

Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*)

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Abstract: Structurally complex environments strongly affect the behaviours and foraging efficiencies of predators and prey. I studied temporal variation in the habitat distribution of perch (*Perca fluviatilis*) and pike (*Esox lucius*) in relation to habitat complexity and prey abundance in a lake. The study involved quantitative estimates of different habitat types, estimates of macroinvertebrate prey availability, and distribution and movement patterns of the fish. The numbers of 80–110 mm perch in the littoral zone decreased rapidly in spring, which was a result of either perch moving to the pelagic zone or predation mortality. Predation mortality is the most plausible explanation because piscivorous perch and pike >160 mm aggregated close to these high abundances of 80–110 mm perch, and 80–110 mm perch used only vegetated habitats as a possible protection against predators. Both the biomass and diversity of macroinvertebrates increased with vegetation density, whereas perch abundance was highest in an intermediate vegetation density. Pike size was inversely related to vegetation density as a result of potential cannibalism from the largest pike individuals, which preferred the tree structure habitat. Perch group size decreased with increasing vegetation density, and perch <80 mm always occurred in group sizes larger than three individuals and never occurred in the same groups as perch >160 mm. In contrast, perch >160 mm occurred at decreasing numbers with increasing group size and mainly stayed solitary or in pairs. Perch >160 mm showed no tendencies for homing behaviour and moved actively around the whole lake, whereas pike showed a strong homing behaviour. My study suggests that the structural complexity in the littoral zone can both qualitatively and quantitatively change the interaction between piscivorous predators and their prey.

Résumé : La variation temporelle touchant la distribution de la perche commune (*Perca fluviatilis*) et du grand brochet (*Esox lucius*) dans l'habitat d'un lac a suggéré que la complexité structurale de la zone littorale puisse modifier, qualitativement et quantitativement, les interactions entre les prédateurs piscivores et leurs proies. Le nombre de perches de 80–110 mm dans la zone littorale a diminué rapidement au printemps. La mortalité par prédation est une explication plus plausible de ce phénomène que la migration des perches vers la zone pélagique parce que les percidés et les brochets piscivores de taille 160 mm se rassemblaient près de ces zones de forte abondance de petites perches (80–110 mm), qui n'utilisent que les habitats couverts de végétation comme protection possible contre les prédateurs. La biomasse et la diversité de macroinvertébrés ont augmenté avec la densité de la végétation, tandis que l'abondance des perches était la plus élevée lorsque la densité de la végétation était intermédiaire. La taille du grand brochet était inversement proportionnelle à la densité de la végétation en raison de la possibilité de cannibalisme par les brochets de plus grande taille qui préféraient un habitat comportant des arbres. La taille des perches, en groupe, diminuait avec l'augmentation de la densité de la végétation et les percidés de taille < 80 mm se présentaient toujours en groupe de plus de trois individus et jamais dans les mêmes groupes que les percidés > 160 mm. Ces derniers vivaient principalement en solitaires ou en paires, ne présentaient aucune tendance en ce qui a trait au comportement de retour, et se déplaçaient activement autour du lac entier; le grand brochet présentait un comportement de retour très prononcé.

[Traduit par la Rédaction]

Introduction

Spatial heterogeneity in the environment may have large effects on the stability properties of predator–prey interactions and is an important structuring factor of communities (Murdoch and Oaten 1975; Caswell 1978; Holt 1984; Taylor 1984; McNair 1986). An increase in spatial heterogeneity may increase habitat dimensionality resulting from changes in structural complexity,

habitat morphology, or other environmental variables (Schoener 1989; Warren 1989; Whitehead and Walde 1992). The dimensionality of the habitat is an important determinant of community structure because environmental dimensionality may interact with individual level variables such as the encounter rate between predators and prey (Briand and Cohen 1987; Whitehead and Walde 1992).

Structural complexity is one of those dimensions that has strong effects on the behaviours and efficiencies of predators and prey (Savino and Stein 1982, 1989; Werner et al. 1983; Eklöv and Diehl 1994; Persson and Eklöv 1995). Both the quality and quantity of structural complexity strongly affect the interaction between predators and prey as a result of

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species-specific differences in predator efficiency and prey antipredator response (Savino and Stein 1989; Angermeier 1992; Christensen and Persson 1993; Eklöv 1995). Different types of predators are differentially affected by varying degrees of structural complexity as a result of both structural complexity interacting with foraging mode and encounter frequency with prey decreasing with an increase in structural complexity (Savino and Stein 1982, 1989; Eklöv and Diehl 1994).

In lakes, habitat heterogeneity is most commonly present in the form of littoral zone vegetation or a depth-gradient diversity both of which may have profound effects on species abundance and diversity (Werner et al. 1977; Tonn and Magnusson 1982; Eadie and Keast 1984; Benson and Magnusson 1992). Greater diversity of habitats within a lake appears to create an opportunity for a more species diverse fish community (Benson and Magnusson 1992), and different forms of structural complexity may provide shelter for fish to escape predators (Werner and Hall 1988; Mittelbach 1988). Prey refuges are species specific, suggesting that the survival of prey will depend on the availability of different types of refuges in the environment (Christensen and Persson 1993). Alternatively, prey may use schooling as an antipredator strategy (Christensen and Persson 1993; Eklöv and Persson 1995). The efficiencies of piscivorous predators are affected by the degree of structural complexity: the efficiency of sit-and-wait predators increases with an initial increase in structural complexity whereas the efficiency of active group foraging predators decreases with an increase in structural complexity (Savino and Stein 1982, 1989; Anderson 1984; Eklöv and Diehl 1994). Size-dependent spatial distributions of piscivores as a function of interactions between individual predators of different sizes may also affect the efficiency of piscivorous predators (Eklöv 1992; Eklöv and Diehl 1994). For example, large piscivorous pike (*Esox lucius*) were found to interact with smaller pike and stayed closer to the prey than did smaller pike (Eklöv 1992; Eklöv and Diehl 1994).

The aim of this study was to test predictions concerning patterns of the temporal variation in habitat distribution of perch (*Perca fluviatilis*) and pike in relation to habitat availability and structural complexity in a small lake. The predictions were created from previous experimental results that revealed mechanistic explanations for the outcomes of predator-prey interactions between large and small individuals of perch and pike (Eklöv 1992; Eklöv and Diehl 1994; Diehl and Eklöv 1995; Eklöv and Persson 1995).

Perch and pike are the two most widely distributed fish species in Scandinavian lakes (Svärdson 1976). In lakes where they co-occur, perch totally dominate numerically in the pelagic zone whereas both species commonly occur in the littoral zone (Persson et al. 1991). The two species have been found to have both numerical and behavioural effects on prey fish populations (Persson et al. 1996). During their ontogenetic development, perch undergo several niche shifts with respect to food resources and habitat use (Persson 1988). With increasing body size, perch switch from being zooplanktivorous mainly in the pelagic zone to benthivorous feeding mainly in the littoral zone. If they become large enough, perch feed mainly on fish and use both the littoral and pelagic zones (Persson 1988). As piscivores, perch are efficient group foragers (Eklöv 1992), but their efficiency decreases in structurally complex environments (Eklöv and Diehl 1994; Persson and Eklöv 1995). Pike

are sit-and-wait predators that occupy vegetated zones of lakes (Diana et al. 1977; Diana 1980). The foraging efficiency of pike increases at low vegetation densities and decreases at high vegetation densities (Savino and Stein 1989). As a consequence, pike are less affected by the presence of structurally complex prey refuges than piscivorous perch (Eklöv and Diehl 1994). In relation to differential predation risks and predator efficiencies in different habitats, the abundances of the smaller sizes of perch and pike were predicted to be positively related to an increase in structural complexity, whereas the abundances of larger sizes of perch and pike were predicted to be negatively related to an increase in structural complexity. The abundance of smaller sizes of perch was predicted to be positively related to an increase in abundance and diversity of macroinvertebrates. As a result of the social behaviour of perch and the territorial behaviour of pike (Eklöv 1992; Eklöv and Diehl 1994), perch could be expected to be active and form groups whereas pike could be expected to be sit-and-wait and solitary. However, because the shoaling ability of fish interact with structural complexity (Pitcher 1986), the group size of perch was predicted to be inversely related to vegetation density, and large perch were predicted to stay solitary and inactive, which has also been found for large perch with increasing structural complexity (Eklöv and Persson 1995). The abundances of large perch and pike were predicted to be positively related to the abundance of small perch.

