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Article *in* Aquatic Sciences · March 1996

DOI: 10.1007/BF00877636

Aquatic Sciences 58/1, 1996

1015-1621/010001-14 $ 1.50 + 0.20/0

Influence of submerged aquatic vegetation on size class distribution of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in the littoral zone of Lake Geneva (*Switzerland*)

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Key words: Perca fluviatilis, Rutilus rutilus, littoral, habitat selection, aquatic vegetation, Lake Geneva.

ABSTRACT

The abundance of different size classes of perch and roach in the littoral zone of Lake Geneva was compared between submerged aquatic vegetation and unvegetated zones. Samples were taken with gillnets during four periods between June and October 1993. During the vegetation period (June to September), perch ≤9 cm and roach ≤10 cm were more abundant in vegetation whereas roach > 20 cm were more abundant in open water. Perch larger than 18 cm and medium roach were equally distributed in both habitats whatever the period, whereas medium perch distribution fluctuated according to the period. In October, after the decline of the vegetation, no more differences in fish distribution were observed except for small roach, which were always more abundant in the "vegetated sites".

Introduction

Submerged aquatic vegetation, bottom substrate, water depth, temperature and dissolved oxygen are the most important factors influencing the distribution of fishes in littoral zones (Hall and Werner, 1977; Werner et al., 1977; Keast, 1984; Stang and Hubert, 1984; Benson and Magnuson, 1992). Especially, several studies have shown that fish abundance is generally higher in vegetated than in unvegetated areas, both in freshwater and marine environments (e.g. Werner et al., 1977, 1978; Orth and Heck, 1980; Rozas and Odum, 1987; Dewey et al., 1989; Killgore et al., 1989; Lubbers et al., 1990). Aquatic vegetation is known to support usually higher abundance of macroinvertebrates than unvegetated areas (Gilinsky, 1984; Orth et al., 1984; Rabe and Gibson, 1984; Gregg and Rose, 1985) and can thus provide a rich foraging area for some fish species. In addition, the presence of vegetation mediates the predator-prey relationships through the increase of habitat structural complexity (Crowder and Cooper, 1979) and experimental studies have proved that the predation rate of piscivorous fishes decreases when plant density (complexity) increases (Savino and Stein, 1982; Gotceitas and Colgan, 1987; Nelson and Bonsdorf, 1990). Macrophyte beds thus provide an effective shelter against predation for juvenile fishes (Werner et al., 1983) and several studies have demonstrated the nursery role played by vegetation for some species (e.g. Hall and Werner, 1977; Orth and Heck, 1980; Holt et al., 1983; Burchmore et al., 1984; Paller, 1987; Conrow et al., 1990). Thus macrophyte presence could influence not only species distribution but also size class distribution by providing a shelter for young individuals or an important feeding area for some developmental stages.

Perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) are the most abundant fish species in Lake Geneva (Büttiker, 1984). They stay in deep water during winter and colonize the littoral zone in spring for the breeding period (Thorpe, 1974; Hartmann and Löffler, 1978, 1989; Lang, 1987). Many young-of-the-year and older fish stay in the littoral zone of Lake Geneva until autumn (Rossier, 1995). The simultaneous presence of several size classes of each species in this relatively small area (about 5.3% of the total lake area (Lachavanne and Wattenhofer, 1975)) enhances intra and interspecific interactions. Different studies have shown that, in some occasions, competition for food can occur between perch and roach or within the perch population (Persson, 1983, 1987a, b, c; Bergman, 1990; Persson and Greenberg, 1990a, b). Predator-prey relationships could likewise occur in this community. Perch are piscivorous from a size of 2.5 cm in Lake Geneva if smaller prey are available (D. Ponton, pers. comm.) and feed, among other prey, on smaller roach or perch (Craig, 1987; Hartmann, 1992). A recent study (Rossier, 1995) has shown that, in the littoral zone of Lake Geneva, perch and roach were distributed differently according to the distance from the shore, but little information exists on the influence of macrophyte stands on their spatial pattern. This study is intended to compare abundance of different size classes of perch and roach in vegetated and unvegetated zones to determine the influence of vegetation on their distribution.

