Bonnie Blessing

Salmon get preyed on by bass blugill and perch that tend to use different amounts of littoral aquatic vegetation. At some point, Ecology should consider reviewing the literature on how much littoral vegetation should be removed. Here's 3 articles related to use of littoral vegetation by salmon predators. Perhaps this has already been done but if not, maybe its useful

Influence of submerged aquatic vegetation on size class distribution of perch (Perca fluviatilis) and roach (Rutilus rutilus) in the littoral zone of La....

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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

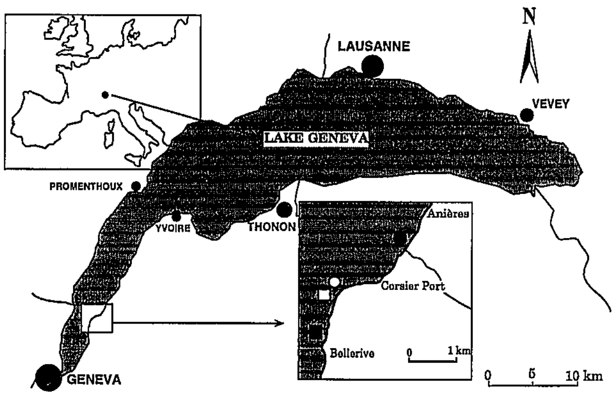

Figure 1. Location of sampling sites (black symbols: vegetation and white symbols: unvegetated, circle: site 1, square: site 2) in the littoral zone of Lake Geneva, Switzerland

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.

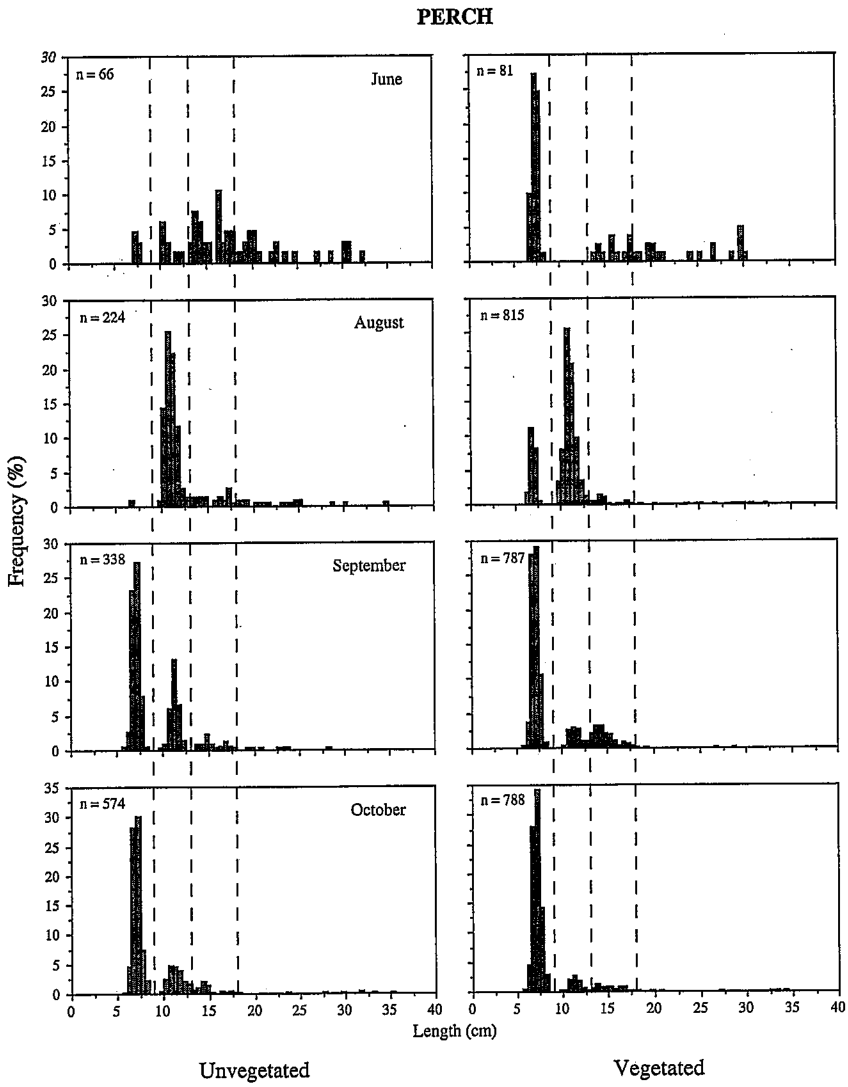

Figure 3. Length-frequency distribution of perch caught in gill nets in vegetated and unvegetated habitats during each sampling session. Dashed lines indicate size class separations

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.

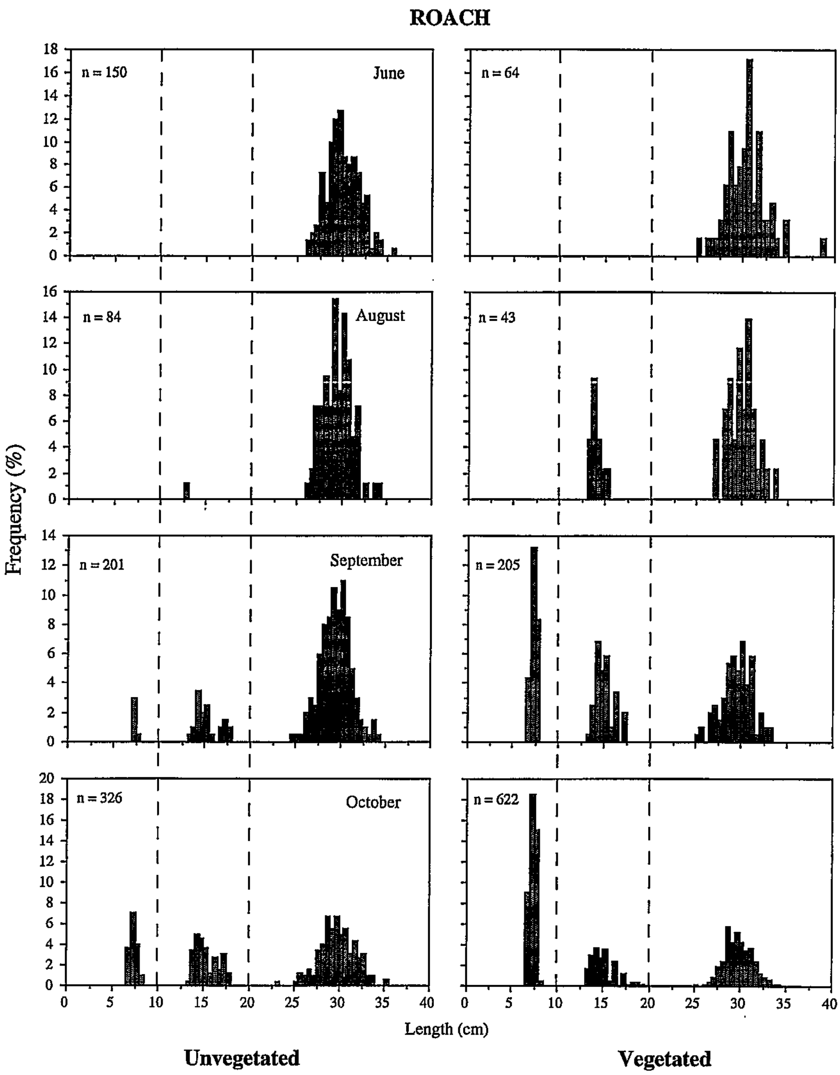

Figure 2. Length-frequency distribution of roach caught in gill nets in vegetated and unvegetated habitats during each sampling session. Dashed lines indicate size class separations

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

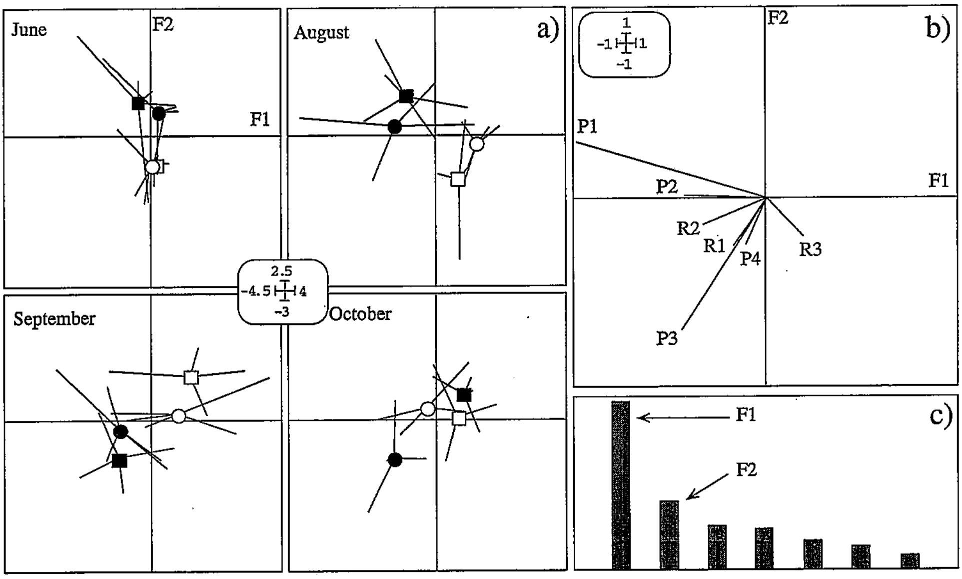

Figure 4. Within-periods centered PCA of the three size classes of roach (R) and four size classes of perch (P) by 72 samples data matrix. a: split of the F1 × F2 factorial plane of the 72 samples according to the 4 periods (black symbols: vegetated sites; white symbols: unvegetated sites, circles and 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

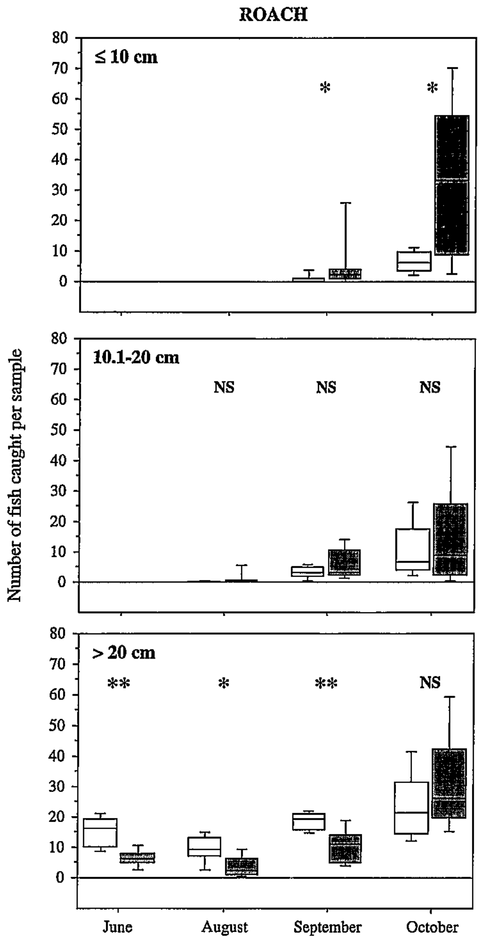

Figure 5. Comparison of roach mean abundance (number of fish per sample) in vegetated (shaded) and unvegetated (white) habitats for each size class during the four sampling periods. Plots indicate the 10th, 25th, 50th, 75th and 90th percentiles of the variables. Samples series were 10 in June, 9 in August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

