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A 15-year Study of the Spatial Distribution of *Rutilus rutilus* and *Perca fluviatilis* in Late Summer in Two Shallow Lakes with Contrasting Trophic State

Zeynep PEKCAN HEKIM [1,2], **Torben LINDING LAURIDSEN** [1,3] **Martin. SØNDERGAARD**[1,3] **Liselotte SANDER. JOHANSSON**[1] **Tserenpil SH**[4] **Erik JEPPESEN**[*1,3,5,6]

[1]Ecoscience and Center for Water Technology (WATEC), Aarhus University, 8600 Silkeborg, Denmark
[2]Swedish University of Agricultural Sciences, Uppsala, Sweden
[3]Sino-Danish Centre for Education and Research, University of Chinese Academy of Sciences, Beijing, China
[4]Nuclear Research Center, National University of Mongolia, 14201 Ulaanbaatar, Mongolia
[5]Limnology Laboratory, Department of Biological Sciences and Centre for Ecosystem Research and Implementation, Middle East Technical University, 06800 Ankara, Turkey
[6]Institute of Marine Sciences, Middle East Technical University, 33731 Mersin, Turkey

ABSTRACT

Roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) are dominant species in northern-temperate lakes of Europe, their relative importance depending on trophic state and habitat complexity. We studied the habitat distribution of roach and perch over a 15-year period in two Danish lakes, Lake Væng, undergoing major changes in water clarity and macrophyte coverage, and the permanent turbid Lake Søbygård. We used multi-mesh sized gill nets in 5-6 different sections of the lakes following the same program in all years. Both species were evenly distributed in the sections and among habitats, in Lake Væng during the turbid period and in Lake Søbygård during the whole study period. During the clear-water period in Lake Væng, however, the distribution of roach and perch was uneven and the density negatively correlated with macrophyte coverage and density, but the strength of the relationship differed between the two species and between small (≤ 8 cm for roach and <10 cm for perch) and larger fish. Our results suggest that water clarity and macrophyte density were of key importance in determining roach and perch distribution in these two shallow lakes.

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**** CORRESPONDING AUTHOR***

ej@ecos.au.dk

Keywords: Roach, perch, habitat distribution, turbidity, eutrophication

Farklı Trofik Duruma Sahip İki Sığ Gölde *Rutilus rutilus* ve *Perca fluviatilis*'in Yaz Mevsimi Sonundaki Mekansal Dağılımı Üzerine 15 Yıllık Bir Çalışma

Öz: Yapısal karmaşa ve bulanıklık (türbidite), balıkların habitat seçiminde önemli roller oynayabilmektedir. Kızılgöz balığı (*Rutilus rutilus*) ve tatlısu levreği (*Perca fluviatilis*) Avrupa'nın kuzey ılıman göllerinin baskın (dominant) türleridir. Bu türlerin görece önemi, genel olarak trofik seviyeye ve habitat karmaşıklığına bağlıdır. Kızılgöz ve tatlısu levreğinin, su berraklığı ve makrofit yayılımı sürekli değişen Væng gölü ile bulanık Søbygård gölündeki dağılımları 15 yıllık bir dönem boyunca çalışılmıştır. Örnekleme, her yıl aynı program takip edilerek, göllerin çeşitli kısımlarından, farklı göz açıklıklarına sahip galsama ağları kullanılarak gerçekleştirilmiştir. Türler, Væng gölünün bulanık olduğu dönemde, Søbygård gölünde ise tüm çalışma sürecinde, göllerin tüm kısımlarında ve tüm habitatlarda eşit dağılmışlardır. Væng gölünün berrak döneminde ise kızılgöz ve tatlısu levreğinin dağılımları eşit değildir. Türlerin bolluğu, makrofit yayılımı ve yoğunluğu ile negatif korelasyon gösterirken, bu ilişkinin kuvvetinin türlere ve balık boylarına göre farklı olduğu ortaya konulmuştur. Sonuç olarak, çalışılan iki gölde, kızılgöz ve tatlısu levreğinin dağılımında, suyun berraklığı ve makrofit yoğunluğunun anahtar belirleyici faktörler olduğu bulunmuş, bu durumun diğer benzer kuzey-ılıman sığ göllerde de gözlenebileceği öngörülmüştür.

Anahtar kelimeler: Kızılgöz balığı, tatlısu levreği, habitat dağılımı, bulanıklık (türbidite), ötrofikasyon

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Introduction

Biotic, abiotic and spatial factors influence the habitat distribution of fish in lakes (Donald et al. 2000). Spatial complexity plays an important role in the distribution patterns of fish by offering a refuge from predators (Jacobsen and Berg 1998) or a habitat that is rich in food resources (Diehl 1988; Diehl and Kornijow 1997). Habitat shifts can be a result of changes in competition or predation risk, which is closely linked to the size of individuals (Werner and Hall 1988; Ebenman and Persson 1988; Byström et al. 2003). The resource use of fish also differs with size, potentially influencing their habitat choice (Werner and Hall 1979). Together with structural complexity, size can therefore play a role in the interactions among fish and thus impact their habitat choice (Rossier et al. 1996; Persson and Crowder 1997).

Water clarity can also affect fish habitat distribution (Blaber and Blaber 1980; Skov et al. 2002; Jacobsen et al. 2004; Jeppesen et al. 2006; Pekcan-Hekim et al. 2010; Nurminen et al. 2010). High turbidity can reduce the predation risk and thereby enhance the foraging activity of the prey fish (Gregory and Northcote 1993). It can also influence diel and seasonal migratory activity (Ginetz and Larkin 1976) by reducing the use of shelter and increasing the use of open water by prey fish (Miner and Stein 1996; Utne-Palm 2002; Snickars et al. 2004; Pekcan-Hekim et al. 2005).

Roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) are both dominant species in temperate lakes of Europe, their relative abundance depending on several factors including trophic state (Persson et al. 1991; Jeppesen et al. 2000; Olin et al. 2002) and habitat complexity (Persson et al. 1992). Perch is dominant in lakes with high structural complexity, whereas roach is abundant in more productive and structurally simpler systems (Persson et al. 1991, 1992; Diehl 1988). Perch depends on good light conditions, and thus clear water conditions, for effective foraging (Ali et al. 1977; Bergman 1988), while roach manage in more turbid waters, where is a superior feeder to perch (Diehl 1988). Changes in structural complexity and water clarity along a nutrient gradient affect the habitat choice of the two species. Using data from 53 Danish lakes, Menezes et al. (2015) found increasing homogenisation of the fish community with increasing trophic state, as it has been seen previously for other organisms in lakes and terrestrial ecosystems (Stevens et al. 2004; Donohue et al. 2009; De Schrijver et al. 2011). However, different size classes may respond differently to eutrophication. Thus, in a study of 34 Danish lakes, Jeppesen et al. (2006) found that the proportions of large roach and perch inhabiting the littoral zone rose with increasing nutrient concentrations, most pronouncedly for roach. Moreover, in low nutrient clear water lakes with submerged macrophytes, juvenile roach and perch both increased their use of submerged vegetation in the presence of predators (Persson and Eklöv 1995), and the habitat distribution of roach shows a shift from vegetation to open water with increasing size, while small perch particularly use the macrophyte beds (Rossier et al. 1996).

Long-term studies of spatial variations in the distribution of roach and perch in lakes are scarce. In this 15-year study, habitat distribution of roach and perch was investigated in two different lakes with changing water clarity and macrophyte coverage. We predicted that an increase in turbidity and changes in macrophyte coverage would affect the interactions between the two fish species and thereby their habitat choice. We expected that in the presence of macrophytes, small roach and perch would take refuge in the vegetation. However, with increasing turbidity, the risk of the predation would be lower and allow roach and perch to forage more evenly within the different lake habitats. This would also lead to different distribution patterns and behaviour of small and large-sized fish within the lake, depending on trophic state.

Study Areas

Fish samples were collected from 1988 to 2002 in Lake Væng and Lake Søbygård situated in Central Jutland (56° N; 9° E), Denmark. Both lakes are shallow and eutrophic. Lake Væng (16 ha) has a mean depth of 1.2 m and Lake Søbygård (40 ha) a mean depth of 1.0 m (Figure 1. A and B).

In Lake Væng, nitrogen and in particular phosphorus loading decreased significantly following sewage diversion in 1981; however, only minor improvements in water quality were observed in the following 5 years (Jeppesen et al. 1990; Søndergaard et al. 1990). To accelerate the improvement towards a clear-water state, 50% of the planktivorous fish biomass was removed between October 1986 and July 1988. The fish removal had significant effects on the water quality and resulted in low phytoplankton biomass and colonisation of macrophytes (Jeppesen et al. 1990; Lauridsen et al. 1993; Søndergaard et al. 2017). Before the fish removal, the planktivorous fish community was dominated by bream (*Abramis brama*), roach (*R. rutilus*) and rudd (*Scardinius erythrophthalmus*), while pike (*Esox lucius*) and perch (*P. fluviatilis*) were the most abundant piscivores.

In Lake Søbygård, Secchi depth is typically < 0.5 m, the turbid conditions being caused by the high density of phytoplankton. In 1982, the phosphorus loading decreased from 90 to 18 mg TP m^{-2} d^{-1} due to the implementation of chemical treatment at the nearby sewage plant, and in 1987 the nitrogen supply also declined (300 to 250 mg TN m^{-2} d^{-1}) after the closing of a large slaughterhouse. Despite these changes the lake remained eutrophic and phytoplankton dominated due to high phosphorus release from the sediment (Søndergaard et al. 1993; Jeppesen et al. 1998). The fish community in Lake Søbygård was dominated by cyprinids and the fish biomass remained high for many years. However, 14 years after the loading reduction the percentage of piscivorous fish increased and the abundance of planktivorous fish declined (Jeppesen et al. 2003).

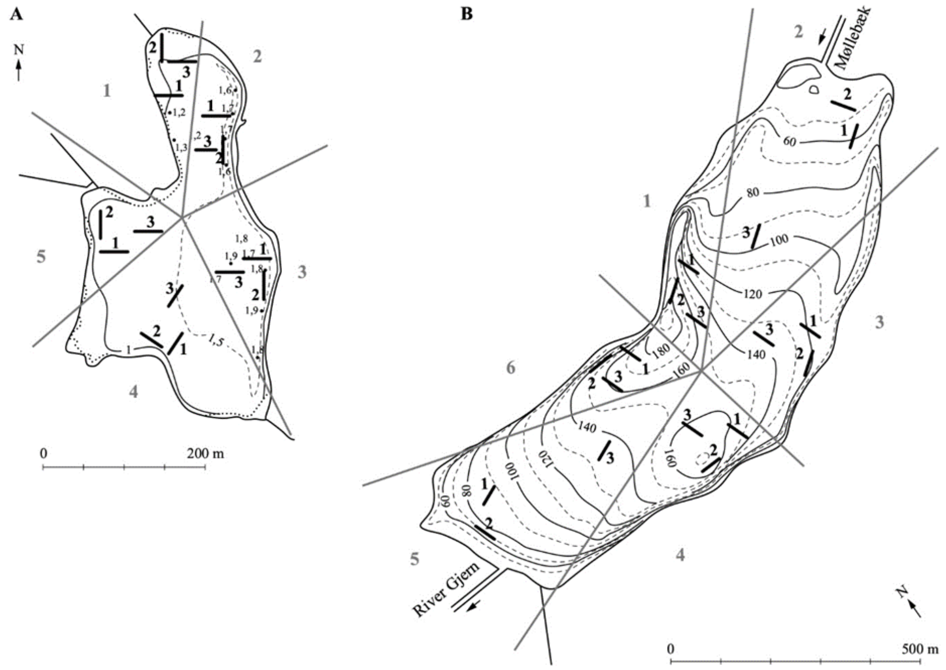

Figure 1. Map of a) Lake Væng and b) Lake Søbygård with number of sections and the locations and numbers of the three nets in each section marked.