Study site

Lake Geneva (Switzerland-France, 582.4 km^2, average depth 152.7 m, alt. 372 m) is a deep meso-eutrophic, monomictic lake, thermally stratified between May and November (thermocline depth between 10 and 25 m). In 1993, the minimum temperature of surface water was about 6 °C in February and the maximum was about 22 °C in August. Water transparency fluctuates greatly throughout the year but Secchi disk visibility remains between 8 and 12 m in November-March and between 2 and 8 m in April-October (Blanc et al., 1994).

Macrophyte communities colonize the littoral zone down to a depth of 6 m (12 m for Characea, R. Baenziger, pers. comm.), and are dominated by Potamogetonaceae, especially by *Potamogeton pectinatus* and *P. perfoliatus* (Lachavanne and Wattenhofer, 1975; Lachavanne et al., 1986).

Two sites without and two sites with vegetation were chosen to study the influence of vegetation on the distribution of perch and roach. All sites were located on the southern shore of the lake, between Anières and Bellerive (46°16′N; 6°12′E) and were very similar except for vegetation and substrate (Fig. 1, Table 1). In this area, the bottom slope was very gentle and there was no significant depth

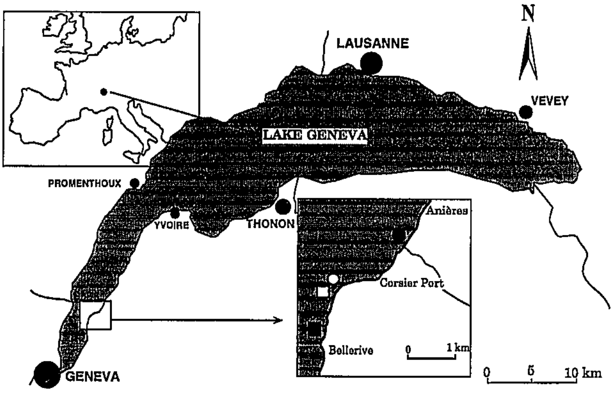

Figure 1. Location of sampling sites (black symbols: vegetation and white symbols: unvegetated, circle: site 1, square: site 2) in the littoral zone of Lake Geneva, Switzerland

Table 1. Description of the four sampling sites

Site	Depth (m)	Substrate	Distance from the shore (m)	Width of the littoral zone (m)	% of vegetation cover	Macrophyte composition
Unvegetaged 1	4.5	Silt Boulder Cobble	~150	~300	<5%	*P. perfoliatus*
Unvegetated 2	4	Silt Boulder Cobble	~100	~250	<5%	*P. perfoliatus*
Vegetated 1	4	Silt	~100	~250	60–70%	*P. lucens* 40% *P. perfoliatus* 40% *P. pectinatus* 20%
Vegetated 2	3.5	Silt	~150	~325	70–80%	*P. lucens* 60% *P. perfoliatus* 30% *P. pectinatus* 10%

difference within each site. The study sites were chosen on the basis of previous vegetation surveys carried out in 1991 by Ecotec Environment S.A. (pers. comm.).

Each vegetated site consisted of several patches of vegetation within which sampling was carried out. These patches were separated by small areas without macrophytes. The macrophyte patches were composed mostly of *P. lucens* and *P. perfoliatus* which grew to the surface, and a smaller proportion of *P. pectinatus* (Table 1) which extended about one meter above bottom at this depth. In macrophyte patches, stem density was about 100–120 per m^2 at the end of July. Macrophyte growth began generally in April and the maximum biomass occurred between July and August. During September, macrophyte density was still high, but almost all vegetation disappeared during October. A detailed description of growth and biomass of the three macrophytes species in Lake Geneva is given by Lehmann et al. (1994).

Material and methods

Between June and October 1993, four sampling series consisting of 10, 9, 9 and 8 samples, respectively in each habitat (vegetated and unvegetated), were carried out during the following periods: period I (June): 8.6–29.6; period II (August): 27.7.–6.8; period III (September): 31.8–8.9; period IV (October): 30.9–12.10 (a total of 72 samples). Samples were taken simultaneously at the two vegetated sites and the two sites without vegetation, though only one site per habitat type was sampled on some occasions. The first three sampling periods occurred during the vegetation period, whereas in October almost all the macrophytes had disappeared.