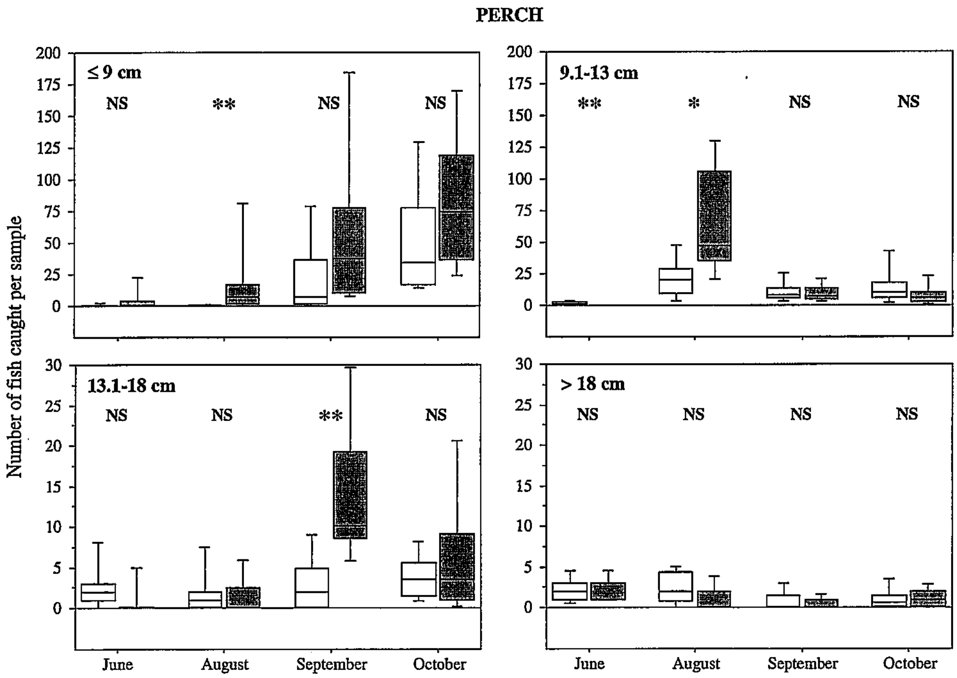

Figure 6. Comparison of perch mean abundance (number of fish per sample) in vegetated (shaded) and unvegetated (white) habitats for each size class during the four sampling periods. Plots indicate the 10th, 25th, 50th, 75th and 90th percentiles of the variables. Samples series were 10 in June, 9 in August 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 (1987 b) 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, 1987 a).

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.

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Effect of Fluridone on Macrophytes and Fish in a Coastal Washington Lake

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ABSTRACT

Loomis Lake, a long narrow shallow lake on the coast of Washington State, had a submersed plant community dominated by the invasive non-native species Eurasian watermilfoil (*Myriophyllum spicatum* L.) and egeria (*Egeria densa* Planch.). In 2002, the whole lake was treated with the liquid formulation of the aquatic herbicide fluridone (1-methyl-3-phenyl-5-[3-(trifluoromethyl) phenyl]-4(1*H*)-pyridinone). We monitored aquatic plant frequency of occurrence and biomass before herbicide application (2002) and for three years after the treatment (2003 to 2005). The fish population was assessed one year prior to herbicide treatment (2001) and three years post treatment (2005). Prior to domination by invasive macrophytes, the lake had a diverse native plant community with low growing species in the deep water providing open water. During that time the lake supported a stocked rainbow trout (*Oncorhynchus mykiss* Walbaum) and warmwater fishery. As invasive macrophytes took over, the native plant richness decreased, the trout stocking program ceased, and small yellow perch (*Perca flavescens* Mitchill) dominated the fish community. The herbicide treatment resulted in a significant reduction in frequency (86% for egeria, 84% for Eurasian watermilfoil) and biomass (98% for egeria, 99% for Eurasian watermilfoil) of the invasive species for three years. The native submersed plant community was also significantly reduced for the study duration. We attributed this to fluridone use at a nonselective rate and poor light penetration caused by wind-induced sediment entrainment. After treatment the growth of largemouth bass (*Micropterus salmoides* Lacepede) and pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus) increased. In addition, the abundance of small yellow perch decreased while abundance of larger pumpkinseed sunfish increased.

Key words: Egeria densa, Eurasian watermilfoil, herbicide, largemouth bass, *Myriophyllum spicatum,* pumpkinseed sunfish, yellow perch.

INTRODUCTION

To better understand the impacts of aquatic herbicides on nontarget plants under local conditions, the Washington De-

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partment of Ecology (WDOE) has conducted monitoring studies for each of the herbicides allowed for use in Washington. Prior to inception of this project, fluridone (1-methyl-3-phenyl-5-[3-(trifluoromethyl) phenyl]-4(1*H*)-pyridinone) combined with follow-up spot treatment methods had been used to achieve control and occasional eradication of Eurasian watermilfoil (*Myriophyllum spicatum* L.) from specific waterbodies in the state. However, no data on impacts to nontarget plants or fish had been collected during those projects. The purpose of this project was to provide those data.

Loomis Lake, the study site, is a 69-ha lake located in the coastal dunes of southwestern Washington (Figure 1). It is on a peninsula, with the Pacific Ocean about 1 km to the west and Willapa Bay about 1 km to the east. The climate is wet and cool, with frequent strong storms during the winter. The lake is 3.2 km long by 250 m wide, with 6.9 km of shoreline. Development of the shore is limited to several houses and a public boat launch with a fishing dock on the west shore. The maximum depth is 3 m with an average depth of 1.5 m (Bortleson et al. 1976). Tannins stain the water, and high levels of nutrients result in a eutrophic classification (O'Neal et al. 2001). The shallow nature of the lake prevents development of a thermocline.

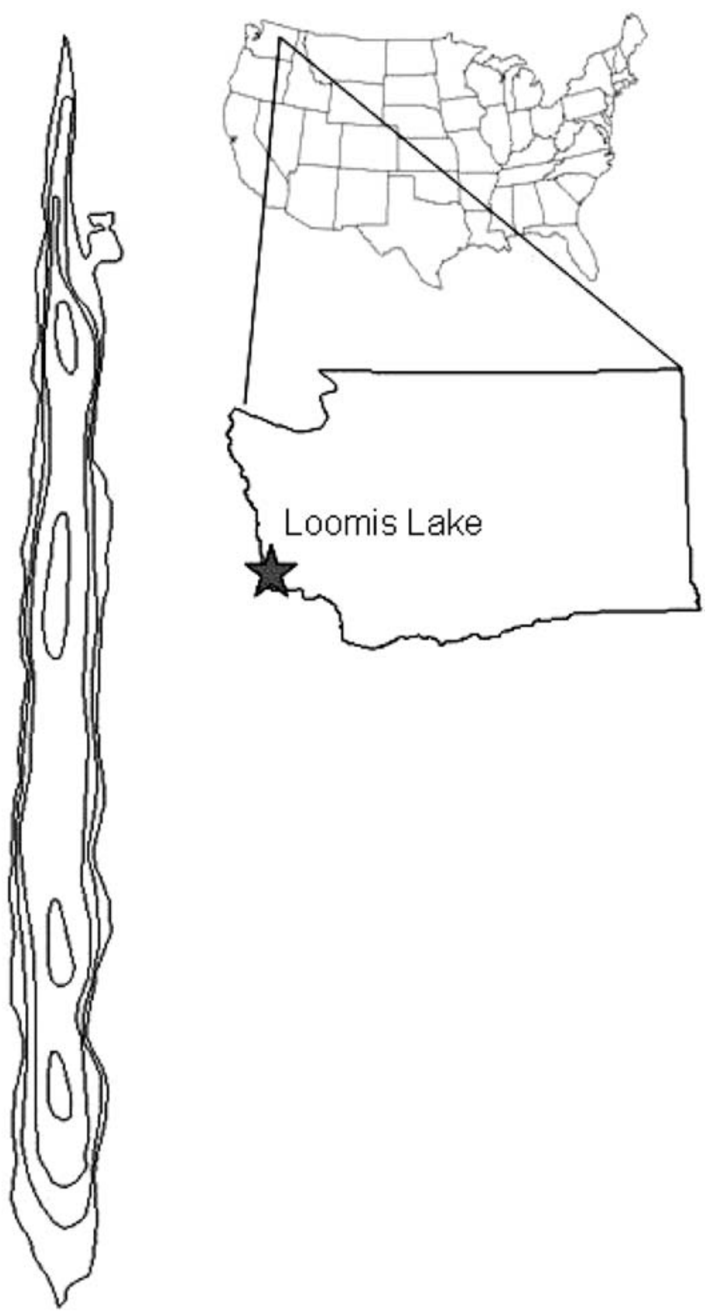

Figure 1. Loomis Lake, Washington. Depth contour intervals are 0.9 m.

Aquatic plants historically grew throughout Loomis Lake, although in deeper water they were limited to low-growing plant-like macroalgae prior to the invasion by non-native species. Eurasian watermilfoil was first observed in the lake in 1996 and egeria (*Egeria densa* Planch.) was found in 1999. Both species are invasive non-native plants in Washington State. Eurasian watermilfoil has been in Washington since at least 1965 and is currently present in many waterbodies throughout the state. Egeria was first found in Washington in the early 1970s and is currently found in more than 20 lakes in the western part of the state (Parsons 2007). When introduced outside their native range, both species can dominate the submersed plant community to the detriment of native plant diversity, fish and wildlife habitat, water quality, flood control, recreation, and aesthetics (Nichols and Shaw 1986, Smith and Barko 1990, Madsen et al. 1991, Wells and Clayton 1991, Boylen et al. 1999, Valley and Bremigan 2002, California Department of Boating and Waterways 2006). Loomis Lake was no exception; within a few years these two species dominated the submersed plant community, forming a surfacing canopy throughout.

Loomis Lake was historically stocked with rainbow trout (*Oncorhynchus mykiss* Walbaum). However, as invasive macrophytes filled the lake the quality of the fishery declined, so stocking was eliminated from 2000 to 2002. In 2003 limited stocking resumed, was suspended in 2004, and resumed again in 2005. In addition to the rainbow trout, introduced warmwater species included yellow perch (*Perca flavescens* Mitchill), largemouth bass (*Micropterus salmoides* Lacepede), pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus), black crappie (*Pomoxis nigromaculatus* Lesueur), brown bullhead (*Ameiurus nebulosus* Lesueur), and bluegill (*Lepomis macrochirus* Rafinesque). Two native species, sculpin (*Cottus* sp.) and three-spine stickleback (*Gasterosteus aculeatus* Linnaeus) were also present (Mueller 1998).

In 2002, the U.S. Army Corps of Engineers, Seattle District, and WDOE jointly funded this study on the use of fluridone to control both the Eurasian watermilfoil and egeria in Loomis Lake. The WDOE monitored macrophytes pre-treatment (2002) and for three years post-treatment (2003 to 2005) to assess the herbicide's effectiveness at controlling the two target invasive species as well as impacts on native vegetation. In addition, the Washington Department of Fish and Wildlife conducted a fish population assessment of Loomis Lake one year prior to treatment (2001), and three years after the herbicide treatment (2005). These assessments determined species richness, relative abundance (as measured by catch rates), and growth rates, all of which may be affected by the density and abundance of macrophytes.

MATERIALS AND METHODS

Herbicide

The typical scenario for a whole-lake fluridone treatment is to maintain low concentrations for a long time period. Concentration and exposure time (CET) requirements to control Eurasian watermilfoil are well documented (Getsinger and Netherland 1997, Netherland et al. 1997). To achieve selective Eurasian watermilfoil control, the recommended CET is 4 to 5 ppb for 60 days (Cockreham and Netherland 2000, Madsen et al. 2002, Pedlow et al. 2006, Wagner et al. 2007). When this study began, less work had been done on CET requirements for egeria than for Eurasian waterfoil. Laboratory studies indicated that concentrations of 8 to 12 ppb were lethal to egeria (Cockreham and Netherland 2000). To substantiate this, we used the SePRO Corporation PlanTEST® method to determine the target CET. This required that egeria from Loomis Lake be sent to the corporate lab for individual susceptibility tests. Results recommended a CET of 12 ppb for a minimum of 8 weeks for control. This treatment rate is above what Netherland et al. (1997) recommended for selective control, therefore die-off of native plant species, while not desired, was expected.