Materials and methods

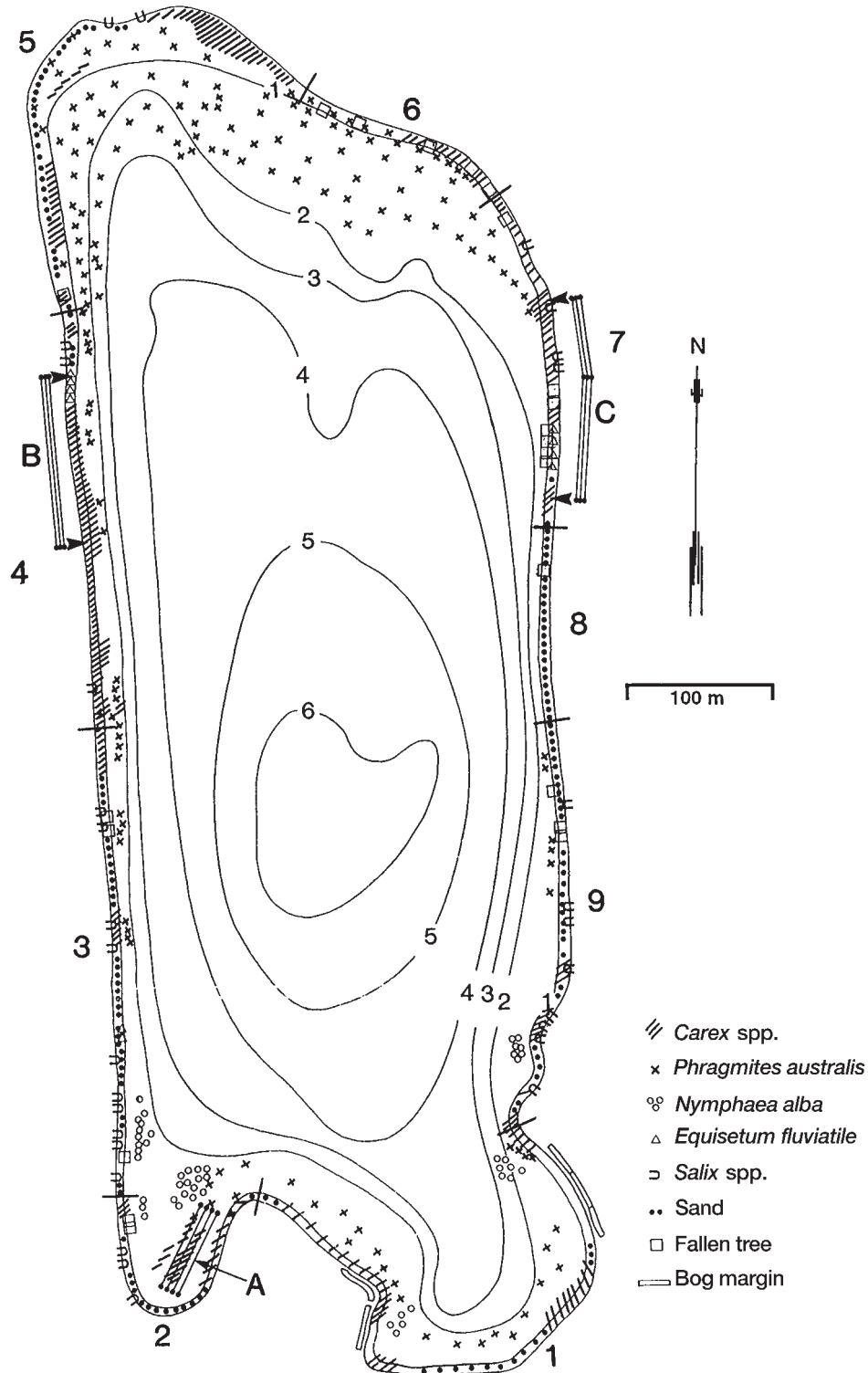
System studied

The study was performed in Lake Degersjön 25 km west of Umeå, Sweden (63°50'N, 20°1'E), during 1990–1991. All data presented were collected in 1990 except for the gillnet samples and movement patterns of perch and pike >160 mm from 1991, which were included to estimate variability of movement patterns between years. Lake Degersjön is a primarily spring-fed, low-productivity lake with a small outlet that dries out in summer. The lake is shallow (maximum depth 6 m) and has a surface area of 27.3 ha. Water transparency (Secchi depth) varies between 3.5 and 4.6 m. The lake is surrounded by a mixed spruce and pine forest except for a deforested area, which covers one third of the western shore. The littoral zone vegetation consists of the following emergent macrophytes in descending order of abundance: *Carex rostrata*, *Phragmites australis*, and *Equisetum fluviatile* (Fig. 1). Submerged and floating leaf vegetation are also present at lower abundances and consist of *Isoetes* sp., *Lobelia dortmanna*, *Nymphaea alba*, *Potamogeton natans*, and *Sparganium* sp. Along the shore, several dead trees have fallen into the lake.

Physical structure

The physical structure of the lake was quantified from aerial photographic slides that covered the whole littoral zone of the lake taken from an approximate height of 100 m in July 1990, and from observations obtained during the electrofishing (see methods for fish abundance estimates below). The littoral zone was classified into the following eight categories: *Carex rostrata*, *Equisetum fluviatile*, *Phragmites australis*, *Salix* spp., sand, tree structure, and bog margin. *Equisetum fluviatile* constitutes a similar structure type as *Carex rostrata* so their abundance were pooled. The locations of the fish were related to the habitats quantified from the photo slides. Physical structures in transects were at three locations in the lake (Fig. 1) estimated on one occasion in July 1990 by an observer, who classified vegetation into five density categories (very dense, 150 stems/m²; dense, 60–150 stems/m²; sparse, 40–60 stems/m²; very sparse, 5–40 stems/m²; and no vegetation) for every square metre of the transects. The

Fig. 1. Morphometric map of Lake Degersjön. The numbers 1–9 indicate the different zones and A–C indicate the three locations where underwater observations were conducted.



presence of trees fallen into the lake and water lilies (*Nymphaea alba*) was also noted. All categories of vegetation density were present at the three locations.

Fish abundance estimates

The main fish species present in the lake are perch and pike. In

addition, roach (*Rutilus rutilus*) and burbot (*Lota lota*) occur in small numbers. A small population of large roach (range 240–310 mm) was also present in the lake. During the electrofishing, schools of smaller roach were only observed twice in the littoral zone (15–20 individuals of 1-year-old roach). A small number of burbot were also caught in the littoral zone. The size distributions of the fish species in the lake

Table 1. Mean depth (cm) and range (given in parentheses) for transects at locations A, B, and C.

Transect	Location A	Location B	Location C
1	80 (62–98)	39 (37–41)	38 (25–44)
2	75 (58–91)	63 (60–65)	67 (40–80)
3	70 (57–83)	90 (86–96)	94 (43–145)
4	63 (55–70)		

were estimated in July 1991 based on gillnet samples (benthic multi-mesh gill nets, 56 m total length, mesh sizes: 9.5, 14.5, 18, 24, 29.5, 33, 38, and 46 mm) and expressed as numbers per four net panels. Two nets were set in the deepest part of the lake and two nets were set immediately outside the littoral zone. All nets were set in the afternoon (15:00) and lifted the following morning (09:00).