The areas were sampled with a set of experimental monofilament bottom gill nets modified from Stang and Hubert (1984). A set consisted of three bottom gill nets (15 m × 1.5 m), each net consisting of three panels of the same surface area (5 m × 1.5 m) but of a different mesh size (8–13–17 mm, 21–25.5–32 mm and 40–50–60 mm knot to knot, respectively). At the vegetated sites, gill nets were deployed within macrophyte patches of sufficient surface area for the whole length of net to be surrounded by vegetation and to avoid edge effect. Supplementary weights were added to the base of these gill nets to force them to sink and to open correctly within macrophyte stands.

At each sampling site the three nets were positioned side by side (spaced approximately 25 m apart), perpendicular to the shore, and were left for about 18 hours (from 15 h until 9 h the next day). All fish captured were identified and measured (total length) to the nearest millimeter immediately after the net was lifted in order to release a maximum number of fish.

In the data analysis, we first grouped the individuals in size classes based upon the size distribution of the two species. The number of individuals of each size class captured by a set of nets during 18 hours (= one sample) was used as the basic unit (catch per unit effort, CPUE) to describe the relative abundance.

A within-period centered Principal Components Analysis (PCA) of the log transformed CPUE of each size class was used to concentrate on the general differences between sampling sites at each period. This type of constrained ordination produces factorial scores that center the samples belonging to the same category (here the period) and maximizes the dispersion of samples within each period (Dolédec and Chessel, 1989, 1991).

Effects of habitat type on fish abundance were tested for each size class during the vegetation period (June, August and September) with two-way ANOVAs performed on rank transformed CPUE data because the data were not normally distributed (Conover and Iman, 1981). Mann-Whitney U-tests were used in parallel to the ANOVAs to compare relative abundances between habitats for each period. For the purpose of the tests, the data were grouped per habitat type (2 sites merged) for each size class.

The ordinations and the related graphical outputs were realized using the 3.6. version of the ADE hypecard© stacks and Quickbasic Microsoft© program library (Chessel and Dolédec, 1992) and the Graph Mu program (Thioulouse, 1990).

The size class composition of perch and roach populations was very different (Table 2). Fish smaller than 13 cm were clearly dominant in perch catches (nearly 90% of total perch catches) whereas adults (> 20 cm) were more numerous in roach catches. Roach smaller than 10 cm were absent in June and August because young-of-the-year fish were too small to be caught in gill nets during these periods. On the other hand, perch smaller than 9 cm were present during each period but fish caught in June were the smallest individuals of the 1992 cohort whereas fish caught thereafter were young-of-the-year.