The initial herbicide treatment took place on June 28, 2002, using the liquid fluridone formulation (Sonar AS®). This treatment date was chosen because plants are typically still in a pattern of rapid spring growth in the wet cool climate of Loomis Lake, and it is at the end of the rainy season so herbicide dilution would be minimized. Approximately every two weeks from mid-July until the end of August water samples from three sites were tested for fluridone concentration using FasTEST® (an enzyme-linked immunosorbent assay (Netherland et al. 2002). Results of these tests indicated that additional herbicide was periodically required to maintain the target concentration of 12 ppb. The herbicide was added on July 11, July 30, August 14, and August 28 (T. McNabb, Aquatechnex, 2002, pers. comm.).

We did not expect the herbicide treatment to fully eradicate the egeria and Eurasian watermilfoil because previous experience had shown some form of follow up treatment is nearly always required. The Aquatic Plant Management Plan for Loomis Lake identified diver hand pulling as the follow-up method of choice to remove surviving invasive plants (Envirovision 1998). If the recovering plants were too numerous or widely scattered for diver hand pulling to be practical, additional herbicide treatments were considered.

Aquatic Plants

Aquatic plant biomass and frequency of occurrence data were collected in June of each year; once before the herbicide treatment (2002) and for three years after treatment (2003 through 2005). Species richness was also determined by listing all aquatic plant species observed, both at sample points and any new ones observed between points.

The point-intercept method was used to gather presence-absence data for species frequency of occurrence as per Madsen (1999). We created a 50 by 50 m grid covering the whole lake using a Geographic Information System. Each grid intersection was a sample point, provided as UTM (Universal Transverse Mercator) coordinates. In 2002, the grid produced 251 sample points; from 2003 to 2005 the grid was modified slightly and resulted in 238 points. A Geographical Positioning System (GPS) unit was used to locate the points in the field. At each point macrophyte data were collected by using a sampling rake. The rake was deployed twice at each point, and all species collected were recorded. The data were analyzed using Chi square two-by-two analysis for the species present in at least 10% of samples during at least one sampling event.

Biomass samples were collected by a SCUBA diver from 50 points randomly selected from the frequency data grid. At each point the diver collected the sample using a 0.1-m^2 frame placed on the sediment (Madsen 1993). All above-ground plant matter was collected and placed in a mesh bag. The samples were sorted by species and dried in a forced air oven at 60 to 70 °C to a constant weight and weighed to 0.01 g accuracy. Analysis of variance was performed on log transformed data to check for significant differences before and after treatment. The resultant p-values were adjusted using a Bonferroni post-hoc test to adjust for multiple comparisons.

Water transparency data were also collected during each visit using a standard 20-cm secchi disk.

Fish

The fish community was surveyed in June of 2001 and 2005 following methods outlined by Bonar et al. (2000). Sampling occurred during the evening hours to maximize the type and number of fish captured. Fish were captured using three sampling techniques: electrofishing, gill netting, and fyke-netting. The electrofishing unit consisted of a Smith-Root SR-16s electrofishing boat, with a 5.0GPP pulsator unit. Experimental gill nets, 45.7 m long by 2.4 m deep, were constructed of four sinking panels (two each at 7.6 m and 15.2 m long) of variable-size (1.3, 1.9, 2.5, and 5.1 cm stretch) monofilament mesh. Fyke (modified hoop) nets were constructed of five 1.2-m diameter hoops with two funnels, and a 2.4-m cod end (6 mm nylon delta mesh). Attached to the mouth of the net were two 7.6-m wings, and a 30.5-m lead.

The 2001 survey spanned four days (June 12-15) and the 2005 survey spanned three (May 31-June 2). Each survey consisted of 12 electrofishing sections, 6 to 8 gillnet sections, and 6 to 8 fyke net sections (6 each in 2001; 8 each in 2005). Electrofishing sample locations were selected from a map by dividing the entire shoreline into 400-m sections, numbering them consecutively, and randomly choosing them without replication. The electrofishing boat was maneuvered slowly through the shallows (1 to 3 m deep) for 600 sec in each section. Gill nets were fished perpendicular to the shoreline; the small-mesh end was tied off to shore, and the large-mesh end was anchored off shore. Fyke nets were fished perpendicular to the shoreline as well. The lead was tied on shore, and the cod-end was anchored off shore, with the wings anchored at approximately a 45° angle from the net lead. Fyke nets are fished with the hoops 0.3 to 0.5 m below the water surface, which sometimes requires shortening the lead. Both nets types were set at dusk and retrieved in the morning, with soak time recorded as "net nights" (1 net set over 1 night = 1 net night).

With the exception of sculpin (family Cottidae), all captured fish were identified to species level. Most fish were measured to the nearest millimeter (mm) total length, and weighed to the nearest gram (g). Fish <70 mm were not weighed due to inadequate scale precision. To reduce handling stress on fish, where large numbers (>200) of obviously similar-sized fish were collected simultaneously, a subsample was measured to the nearest millimeter and weighed to the nearest gram. The remaining fish were counted and the subsampled data expanded. Weights were then assigned using a length-weight regression formula. Scales were taken from five individuals of each warmwater game species per centimeter size class (>70 mm) for aging purposes. Total and incremental lengths at annulus formation were back-calculated using the Fraser-Lee method with *y*-axis intercepts specified by Carlander (1982).

The species composition expressed as the number of fish captured was determined by counting all the fish in a given species. Species composition expressed as weight percentage (%w) of fish captured was determined by dividing the total weight of fish of a given species by the total weight of the sample. All fish, including young-of-the-year, were used to determine biomass and species composition; the impact of young-of-the-year fish on data analysis was minimal due to sample timing (early June for both surveys).

Catch-per-unit-of-effort (CPUE) data, which measures the number of fish in each species collected with a given sampling gear over a standardized unit of time, was used to compare the relative abundance of stocks between lakes or over time. For electrofishing, the results were expressed as the number of fish caught per hour. The CPUE for gill nets and fyke nets is expressed as the number of fish caught per net-night. An average CPUE (across sample sections) with an 80% confidence interval was calculated for each species and gear type. The CPUE of stock length and sub-stock length fish was calculated separately (stock length is approximately 20 to 26% of the all-tackle, world record length for each species, and often correlates to age of maturity (Gablehouse 1984). Analyses of means for CPUE data were calculated using the Mann-Whitney rank-sum test with $\alpha = 0.05$.

To evaluate fish growth in the years immediately adjacent to the herbicide treatment, growth rate assessments were conducted using incremental length-at-age data (growth that occurred between annulus formation). Incremental length-at-age date was considered superior to total length-at-age data because the former provides growth data specific to one year, whereas the latter is the cumulative growth of a fish's entire lifespan and is therefore influenced by previous years' growth rates. To limit the potential influence of age effects on growth (different growth rates inherent to different age fish), comparisons were limited to like age-classes.

For each calendar year, mean incremental lengths-at-age for each cohort were produced. From these data a cumulative mean for each age-class was calculated spanning 1997 to 2004 (growth data from a 1997 Loomis Lake fish inventory (Mueller 1998) was included.) The mean incremental length-at-age for each cohort in each calendar year was then compared to the cumulative incremental length-at-age for the corresponding age-class and expressed as a percent difference. For example, the mean incremental length of age-1 largemouth bass from 2001 (64.27 mm) was compared to the mean incremental length of all age-1 largemouth bass from 1997 to 2004 (77.24 mm) and expressed as a percent difference (-16.8%). A comparison of means to determine a statistically significant difference between these data sets was conducted using the Mann Whitney rank sum test per Klumb et al. (1999).

RESULTS AND DISCUSSION

Herbicide

The average herbicide concentration varied between 10 and 26 ppb throughout the treatment period (Figure 2). This was above the target CET normally used for Eurasian watermilfoil control, and only dipped below the target concentration for egeria during a short period at the end of July. An additional water sample collected October 30, 2002, showed the fluridone persisted into autumn, with a concentration of 10 ppb at that time (T. McNabb, Aquatechnex, 2003, pers. comm.).

Aquatic Plants

During routine monitoring before the submersed plant community became dominated by egeria and Eurasian watermilfoil, 16 submersed and floating-leaved aquatic plant species had been observed (Table 1; pre-2000 column). In 2002, just before the herbicide treatment, the number of species was reduced to 12; four pondweed species were not found. At that time the invasive species were growing to the surface nearly throughout the lake. They were the most frequently encountered species (Table 2) and accounted for 91% of the plant biomass (Table 3). Other studies have also documented declines in native macrophyte species richness corresponding to dominance by invasive macrophytes (Madsen et al. 1991, Trebitz et al. 1993, Boylen et al. 1999). Thus the egeria and Eurasian watermilfoil were dominating the plant community to the extent that several native plants were elim-

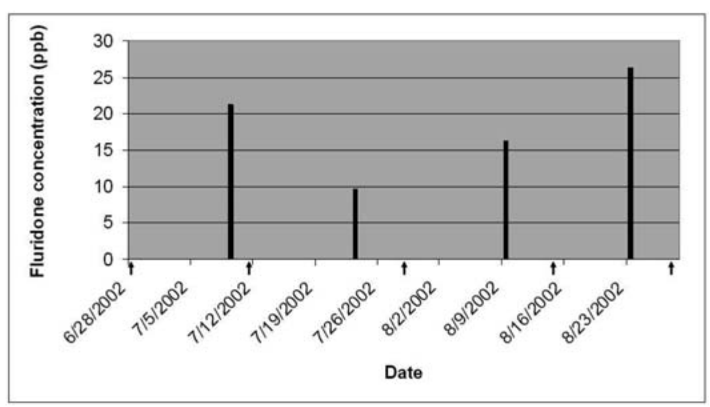

Figure 2. Fluridone concentration results from FasTEST® for Loomis Lake, WA. Arrows indicate dates when herbicide was added to maintain levels at or above the target concentration of 12 ppb.

Table 1. Submersed (s) and floating leaved (fl) aquatic plant species and year of observation in Loomis Lake, WA. Herbicide treatment began three days after the 2002 inventory.

Scientific name	Common name	Growth form	Pre-2000	2002	2003	2004	2005
Ceratophyllum demersum	coontail; hornwort	s	√	√			√
Egeria densa	egeria	s	√	√	√	√	√
Elodea sp.	common elodea	s	√	√			√
Hydrocotyle ranunculoides	water-pennywort	fl	√	√	√	√	√
Myriophyllum spicatum	Eurasian watermilfoil	s	√	√		√	√
Najas sp.	water-naiad	s	√	√		√	√
Nitella sp., Tolypella sp.	macro-algae	s	√	√		√	√
Nuphar polysepala	yellow waterlily	fl	√	√	√	√	√
Nymphaea odorata	fragrant waterlily	fl	√	√			√
Potamogeton amplifolius	large-leaf pondweed	s	√			√	
Potamogeton epihydrus	ribbon-leaf pondweed	s	√			√	√
Potamogeton natans	floating leaf pondweed	fl	√				
Potamogeton praelongus	whitestem pondweed	s				√	√
Potamogeton richardsonii	Richardson's pondweed	s	√	√			√
Potamogeton sp.	thin leaved pondweed	s	√			√	√
Potamogeton zosteriformis	eelgrass pondweed	s	√	√	√	√	√
Utricularia sp.	bladderwort	s	√	√		√	√

inated from the lake or had become so rare that they were not observed using any of our sampling methods.

One year after treatment (YAT), in June 2003, the submersed and floating-leaved plant community had changed substantially. Four sparsely distributed submersed or floating-leaved species were recorded (Table 1), 75% of sample points contained no plants (Table 2), and total plant biomass was reduced by 97% (Table 3). Egeria and a small amount of eelgrass pondweed were the only submersed plants found. Most of the egeria had black stems and leaves, with only a green inner stem to indicate it may be viable. A large die off of native plant species during the year of treatment was expected because of the concentration of fluridone administered to control egeria. Concentrations of 10 ppb or higher with an exposure time of several months will significantly reduce many native species (Netherland et al. 1997, Welling et al. 1997, Wagner et al. 2007). However, we expected to see greater recovery by one YAT.