The lake was divided into nine zones (100–440 m long; Fig. 1) whose demarcations were based on physical structure and lake morphometry. Fish abundance was estimated by electrofishing, covering all zones of the lake and repeated at approximately 1-week intervals during the same time of the day (between 09:00 and 15:00) between May and September. This was done both in 1990 and 1991. Data is expressed as catch per unit effort (CPUE) (catch per one electrofishing round the lake). I used mark and recaptures of perch and pike >160 mm to estimate population size. The electrofishing was conducted from a row boat. The anode was dipped into the water at 3-m intervals and stunned fish were counted and classified. Perch were grouped into four size-classes (<80, 80–110, 111–130, 131–160, and >160 mm; perch <80 mm and >160 mm are hereafter called small and large perch, respectively) and pike into two size-classes (<160 and >160 mm; hereafter called small and large pike, respectively). Fish from the largest size-class were placed in a tub with lake water for later tagging. The number of dips of the anode into the water was counted for each zone to be able to keep track of the location of the captured fish. When a zone had been fished, all collected large perch and pike were anaesthetized with ethylene glycol monophenylether and individually tagged with floy tags (Floy Tag & Manufacturing, Seattle, Wash.). Fish were allowed to recover in a tub containing lake water before they were released back into the lake. Because large perch and pike were released at the boundary between two zones after the tagging procedure, they had the possibility to choose between going back to the zone in which they had been caught, going to the next zone (neighboring zone), or going to one of the other zones. Given these options, the homing behaviour and movements within and among zones of later recaptured large perch and pike could be estimated. This was done by noting the locations of recaptured tagged large perch and pike at the next and later electrofishing samplings.

Underwater methods

Underwater estimations of fish abundance in relation to habitat type were performed using a visual census strip count technique (Keast and Harker 1977; Turner and Mackay 1985; Helfman 1983). At three locations in the lake (A, B, and C), transects parallel to the shore were constructed using 60–137 m long nylon cords (Fig. 1). The four transects at location A were placed to cover the macrophyte vegetation in the small bay at the southern end of the lake. The three transects at each of the other two locations were placed 3 m from the shore separated by 3 m extending 9 m out in the lake. The transects at location A were numbered starting with the most eastern transect as number one. The transects at locations B and C were numbered starting with the transect closest to the shore as number one. The water depth was measured at the ends and at the center of the transects (Table 1). Different colored plastic bands were attached to each cord, dividing them into 1-, 5-, and 10-m intervals. The cords were about 20 cm from the bottom and the end of the cords were attached to wooden poles that were buried into the sediment.

All transects were visually censused using face mask and snorkel

on eight occasions during July and August in both 1990 and 1991. The surveys were conducted between 10:00 and 15:00 using the same census method. At all observations, the water was clear enough to allow an observation distance of at least 4 m. Location censused was selected at random. At the chosen location, the observer swam down to the center of transect number one recording all observed fish within a 3 m wide strip. For every meter the fish were classified by species and size using the same classification norms as for the electrofishing samplings. In addition, perch were classified into four group sizes (1, 2, 3–10, >10 individuals). Because perch groups consisted of different-sized perch individuals, the numbers of perch of each size-class were estimated for each group size. The second transect selected was number three and when this transect had been covered, the observer changed to another location. After these two transects in each location had been surveyed, the same procedure was repeated for the remaining transects. This procedure was used to minimize the risk that potential disturbance of fish when surveying the other transects biased observations of the middle transect. Before the survey started, the observer was trained in the observation procedure to minimize disturbance of the fish, as perch and pike reacted differently to the observer. A constant swimming speed (approximately 10–15 m/min) of the observer was of major importance when encountering perch because perch tended to aggregate around an immobile observer. In contrast, when encountering pike it was important that the observer moved very slowly (<10 m/min) not to frighten the pike over to another transect that had not yet been surveyed. If the observer moved slowly, the pike retreated, swam slowly around the observer, and ended up at the same location as when encountered by the observer. This method has been shown to be successful for estimating population sizes of pike (Turner and Mackay 1985).

Macroinvertebrates

Macroinvertebrates were sampled in July 1990 at eight sites each in locations B and C. Three sites were chosen at each vegetation density except for the highest vegetation density, where four sites were chosen. At each site, six samples were taken with a Plexiglas core (area 38 cm²) and the samples were sieved through a 0.5-mm net, preserved in 70% ethanol and stained with rose Bengal. In the laboratory, the animals were classified by taxa, measured, and counted. Lengths were converted to dry masses using length–mass regressions (Persson and Greenberg 1990).

Statistical methods

All relationships between fish abundances or group size and depth or vegetation density were tested by linear or quadratic regressions. Diversity of littoral macroinvertebrates was estimated by Shannon–Weaver index. Large perch, small pike, and large pike selectivities for high density of perch (80–110 mm) were tested with Mann–Whitney *U* test based on estimates from Ivlev's electivity index. All proportions were tested with the *G* test and all other statistical analyses were done using ANOVAs. Data were $\ln(x)$ or $\ln(x + 1)$ transformed when necessary to stabilize variances.

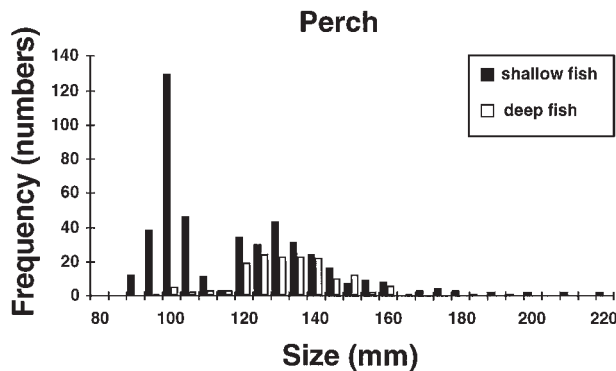
Results

Littoral and benthic fish abundance

Based on gillnet and electrofishing data combined, perch were the numerically dominant fish species in the lake, and the population size structure showed a distinct year-class of 2+ perch ranging from 85 to 110 mm (Fig. 2). Larger perch consisted of a wide distribution of perch sizes >120 mm. All pike were caught by electrofishing except for one individual caught in the littoral net.

Perch between 80 and 130 mm were abundant in the littoral zone in May, after which they rapidly decreased to about one

Fig. 2. Size–frequency distribution of perch caught close to the littoral zone (shallow fish) and in the deepest part (deep fish) of the lake in 1990.



quarter of the level in May (Fig. 3). The numbers of small and large pike captured in the littoral zone were similar and did not depend on whether the high abundance of small pike in September was included in the analyses (September observation included $t = -0.208$, $df = 8$, $p = 0.841$, September observation excluded, $t = -1.389$, $df = 7$, $p = 0.207$).

Littoral population sizes of large perch and pike were estimated to be 114 ± 43 (mean \pm 95% CL) and 205 ± 95 individuals, respectively, in 1990 and 164 ± 93 and 140 ± 62 individuals, respectively, in 1991. None of the tagged large perch or pike were captured in the gill nets, suggesting that movement between the littoral and pelagic zones was limited.