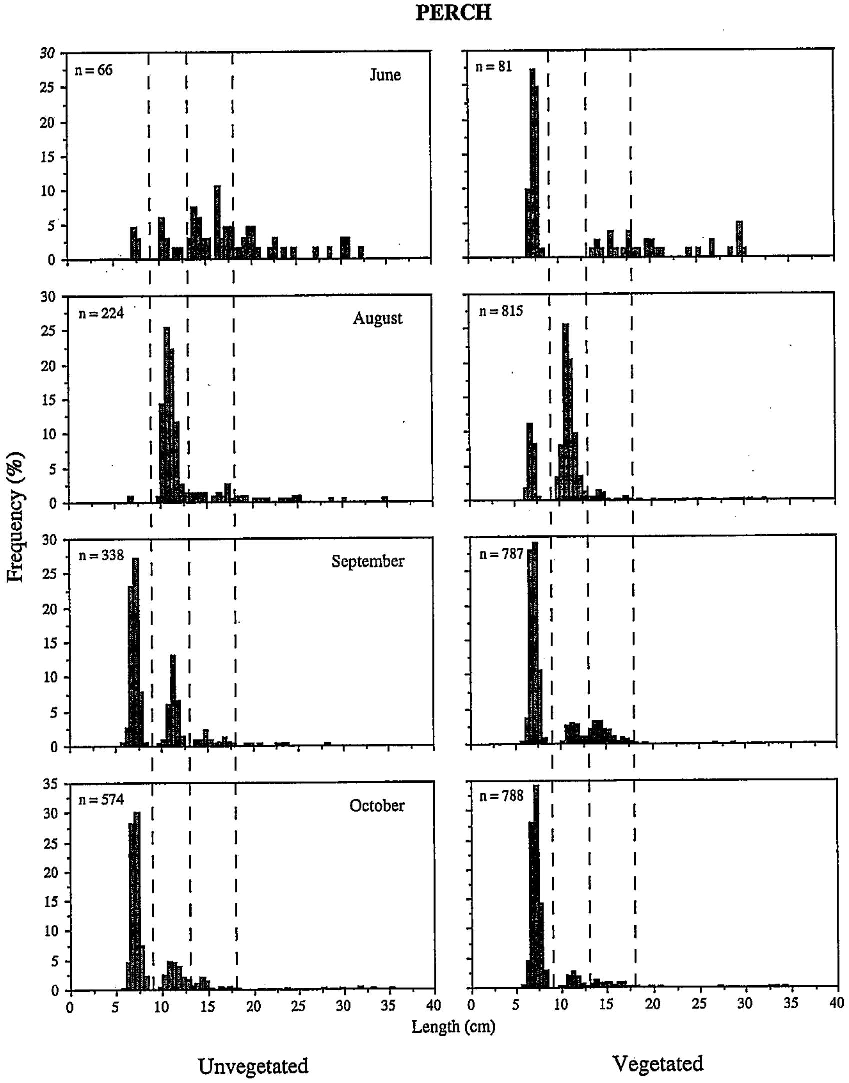

Figure 3. Length-frequency distribution of perch caught in gill nets in vegetated and unvegetated habitats during each sampling session. Dashed lines indicate size class separations

Results

Roach exhibited clear size class separation with three non-overlapping size groups in the catches (Fig. 2) whereas less clear division existed for perch (Fig. 3). For this species, the length-frequency histogram still allowed to visually split the data in four classes (Fig. 3). The size class intervals and the number of fish corresponding to these categories are given in Table 2. According to the selectivity of mesh sizes, some size classes were not caught. Therefore, perch and roach smaller than 6 cm were absent as were some intermediate sizes.