A corresponding difference one YAT was a reduction in water clarity. Because Loomis Lake is long, narrow, shallow, and subject to strong winds that accompany frequent storms off the Pacific Ocean, the fetch is the entire 3.2 km length of the lake. Notable sediment entrainment occurred when plant death left large areas of the lake bed unprotected. This was evidenced in the Secchi depth, which averaged a tannin-stained 1.5 m in summers 1997 and 1999 prior to treatment (Smith et al. 2000, O'Neal et al. 2001), but fell to a muddy-looking 0.6 m during sample collection one YAT. Loomis Lake is also prone to periodic algae blooms, which may have contributed to the reduction in water clarity. Decreases in water clarity have corresponded with other whole lake fluridone treatments, especially in nutrient-rich lakes where planktonic algae take advantage of reduced competition from macrophytes and in lakes where the CET of fluridone was high enough to reduce native plant growth (Valley et al. 2006, Wagner et al. 2007). Thus, it was likely a combination of the long exposure to relatively high levels of fluridone along with reduced water clarity one YAT that prevented native macrophytes from recovering quickly from the herbicide treatment. By June 2004 (two YAT) the Secchi depth had improved to pretreatment values (1.7 m).

Healthy looking egeria was found at a few sample points two YAT (2004; Tables 2 and 3). We also noticed egeria patches outside the sample points, especially at the north end of the lake where sediment is deep and flocculent. A SCUBA diver was contracted to hand-pull the recovering plants in August 2004. The diver pulled some egeria, but after a short time in the water, realized the amount of egeria present was more than could be controlled within the project budget (D. Freeland, ACE Diving, 2004, pers. comm.). Although Eurasian watermilfoil was not collected at any sample points in June 2004, it was spotted by the diver in August, and a few plants were removed. By June 2005 (three YAT) both Eurasian watermilfoil and egeria samples were collected in frequency of occurrence (Table 2) and biomass (Table 3). We had hoped the combination of fluridone and hand pulling would eradicate the two invasive weeds, as has been the case with Eurasian watermilfoil in other Washing-

Table 2. Aquatic plant frequency of occurrence data chi-square analysis results for common species. Numbers are the percent of samples where the plant was found in Loomis Lake, WA, June 2002 to 2005.

	% present			
Plant	June '02	June '03	June '04	June '05
Egeria	59	16*	0.4*	8*
Eurasian watermilfoil	82	0*	0*	13*
Coontail	16	0*	0*	5*
eelgrass pondweed	56	2*	3*	20*
Elodea	33	0*	0*	0.4*
water-naiad	0.8	0	18*	32*
macroalgae	2	0	47*	52*
No Plants	3	75*	42*	30*

*significantly different from pretreatment frequency of occurrence (June 2002). Significance level corrected for multiple comparisons is $p < 0.017$.

TABLE 3. AQUATIC PLANT MEAN DRY WEIGHT BIOMASS WITH STANDARD DEVIATION IN PARENTHESES AND BONFERRONI ADJUSTED ANOVA RESULTS FROM COMMON SUBMERSED SPECIES IN LOOMIS LAKE, WA, JUNE 2002 TO 2005.

	Biomass (g/m^2)			
Plant	June 2002	June 2003	June 2004	June 2005
Egeria	157.7 (263.9)	9 (16.5)*	0.5 (3.4)*	3.15 (17.3)*
Eurasian watermilfoil	129.4 (165.5)	0*	0*	0.5 (1.6)*
Coontail	1.3 (6.4)	0	0	0.3 (1.5)
eelgrass pondweed	13.2 (23.8)	0*	0.2 (0.8)*	1.1 (3.5)*
Elodea	3.56 (12.6)	0*	0*	0*
water-naiad	0	0	0.07 (0.2)	0.2 (0.3)*
macroalgae	0.07 (0.34)	0	0.9 (3.5)	18.7 (43)*
Total of all plants	313.9 (256.7)	9 (16.5)*	1.7 (4.9)*	26 (45.9)*

*significantly different from pretreatment biomass (June 2002) at $p \leq 0.05$.

ton lakes; however, the degree of plant recovery, along with the poor water clarity, made diver hand pulling impractical.

Although eradication was not realized, the treatment achieved 100% control of Eurasian watermilfoil one YAT that lasted into early summer two YAT. The treatment also provided control of egeria for the duration of the study. There was a 73% reduction of frequency and 94% reduction in biomass of egeria one YAT. These numbers were higher two YAT (>99% reduction in frequency and biomass), likely due to our overestimation of the viability of egeria remaining on the sediment during the one YAT sampling. By three YAT Eurasian watermilfoil, as well as egeria, were present in samples, though they were still significantly reduced compared with pretreatment (Eurasian milfoil, 84% reduction in frequency and >99% biomass reduction; egeria, 86% reduction in frequency and 98% biomass reduction). In 2006, herbicides were again used to control the recovering Eurasian watermilfoil and egeria.

At two YAT, native macrophyte richness was beginning to recover, and by three YAT, 15 submersed and floating leaved species were found (Table 1). Floating-leaved pondweed was the only species historically present in the lake that was not seen after the treatment. We did not see large-leaf pondweed three YAT but found a very small patch two YAT. Whitestem pondweed was not known from the lake prior to the treatment, but was present two and three YAT.

In spite of recovering species richness, the frequency of sample points with no plants was significantly higher than pre-treatment for three YAT (Table 2). Common elodea, eelgrass pondweed, and coontail, all common before treatment, were significantly reduced for three YAT (Tables 2 and 3). Common elodea was the slowest of the three to show signs of recovery. It was absent from samples until three YAT, and then frequency of occurrence was reduced 99% compared with pretreatment data (it was not collected in biomass samples). Frequency of coontail was reduced 69% three YAT. Other studies have also found that elodea and coontail are susceptible to fluridone at the CET used in Loomis Lake and are reduced or eliminated after treatment (Netherland et al. 1997, Smith and Pullman 1997, Poovey et al. 2004, Harmon et al. 2005, Valley et al. 2006, Wagner et al. 2007). Eelgrass pondweed is susceptible to fluridone at concentrations >20 ppb, and intermediately susceptible at concentrations <20 ppb (Hauxwell and Wagner in prep). For the majority of this study, fluridone concentrations were between 10 and 20 ppb (Figure 2). Also, plants that produce vegetative reproductive structures recover more quickly from fluridone treatments (Netherland et al. 1997), and eelgrass pondweed produces leafy turions (Haynes and Hellquist 2000). Thus the combination of its higher tolerance to fluridone, the dormant turions, and the fact that it was the most common native plant prior to treatment likely enhanced the recovery of eelgrass pondweed above that of most other native species.

The two most common submersed species two and three YAT were macroalgae and water-naiad. Their frequency of occurrence and biomass were significantly higher than prior to treatment (Tables 2 and 3). These were also shown to recover most quickly from fluridone in mesocosm experiments (Netherland et al. 1997) and increased quickly after some whole-lake treatments (Crowell et al. 2006), although in a different study, Wagner et al. (2007) showed naiad species took three to five years to recover from whole lake fluridone treatments. Naiad is an annual plant that relies on seed for reproductive success (Wingfield et al. 2004), so its recovery was likely driven by seed germination. Macroalgae have demonstrated tolerance to fluridone in other studies (Welling et al. 1997; Hauxwell and Wagner, in prep,); therefore we suspect the absence of this plant from samples one YAT was due more to growth inhibition from turbidity than direct impacts by the herbicide. After the water cleared, the macroalgae colonized much of the area opened up by the vascular plant removal.

Fish

Nine fish taxa were collected from Loomis Lake in 2001. In 2005, bluegill were missing from the sample, for a total of eight taxa (Table 4). Largemouth bass, pumpkinseeds, and yellow perch dominated the species composition of both surveys. Combined, they account for 97% of the abundance by number and 89% of the weight in 2001, and 94% of the abundance by number and 76% of the weight in 2005 (Table 4). With the possible exception of the hatchery-planted rainbow trout, whose abundance is independent of the lake environment, no other taxa had sufficient samples sizes to assess.

TABLE 4. FISH SPECIES COMPOSITION BY WEIGHT PERCENTAGE (%W) AND NUMBER (#) FOR FISH COLLECTED FROM LOOMIS LAKE, PACIFIC COUNTY, WA, IN JUNE 2001 AND JUNE 2005.

		Species Composition			
		2001		2005	
Fish Species	Scientific Name	(%w)	(#)	(%w)	(#)
Yellow perch	*Perca flavescens*	45.56	1178	35.88	242
Largemouth bass	*Micropterus salmoides*	41.35	116	26.12	49
Rainbow trout	*Oncorhynchus mykiss*	7.74	16	22.80	25
Pumpkinseed	*Lepomis gibbosus*	2.34	100	13.88	355
Brown bullhead	*Ameiurus nebulosus*	2.43	4	0.36	2
Bluegill	*Lepomis macrochirus*	0.25	5		
Black crappie	*Pomoxis nigromaculatus*	0.16	3	0.53	5
Sculpin	*Cottus spp.*	0.15	13	0.41	8
Three-spine stickleback	*Gasterosteus aculeatus*	0.01	4	0.02	3

Stock lengths for the three most abundant species in Loomis Lake are 20 cm for largemouth bass, 8 cm for pumpkinseed, and 13 cm for yellow perch (Anderson and Neumann 1996). We collected CPUE data for stock length largemouth bass, pumpkinseed, and yellow perch (Table 5), and data for sub-stock length fish (excluding stock length and above; Table 6). The stock length data show a significant decline in gill-netted largemouth bass ($P = 0.0084$) and a significant increase in electrofished ($P = 0.0078$) and fyke-netted ($P = 0.001$) pumpkinseeds in 2005 compared with 2001. The CPUE data for sub-stock length fish showed a significant decline of fyke-netted largemouth bass ($P = 0.0102$), and both electrofished ($P < 0.0001$) and fyke-netted ($P = 0.006$) yellow perch. The sub-stock length gill-net CPUE samples for all three species were very small in both surveys, which is probably due to the inefficiency of gill nets in capturing small fish.

Both the CPUE and species composition data show the fish community in 2001 was comprised of high numbers of small fish (yellow perch), typical for lakes with high plant density throughout the lake (Dibble et al. 1997). Although the CPUE of stock length yellow perch did not change significantly after the herbicide treatment, the number of sub-stock length yellow perch declined significantly. Conversely, stock length pumpkinseeds increased post-treatment, with no significant change in sub-stock length pumpkinseeds. The decline in small yellow perch may be attributed to increased largemouth bass predation (Guy and Willis 1991) because decreased macrophyte density is known to improve

TABLE 5. AVERAGE CATCH PER UNIT EFFORT FOR STOCK SIZE FISH COLLECTED AT LOOMIS LAKE, WA, JUNE 2001 AND 2005 WITH 80% CONFIDENCE INTERVAL IN PARENTHESES.

	electrofishing (#/hour)		gill netting (#/net night)		fyke netting (#/net night)	
	2001	2005	2001	2005	2001	2005
largemouth bass	7.0 (2.3)	7.4 (3.8)	2.7 (0.9)	0.4 (0.2)*	0	0
pumpkinseed	9.0 (4.2)	27.2 (8.9)*	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	12.9 (3.2)*
yellow perch	75.0 (15.4)	89.3 (26.1)	5.8 (1.6)	3.1 (1.3)	5.0 (3.9)	3.3 (2.1)

*significantly different from 2001 CPUE (p ≤ 0.05).