In Lake Væng, after the biomanipulation, *Elodea canadensis* and *Potamogeton crispus* first developed in 1988 where the total coverage of macrophytes reached 2% (Figure 2. a). Initially, the macrophyte species consisted of *P. crispus* and *E. canadensis*. Later, *E. canadensis* became dominant and reached

(Figure 2. a). Reeds were present at the western and southern sides of the lake (Figure 1). Floating high densities by spreading and colonising the lake from the deepest eastern part towards the shallow and sheltered locations (for more details see Lauridsen et al. 1994; Søndergaard et al. 2017). Submerged macrophytes disappeared from the lake after 1996 and were absent until the end of the study period plants were scarce and the lake is surrounded by forest and meadows.

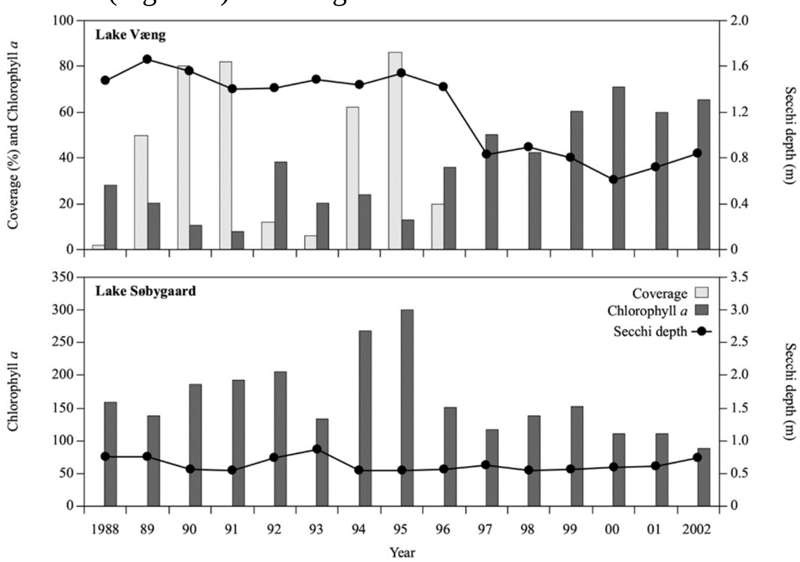

Figure 2. Total coverage of macrophytes (Coverage %) (bars) during fish sampling and mean summer chlorophyll *a* (µg l^{-1}) values (bars). Secondary y-axis shows the Secchi depth (m) (line) in a) Lake Væng and b) Lake Søbygård from 1988 to 2002.

In Lake Søbygård, submerged macrophytes were absent during the whole study period from 1988 until 2002, and mean summer chlorophyll *a* values ranged between 88 and 300 µg l^{-1} (Figure 2. b). Floating plants were scarce. Belts of reeds (*Phragmites australis*) were found along the shore in 80-90% of the area. The lake is surrounded by forest.

Materials and Methods

Fish Sampling

The lakes were divided into sections consisting of equal-sized pies with a mid-lake station acting as centre (Figure 1). The number of sections in the lakes depended on surface area and shoreline length (Mortensen et al. 1990). Accordingly, Lake Væng was divided into five and Lake Søbygård into six sections.

Fishing was conducted in between August 15 and September 15 (when YOY fish have reached a size rendering them likely to be caught in the gill nets) using gillnets made of monofilament nylon. The nets were 1.5 m high and 42 m long and consisted of 14 units of 3 m with different mesh sizes placed in random order (6.25, 8, 16.5, 75, 38, 25, 12.5, 33, 50, 22, 43, 30, 60 and 10 mm). Three multi-mesh size gill nets were set in all sections. Two nets were placed at a distance of ~25 m away from shore, one being set perpendicular to shore (net 1) and the other parallels to shore (net 2) (Figure 1. a and b). The third gillnet was set about half distance to the middle of lake in a perpendicular position to shore (net 3) (Figure 1. a and b). The nets were set in late afternoon and retrieved the following morning (after ~18 h). For each net we calculated catch per net (CPUE).

Electrofishing was conducted in the outer reed zone or near shore (plant-free) in 300 m (Lake Søbygård) and 150 m (Lake Væng) zones randomly selected in the chosen six and five sections in the two lakes, respectively (for details see Jeppesen et al. 2006). For electro-fishing, a pulsating DC generator with a minimum effect of 1000 W and a landing net with a mesh size of ~4 mm were used. In this study, electrofishing data were only used to provide information about pike distribution and abundance as pike were not well represented in the net catch.

For both lakes, the fish caught in the nets were divided into two size classes (≤ 8 cm and > 8 cm for roach and ≤ 10 cm and > 10 cm for perch). The classification was based on the length distribution identifying roach ≤ 8 cm and perch ≤ 10 cm as YOY fish.

Water Quality

We used weighted data (1 May – 1 Oct.) on total phosphorus (mg l^{-1}), chlorophyll *a* (µg l^{-1}), pH, dissolved oxygen percentage (%) and water temperature (ºC), based on samples taken at a mid-lake station weekly to biweekly (integrated sample from top to bottom). Total phosphorus was measured according to Søndergaard et al. (1992) and the other variables were measured in the field using Horiba field sensors. Ethanol was used for chlorophyll *a* extraction (Jespersen and Christoffersen 1987). Secchi disc depth was recorded as well. If the disc reached the bottom, the depth at the sampling station was used.

Macrophytes

In Lake Væng, submerged macrophyte samplings were conducted along 14 transects that covered the whole lake. Macrophyte coverage (COV), height and water depth were measured equidistantly along the transects using a water glass in combination with a rake. The vegetation was assigned to the following categories: 0, 1-5, 6-25, 26-50, 51-75 and 76-100% COV. Macrophyte coverage was calculated for all sections and integrated to a whole lake average. Plant Volume Infested (PVI) was also calculated as PVI=COV*(plant height/water mean depth) for each area and subsequently for the entire lake.

