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Diel migration and spatial distribution of fish in a small stratified lake

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Abstract

The diel migration and spatial distribution of fish were explored using six sequential 4-h sample gillnettings in the pelagic and littoral zones of Lake Verevi (Estonia, 12.6 ha, max. depth 11 m, hard-water, deoxygenated hypolimnion) in August 2001 and July 2002. Considering abundance, two-thirds of the total fish moved to the littoral zone. The biomass of fish was distributed evenly between the littoral and pelagic zones, where the topmost epilimnion accounted for 80–85% leaving 10–15% for the lower epilimnion in the pelagic zone. Just above the thermocline only some large specimens of perch *Perca fluviatilis* (L.) and roach *Rutilus rutilus* (L.) (1–5%) during the daytime were captured. No fish movements were recorded under the thermocline. Rudd *Scardinius erythrophtalmus* (L.) inhabited only the littoral zone; all the other species were captured in both zones. Juvenile perch stayed in the littoral zone, whereas juvenile roach was caught in both zones and was active over a 24-h period. Piscivores, perch and pike *Esox lucius* L., were inactive in the dark. Perch inhabited mostly the littoral zone and the duration of its activity increased with age. In summer-stratified Lake Verevi, sharp change in the values of oxygen in the metalimnion along with species interaction affected the spatial distribution of fish, while diel migration was light-dependent.

Introduction

In lakes, the biota is mostly determined by water quality and lake morphometry, while fish composition and biomass are related to the content of dissolved solids *per* mean depth of the water column (Ryder et al., 1974; Moss, 1998). The catchability of passive fishing gears is directly related to moving activity of fish. The activity of fish depends on season, light conditions and temperature, besides mutual interaction of fish species (Davenport & Sayer, 1993; Rowe, 1994; Jurvelius & Sammalkorpi, 1995; Persson et al., 1996; Ekloev, 1997; Horppila, 1998; Dörner et al., 1999; 2001; Jepsen et al., 1999; Hölkner & Breckling, 2002). Vegetated sites had higher densities of fish, specially smaller fish and greater species richness than unvegetated sites (Randall et al., 1996; Jacobsen et al., 2002a). Inter-annual variation in fish community structure, in biomass–size distributions of benthic lake fish communities, in mutual interaction of species and in activity are well-known (Holmgren, 1999; Holmgren & Appelberg, 2000; Olin et al., 2002). The dominant fish species in Lake Verevi as in most eutrophic small Estonian lakes were roach and perch (Mäemets, 1977; Pihu 1993). Our goal was to study the diel migration and spatial distribution of fish in this small hard-water lake at the time of sharp summer stratification.

Material and methods

Verevi (South Estonia) is a small (12.6 ha), slightly exorheic, sheltered, and hence a stratified lake with a steep thermocline, and a small drainage basin of 1.1 km^2. The maximum depth is 11 m, and the average depth 3.6 m. At the time of the study, the Secchi disc transparency of water in Lake Verevi was 3 m, bottom was covered with submerged plants to a depth of 3.5 m, and values of pH ranged from 8.2 in the upper epilimnion to 7.5 at 4 m, and to 7.0 at 5 m.

According to the literature data, 12 fish species inhabited L. Verevi (Eesti järved, 1968; Mäemets, 1977). Roach and perch are still the most abundant in the lake, while pike, rudd, tench *Tinca tinca* (L.) and crusian carp *Carassius carassius* (L.) are of second-rate abundant. The common benthophagous species, bream *Abramis brama* (L.) and ruffe *Gymnocephalus cernuus* (L.) of L. Verevi between 1950 and 1980, have obviously disappeared by now.

The fish composition was explored on 2–3 August in 2001, and on 8–9 July in 2002. We used Danish type of multi-mesh nylon monofilament gillnets (of 14 randomly placed 3 × 1.5-m mesh panels). The gillnets were arranged to catch at depths of 0–1.5 , 2.5–4 , 4.5–6 , and 6.5–8 m in the pelagic zone. In every depth one gillnet was used. Two gillnets were placed at a depth of 1–2.5 m in the littoral zone. This zone was characterised by the *Typha–Phragmites–Chara–Potamogeton–Nuphar* complex. All captured fish were sorted by mesh size and species, and measured by total length (TL, to the nearest 1 mm), and total weight (TW, to the nearest 0.1 g); sex and consumed prey (fish) were identified. The age of perch by *operculum* and of roach by scales was determined.

Since noon, the gillnets were checked in sequential 4 h over a 24-h period (altogether six times). In both years, the days of experiment were sunny. The specific feature of weather in the morning of the experiment day in 2001 was a weak thunderstorm. In both years, the mornings were foggy and direct sunlight irradiated the water column for 14 h in 2001 (the morning was foggy from 4 to 8 a.m.), and only for 11.5 h in 2002 (clouds dispersed at 10 a.m.) out of possible 16–17 h characteristic of the season. The water temperature of the topmost epilimnion was 22.4 °C in August 2001 and somewhat lower (21.6 °C) in July 2002. The temperature and oxygen gradients over the water column in the pelagial at gillnetted depths are presented in Figure 1.