TABLE 6. AVERAGE CATCH PER UNIT EFFORT FOR SUB-STOCK SIZE FISH (EXCLUDING STOCK SIZE AND LARGER) COLLECTED AT LOOMIS LAKE, WA, JUNE 2001 AND 2005 WITH 80% CONFIDENCE INTERVAL IN PARENTHESES.

	electrofishing (#/hour)		gill netting (#/net night)		fyke netting (#/net night)	
	2001	2005	2001	2005	2001	2005
largemouth bass	29.0 (9.3)	15.0 (4.8)	0.3 (0.3)	0	4.3 (2.0)	0.3 (0.2)*
pumpkinseed	22.5 (11.5)	48.5 (17.2)	0	0	5.7 (3.2)	12.5 (3.2)
yellow perch	398.9 (41.0)	7.5 (3.3)*	1.5 (1.4)	0	26.0 (13.7)	0.1 (0.2)*

*significantly different from 2001 CPUE (p ≤ 0.05).

predator efficiency (Crowder and Cooper 1982, Hayse and Wissing 1996, Dibble et al. 1997). The changes we observed in the size structure of the yellow perch population, from one with many small fish to one with fewer but larger fish, is a well known result of increased predation (Novinger and Legler 1978, Tonn and Paskowski 1986). However, the increase in pumpkinseed abundance is unexpected because largemouth bass would be expected to prey on them as well, unless they preferentially feed on yellow perch over pumpkinseeds. The increase in pumpkinseed abundance could also be caused by reduced competition for resources with the decline in yellow perch. Resource utilization overlap occurs in small fish of both species feeding on zooplankton (Hubert and Sandheinrich 1983, Mittelbach 1984, Lott et al. 1996).

A potentially confounding factor to the CPUE data is the effect the removal of vegetation may have had on the capture efficiency of the various collection gears. Unfortunately, published research on the subject is limited. Bayley and Austen (2002) found that the catch efficiency of a boat electrofisher was related to the percentage of a lake covered by macrophytes. Gill-net efficiency can be affected by twine diameter and color, both of which alter the net's visibility (Hansen 1974, Jester 1977), which could also be affected by the presence or absence of macrophytes. Weaver et al. (1993) found differences in catch rates of fyke-nets fished at multiple sites with a range of macrophyte density and species composition, although whether the results reflect differences in fish abundance at each site or differences in gear efficiency is unclear. Anecdotal reports from the 2001 survey of Loomis Lake suggests that the macrophyte density may have prevented the lead lines of both net types from laying flush on the lake bottom. Thus we do not know how much the presence or absence of macrophytes may have altered catch efficiency. Adding further complexity, alterations in the catch efficiency for each gear type may have species-specific impacts.

Age data were collected on 53 largemouth bass, 24 pumpkinseeds, and 62 yellow perch in 2001, and 44 largemouth bass, 36 pumpkinseeds, and 48 yellow perch in 2005. Combined growth rate data for all three species indicate improved population growth for the two years subsequent to the herbicide treatment (Figure 3). For four years prior to the herbicide treatment (1997-2000) the combined growth rate (measured as incremental lengths-at-age) of these three species was 0.3% below the mean. After treatment (2003 and 2004), the combined growth rate was 7.9% above the mean. When considering individual species cohorts, incremental length-at-age data for 2004 for age-1 and age-2 largemouth bass and age-1 pumpkinseed were significantly higher than average ($P = 0.0018$ to <0.0001). Other studies have also shown that largemouth bass and sunfish (bluegill and redear sunfish) growth increased with total macrophyte removal (Dibble et al. 1997). Age-1 largemouth bass from 2003 and age-1 yellow perch from both 2003 and 2004 showed no significant difference from the mean of all three surveys ($P \geq 0.05$). Other age-classes had insufficient data to analyze.

When considering combined growth and abundance data, fish growth typically has an inverse relationship to fish abundance; fewer fish mean reduced competition for resources and increased growth for the remaining individuals (Swingle and Smith 1941, Partridge and DeVries 1999, Sass et al. 2004,

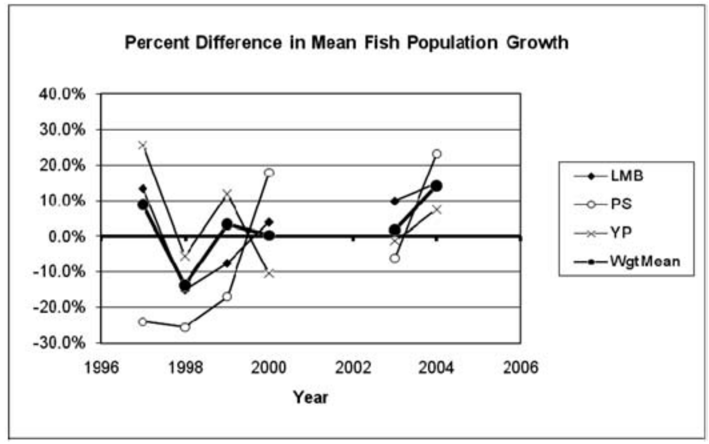

Figure 3. Percent difference in cohort growth per year measured as incremental lengths-at-age for largemouth bass (LMB), pumpkinseed sunfish (PS) and yellow perch (YP) collected from Loomis Lake in June 2001 and 2005. Data compare the mean incremental lengths-at-age for Loomis Lake. The weighted mean (Wgt Mean) of all three species is also shown.

Aday et al. 2005, Headley and Lauer 2008). Our findings appear to disagree with this. In this study, largemouth bass exhibited increased growth post-treatment (compared to pretreatment growth) despite essentially unchanged abundance. Pumpkinseed showed significant increases in both growth and abundance post-treatment. Yellow perch showed no significant growth increase post-treatment (again, compared to pretreatment growth) despite significantly reduced relative abundance.

The impact of vegetation removal on fish abundance, growth, survival, and diversity has mixed results in literature (Maceina et al. 1991, Bettoli et al. 1993, Olson et al. 1998, Pothoven et al. 1999, Unmuth et al. 1999). Most found significantly increased growth in at least some age classes of some species. Changes in abundance were highly variable depending on species, sampling gear, and predator-prey relationships. Betolli et al. (1993) discovered significant alterations in species richness and diversity as prey species adapted to highly vegetated habitats gave way to those that prefer less vegetation. They also found that although some changes could be explained by species life histories, others could not. In a study similar to Loomis Lake, Pothoven et al. (1999) followed two lakes given whole-lake Sonar treatments and compared results to three control lakes. Largemouth bass and bluegill exhibited increased growth rates, but showed mixed results for abundance, depending on species, age, and gear type.

Fish response to vegetation removal appears to be highly dependent on the underlying ecosystem dynamics. The density of macrophytes before and after removal, the difference in density as a result of removal, and the persistence of the removal all appear to be factors. Fish life histories and predatory and competitive pressures, both intra- and inter-specific, also play a role.

In conclusion, the fluridone treatment at Loomis Lake achieved a significant reduction in frequency (86% for egeria; 84% for Eurasian watermilfoil) and biomass (98% for egeria; 99% for Eurasian watermilfoil) for three YAT. Because the CET was above that which will achieve species selectivity, the herbicide treatment also significantly reduced native plant frequency of occurrence and biomass for the same time period. This allowed the lake to become more turbid for one YAT. The fish community experienced a decline of small fish, which had become abundant due to dense vegetation prior to treatment. After treatment, the growth of largemouth bass and pumpkinseed and abundance of stock size pumpkinseed increased. Whole-lake herbicide treatments that reduce native plant cover in shallow nutrient rich systems run the risk of producing an algae-dominated system. The native plant community composition and tolerance to herbicide CET, as well as the potential for algae and sediment entrainment, should be considered before use to avoid potential long term impacts to the lake biota.

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Quantifying littoral vertical habitat structure and fish community associations using underwater visual census

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Key words: community ecology, lake, microhabitat, quadrat sampling, canonical correspondence analysis, vertical structure, littoral

Synopsis

We developed and tested a new visual census technique to quantify the importance of vertical habitat structure on the associated fish assemblages in the littoral zone of a freshwater lake. We demonstrated that the primary environmental gradient, accounting for the most variation in the species data, represented a temporal gradient of seasonal characteristics. The secondary environmental gradient was related to the vertical structure at the sampling locations, showing the importance of the vertical component of the environment on fish community structure. Characterizing the vertical component at different resolutions provided different interpretations. The primary difference was the strength of influence of woody material on community structure. Woody material had a stronger influence on community structure throughout the water column when a single vertical unit defined the fish data. The appropriateness of defining the data by either multiple vertical strata or by a single vertical one would be dependent on the objectives of the study, as neither approach was found to explain substantially more variation in the species data. The current study demonstrates that fish are closely associated with particular elements of habitat structure in the littoral zone, even in the absence of major piscivorous predators. We provide a novel study quantifying the vertical multiple habitat structures and habitat use by fish in the water column of a freshwater lake. The new vertical visual census technique can be used to more comprehensively sample the three-dimensional environment of lake littoral zones, and quantify the fish–habitat spatial relationships across a range of abiotic and biotic habitat features.

Introduction

Aquatic ecosystems are naturally complex, making it difficult to understand the processes that structure communities (Jackson et al. 2001). To discern the processes that influence community structure, the differential responses of assemblages and individual species to environmental factors must be examined (Weaver et al. 1996). To understand the relationship between habitat and fish distribution, it is necessary to characterize and quantify aspects of the environment that are important to fishes. Considering spatial and temporal changes on a microhabitat scale may help to unravel some of the complexity of aquatic ecosystems.

Habitat complexity or heterogeneity has been shown to influence fish distribution in the littoral zone of freshwater lakes (e.g. Pratt & Smokorowski 2003). Fish distribution has been linked to environmental variables including the presence or diversity of macrophytes (e.g. Pratt & Smokorowski 2003), shoreline aspect and substrate composition (Gido et al. 2002), distance from shore, and lake morphological features including lake size, lake depth and the associated thermal stratification. However, whereas studies of other aquatic and terrestrial systems have long recognized the importance of vertical habitat complexity and heterogeneity (e.g. Catsadorakis 1997, Grossman et al. 1998), lake studies have lacked a similar focus on the three-dimensional aspect of the environment.

Habitat structure in freshwater lakes has often been measured by considering the amount and distribution of macrophytes. Studies have relied on removing sections of vegetation from natural lake habitat to determine the importance of macrophyte composition (e.g. Weaver et al. 1997). However, more traditional approaches of quantifying the vertical component of vegetation involve the visual inspection of macrophytes to estimate their relative abundance in an area of interest (e.g. Tonn & Magnuson 1982) or to classify aquatic plants as submerged, emergent, or floating types. Estimating the percentage cover of vegetation has not always been the best measure of habitat structure because the vertical component of the vegetation is often ignored. In such instances, two very different types of vegetative structure may be given the same weight in the analysis related to fish community structure.

Macrophytes are the most commonly measured element of habitat structure in the littoral zone of freshwater lakes. Additional physical habitat features such as woody material, also referred to as woody debris or necromass, may influence fish distribution in the littoral zone but have received limited attention (e.g. Mallory et al. 2000). There is a need for improved knowledge of a broader base of habitat structures and their relation to fish distribution; a comprehensive quantitative method of sampling habitat and fish associations is the most valuable approach. Quantifying woody debris and fish use of woody structure, other than that associated with predator–prey interactions, would be valuable for enhancing the current state of knowledge of the role that woody debris plays in structuring littoral zone fish communities.

Visual census

To understand fish community structure, both the habitat and the fish must be sampled. Many methods of fish sampling have limitations and biases associated with them (Jackson & Harvey 1997). Visual census is a commonly used technique for observing fish habitat and fish species associations in aquatic systems. The technique involves either snorkeling or using SCUBA to remain in the water for extended periods of time, using quadrats, point-abundance sampling, or strip counts to sample a variety of sites.

Our study developed and tested a new quadrat-based, visual-census technique that quantified the vertical-habitat structure and vertical habitat use by fish. To most effectively test this technique, we chose a small lake, Poorhouse Lake, which had no development on the shoreline and lacked major littoral predators such as bass, *Micropterus* species, or pike, *Esox lucius*. The lack of major predators resulted in a lake system with a large number of cyprinids that did not display predator-escape behaviour in the presence of a snorkeling observer (MacRae and Jackson 2001). The lack of shoreline development ensured undisturbed littoral-zone habitat and suggested the presence of a natural fish community, unaffected by introduced or invading species. Within Poorhouse Lake, we sampled 20 sites; we quantified both the habitat structure and fish associations in three-dimensions.