Macroinvertebrates

Benthic macroinvertebrates were sampled during early spring in the period of 1988-2001 (except 1995) in Lake Væng and in 1988-1993 and 1998 in Lake Søbygård. In 1988, ten samples were taken randomly from each of three locations in Lake Væng and five samples randomly from each of five locations in Lake Søbygård. In the other years and in both lakes, ten samples were taken at random locations. Kajak cores (diameter of 5.2 cm) were used for sampling and each sample (down to 10 cm in the sediment) was sieved through a 212 µm sieve. Chironomids, oligochaetes and ostracods were the most abundant benthic macroinvertebrates (Boll et al. 2012). Therefore, the benthic macroinvertebrates were divided into groups for the statistical analysis; Chironomidae indet., Oligochaeta indet., Ostracoda indet. and other macroinvertebrates.

Zooplankton

Zooplankton densities were determined on depth-integrated water samples taken with a core sampler at least once a month from May 1 to Oct 1 at a mid-lake station. The samples were filtered through a 20 µm net and the contents were fixed with Lugol. The zooplankton was divided into the following groups: rotifers, *Daphnia*, other cladocerans and cyclopoid copepods.

Data Analyses

For Lake Væng, the data series was divided into two periods covering years with and without submerged macrophytes. Macrophytes were present from 1989 to 1996 and absent in 1988 and from 1997 to 2002 (Figure 2). For comparative purposes the same period of years was used for Lake Søbygård, even though submerged plants were absent during the entire study period. Statistical analysis based on restricted maximum likelihood in a linear mixed model was used to determine the proportional distribution of roach and perch in the two lakes, both among sections and nets between different periods (mixed procedure in SAS, SAS institute 1989). The model included net position (NP), section (S) and years with and without macrophytes (M) in Lake Væng as fixed factors. The square root of the number of fish caught was used as dependent variable and two periods (with macrophytes (1989-1996 years) and without macrophytes (1988 and 1997-2002 years) in Lake Væng were compared for both lakes. A linear mixed model was also used to determine the relationship between fish numbers among sections and the COV and PVI of macrophytes.

All other variables were statistically tested (the non-parametric Kruskal-Wallis rank test) for the differences between the two periods using summer means for physico-chemical variables and zooplankton densities and the annual sample for macroinvertebrates.

Results

Water Quality

In Lake Væng, chlorophyll *a* and Secchi depth differed significantly (all with $p< 0.001$) between the two periods with and without macrophytes. The same was true for total phosphorus ($p< 0.02$). No difference was observed for pH, dissolved oxygen concentration and water temperature ($p> 0.5$) (Table 1). pH, water temperature, oxygen concentration and Secchi depth did not differ significantly in Lake Søbygård between the two selected periods with macrophytes (1989-1996) and without macrophytes (1988, 1997-2002) in Lake Væng (Table 1). Total phosphorus and chlorophyll *a* were significantly lower in the second period ($p< 0.03$ and $p< 0.01$, respectively).

Table 1. Physico-chemical variables for Lake Væng and Lake Søbygård during the periods with macrophytes (1989-1996) (M) and no macrophytes (1988, 1997-2002) (NM) in Lake Væng. All physico-chemical variables are averages of summer means for each period (± Standard Deviation).

	Chlorophyll *a* (µg l^{-1})	Total phosphorus (mg l^{-1})	pH	Dissolved oxygen (mg O_2 l^{-1})	Temperature (°C)	Secchi depth (m)
Lake Væng						
M	21.3 ± 11.1	0.08 ± 0.03	8.2	10.0 ± 0.5	16.1 ± 0.7	1.5 ± 0.7
NM	53.9 ± 14.8	0.12 ± 0.03	7.9	11.0 ± 1.5	16.4 ± 1.0	0.9 ± 1.0
Lake Søbygård						
M	196.8 ± 60.2	0.7 ± 0.2	9.1	10.9 ± 0.7	16.3 ± 0.7	0.6 ± 0.1
NM	125.5 ± 25.5	0.4 ± 0.2	9.1	12.0 ± 2.4	16.6 ± 0.9	0.6 ± 0.1

Fish

Proportionally, roach and perch were the species most frequently caught in both lakes during the sampling period of 1988-2002. In Lake Væng, small (≤ 8cm) roach dominated the catch from 1988 to 1995, with the exception of 1993, when large (> 8 cm) roach constituted about 60% of the total roach catch. During 1996-1998, the contribution of small roach was less than 50% of the total roach catch. From 1999 to 2002, small roach exceeded 60% of the overall catch and peaked with 80% in 2002. In most years, the major part of the perch in Lake Væng consisted of small-sized (≤ 10 cm) individuals, constituting about 80% of the total catch from 1998 to 2002. Other fish species caught in low numbers in Lake Væng included bream, rudd, pike and ruffe (*Gymnocephalus cernuus*).

In Lake Søbygård, the perch catch was low until 1995. Large roach (> 8 cm) and perch (> 10 cm) dominated total catches throughout the whole study period, with an average percentage of 72% and 76%, respectively. However, in 1997 and 2000-2002, small perch dominated the catches. Other fish species caught were bream and pikeperch, though in low numbers, while rudd and three-spined-stickleback (*Gasterosteus aculeatus*) were caught in high numbers only from 1988 to 1991 (Jeppesen et al. 1998).

For Lake Væng, linear mixed modelling showed a significant difference in the distribution of roach among sections between the years with and without macrophytes (Table 2). The abundance of roach in sections 1 and 2 (north) differed from section 3 (east) ($p < 0.05$). When macrophytes were present (with the highest PVI), the proportion of roach was low in the two northern sections. Here, however, the proportion of roach increased after 1994 (Figure 3. a). For Lake Søbygård, no significant difference was observed in the distribution of roach either among the sections or between the two periods (Table 2, Figure 3. c).