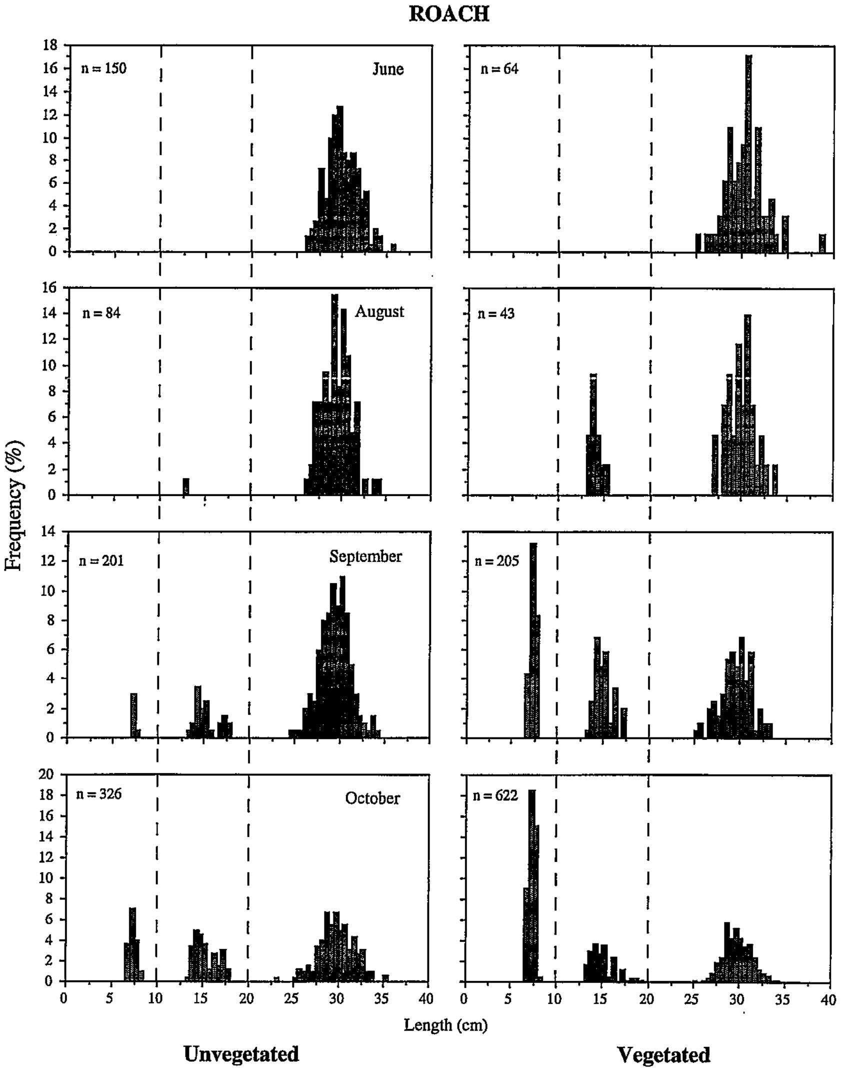

Figure 2. Length-frequency distribution of roach caught in gill nets in vegetated and unvegetated habitats during each sampling session. Dashed lines indicate size class separations

Table 2. Size class limits for perch and roach with class code and number of fish caught per class

Species	Size class (cm)	Class Code	N
Perca fluviatilis	≤9	P1	2096
	9.1–13	P2	1158
	13.1–18	P3	312
	>18	P4	106
Rutilus rutilus	≤10	R1	379
	10.1–20	R2	301
	>20	R3	1035

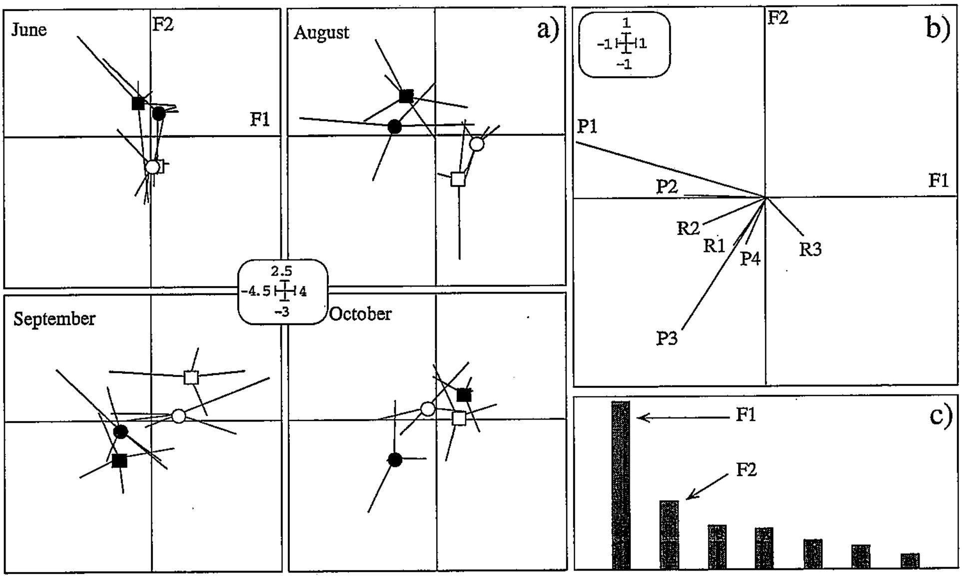

Figure 4. Within-periods centered PCA of the three size classes of roach (R) and four size classes of perch (P) by 72 samples data matrix. a: split of the F1 × F2 factorial plane of the 72 samples according to the 4 periods (black symbols: vegetated sites; white symbols: unvegetated sites, circles and squares: sites as in Figure 1), b: F1 × F2 plot of the 7 size classes, c: eigen values. The axes explain 42.7% (F1) and 17.4% (F2) of the total inertia

The within-period PCA (Fig. 4) aimed at removing the differences between sampling periods, in order to maximize and compare the variability of samples within each period. This analysis showed that in June, August and September, during the vegetation period, differences between vegetated and unvegetated habitats were larger than between sites of a similar habitat type. In October, at the end of the vegetation period, a more important difference occurred between the two vegetated sites.