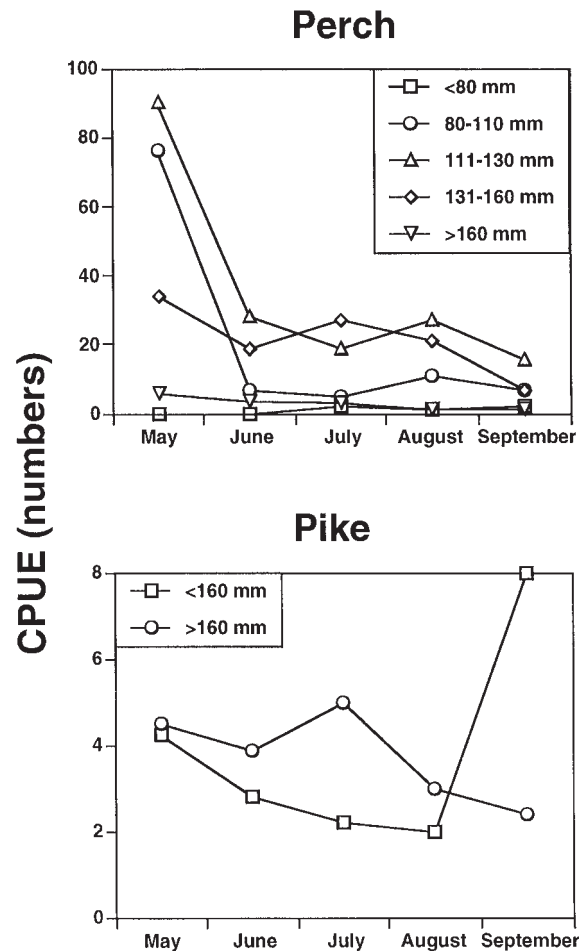
Littoral resources

The biomass and diversity of littoral macroinvertebrates did not differ between locations B and C (biomass, $t = 1.149$, $df = 14$, $p = 0.270$; diversity, $t = -0.129$, $df = 14$, $p = 0.899$); hence, the data from the two locations were pooled (Fig. 4). The biomass and diversity of littoral macroinvertebrates increased with vegetation density (one-way ANOVA on biomass, $F_{4,11} = 4.587$, $p = 0.023$; on diversity index, $F_{4,11} = 3.920$, $p = 0.036$). The tendency for higher biomasses in the zero vegetation samples was a result of the high biomasses of Oligochaeta and Chironomidae in these samples, the dominance of which was reflected in low diversity.

Perch and pike habitat selection

All perch size-classes, except the smallest, differed in habitat use from what could be expected if they were using habitats randomly (Fig. 5, Table 2). The lack of a significant deviation from a random use for the smallest size-class of perch was probably due to the low sample size. The significant difference between habitat use of perch 80–160 mm and random habitat use was mainly a result of a higher proportional use of the *Carex* habitat and a lower proportional use of the sand habitat (Fig. 5, Table 2). Large perch used a higher proportion of mainly tree structure and *Salix* habitats compared with random habitat use (Fig. 5, Table 2). Perch ranging from 80 to 110 mm and large perch changed habitat over time (Fig. 5, Table 2). The only habitat preferred by perch between 80 and 110 mm in July was the *Carex* habitat, whereas they increased the use of the *Salix* habitat in September (Fig. 5, Table 2). Overall, large perch used a higher proportion of the tree structure and

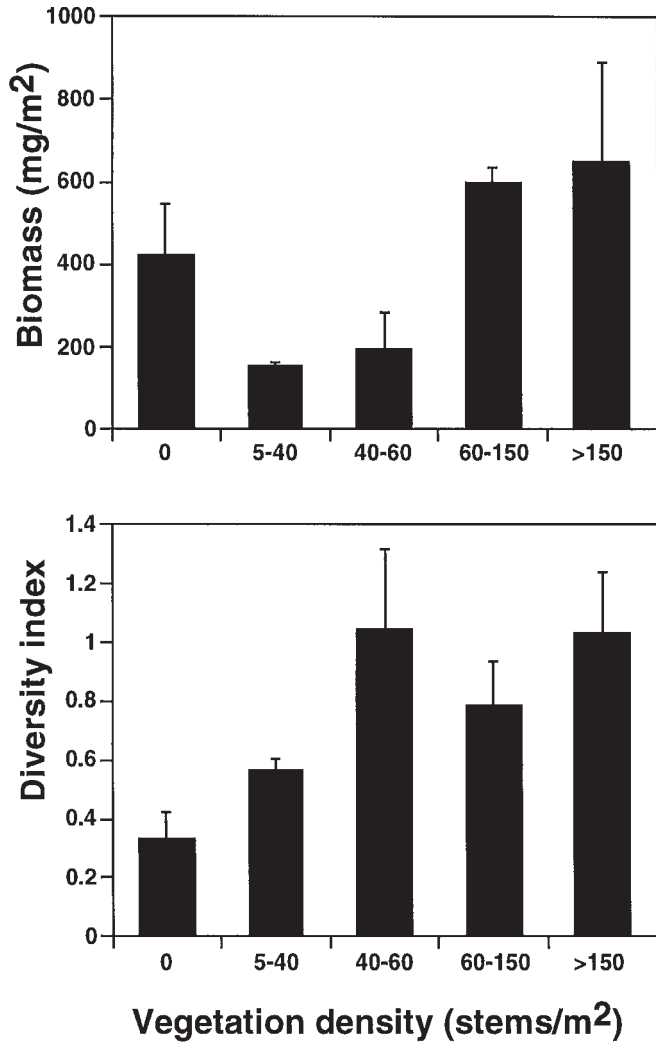
Fig. 3. Numbers (CPUE) (catch per electrofishing round) of perch and pike of different sizes caught by electrofishing from May to September 1990.



Salix habitats. They increased their use of the tree structure habitat from May to July at the same time as they decreased their use of the *Carex* habitat. In contrast, large perch decreased the use of tree structure from July to September and increased their use of *Carex* and *Salix* habitats. The fact that more than 60% of the habitats used during July and August consisted of bog margin, tree structure, and *Salix* demonstrate that large perch selected more open habitats during these months.

Both size-classes of pike differed in habitat use from what could be expected if they were using habitats randomly (Fig. 5, Table 2). For both small and large pike, this was mainly due to their preference for the *Salix* habitat and avoidance of the sand habitat (Fig. 5, Table 2). Small pike did not use *Phragmites* habitats at all, and their habitat use did not change over time (Table 2). Large pike used the *Salix* habitat heavily in May and increased their use of the tree structure habitat from May to July. The use of tree structure decreased in August and the use of *Salix* increased during September (Fig. 5, Table 2). The high use of bog margin, tree structure, and *Salix* habitats in July suggest that large pike preferred more open habitats during this month. Large pike that were found in tree structure were also the largest pike found in the lake.

Fig. 4. Biomass (mg/m²) and diversity (Shannon–Weaver index) of littoral macroinvertebrates in location B and C 1990. Values are means ± SEs of three replicates per vegetation density level, except at the highest vegetation density where four replicates were measured.



Perch abundance, vegetation density, and depth

Because of the small difference in depth among transects at location A, no analysis of the variation of vegetation density and perch abundance with depth was performed for this location. The vegetation density at location B decreased with increasing water depth (Fig. 6; $R^2 = 0.529$, $F_{1,22} = 24.69$, $p < 0.0001$), whereas no relationship between vegetation density and water depth was present at location C ($R^2 = 0.004$, $F_{1,38} = 0.168$, $p = 0.684$) because the vegetation was more sparse in the shallow areas of location C than at the other locations.

Perch abundance increased with depth at location B ($R^2 = 0.529$, $F_{1,22} = 24.69$, $p < 0.0001$) but was unrelated to depth at location C (Fig. 6; $R^2 = 0.004$, $F_{1,38} = 0.168$, $p = 0.684$). Perch abundance first increased with vegetation density then decreased at high vegetation density (test of difference between a linear and a second-degree polynomial: location A, $F_{2,37} = 28.61$, $p < 0.0001$; location B, $F_{2,37} = 53.66$, $p < 0.0001$; location C, $F_{2,37} = 158.11$, $p < 0.0001$; regression on second-degree

Fig. 5. Proportional habitat use of the different sizes of perch and pike in May–September 1990. The leftmost bar in the perch panels shows the proportions of the different habitats available in the lake.