Research objectives

The primary objective of the current study was to develop and test a new visual-census technique for quantifying the vertical component of habitat structure and fish use of habitat in the littoral zone of a freshwater lake. We used multiple, discrete vertical strata to quantify vertical habitat structure and fish position in the water column. We employed multiple approaches for integrating or pooling the data to determine how differences in the resolution of vertical stratification affected the pattern of fish–habitat interactions. Our approach can vertically quantify both fish and habitat structure whereas to date there has been a lack of focus on the three-dimensional arrangement of habitat in lakes.

Methods

Study area

We chose Poorhouse Lake for this study based on the following criteria: the accessibility of the lake, the absence of major predators, high numbers of cyprinids and known species composition (Jackson 1992), adequate water clarity for visual census, and heterogeneity of the littoral zone habitat. Poorhouse Lake, (45°22′ N latitude and 78°45′ W longitude) has an area of 29.4 ha and a depth of 12.5 m at its deepest point, although this study focused on the littoral zone.

Site selection

We first surveyed the entire shoreline to determine the range of habitat types, from simple to complex. We selected 20 sites around the perimeter of Poorhouse Lake, each at approximately 1 m depth within the littoral zone, for sampling throughout the summer of 2001. We selected 15 of the 20 sites based on the relative occurrence of particular habitat types within the lake, and we chose five sites at random. We selected each sampling site by choosing a section representative of the general area within each habitat type. We marked quadrat sites with a short length (2–3 cm) of flagging tape tied to a nail pushed into the sediment. The sites chosen ranged from simple sandy sites to complex sites, consisting of various combinations of woody and rocky structures with vegetation, and a variety of substrates. We mapped all sites to confirm the habitat type within a radius of approximately 2 – 3 m of the quadrat marker.

We followed a standard protocol for collecting habitat details at all sites. We set a temperature logger at each site on 30 May, which remained in the water until 29 September. Loggers were placed at least 3 m from each quadrat center to prevent the logger from becoming part of the three-dimensional habitat of the site at locations lacking vertical relief. Depth of the water column at all quadrat markers was initially recorded in May and monitored each month throughout the summer. We measured the distance to shore from each quadrat center once in May and once in August, and set minnow traps at different times throughout the summer to verify species identification.

For each trial, we approached the site slowly from at least 5 m away by snorkeling and placed a quadrat at the marker. Small fishing bobbers tied to the ends of fishing line attached at each corner floated to the surface and held the line vertical in the water (Figure 1a). The lines were stratified vertically, at 25 cm intervals and were numbered consecutively from the lower most to the top. The activity trial began 3–5 min after the quadrat was in place so that the fish were acclimated to the presence of the motionless swimmer and quadrat. We recorded the following details underwater on a clear Plexiglass slate, every minute for 10 min: the abundance of each species of fish present in the quadrat, the behaviour and activity exhibited by each species, and the vertical position of the fish in the water column. When more than 50 fish were present at the site, single-minute observations could not be made. In these cases, we recorded the following information: total number of fish ob-

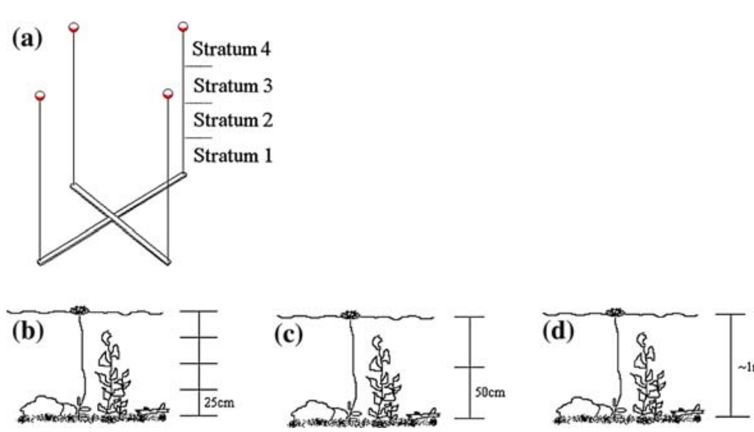


Figure 1. Quadrat used to quantify vertical and horizontal habitat structure (1 m^2) in Poorhouse Lake littoral zone (a), and the three resolutions of vertical stratification used for data organization: 25 cm strata (b), 50 cm strata (c), and the full water column as a single vertical unit (d).

served, an estimated percentage of each species present, and the activity, behaviour, and position of each species. To minimize disturbance to the fish and habitat, there was little fin or arm movement by the observer throughout each trial; a position was chosen for observation that would avoid casting a shadow onto the site. After the trial, we recorded the amount of wood, rock, and vegetation within each stratum using a modified Domin scale (Kershaw 1973). Environmental data collected included surface water temperature, air temperature, time of day, and weather conditions; the Beaufort wind scale was used to estimate wind speed. Additional notes were made on the fish observed in the general area and conditions specific to that day and trial. We determined substrate type using a modified Wentworth scale (Cummins 1962); we estimated percentage cover of each substrate type using the modified Domin scale, at the end of the summer sampling period. In May through August, we sampled Poorhouse Lake twice per month. Within each sampling period, we ran two sets of trials for all 20 sites. In September, we sampled Poorhouse once with one set of trials.

Both shore distance and temperature range data were log-transformed to approximate normal distributions and improve linearity between variables; we performed square transformations on depth and water temperature data. We used principal coordinates analysis (PCoA; Legendre & Legendre 1998) with the Euclidean distance coefficient to summarize the gradient among the eight substrate variables used in data collection. A gradient of coarse substrate types (e.g., boulder) to fine substrate (organic silt) was summarized along the first PCoA axis. We replaced the eight different substrate variables by this single substrate variable, which summarized a gradient from fine to coarse substrate.

Fish species presence–absence data were organized into three different resolutions of vertical stratification (Figure 1b–d) to better elucidate the effectiveness of the new technique in capturing community interactions. The finest level of resolution treated the data as it was collected in the field: the data was defined by vertical strata 25 cm high, from the substrate to the surface, with each site having four or five strata in total depending on the site depth. The coarser level of resolution used pooled data so that the water column was divided into only two strata: the first extended from the substrate to 50 cm above it, and the second extended from 50 cm above the substrate to the water's surface. The final, coarsest resolution used pooled fish data that was defined by the single vertical unit of the full water column (i.e. each site had only one set of observations per survey). However, in this final consideration of the data, the vertical habitat measurements of wood, rock and vegetation were included as separate variables so that the role of these habitat structures could be considered in the four vertical strata (25 cm) of the water column. At this coarsest resolution, the fish data were defined by the full water column but the physical habitat attributes were still considered in multiple vertical units. This approach allowed a comprehensive evaluation of the influence of individual habitat structures throughout the water column on fish distribution.

We used correspondence analysis to summarize species association relationships at each of the three resolutions of vertical stratification. Biplot scaling was used, with a symmetric focus. We excluded samples in which no fish were observed from the analysis, as these cannot be included in a CA approach. In total, we included 17 species and classifications of fish in the analyses (Table 1).

Canonical correspondence analysis (CCA) was used with each vertical resolution of data to quantify the relative importance of vertical habitat structure in influencing community structure, compared to other environmental variables. As in the CA, biplot scaling was used with a symmetric focus, and only samples in which fish were observed were included. To assess the importance of the vertical component of habitat structure, stratum designation was included as an environmental variable at the two finest vertical resolutions. In total, 10 environmental variables were included in the CCA analysis of two out of the three levels of data organization: data defined vertically at 25 cm stratification and 50 cm stratification. When data were pooled to represent the full water column, vertical-habitat measurements were included to evaluate the role of habitat structure in specific sections of the water column: the percentage of cover provided by vegetation, rock, and wood was recorded for each stratum and treated as a separate environmental variable. In total, 15 environmental variables were included. Certain

Table 1. Species list and codes for the 17 species and classifications of fish included in the analyses and graphical results.

Species code	Common name	Scientific name
bln-dc	Blacknose dace	*Rhinichthys atratulus*
blt-ns	Bluntnose minnow	*Pimephales notatus*
brk-sb	Brook stickleback	*Culaea inconstans*
cmn-sn	Common shiner	*Luxilus cornutus*
crk-cb	Creek chub	*Semotilus atromaculatus*
fat-hd	Fathead minnow	*Pimephales promelas*
"fry"	Very small fish that could not be visually identified while in the water	
gld-sn	Golden shiner	*Notemigonus crysoleucas*
pkn-sd	Pumpkinseed	*Lepomis gibbosus*
rbl-dc	Northern redbelly dace	*Phoxinus eos*
Trout	Brook trout	*Salvelinus fontinalis*
Ukn	Last year's young-of-the-year	*N/A*
ukn-cyp	Unidentified cyprinid	*Cyprinidae*
ukn-sn	Unidentified shiner	*Cyprinidae*
ylw-pr	Yellow perch	*Perca flavescens*
yoy	This year's young-of-the-year	*N/A*
ypkn-sd	Young-of-the-year pumpkinseed	*Lepomis gibbosus*

environmental variables were measured at a single point in time for each observation. As such, the data collected for these variables did not accurately reflect the potential influence of the variables on the habitat; they were therefore included as covariables in all CCA analyses. In total, five covariables were included in the analysis: cloud cover, wind strength, wind–gust strength, time, and air temperature. By making these five variables covariables, any confounding effects on the remaining environmental variables or the fish species patterns were removed.

Results

Correspondence analysis

Ordination plots illustrated the physical separation between the young and adult fish at all three levels of data organization (Figures 1b–d). The general pattern was the same across the three resolutions of data (Figures 2a–c); the two young species classifications grouped together, the adults grouped at the opposite end of the same axis, and the "fry" (denotes very small fish that could not be visually identified while in the water) aligned with the alternate axis, separated from both groups. The percentage inertia represents the percentage of the total species inertia explained by each axis, a measure similar to variance. The percentage of inertia of species data explained (Table 2) increases from the finest resolution of four vertical strata (14.1 and 13.4% for axis 1 and 2, respectively) to the coarsest level of resolution, the full water column (17.4 and 16.2% for axis 1 and 2, respectively). However, note that the total inertia decreases substantially from the four strata vertical component to the combined data format due to the reduction in the size of the data matrix. Therefore, as the total amount of variation explained by the species relationships decreases from the level of four strata (4.006) to the full water column (2.645) each axis' eigenvalue represents a greater percentage of that smaller total. The 6.1% difference in the amount of variation explained by the first two axes from the finest to the coarsest vertical resolution was not substantial enough to determine which resolution was the better method of considering the data given the associated change in the size of the matrices being considered.

