copepodits; *ad* adults

toplankton in the gut of roach larvae has been observed in other populations of this species as well (Hammer 1985; Mark et al. 1987). Since this kind of food cannot be digested by the fish one has to assume that bacteria or ciliates associated with the algae are the major source of food during this period. At any rate, growth is slow, not exceeding 8% fbw.d^{-1} even if corrected for the low temperature prevailing in the lake at that time (Wieser et al. 1988). In other lakes rotifers, and sometimes nauplii, comprise the dominant diet during the first weeks after hatching (Grigorash et al. 1972; Weatherley 1987). The high percentage (Table 4) of indigestible phytoplankton in the gut may also be taken as a sign of the not yet fully developed sensory and locomotory capacities of the young fish. Up to a body length of 10–12 mm the swimming muscle are not yet fully differentiated (El-Fiky et al. 1987; El-Fiky and Wieser 1988). The larvae move in irregular bursts and are not yet capable of lateral rotation (Grigorash et al. 1972). Correlated with these motoric deficiencies we may expect deficiencies of the sensory organs (Blaxter 1986, and unpublished observations).

As the fish grow the composition and volume of the diet changes drastically. As in other populations of roach (Grigorash et al. 1972; Hammer 1985; Cryer et al. 1986; Townsend et al. 1986) cladocerans are becoming the dominant component of the diet. In August, *Alona* spp., *Graptoleberis testudinaria, Pleuroxus laevis* and *Ceriodaphnia pulchella,* may represent up to 90% of diet volume. Simultaneously the total volume of the gut contents increases. This is documented by Table 6, in which diet volume is expressed in per cent of average fresh body weight (the latter taken from Wieser et al. 1988).

The increase in relative volume of the gut contents which takes place in the second half of July correlates with an equally distinct change in the form and relative length of the gut (Fig. 4; Table 6). There may also be non-linear increases in proteolytic activity involved since a break in "proteolytic action" (tryptic activity multiplied by gut passage time) was observed in the larvae of *R. rutilus* at a fresh body weight of about 20 mg (Hofer and Nasir Uddin 1985).

In Seefelder See the increase in relative gut length and

Table 6. Length, fresh body weight (fbw), absolute and relative volume of diet, relative length of gut in larvae and juveniles of roach, and density of all crustaceans (crust.) in water samples from Seefelder See. The latter figure includes not only pelagic but also benthic cladocerans collected by means of the Ruttner sampler

date		average length (mm)	average fbw (mg)	average volume of diet (μl/fish)	relative length of gut (% of body length)	relative volume of diet (% of fbw)	density of crust. in water ($N.L^{-1}$)
day	month						
12	6	8.5	2.4	0.0112	42.5±2.1	0.47	16.5
21	6	8.7	3.7	0.0154	41.4±3.3	0.42	48.5
12	7	11.2	6.9	0.0544	38.5±2.7	0.78	19.8
19	7	13.5	27.1	0.277	36.8±2.6	1.02	6.4
30	7	16.2	56.2	0.685	51.8±4.4	1.22	2.3
2	8	19.5	63.9	0.947	51.7±3.4	1.48	n.d.
14	8	23.0	88.8	1.331	58.1±7.2	1.50	3.3

the switch from a phytoplankton dominated to a cladoceran dominated diet was accompanied by an increase in relative growth rate ($\%fbw.d^{-1}$) by nearly one order of magnitude (Wieser et al. 1988). It may be that such a close correlation between developmental processes and diet composition becomes visible particularly under poor food conditions as they prevail in this oligotrophic lake. In a Canadian lake Keast (1980) found a much closer relationship between diet and food availability in the larvae and juveniles of several species of percids and centrarchids.

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