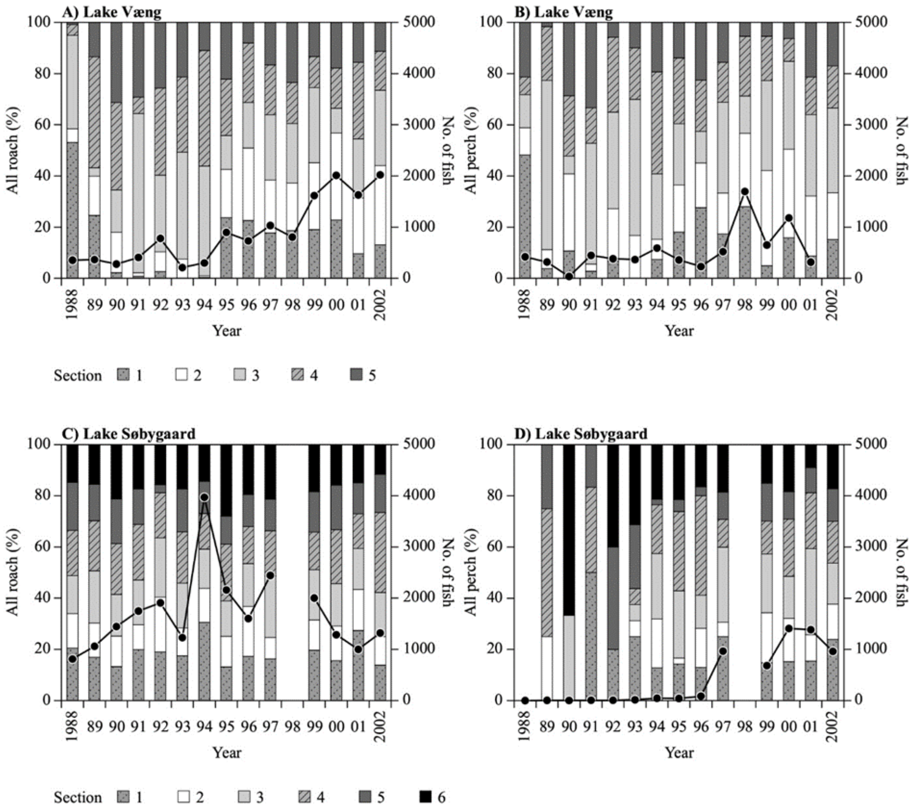

Figure 3. Distribution of a) all roach and b) all perch among the five sections in Lake Væng, c) all roach and d) all perch among the six sections in Lake Søbygård from 1988 to 2002. Secondary y-axis shows total number of fish caught in all nets per year.

In Lake Væng, perch was mostly caught in the sections in the southern part of the lake before 1994 (Figure 3. b). After 1994, perch were caught in all sections and its occurrence increased in the northern part of the lake. However, the proportion in the different sections was not statistically different between years with and without macrophytes (Table 2). In Lake Søbygård, perch appeared in almost equal proportions in all sections (Figure 3. d). However, the number of perch was low in the period corresponding to the macrophyte years in Lake Væng, precluding a solid comparison of distribution (Table 2).

Table 2. Statistical analysis based on restricted maximum likelihood in a linear mixed model testing the distribution of roach and perch in Lake Væng and Lake Søbygård among sections (S) and the net position (NP) between macrophyte and no macrophyte years (M). ns = not significant ($p > 0.05$).

		Roach			Perch		
		All	≤ 8 cm	> 8 cm	All	≤ 10 cm	> 10 cm
Lake Væng	S*M	0.048	0.068	ns	ns	ns	ns
	NP*M	ns	ns	0.039	ns	ns	ns
Lake Søbygård	S*M	ns	ns	ns	-	-	-
	NP*M	ns	ns	ns		-	-

Linear mixed modelling was also used to determine the distribution of the two size classes of roach (≤ 8 cm and > 8 cm) and perch (≤ 10 cm and > 10 cm) (Table 2). We only found a marginally significant difference in the distribution of small roach among sections between the periods with and without macrophytes (Table 2). However, the proportion of small roach among sections had a significant negative relationship with COV and PVI (Table 3). The distribution of small roach among net types was not significantly different between years with and without macrophytes (Table 2). Liner mixed modelling showed no significant difference in the distribution of large roach between the sections (Table 2). A significant negative relationship of large roach with COV and PVI was detected (Table 3), and the distribution among net types was significantly different for large roach when comparing the years with and without macrophytes in Lake Væng (Table 2). The catches in the macrophyte and no macrophyte years differed between net 1 (near shore, perpendicular) and net 3 (further from the shore, perpendicular) ($p <0.05$). Also net 1 and net 2 (near shore, parallel) differed significantly for large roach ($p <0.05$), while there was no significant difference between net 2 and net 3 during the two periods. Net 1 had the highest catch in the no macrophyte years.

Table 3. Statistical analysis based on restricted maximum likelihood in a linear mixed model testing the relation of two size classes of roach and perch with macrophyte coverage (COV) and plant volume inhabited (PVI) in Lake Væng during the years with macrophytes.

	Roach		Perch	
	≤ 8 cm	> 8 cm	≤ 10 cm	> 10 cm
COV	- 0.020	- 0.021	- 0.010	- 0.0002
PVI	- 0.026	- 0.0005	- 0.001	- 0.0036

In Lake Væng (Figure 4. a and b), there was no significant difference in the distribution of small roach among sections and nets, while the position of nets had different effects in macrophyte and no macrophyte years for large roach (Table 2) with proportionally higher catches in Net 1 in no macrophyte years. In Lake Søbygård (Figure 4. c and d), there was no significant difference in the distribution of the selected size classes of roach among the sections or nets during the two time periods (Table 2). Small and large roach appeared in all sections in the lake, and for large roach with an almost equal distribution among sections. In Lake Væng (Figure 5. a and b, there was no significant difference in the distribution of the two size classes of perch between the macrophyte and no macrophyte years (Table 2). Large perch were caught in all sections after 1994 and they tended to be more equally distributed than the small perch (Figure 5. a and b). The presence of both size classes of perch increased in the northern sections after 1994; however, the high variability between years among the sections weakened the analysis. A significant negative relationship was found between the distribution of both small and large perch and COV and PVI (Table 3). The distribution among net types for both size classes of perch did not differ significantly between the macrophyte and no macrophyte years (Table 2). In Lake Søbygård, no tests for perch were conducted due to the low number of fish. However, both small and large perch were found in all sections (Figure 5. c and d).