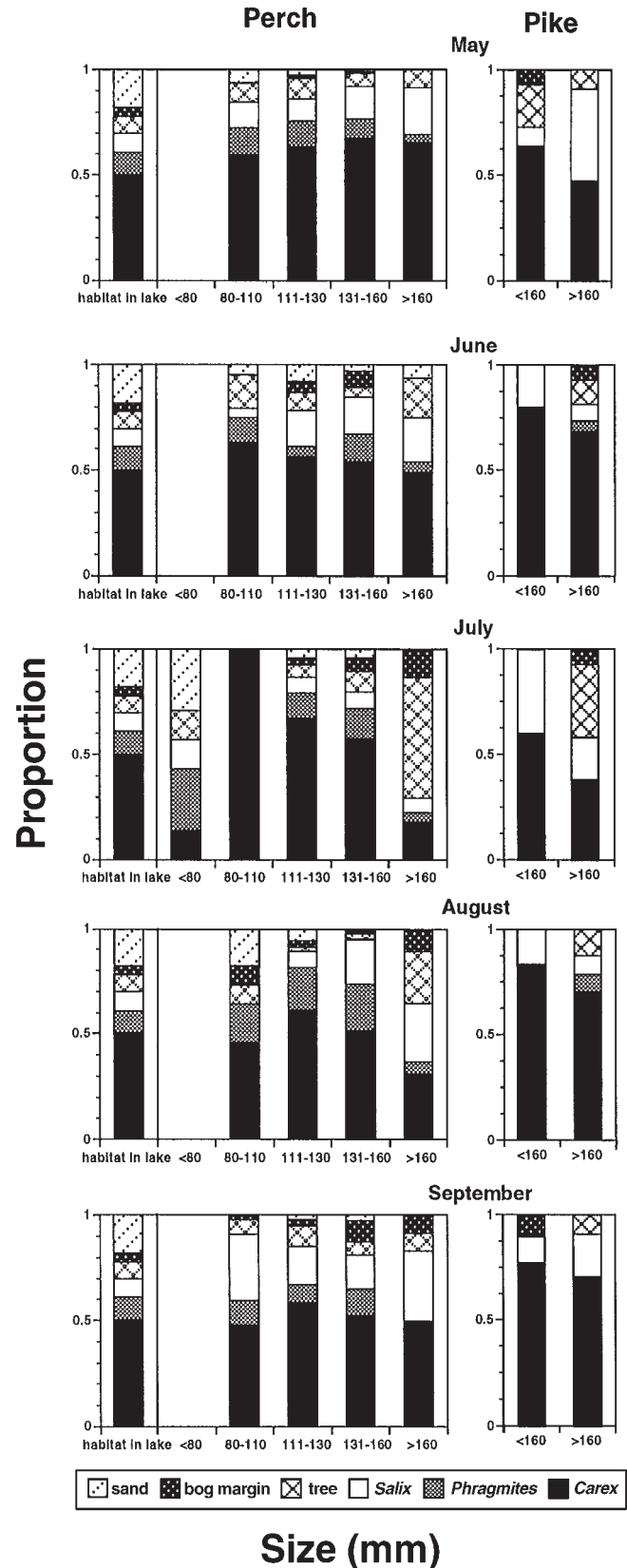


Table 2. G tests of the proportions of different habitats used by five size-classes of perch and two size-classes of pike compared with the proportions of the habitats available in the lake.

	df	G	p
Perch H ₀ habitat ^a			
<80 mm	5	3.16	0.532
81–110 mm	5	43.48	<0.0001
111–130 mm	5	97.46	<0.0001
130–160 mm	5	94.27	<0.0001
>160 mm	5	91.46	<0.0001
Perch H ₀ time ^b			
81–110 mm	5	11.88	0.036
111–130 mm	5	0.71	0.983
130–160 mm	5	1.72	0.886
>160 mm	5	12.35	0.030
Pike H ₀ habitat ^a			
<160 mm	5	29.58	<0.0001
>160 mm	5	53.79	0.0008
Pike H ₀ time ^b			
<160 mm	3	1.99	0.57
>160 mm	3	8.10	0.044

^aH₀ habitat, proportion of habitat used by perch and pike did not differ from the proportions of habitat present in the lake.

^bH₀ time, the proportion of habitat used by perch and pike did not vary with time.

polynomial (Fig. 6): location A, $R^2 = 0.436$, $F_{2,37} = 14.298$, $p < 0.0001$; location B, $R^2 = 0.592$, $F_{2,37} = 26.832$, $p < 0.0001$; location C, $R^2 = 0.810$, $F_{2,37} = 79.096$, $p < 0.0001$).

The size distribution of pike and vegetation density

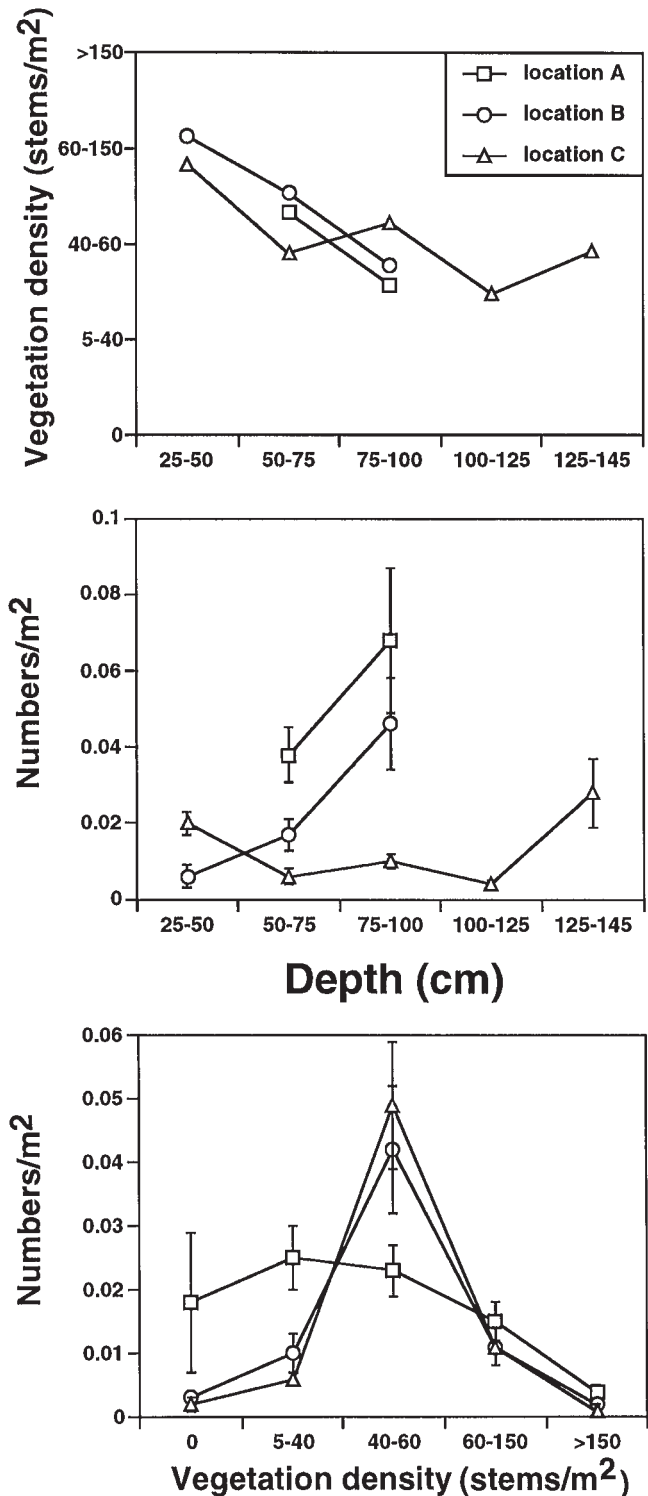
The size of pike was inversely related to vegetation density at all three locations (Fig. 7; location A, $R^2 = 0.44$, $F_{1,25} = 19.618$, $p < 0.0001$; location B, $R^2 = 0.302$, $F_{1,35} = 15.125$, $p < 0.0001$; location C, $R^2 = 0.307$, $F_{1,20} = 8.873$, $p = 0.007$).