Table 3. p values of two-way ANOVAs of the effects of habitat and period on the abundance of the different size classes of roach and perch (rank transformed data)

Source of variation	df	Roach			Perch			
		≤10 cm	10.1–20	>20 cm	≤9 cm	9.1–13	13.1–18	>18 cm
Habitat	1	0.031	0.147	<0.001	<0.001	0.504	0.543	0.426
Period	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.002
Habitat × period	2	0.12	0.559	0.678	0.33	<0.001	<0.001	0.94

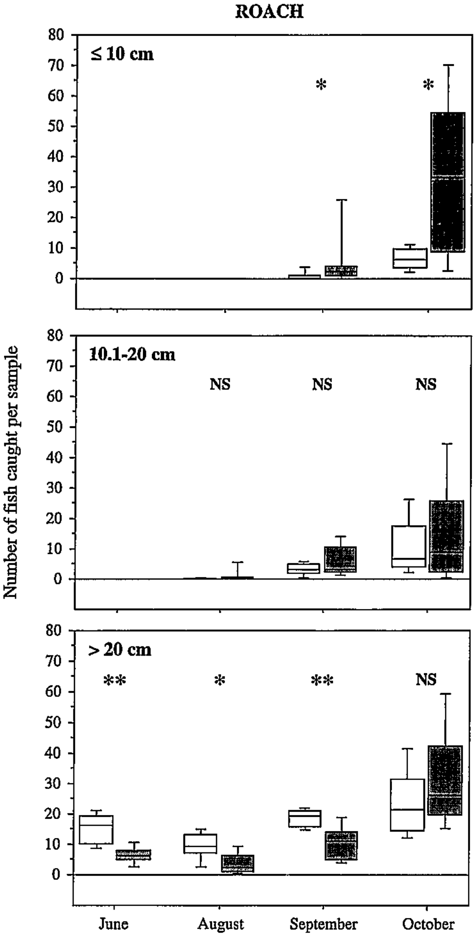

Figure 5. Comparison of roach mean abundance (number of fish per sample) in vegetated (shaded) and unvegetated (white) habitats for each size class during the four sampling periods. Plots indicate the 10th, 25th, 50th, 75th and 90th percentiles of the variables. Samples series were 10 in June, 9 in August and September and 8 in October. Mann-Whitney U-test between habitats for each period: NS: non significant; *: $p < 0.05$; **: $p < 0.01$