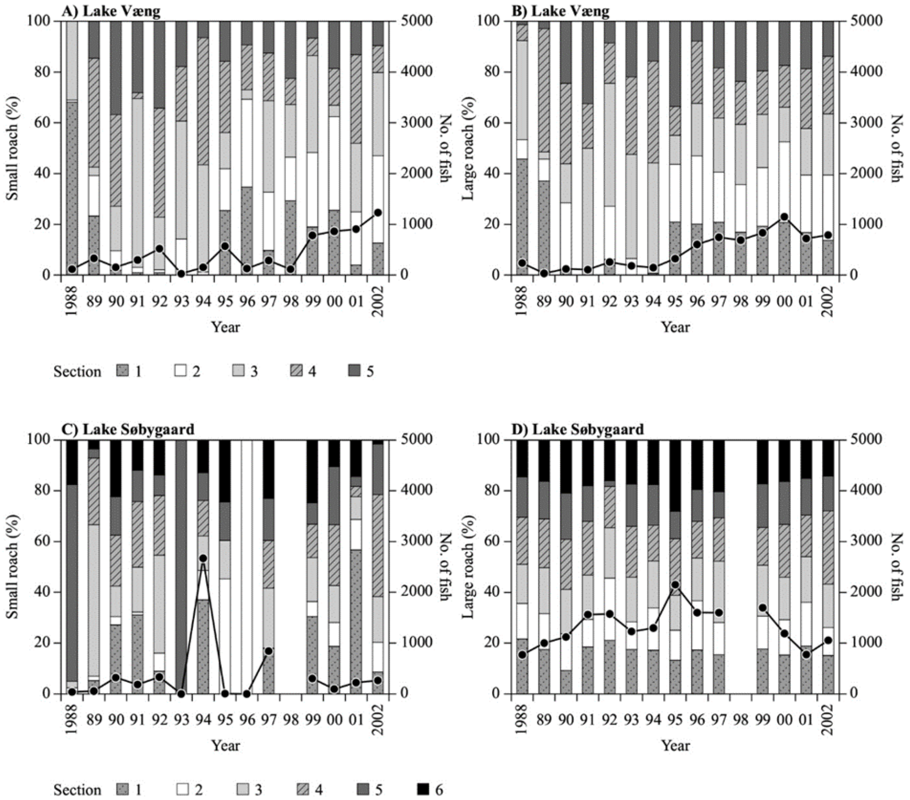

Figure 4. Distribution of a) small roach (≤ 8 cm) and b) large roach (> 8 cm) among the five sections in Lake Væng and of c) small roach (≤ 8 cm) and d) large roach (> 8 cm) among the six sections in Lake Søbygård from 1988 to 2002. Secondary y-axis shows the total number of fish caught in all nets per year.

In Lake Væng, pike > 20 cm were caught by electrofishing in all years, being particularly abundant in 1991 and 1992 (in sections 1, 2, 4 and 5) (Figure 6. a). In Lake Søbygård, pike > 20 cm was caught in very low numbers in all sections (Figure 6. b). No pikeperch was caught in Lake Væng irrespective of the fishing gear used. In Lake Søbygård, pikeperch > 8 cm was caught in the nets in low numbers, the highest catch of 60 individuals occurring in 1997 (Figure 7).

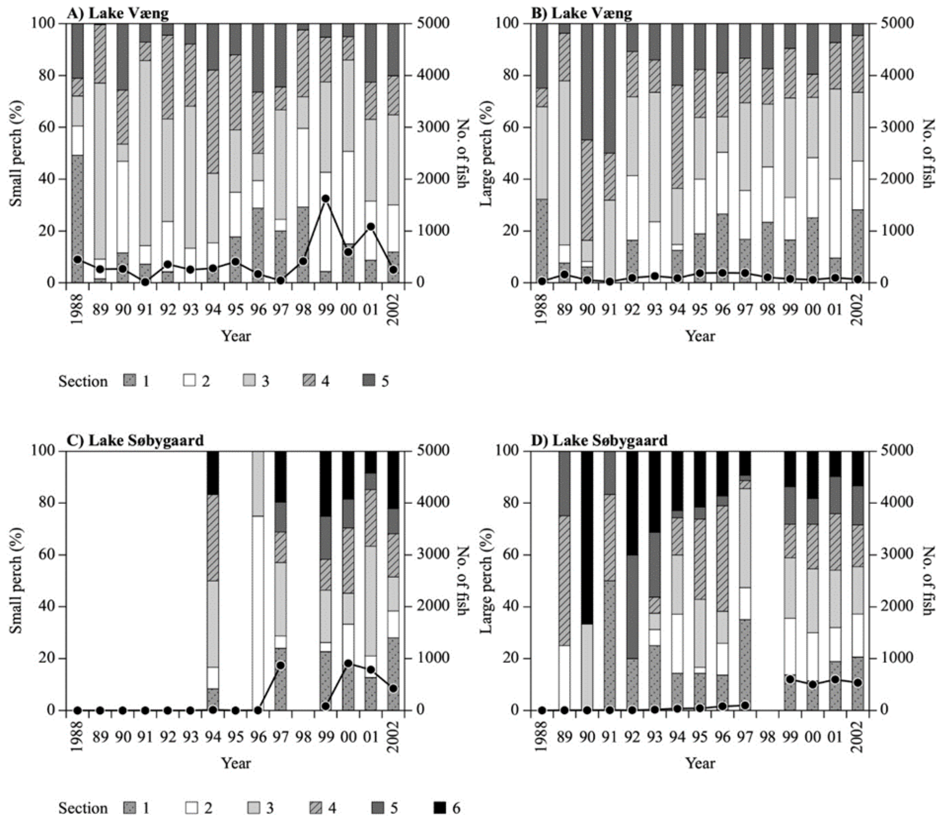

Figure 5. Distribution of a) small perch (≤ 10 cm) and b) large perch (> 10 cm) among the five sections in Lake Væng and of c) small perch (≤ 10 cm) and d) large perch (> 10 cm) among the six sections in Lake Søbygård from 1988 to 2002. Secondary y-axis shows the total number of fish caught in all nets per year.