Cumulative percentage variation of species data was low in the CCA results for all three resolutions of vertical stratification (Table 3). CCA can produce low percentage inertia of species data because data can be very noisy, especially presence–absence data (ter Braak 1998), or because the fish community is not structured along the variation in the environmental conditions. Nearly three quarters (73.8%) of the explained variation was

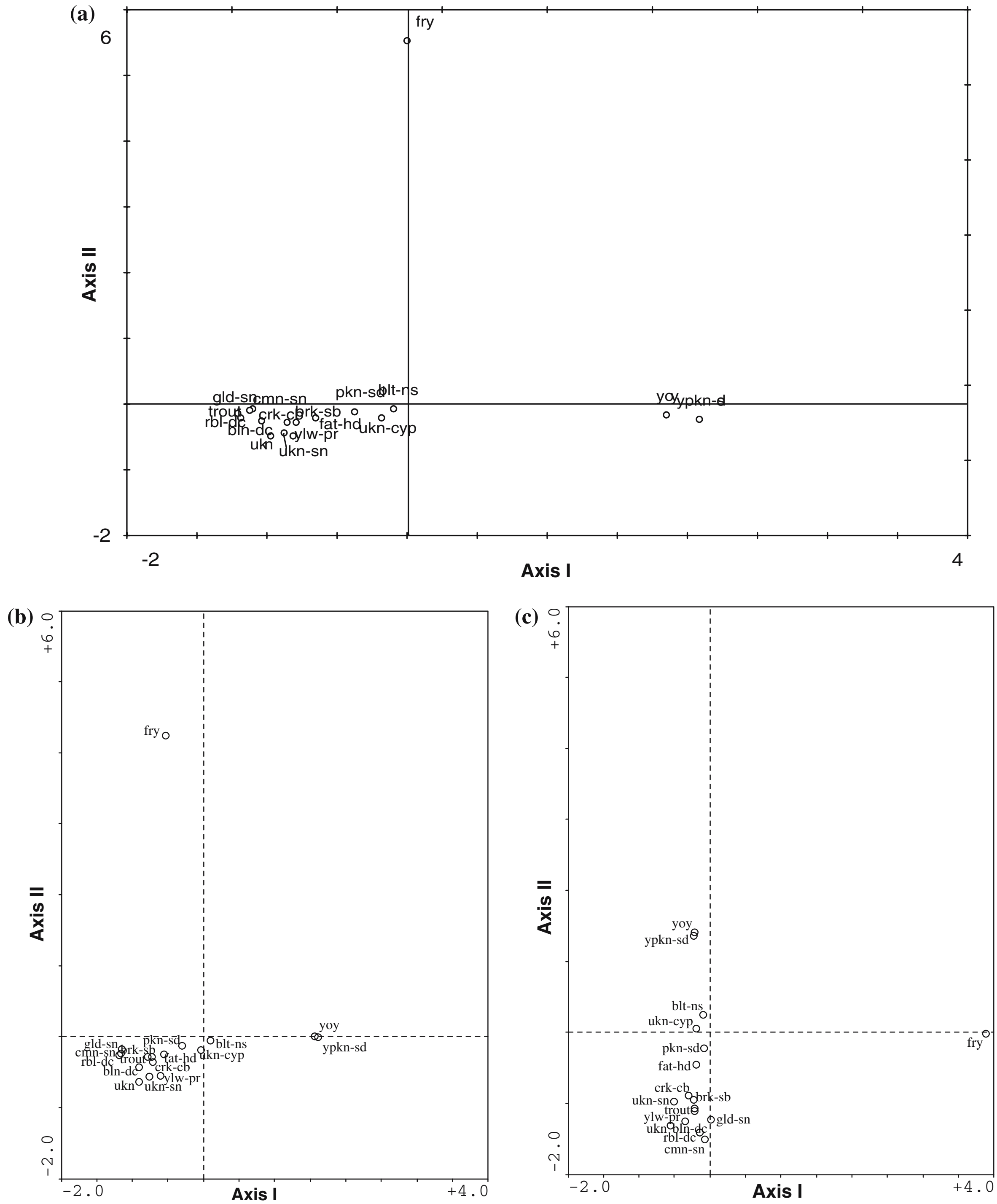


Figure 2. Correspondence analysis axes one and two, showing the association of fish species based on presence–absence data defined by (a) 25 cm vertical stratification, Axis I and II summarized 14.1 and 13.4%, respectively, of the variation in the species data, (b) 50 cm vertical stratification, Axis I and II summarized 15.3 and 14.7%, respectively, of the variation in the species data and (c) the single vertical unit of the full water column, Axis I and II summarized 17.4 and 16.2%, respectively, of the variation in the species data.

Table 2. Eigenvalues and percentages of variation from correspondence analyses of species presence–absence data at three resolutions of vertical stratification; the number of samples in the fully collapsed data is not half that of the two strata vertical component because not every site had fish present in the second strata and therefore, when it was collapsed the sample number only reduced by the number of samples that had fish present in the second strata (i.e. 124 samples).

Axes	1	2	3	4	Total inertia
Four strata vertical component ($n=676$)					
Eigenvalues	0.564	0.539	0.304	0.29	4.006
% Variation of species data	14.1	13.4	7.6	7.3	
Cumulative % of species data	14.1	27.5	35.1	42.4	
Two strata vertical component ($n=426$)					
Eigenvalues	0.5	0.48	0.26	0.24	3.274
% Variation of species data	15.3	14.7	7.9	7.3	
Cumulative % of species data	15.3	30	37.9	45.2	
Collapsed data-full water column ($n=302$)					
Eigenvalues	0.459	0.43	0.215	0.19	2.645
% Variation of species data	17.4	16.2	8.1	7.2	
Cumulative % of species data	17.4	33.6	41.7	48.9	

represented by the species–environment relations of the first two axes portrayed for the finest vertical resolution of 25 cm strata. The amount of variation decreased slightly at the level of 50 cm strata to 73.2%. When data were collapsed and the water column was treated as a single vertical unit, the cumulative percentage variation of species–environment relations for the first two axes dropped to 63.6%. Similar to the CA results, the total inertia was smaller at the coarsest level of vertical resolution: 2.645 versus 4.006 for the finest resolution.

The Monte Carlo test of significance of the first canonical axis and the test of significance of all canonical axes illustrated that the relationship between the species and the environmental variables was highly significant ($p=0.005$) for the three vertical resolutions used to study the community structure.

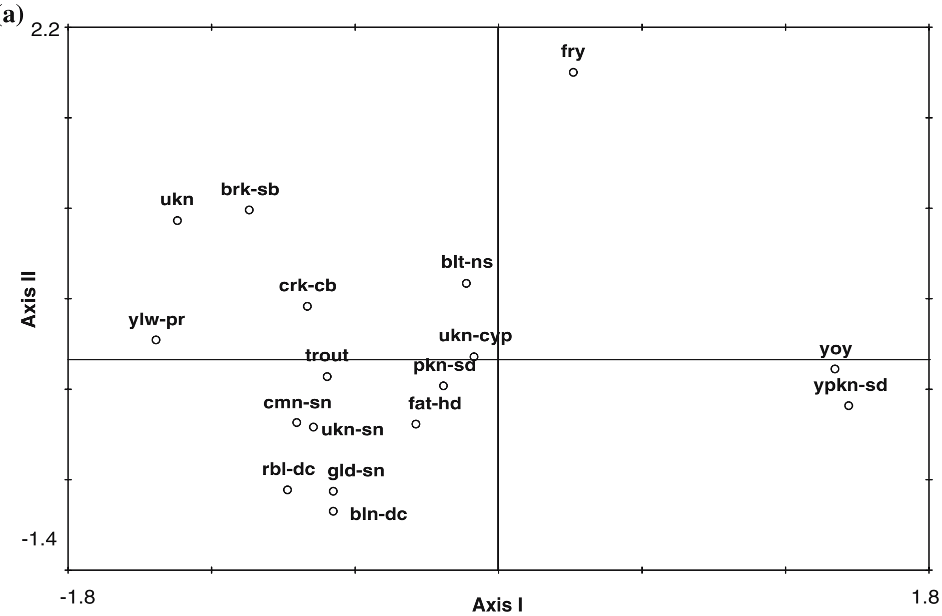
The community structure at each resolution of vertical stratification can be depicted by CCA ordination diagrams. The finest resolution of stratification was 25 cm stratum, with four or five strata per site, depending on site depth. The first axis of the ordination diagram at this resolution represented a seasonal gradient (Figure 3a). The depth, water temperature, and date variables were closely aligned with the first axis and strongly correlated with each other, as indicated by the small angles between the vectors.

The second axis summarized a gradient in the vertical habitat across sites. Vegetation was correlated with fine substrate, increasing shore distance and decreasing stratum level, suggesting that vegetation was found more in the lower part of the water column, growing in fine substrate, and at sites that were found on the gentler sloping shores of the lake

Table 3. Eigenvalues and percentages of variance from canonical correspondence analyses of species presence–absence and environmental data at three resolutions of vertical stratification; Monte Carlo significant probabilities are shown in italics.

Axes	1 (p)	2	3	4	Total inertia
Four strata vertical component ($n=676$)					
Eigenvalues	0.313 (*0.005*)	0.072	0.04	0.032	4.006
Cumulative percentage variance of species–environment relation	59.9	73.8	81.4	87.4	
Two strata vertical component ($n=426$)					
Eigenvalues	0.29 (*0.005*)	0.072	0.033	0.025	3.274
Cumulative percentage variance of species–environment relation	58.7	73.2	80	85.1	
Collapsed data-full water column ($n=302$)					
Eigenvalues	0.268 (*0.005*)	0.075	0.046	0.038	2.645
Cumulative percentage variance of species–environment relation	49.8	63.6	72.1	79.1	

(a)



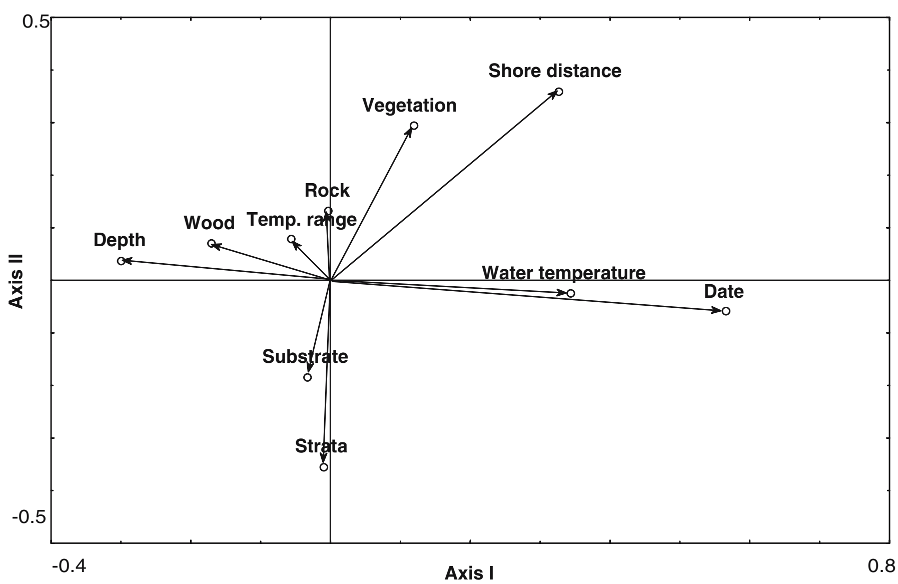


Figure 3. Canonical correspondence analysis axis one and two, showing the association of fish species and habitat characteristics based on presence–absence and environmental data defined by (a) 25 cm vertical stratification, Axis I and II summarized 8.1 and 1.9%, respectively, of the variation in the species data, (b) 50 cm vertical stratification, Axis I and II summarized 9.3 and 2.3%, respectively, of the variation in the species data, and (c) the single water-column stratum, Axis I and II summarized 10.7 and 3.0%, respectively, of the variation in the species data.

(therefore were further from shore at ~1 m depth). "Fry" and bluntnose minnows, *Pimephales notatus*, were most strongly associated with the vertical gradient. Wood was not correlated with the vertical component, but the amount of wood increased in deeper sites, even though the variation in depth among sites was relatively limited. The environmental variables most strongly associated with community structure were shore distance, date, vegetation, water temperature, and vertical stratum.