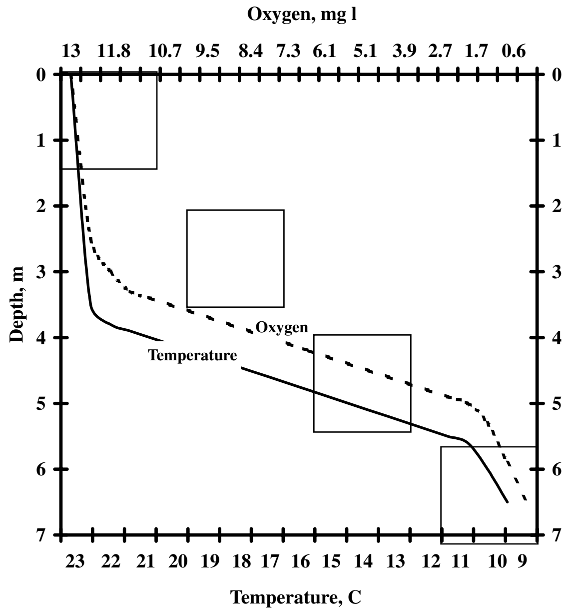

Figure 1. Temperature and oxygen gradients over a water column at the gillnetted (transparent squares) station.

Results

In August 2001, the total landing of 24-h gillnetting (13.8 kg) at two stations (littoral and pelagic) comprised 376 fish from five species: roach, perch, tench, rudd, and pike. The biggest captured fish were a 1188 g tench and a 1090 g pike (accounting 18% for total catch). In July 2002, 301 fish (9.9 kg) were captured at the same stations. In comparison with the catches of the previous year, rudd and juvenile tench were absent, and a juvenile pike and a 1407 g tench were captured.

Spatial segregation

Rudd inhabited only the littoral zone; all the other species were captured in both zones. Roach and perch outweighed the other species accounting for 80% of the total catch. The lengths of the captured perch and roach were distributed evenly in both years (Fig. 2), as did the catches between the net panels of different mesh size (Fig. 3). In the littoral zone, juvenile roach and perch were caught as shoals; rudd and juvenile pike were captured in places with opulent water-plants, while tench inhabited shallow

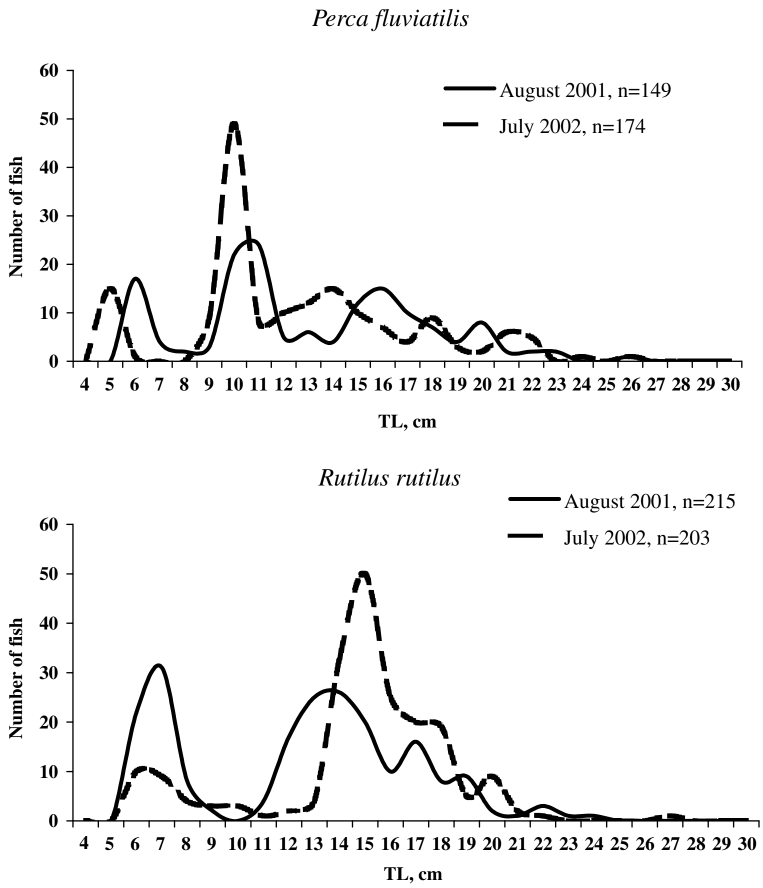

Figure 2. The length distributions of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in lake Verevi; comparison between two sequential summers.

waters with *Typha angustifolia* L. and *Phragmites australis* (Cav.) Trin. ex Steud. At the station of the pelagic zone, most fish inhabited the topmost 1.5 m of the epilimnion of the total 7 m water column (Table 1). In both years, roach and perch were abundant in this layer (Table 2). At a depth of 2.5–4 m, the abundance of fish decreased sharply (up to 10–12% of the total catch in the pelagic zone). Mostly roach, rarely perch and a 5 year-aged pike inhabited this water layer. As many as eight fishes were captured with five gillnets (out of 12) at a depth of 4–5.5 m. Perch (80–100 g, aged 4–5 years; 2001) as well as roach (20–30 g; 2002) were captured at this depth. Our experiments showed that fish avoided this depth in the dark and never occurred in the anoxic hypolimnion below the depth of 5.5 m.