Perch group formation and vegetation density

The group size of perch decreased with increased vegetation density at locations A and B (Fig. 8; location A, $R^2 = 0.673$, $F_{1,28} = 57.54$, $p < 0.0001$; location B, $R^2 = 0.542$, $F_{1,34} = 37.36$, $p < 0.0001$). At location C, the group size of perch first increased with vegetation density but decreased at high vegetation density (test of difference between a linear and a second-degree polynomial: $F_{2,37} = 248.73$, $p < 0.0001$; regression on second-degree polynomial (Fig. 8): $R^2 = 0.822$, $F_{2,37} = 124.52$, $p < 0.0001$). The large variation in group size in the absence of vegetation at location A was due to one observation of 120 individuals of perch 80–110 mm. Schools (>10 individuals) of perch 80–110 mm were also observed in the absence of vegetation at the other two locations. Perch in these schools were also found to forage on zooplankton in the open water.

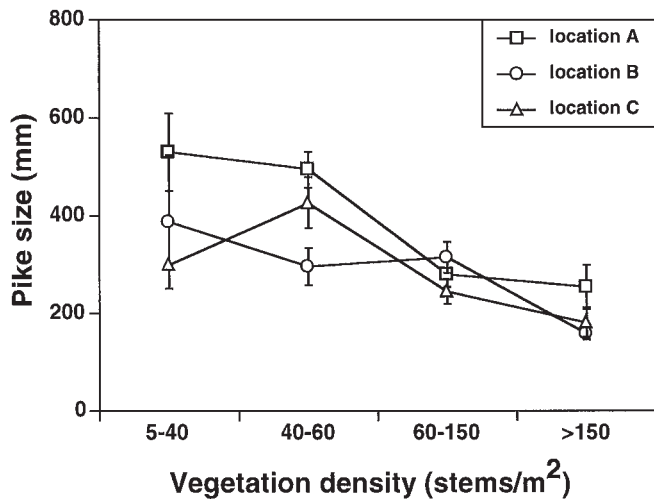
The numbers of perch in each group size (1, 2, 3–10, and >10 individuals) differed between group sizes for all size-classes except for perch of size 111–130 mm (Fig. 9). Perch <111 mm were more frequent in larger groups than in smaller groups and perch <80 mm never occurred in the same groups as large perch (one-way ANOVA on perch <80 mm, $F_{3,8} = 9.37$, $p = 0.005$; on perch 80–110 mm, $F_{3,8} = 8.15$, $p = 0.008$). A Bonferroni-adjusted post-hoc comparison revealed that

Fig. 6. Vegetation density (stems/m²) and perch abundance (no./m²) versus depth (cm), and perch abundance versus vegetation density at locations A, B, and C. Values are means ± SEs for the period May–September 1990.



perch 80–110 mm were more frequent in groups of 1 or 2 individuals than 3–10 individuals (1 vs. 3–10, $p = 0.029$; 2 vs. 3–10, $p = 0.024$). Perch 111–130 mm occurred in similar numbers in the different group sizes (one-way ANOVA, $F_{3,8} = 2.32$,

Fig. 7. Pike size (mm) as a function of vegetation density (stems/m²) at locations A, B, and C. Values are means \pm SEs for the period May–September 1990.



$p = 0.152$). Perch 131–160 mm occurred most frequent in the groups of 3–10 individuals (one-way ANOVA, $F_{3,8} = 9.19$, $p = 0.006$). A Bonferroni-adjusted post-hoc comparison revealed that perch 131–160 mm were less frequent in groups of 2 individuals ($p = 0.05$) and >10 individuals ($p = 0.005$) than in groups of 3–10 individuals. Perch >160 mm decreased in numbers with increasing group size (one-way ANOVA, $F_{3,8} = 5.13$, $p = 0.029$). A Bonferroni-adjusted post-hoc comparison revealed that perch were more frequently solitary ($p = 0.034$) or in pairs ($p = 0.05$) than in groups of >10 individuals.

Movement patterns of large-sized perch and pike

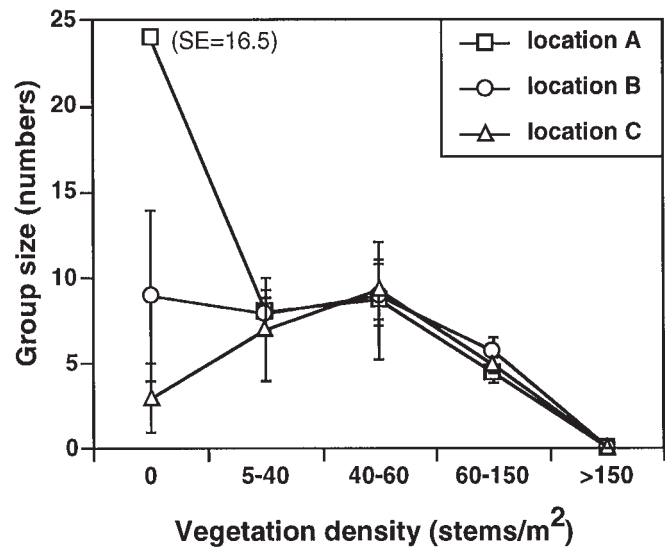
Large perch showed a little tendency to stay in the same zone over time in both 1990 and 1991 (Fig. 10; $G = 1.48$, $df = 2$, $p = 0.478$). In contrast, pike preferred either to stay within the same zone over time or moved to the neighboring zone both in 1990 and 1991 ($G = 14.078$, $df = 2$, $p = 0.0009$). Thus, pike showed a stronger homing behaviour than perch, staying at higher proportions in the same or neighboring zones compared with perch ($G = 11.37$, $df = 2$, $p = 0.0034$). A comparison of perch and pike movements between 1990 and 1991 revealed that both species showed little tendencies to stay within the same zone (perch: $G = 1.55$, $df = 2$, $p = 0.460$ pike: $G = 1.95$, $df = 2$, $p = 0.378$).

The pike that stayed in the same zone between years were the largest pike found (size range 550–800 mm). Both large perch and pike selected the parts of the transects that had the highest densities of perch 80–110 mm (Mann–Whitney U test on Ivlev's selectivity index, both large perch and pike, $n = 3$, $p = 0.05$), whereas small pike avoided these high-density perch patches (Mann–Whitney U test on Ivlev's selectivity index, $n = 3$, $p = 0.05$). At one occasion, a pike (size 400 mm) was observed to attack and capture one perch 80–110 mm.

Discussion

Studies on species interactions have demonstrated that the degree of structural complexity in the environment plays a

Fig. 8. Group size (nos.) of perch at the different vegetation densities at locations A, B, and C. Values are means \pm SEs for the period May–September 1990.