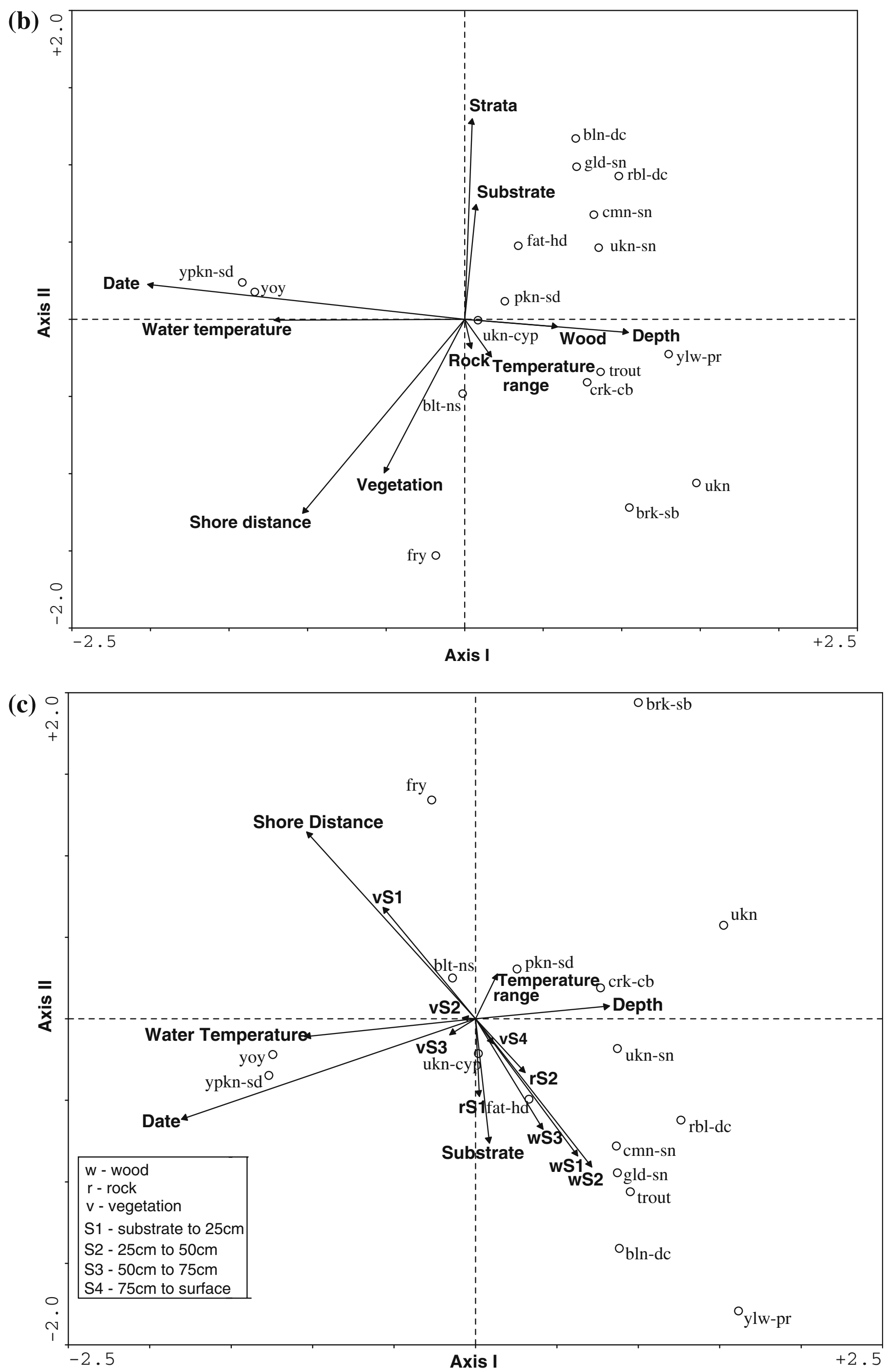


Figure 3. Continued

The ordination diagram for the data defined more coarsely at two 50 cm, vertical strata (Figure 3b) illustrated similar patterns of community structure as those found at the finer resolution. A seasonal gradient was observed along the first axis, and a vertical gradient was observed along the second axis. The following differences in environmental associations were observed: wood and depth were more strongly (positively) correlated with each other and negatively correlated with water temperature and date; however, water temperature showed a weaker association with date than at the finer resolution. Temperature range and rock cover were more closely correlated, but both had shorter vectors relative to the vectors of the other environmental variables, suggesting they were not strongly associated with the community structure extracted from the data included in this study. Vegetation and shore distance were more strongly positively correlated, as were stratum and substrate.

Species associations were very similar as those observed at the finer resolution with the exceptions that brook trout, *Salvelinus fontinalis*, and creek chub, *Semotilus atromaculatus*, were more closely associated with each other and with yellow perch, *Perca flavescens*; all three species were associated with deeper, woodier sites, although the yellow perch were most closely aligned with the depth vector. The shiner group showed a weaker correlation with the depth vector than at the finer vertical resolution. Fathead minnows, *Pimephales promelas*, showed stronger association with the shore distance and vegetation vectors in this analysis, but were closer to the origin than either the shiner group or dace-shiner group; therefore, the fathead minnow association with non-vegetated sites close to shore was weaker than that observed for the two groups. Both the shiner and dace-shiner groups, as well as the fathead minnows, showed a stronger association with the vertical gradient in this analysis than in the previous, finer vertical resolution analysis. The dace-shiner group exhibited a correlation with the upper strata, whereas the shiner group and fathead minnows showed an association with strata lower in the water column.

The CCA results of community relationships at the full water column data set depicted different patterns than those detected when data were defined by finer vertical components (Figure 3c). The primary difference when the fish data from different strata were combined was the increased influence of woody cover on community structure. Shore distance, date, and woody structure appeared to have the strongest association with the community structure when the data included the habitat structural components measured at each section of the water column.

The seasonal characteristics were again correlated: water temperature and date were positively related to each other, but negatively with depth. A complexity gradient was observed in the grouping of most of the remaining environmental variables, although the gradient did not align with either axis. Shore distance was positively correlated with vegetation in the first stratum; the first stratum vegetation vector (vS1) was the longest of all vegetation vectors, which suggested that vegetation closest to the substrate had the most influence on the community structure of the four vertical vegetation components observed.

The species most strongly associated with the vertical woody structure were the larger bodied species, including common shiners, *Luxilus cornutus*, and golden shiners, *Notemigonus crysoleucas*, brook trout and yellow perch. The smaller-bodied blacknose dace, *Rhinichthys atratulus*, was also associated with the vertical woody structure. Wood and depth were more weakly associated at this coarsest vertical resolution; this weaker association illustrated the yellow perch's correlation to wood and the creek chub's correlation to depth. These correlations were not discerned at the finer vertical resolutions. Northern redbelly dace, *Phoxinus eos*, did not exhibit as strong a response to shore distance or vegetation at this resolution but were still weakly associated with the vertical gradient.

When fish data were organized by the single vertical component of the full water column, both the rock and wood vectors showed different trends than when the vertical component was defined on a finer scale. At the coarsest vertical resolution, rocky structure was positively correlated with coarseness of substrate and negatively correlated with temperature range; previously, it was associated with finer substrate and increased temperature range. The length of the rock vector, however, indicates that rocky cover did not have a strong association with the community structure extracted in this analysis, whereas woody structure did. Woody structure was strongly positively related to increased rock cover and coarse substrate, but was negatively related to shore distance and vegetation. When data were defined by finer vertical components in the previous two analyses, woody structure was only very weakly related to either rock or vegetation cover.

Discussion

This study illustrated that quantifying the vertical component of habitat structure and habitat use by fish as multiple, discrete units yielded a comprehensive picture of fish community structure and outlined differences in fish distribution and their relationship to habitat differences. Recording the fish and habitat structural data by discrete vertical units is a new visual census approach for quantifying habitat characteristics and fish associations with habitat. The importance of vertical habitat complexity on species diversity and habitat use has been established in several terrestrial systems, as well as in marine and stream systems. When data were recorded using multiple, discrete vertical units in our study, the second strongest influence on the fish community structure was a vertical complexity gradient, following the more influential seasonal gradient. Our study confirms that vertical habitat structure and habitat use by fish could be quantified in lake littoral zones and that vertical habitat structure plays an important role in regulating the fish community.

The organization of environmental and species data at three resolutions illustrated multiple ways of considering the role of the habitat's vertical component. At the two finest resolutions, the data were defined by multiple vertical components, and a separate environmental variable represented the vertical stratification. This direct approach allowed the overall role of vertical habitat, in terms of structure and fish use, to be evaluated. There was very little difference in the community structure when data were defined by either the finest resolution of 25 cm strata, or by the coarser resolution of 50 cm strata. Therefore, either approach could be taken when sampling a littoral zone; the appropriateness of the technique used would likely be a result of the type of question being asked and the system in which it was being studied. In a typical littoral zone, visual census of the habitat and fish community would be simpler using the coarser resolution of 50 cm strata. This reduces the number of boundaries between sampling units, likely reducing the inaccuracy associated with habitat and fish sampled close to those boundaries. However, in highly vertically complex habitats, the finer resolution may be required to distinguish niches of associated fish species.

When habitat was sampled in the field, three structural habitat components (woody debris, rock, and vegetation) were recorded in each stratum. By defining the fish data vertically, the influence of these habitat components at each section of the water column was not directly illustrated. However, when defining the data by the single vertical unit of the full water column, the structural components of wood, rock, and vegetation can be included as individual variables, allowing direct interpretation of their role throughout various parts of the water column. The influence of habitat heterogeneity on fish communities has been a focus within aquatic ecology. Several studies have evaluated habitat heterogeneity or complexity primarily through vegetation density or diversity and substrate type; however, there has been a lack of attention on other elements of the habitat that enhance heterogeneity. When considering the integrated vertical patterns, we were able to address the lack of focus on other habitat structural elements in the water column and the lack of multivariate analysis of fish associations with both environmental variables and vertical habitat components. Defining the fish data by the full water column allowed the evaluation of the individual influence of woody structure, rock, and vegetation on fish distribution in each of the four strata of the water column.

Analysis of fish–habitat interactions at the coarsest vertical resolution revealed that woody structure both on the substrate and throughout the water column, was strongly associated with several species specifically, as well as the overall community structure. This result confirmed that woody debris is a vital component of littoral-zone habitat structure. No major piscivorous predators exist in Poorhouse Lake, but woody structure may have been used by fishes to escape predation from brook trout, large creek chub, common mergansers, *Mergus merganser*, loons, *Gavia immer*, or belted kingfishers, *Ceryle alcyon*, in the littoral zone. While we show the importance of woody habitat, its importance is likely to be much greater in systems containing piscivorous fishes (MacRae & Jackson 2001).

In all three vertical resolutions of data, "fry" was found to be the only species category associated with the heavily vegetated sites in Poorhouse Lake. Conversely, the majority of adult species categories were either associated with sites that lacked vegetation or were not influenced by the presence or absence of macrophytes. This separation of fry and adult individuals may reflect the recognized behaviour of age 0 fish using submerged vegetation for shelter from predation (Werner et al. 1983). Patchy vegetation may offer the best habitat for age 0 fish to gain protection from predation, but it also gives them more immediate access to the open spaces that harbour zooplankton, one of their preferred food resources (Weaver et al. 1997).

The new vertical visual census method described in this study allows data to be evaluated and interpreted at three different vertical resolutions (i.e. 25 and 50 cm strata, and the full water column); assessing the data in this matter allowed a more detailed evaluation of the role of vertical habitat structure in fish communities. The results of this study suggest that no one treatment of the data explains substantially more variation than another. While the choice of which vertical resolution of data to use may depend upon the question being asked, this type of post-collection data flexibility is a strong advantage of the vertical visual sampling technique.

Our study demonstrated that fish are closely associated with habitat structure in the littoral zone even in the absence of major piscivorous predators. As has been established in several terrestrial systems, this study confirmed the integral role of vertical habitat complexity in structuring community interactions. This is the first known study to quantify multiple vertical habitat structures and habitat use by fish in the water column of a freshwater lake. The lack of focus on the three-dimensional environment of lake littoral zones in aquatic community ecology has left a gap of knowledge concerning freshwater fish–habitat interactions. Based on the results of this study, it can be concluded that the new vertical visual census technique presented here can be employed to successfully address that gap. Both researchers and managers can benefit through application of this technique in additional systems, including those containing major piscivorous predators. Researchers can use this method to enhance their understanding of fish–habitat spatial relationships. Managers can gain a more accurate awareness of the implications that development and subsequent habitat structural changes can have on the fish community. In terms of both academia and application, this vertical visual census method of quantifying habitat structure and fish associations provides a valuable tool that can improve our current state of knowledge concerning fish–habitat interactions.

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