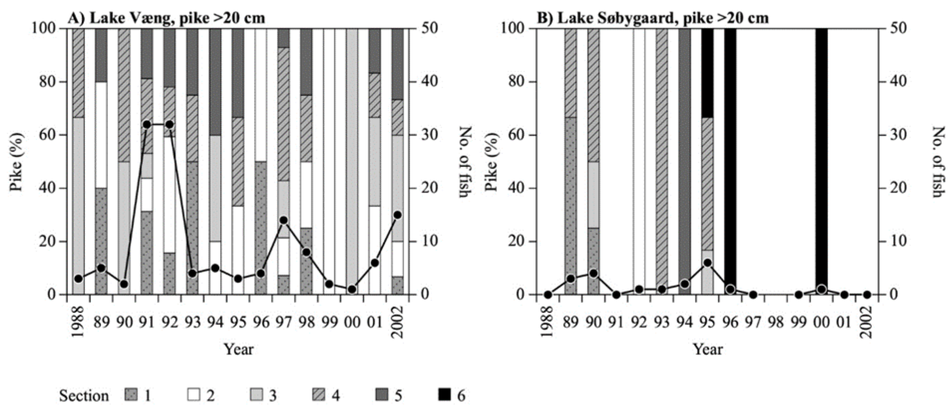

Figure 6. Distribution of pike > 20 cm caught by electrofishing among the sections in a) Lake Væng and b) Lake Søbygård. Secondary y-axis shows the total number of fish caught in all nets per year.

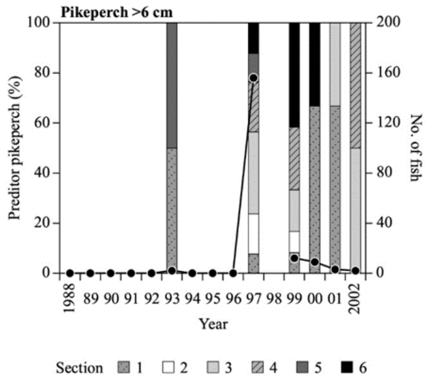

Figure 7. Distribution of pikeperch > 6 cm caught by gillnets among the sections in Lake Søbygård Secondary y-axis shows the total number of fish caught in all nets per year.

Macroinvertebrates

There were significantly ($p < 0.01$) more "other macroinvertebrates" in Lake Væng in the period where the lake was in a clear-water state compared with the turbid period (Table 4). For all other groups of macroinvertebrates in Lake Væng and for all groups of macroinvertebrates in Lake Søbygård, there were no significant differences between the two periods ($p > 0.17$) (Table 4).

Table 4. Summer mean (May-Oct.) (± Standard Deviation) zooplankton densities including rotifers, Daphnia, other cladocerans and copepods (ind. l^{-1}) and macroinvertebrate densities (ind. m^{-2}); Chironomidae indet, Oligochaeta indet., Ostracoda indet and other macroinvertebrates, in Lake Væng and Lake Søbygård during the period with macrophytes (1989-1996) (M) and no macrophytes (1988, 1997-2002) (NM) in Lake Væng

	Zooplankton (ind. l^{-1})				*Macroinvertebrates (ind. m^{-2})*			
	Rotifera	*Daphnia*	Other cladocerans	Copepods	Chironomidae indet.	Oligochaeta indet	Ostracoda indet.	Other macroinvertebrates
Lake Væng								
M	4766 (±6247)	76 (± 44)	9 (±13)	231 (± 131)	1617 (± 2496)	742 (±1180)	109 (±183)	644 (± 829)
NM	7112 (± 4847)	127 (± 130)	80 (± 69)	231 (± 68)	444 (± 557)	1903 (±2420)	267 (± 565)	19 (±13) **
Lake Søbygård								
M	323 (± 393)	99 (± 47)	245 (± 291)	128 (±48)	9688 (±14969)	4787 (± 7454)	0.5 (± 1,1)	0
NM	231 (± 226)	53 (± 38)	169 (±90)	129 (±36)	792 (± 754)	8559 (±532)	1.2 (± 1.7)	1.2 (± 1.7)

There were no significant differences in the total densities (ind. l^{-1}) of rotifers, *Daphnia*, other cladocerans and cyclopoid copepods between the two periods in any of the two lakes ($p > 0.05$) (Table 4).

Discussion

In turbid macrophyte-free Lake Søbygård, both roach and perch occurred in all sections in nearly equal proportions during the entire study period. This distribution pattern was not affected by the shift towards a higher proportion of perch following recovery from eutrophication, likely because the lake remained turbid without submerged macrophytes. In Lake Væng, however, both roach and perch showed a clear difference in habitat distribution between the two periods i.e., with and without macrophytes. During the macrophyte years, roach and perch were mainly found in the southern part of the lake where COV and PVI were lowest. After 1994 when plants were more evenly distributed in the lake (1995) or absent at high turbidity (1996 and onwards), fish abundance increased in the northern part of the lake and both species occurred in all sections in rather similar proportions. In 1988-1995, Secchi depth in Lake Væng was 1.5 m and decreased to 0.8 m in 1997 and remained low until 2002. Thus, the shift from an uneven to an even distribution coincided with the decrease in Secchi depth, suggesting that increased water turbidity acted as a protective cover, allowing fish to disperse equally among the sections. Turbidity can impede the vision of certain fish species and thus diminish the risk of predation for prey fish (Utne-Palm 2002; Horppila et al. 2004; Skov et al. 2002; Pekcan-Hekim and Lappalainen 2006), thereby reducing the anti-predator behavioural response of roach and perch to fish predators (Lehtiniemi et al. 2005) and birds (Gliwicz and Jachner 1992; Jepsen and Berg 2002).