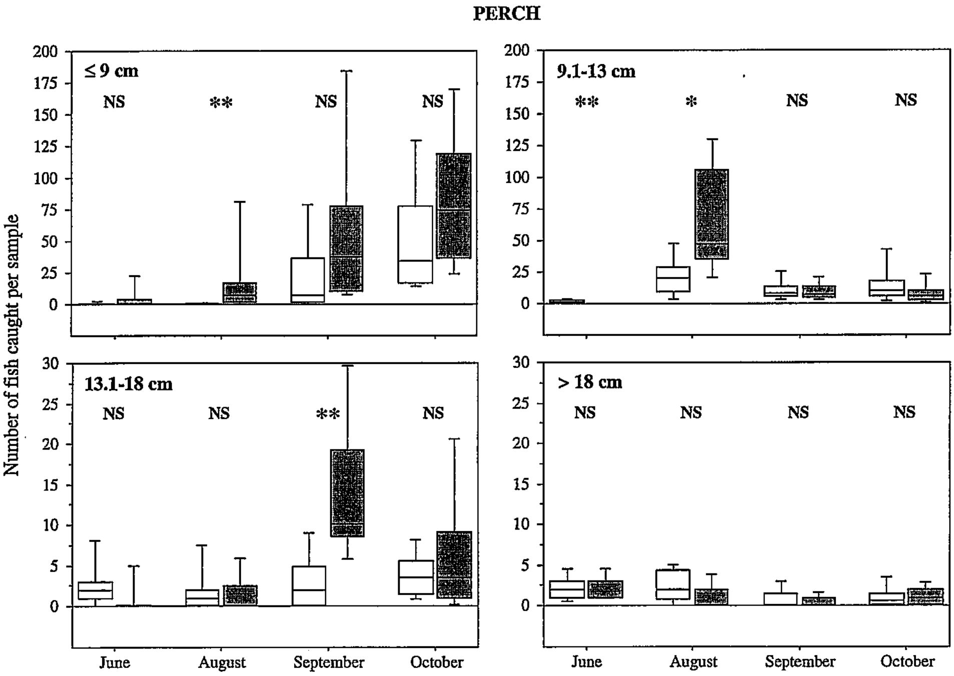

Figure 6. Comparison of perch mean abundance (number of fish per sample) in vegetated (shaded) and unvegetated (white) habitats for each size class during the four sampling periods. Plots indicate the 10th, 25th, 50th, 75th and 90th percentiles of the variables. Samples series were 10 in June, 9 in August and September and 8 in October. Mann-Whitney U-test between habitats for each period: NS: non significant; *: $p < 0.05$; **: $p < 0.01$

Separated two-way ANOVAs performed for each size class during the vegetation period (June, August and September) showed significant abundance differences between habitats for small (R1) and large (R3) roach, and small perch (P1) only (Table 3). Small roach were only captured in September and were more abundant in the vegetated habitat (Fig. 5). Large roach were significantly more abundant in the unvegetated habitat in June, August and September (Fig. 5). Small perch were more abundant in the vegetated habitat during each period but significant differences occurred only in August (Fig. 6).

For several other size classes, significant differences between habitats during periods I, II or III occurred but in a less consistent way. P2 perch (9–13 cm) were more abundant in unvegetated habitats in June, more abundant in vegetation in August and equally distributed in September. The number of fish caught in June was very low compared to other periods (Fig. 6). For 13–18 cm perch, the results showed only significant differences in abundance during period III (more abundant in vegetation). For the other size classes, large perch (P4) and medium roach (R2), abundance differences between habitats were never significant.

Except for small roach (R1) which were more abundant in the vegetation, no other size class showed any distinction between habitats in October (Fig. 5 and 6).

As vegetation had almost disappeared from the littoral zone between September and October, this lack of habitat separation in October suggested that presence or absence of vegetation was responsible for the previous differences. The changes in large roach (R3) abundance were particularly noticeable: during the vegetation periods large roach were always significantly more abundant in unvegetated areas whereas after macrophyte disappearance the mean abundance of adult roach appeared higher in vegetation (Fig. 5).

Discussion

Although gill net catches are usually considered as an indication of fish activity and therefore applied to estimate site utilization (Lagler, 1978), care must be taken in the interpretation of the results. Gill nets are indeed highly selective (review in Hamley, 1975) and mesh sizes used during this study did not recover the total range of fish sizes. For several size classes, the catchability could thus change considerably among periods and influence CPUE. For example, the increase in time of catches of young perch (P1) and roach (R1) was induced by the selectivity of gill nets, fishes gradually reaching a size vulnerable to capture. Because of this bias, it was difficult to explain the abundance differences observed between the periods, nonetheless, comparisons between habitats were possible (Sogard et al., 1989).

Comparison of fish assemblages in vegetated and unvegetated habitats have demonstrated the influence of vegetation on fish distribution. Species composition, species richness and abundance are generally different between these habitats (e.g. Keast et al., 1978; Orth and Heck, 1980; Stoner, 1983; Stang and Hubert, 1984; Killgore et al., 1989; Gelwick and Matthews, 1990; Lubbers et al., 1990). Our results indicated that presence or absence of macrophytes affected perch and roach abundance in the littoral zone of Lake Geneva. Differences between habitats observed in summer disappeared to a large extent in October after the decline of vegetation. A more homogeneous distribution at the end of the vegetation period has been observed previously in other aquatic environment (Lubbers et al., 1990) and suggests that vegetation presence is responsible for previous abundance differences. However, in October, the two vegetated sites differed highly from each other (Fig. 4), perhaps because of the subsistence of some macrophyte stands in one site.

Submerged vegetation influence on the distribution of perch and roach differs highly according to the size class considered. Although the sampling method used during this study did not allow the investigation of the distribution of fish smaller than 6 cm, our results showed that macrophyte beds were particularly used by small perch. Similar habitat selection of young perch has been observed in the littoral zone of Lake Constance by Wang and Eckmann (1994), who noted that perch could hardly be found in areas without macrophytes, and by Coles (1981) in a British lake. For small roach, the influence of vegetation was less clear. Roach abundance was higher in vegetation in September but the same distibution pattern occurred in October after the decline of macrophytes and could indicate that other environmental factors were responsible for these abundance differences. However, direct observations made with SCUBA diving during the summer in different areas denoted that small roach were more abundant in vegetated than in unvegetated areas.