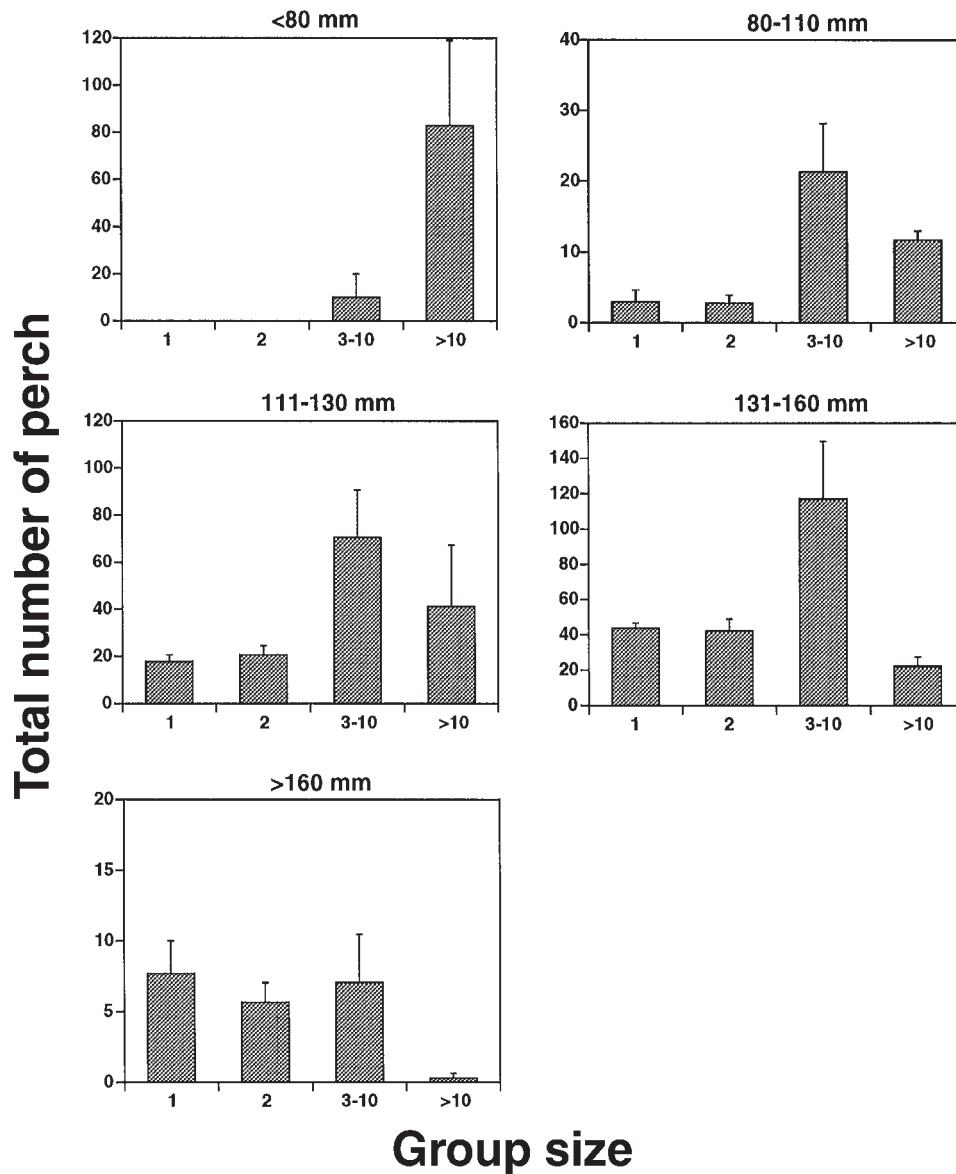


prominent role for the outcome of predator–prey interactions (Savino and Stein 1982; 1989; Werner et al. 1983; Anderson 1984; Werner and Hall 1988; Turner and Mittelbach 1990; Eklöv and Diehl 1994; Persson and Eklöv 1995). Several of these studies demonstrate that structural complexity not only may affect species mortality rates by providing shelter in different forms but also may affect individual growth rate by offering a varying density and diversity of food resources (Crowder and Cooper 1982; Gilinsky 1984; Diehl 1993; Diehl and Eklöv 1995). This study documents that the quality and quantity of habitat structural complexity are of major importance for the distribution patterns of perch and pike. Below, I first discuss some potential mechanisms for the distribution patterns of perch and pike in relation to habitat structure. Then, I develop the implication of the behavioural mechanisms revealed in previous experimental studies for the predator–prey interactions between perch and pike (Eklöv 1992; Eklöv and Diehl 1994; Diehl and Eklöv 1995; Eklöv and Persson 1995). I show that the variation in the distribution patterns of perch and pike that occurred in the lake can mainly be explained by the strong behavioural interactions between predators and prey.

Structural complexity and habitat use of perch and pike

In Lake Degersjön, the highest macroinvertebrate biomass, and also the highest diversity of macroinvertebrates were found in the highest vegetation densities. However, the perch in my study strongly selected the intermediate vegetation density. These observations can be related both to foraging and antipredator strategies of perch. First, the foraging efficiency of perch has been shown to be inversely related to habitat structural complexity (Diehl 1988). At the same time, experimental studies suggest that the higher abundances of resources in vegetated habitats may possibly compensate for the decreased efficiency of foraging perch in that habitat, allowing benthivorous perch to grow at the same rate as perch foraging in open habitats (Diehl 1993). A similar result has been

Fig. 9. Total perch numbers of each perch size class that occurred in different group sizes at locations A, B, and C 1990. Values are means \pm SEs (3 replicates/group size level).

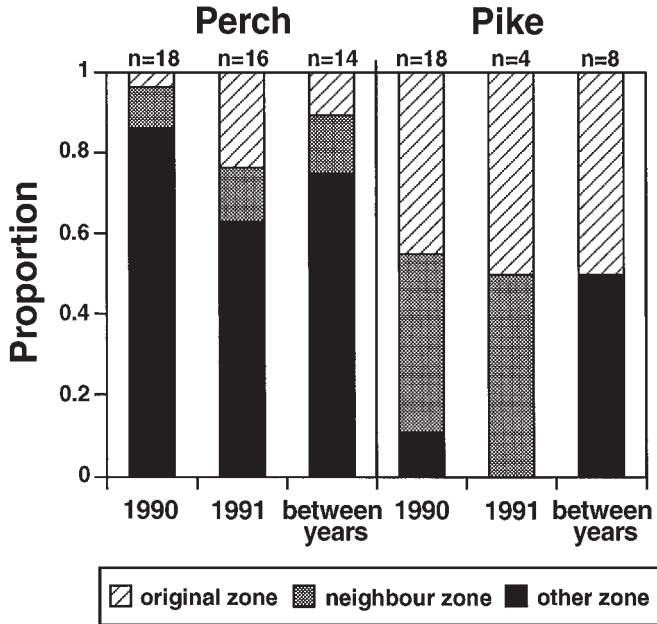


observed for bluegill sunfish (*Lepomis macrochirus*); bluegills foraging at an intermediate vegetation density level had a wider diet breadth and higher growth rate than bluegills foraging in habitats with no vegetation or in habitats with high vegetation densities (Crowder and Cooper 1982). Second, predation risk decreases with an increase in structural complexity (Anderson 1984; Persson and Eklöv 1995). This suggests that vulnerable prey fish in the presence of piscivorous predators should choose densely vegetated habitats to avoid predation, which also have been shown for perch in the size range 80–110 mm (Eklöv and Diehl 1994). In July, perch 80–110 mm were only found in the vegetated habitats, whereas larger size-classes of perch stayed more in open habitats. Thus, the preference for the intermediate vegetation density of perch could possibly be a tradeoff between maximizing foraging advantages and minimizing predation risk of perch.

Although all sizes of perch preferred the intermediate

vegetation density, the different sizes of perch changed their overall habitat choice in different ways over time. The number of perch 80–110 mm collected by electrofishing declined dramatically from May to June, suggesting two possibilities: (1) movement into the pelagic zone or (2) mortality. The observed pattern is most likely explained both by perch 80–110 mm shifting into the densely vegetated habitat (Fig. 5), as a result of predator avoidance, but at the same time suffering from substantial predation (Fig. 3; see also Eklöv and Diehl 1994). A result supporting these hypotheses was that large perch and pike selected more open habitats (e.g., tree structure) located close to the vegetated habitats containing high densities of perch 80–110 mm during the summer months. A possible explanation as to why perch and pike use more open habitats close to vegetation is that this may minimize the negative effect of structural complexity on their foraging efficiency and at the same time maximize encounter

Fig. 10. Proportion of large perch and pike recaptured in the original zone (maximum range 100–440 m, neighboring zone (maximum range 101–565 m), or other zones (maximum range 286–2304 m) in 1990 and 1991 and individuals recaptured 1991 that were tagged 1990 (between years). *n*, Numbers of individuals recaptured.



frequency with prey staying in the refuge habitats. In support of this hypotheses, it has been shown that large perch and pike stay close to or move inside habitats that are used as refuges for prey fish (Eklöv and Diehl 1994; Eklöv and Persson 1995).