Not only water clarity but also plant density may be important for the distribution of fish. During the years with macrophytes in Lake Væng, both size classes of roach and perch preferred the sections in the eastern and southern part of the lake that exhibited the lowest COV and PVI (Table 5), and the distribution of both size classes of the two species were significantly negatively related to COV and PVI (Table 3). Avoidance of dense macrophyte beds by perch and roach is in accordance with the findings of Crowder and Cooper (1982), Werner et al. (1983) and Christensen and Persson (1993), reflecting that high vegetation density impairs the ability of fish to move, thus reducing their foraging efficiency and ability to escape predators. Too complex habitats can impair the prey's ability to use it as a refuge (Bartholomew et al. 2000; Perrow et al. 1996). Snickars et al. (2004) found that 0+ perch avoided the dense vegetation in the presence of predators, but showed anti-predator behaviour at low and medium vegetation density. Eklöv and Hamrin (1989) and Perrow et al. (1996) also found that juvenile perch preferred low vegetation density and pelagic areas in the presence of the predator pike and that mortality was high in dense vegetation. In Lake Væng, pike occurred in high numbers in 1991 and 1992, and in both years, small roach and perch avoided the sections where pike were present. However, in turbid Lake Søbygård, both size classes of roach and perch were found in every section of the lake in almost equal proportions. This suggests that predators may play a role for the habitat choice of roach and perch, but that turbidity can help to provide a safer environment against them.

Table 5. Macrophyte coverage (COV) and plant volume inhabited (PVI) in Lake Væng.

Section	1991	1992	1993	1994	1995	1996
COV %						
1	87.5	6.0	15.4	85.8	87.5	0.1
2	87.5	9.1	20.7	81.7	87.5	16.3
3	75.0	3.8	7.2	61.4	85.6	33.9
4	81.0	15.2	1.9	55.8	86.3	13.8
5	87.5	31.7	2.1	60.9	77.8	0
PVI %						
1	76.8	2.0	6.2	77.6	57.9	0.1
2	75.5	3.0	6.6	54.9	61.6	5.8
3	47.3	0.2	2.0	20.4	64.9	13.9
4	69.8	1.1	0.7	20.0	68.1	6.9
5	57.9	3.6	0.9	27.1	63.3	0

Other environmental factors than water clarity and macrophyte distribution may potentially influence the fish distribution. No major differences were observed in pH, water temperature and oxygen concentration between the two periods, and these variables remained within the range that should not affect fish behaviour (Wootton 1990). Food availability may be another contributing factor. However, the density of zooplankton and that of most of the macroinvertebrates did not differ significantly between the two periods for either Lake Væng or Søbygård. The group "other macroinvertebrates" was, however, significantly more abundant in Lake Væng during the clear period with macrophytes than in the turbid period (Table 4), mainly reflecting the higher abundances of Gastropoda, *Pisidium* spp., *Hirundinae* and *Aselus aquaticus* in the clear period. Nevertheless, the higher density of these mostly plant-associated groups cannot explain why perch and roach preferred areas with less dense vegetation during the clear period. This finding supports the suggestion by Lewin et al. (2004) that habitat type is more important than food resources for the habitat choice of perch.

The changes in the distribution pattern of perch and roach in Lake Væng could potentially also reflect changes in the abundance of fish. The shift from an uneven to an even distribution coincided with an increase in the number of fish, and it has been shown that a higher density of fish can lead to a more even distribution due to increased competition (Werner et al. 1983). In Lake Væng, biomanipulation was conducted during 1986-1988 where 50% of the roach and bream biomass was removed, followed by a gradual increase in roach and in the total catch per unit (CPUE) of fish only after 1994 (Figure 3. a).

Nevertheless, when perch abundance decreased again in 2000-2002 its distribution remained even, suggesting that density does not have key importance for the observed variation in the fish distribution.

In Lake Væng, the proportional differences in the catches of large roach between the three net types differed between the macrophyte and no macrophyte years. Net 1 (perpendicular to the shore) had proportionally higher catch in the no macrophyte years than net 2 and 3, indicating that large roach (but not small roach or both size classes of perch) moved along the near-shore area after the disappearance of macrophytes. This pattern only in part agree with results from a multi-lake study of fish habitat distribution in Danish lakes. Here, Jeppesen et al. (2006) found that not only large roach, but also large perch and small roach increased their usage of the littoral zone with increasing chlorophyll *a* concentration in shallow lakes, while small perch did not show a clear response to such changes.

Our study was conducted during late summer and also the nets were set during both day and night, implying that our results do not describe changes in temporal variation in the distribution at a seasonal or diurnal scale. It is well known that fish show seasonal (Jepsen and Berg 2002; Haertel and Eckmann 2002; Fischer and Eckmann 1997) and ontogenetic (Persson et al. 2000) habitat shifts. Further, it is understood that perch and roach undergo diel horizontal migration in shallow lakes. Thus, during the day, they are commonly found in the littoral zone among the macrophytes to avoid predators and at night they move offshore to find food when the predation risk is low (Bohl 1980; Gliwicz and Jachner 1992; Pekcan-Hekim et al. 2005). Moreover, the pattern of diel horizontal migration has been observed to differ between clear and turbid lakes (Jacobsen et al. 2004).

We conclude that water clarity and macrophyte density were the key determining factors for the distribution of roach and perch (integrated overnight) during summer in our two study lakes; and a similar pattern is likely to be found in other northern-temperate shallow lakes.

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