It is thus possible that juvenile roach stayed in the same areas in October or that the presence of macrophyte remains on the bottom influenced their distribution.

The importance of macrophyte stands as habitat seemed to decrease progressively with increasing fish size. The distribution pattern of roach showed a shift from vegetation to open water as fish size increased. For perch, intermediate size classes (P2 - P3) were only temporarily more abundant in macrophyte beds, whereas larger individuals (P4) were equally distributed in each habitat at all dates. Moreover, adult perch are generally more abundant in the sublittoral zone than in the littoral, at a depth of 6-10 m (Hartmann and Loeffler, 1989; O. Rossier, pers. obs.) where macrophytes are almost absent. A similar pattern of distribution (small individuals restricted to vegetation then colonizing open water as their size increases) was reported for bluegill (*Lepomis macrochirus*) by Hall and Werner (1977) and Werner et al. (1977). These authors hypothesized that small bluegills were restricted to macrophyte beds until they reached a size sufficient to avoid predation. In laboratory experiments, Persson (1991), showed that in presence of predators (large perch), young perch and roach leave vegetation cover less frequently than in their absence. In Lake Geneva, small perch and roach (P1-R1) were potential preys for numerous predators (especially large perch) whereas from a size of 12-13 cm, they can only be eaten by perch larger than about 35 cm or by large predators like trout or pike (Pattay, pers. comm.) that are scarce in the littoral zone of Lake Geneva during summer (Rossier, 1995). In a Norwegian lake, Brabrand and Faafeng (1993) observed that before the introduction of predators (pike-perch: *Stizostedion lucioperca*) both small and large roach used the open water habitat whereas after the introduction only large roach were present in the open water. Therefore, the distribution pattern observed during this study could indicate that small perch and roach were restricted to vegetation by predation pressure whereas larger fish could use the open water habitat to a larger extent. The similar abundance of medium roach (10-20 cm) in both habitats could thus indicate the size interval at which roach become large enough to avoid predation and switch gradually from vegetated to unvegetated habitat.

In addition to shelter against predators, food availability is often invoked to explain the presence of fishes in vegetation (Orth et al., 1984; Rozas and Odum, 1988). Juvenile perch seem to forage mainly in vegetation (Mikheev, 1986) and Jamet (1994) observed that roach migrated from pelagic to littoral areas during the summer to feed on macroinvertebrates and macrophytes. However, Persson (1993) suggested that open water is the preferred habitat of both perch and roach but that in presence of roach, perch shift from open water to vegetation to reduce competition. In a Swedish lake, Persson (1987b) observed that roach were always more abundant in open water whereas perch distribution changed throughout the season according to macroinvertebrate abundance. Moreover, because of dissimilar foraging abilities, habitat use differed according to perch size (Persson, 1987a).

The distribution patterns observed for different size classes of perch and roach in the littoral zone of Lake Geneva could then result from the interaction of several factors. Ontogenetic changes in morphology, behaviour and diet cause different size classes to react to resources differently (Wanjala et al., 1986). In addition to the preferences associated with the size class characteristics, the composition and abundance of coexisting species can greatly influence fish distribution through competitive or predatory interactions. It is thus difficult to identify definitely the factors governing distribution of different size classes of perch and roach observed in our study. Therefore, it would be interesting to test in situ the habitat preferences of each size class in the absence of predators or competitors. Additionally, it would be necessary to assess the utilization of food by fish in relation to the actual prey availability in both vegetated and unvegetated habitats.

ACKNOWLEDGEMENTS

We are very grateful to Dr. G. Copp, Dr. D. Ponton and two anonymous reviewers for critical evaluation of the manuscript. We thank also S. Linker and the members of the "Laboratoire d'Ecologie et de Biologie Aquatique" of the University of Geneva for assistance in the field.

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Received 5 December 1994;
revised manuscript accepted 30 January 1996.