Large pike also preferred the tree structure habitat during the summer months. In fact, the pike captured by electrofishing and observed by snorkeling in or close to the tree structure habitat were the largest pike observed in the lake. Furthermore, pike size was inversely related to vegetation density, suggesting that the smaller pike stayed in dense vegetation to avoid predation. Preference for different habitats by pike has also been found to be size specific in another study, and especially pike <140 mm were often associated with dense submerged vegetation (Grimm 1994). Grimm (1994) suggested that the selection of densely vegetated habitats by small pike enabled them to avoid cannibalism from larger pike. The interaction between pike has also been found to depend on both the availability of prey and size of habitats (Eklöv 1992; Eklöv and Diehl 1994). In the latter study, large pike had effects on both growth rate and habitat use of small pike, and the larger pike were always found closer to the prey than the smaller pike, whereas the smaller pike moved into vegetation patches probably to avoid predation from larger pike. All these results point to direct interactions between pike individuals probably being cannibalistic, which makes the survival of smaller pike dependent on the size and density of the vegetated habitat.

Shoaling behaviour of perch

The group size of perch decreased with increasing vegetation density, suggesting that (i) group foraging was less profitable (or possible) in the vegetation or (ii) that increasing structural

complexity decreased predation risk, decreasing the profitability of using the group as a defense against predators (see Pitcher 1986). Group behaviour has been found to be related to both predator detection and avoidance and to improve individual foraging rate (Pulliam 1973; Powell 1974; Clark and Mangel 1984, 1986; Eklöv 1992). By increased vigilance, individuals within a group can detect predators at longer distances and may also improve the use of information in the presence of scarce patchily distributed prey (Clark and Mangel 1986). My results showed that perch <80 mm preferred large group sizes (>10 individuals) whereas large perch preferred small group sizes (<10 individuals), and the two size-classes of perch never occurred in the same groups. It can be hypothesized that perch <80 mm occurred mainly in large groups, because small individuals are more susceptible to predation, and that the vulnerability of individuals to predation decreases with increasing group size (Pitcher 1986; Magurran 1990). The tendency for large perch to prefer smaller groups or to stay alone can be related to the fact that they switch to a sit-and-wait strategy in structurally complex environments (Eklöv and Diehl 1994; Eklöv and Persson 1995). Whether the effects of shoaling are positive or negative and if there is an optimal group size is ambiguous because an increase in group size may both increase or decrease individual growth rate depending on the social interactions within the group (Metcalf 1986; Cui and Wootton 1989; Eklöv 1992).

Piscivore movement patterns and the significance of different foraging strategies

Large perch showed small tendencies to be recaptured in the same zone on successive samplings, whereas pike were more disposed to stay in the same zone or in a neighboring zone. This suggests that large perch adopted a more active mode, and pike used a more sit-and-wait mode. In addition, the fact that pike stayed in the same zone or moved to the neighboring zone suggests that pike used a specific home range, which also have been found in other studies of pike (Halme and Korhonen 1960; Malinin 1969). The relative predation efficiency of large perch and pike have been found to depend on their different foraging strategies (Eklöv 1992; Eklöv and Diehl 1994; Eklöv and Persson 1995). In the absence of vegetation, large perch were favored by a group foraging strategy, whereas the efficiency of pike decreased with an increase in predator density as a result of interactions between individuals (Eklöv 1992). When prey refuges in the form of submerged vegetation are present, large perch switch from an active group foraging mode to an inactive solitary mode or stay in pairs in which they have a lower foraging efficiency than sit-and-wait foraging pike (Eklöv and Diehl 1994; Eklöv and Persson 1995). Large perch in Lake Degersjön stayed solitary or in small groups with other size-classes of perch, which indicates that they did not use a group foraging strategy in the littoral zone.

The observed activity pattern of large perch can be suggested to depend on the time scale used in the study. On a short time scale, large perch may appear to be inactive sit-and-wait predators (see Eklöv and Diehl 1994; Eklöv and Persson 1995), whereas on a long time scale, they appear to be active and move around the lake. Two explanations can be advanced to explain the functional significance of this time scale dependent activity pattern in perch. First, on a long time scale, large perch can use an active mode to more efficiently track spatial

changes in resource levels. Second, on a short time scale, large perch may switch to a sit-and-wait mode if prey are located in or close to structured environments, such as littoral zone vegetation (Eklöv and Diehl 1994). In fact, large perch in Lake Degersjön were found to select high-density patches of perch 80–110 mm, a size range that is possibly subject to piscivorous predation (Bagenal 1977; Van Densen 1994; Persson et al. 1996). Furthermore, perch are active and social predators and are also morphologically adapted to an active mode (see Webb 1984; Eklöv and Persson 1995). Thus, the activity of littoral large perch in Lake Degersjön may also simply be a result of their life-style (*sensu* Sih 1987). An interesting circumstance in this context is the low exchange rate of large perch between the littoral and pelagic zones. Based on the lower foraging efficiency of large perch in structured versus nonstructured environments (Eklöv 1992; Eklöv and Diehl 1994), one would expect visits to the littoral zone to be sporadic by large perch. However, no tagged large perch were caught in the gill nets despite the fact that recapture of eight tagged individuals was expected based on the numbers of tagged and recaptured large perch in the littoral zone. Even if a total mixture of pelagic and littoral perch was not expected, the data shows that the interchange of large perch between the littoral and pelagic zones was low.

The implications of movement and habitat use of pike in terms of potential effects on the prey population are more easy to interpret because pike occur mainly in the littoral zone even if small numbers of large pike have been observed offshore (Diana et al. 1977; Diana 1980; Vøllestad et al. 1986). In the littoral zone, pike have been found to affect the abundance of prey ranging in sizes between 80 and 130 mm (Bagenal 1977; VanDensen 1994; Persson et al. 1996). The fact that large pike were located close to high density patches of perch 80–110 mm indicates that this size-class of pike select home ranges that coincide with high densities of prey. The home ranges of the largest pike lasted over years. The strong tendency of pike to stay close to high-density prey patches was also found in an enclosure experiment, where the largest pike were always found closest to the prey (Eklöv and Diehl 1994).

The habitat preferences of large perch and pike indicate that they used the same sites in the lake. Large perch and pike affect different size-classes of prey differently (Diehl and Eklöv 1995; Persson et al. 1996). For example, pike have been shown to have strong effects on the refuge use, survival, and growth of both 0+ and 1+ perch, whereas piscivorous perch only affected 0+ perch (Eklöv and Diehl 1994; Diehl and Eklöv 1995; Persson et al. 1996). Furthermore, in the absence of pike and in the presence of large-sized perch, 1+ perch moved out of the refuge, suggesting a potentially lower competition between size-classes of perch when pike is not present in the system (Diehl and Eklöv 1995).

In conclusion, my study suggests that the structural complexity in the littoral zone can both qualitatively and quantitatively change the interaction between piscivorous predators and their prey. Vegetation density appeared to be especially important in potentially mediating predator–prey interactions both by supporting macroinvertebrate food resource for benthivorous perch and as protection from piscivorous predation. Although I was not able to evaluate the predation impact of large perch and pike on prey fish, the spatial distributions of the different size-classes of perch and pike suggest a strong

behavioural interaction between predators and prey. These results were supported by previous enclosure or pond experiments in which mechanistic explanations for the distribution patterns of perch and pike were given (Eklöv 1992; Eklöv and Diehl 1994; Eklöv and Persson 1995). My study in Lake Degersjön further suggests that the foraging efficiency of piscivorous perch and pike might be altered by interspecific interaction as a result of their tendency to exploit the same food resource patches. To be able to answer the question on how such interspecific effects are created and what potential effects they may in turn have on other species, manipulative studies using treatments with both predators present are necessary.

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