Diel migration

Fish, mainly roach and perch, inhabited the topmost 1.5 m layer of the epilimnion throughout the 24-h study period in both years. In 2001, the TW of 4-h catch in the topmost layer ranged from 544 to 916 g. Under the conditions of intensive solar radiation in July 2002, the catch at 2–3.5 m outweighed the catch from the topmost layer. In two periods, one at sunrise and the other in the afternoon, 3–5-years-old roach and perch descended into the deeper water layers of the pelagial zone. In the littoral zone, juvenile fish was the most active and hence abundantly entrapped in the morning just after sunrise.

Gillnets caught most evenly roach that, unlike perch, was active in the pelagial even at night. Perch migrated most frequently at noon and at

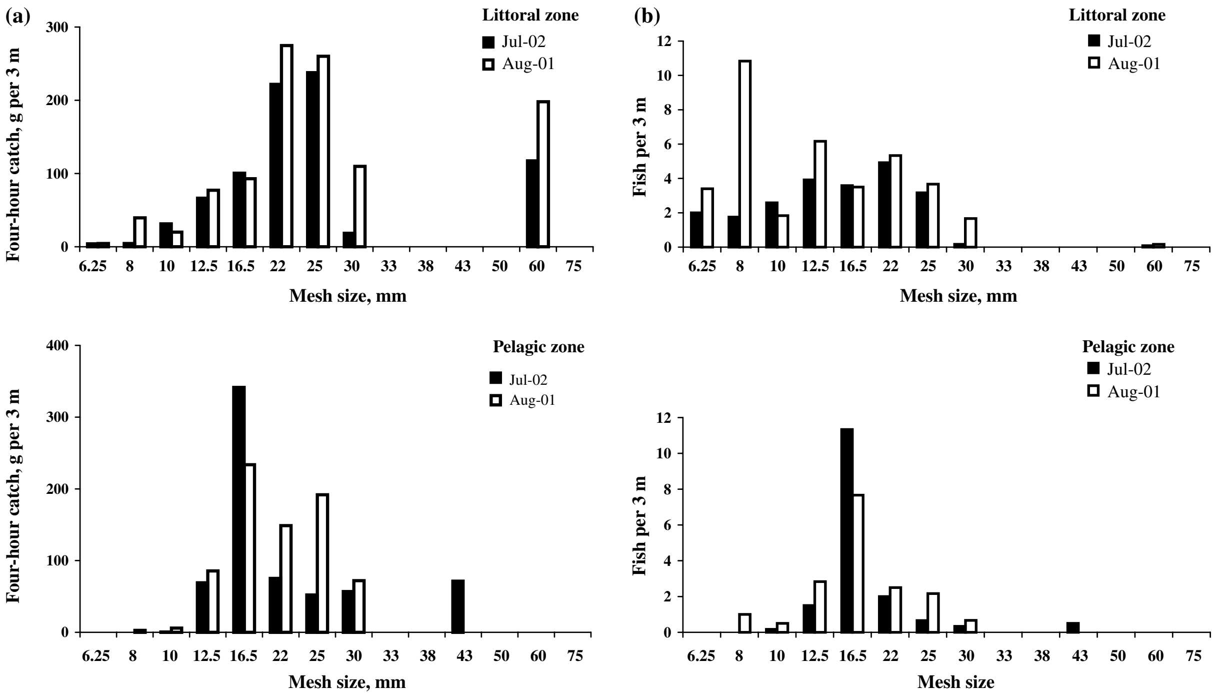

Figure 3. Comparison between the catches of explored mesh-sizes (3-m net-panels); a in biomass, b in abundance.

Table 1. The gillnet catches of four-h samplings at different depths over a 24-h period in August 2001 and July 2002

Time	Year	CATCH, g multi mesh-sized gillnet^{-1}			
		Pelagic zone			Littoral zone
		0–1.5 m	2–3.5 m	4–5.5 m	1–2.5 m
4–8 p.m.	2001	675	1290	0	845
	2002	911	157	51	1026
8–12 p.m.	2001	544	92	0	32
	2002	214	339	31	1246
0–4 a.m.	2001	701	0	0	795
	2002	691	112	0	631
4–8 a.m.	2001	856	39	34	860
	2002	571	233	0	580
8–12 a.m.	2001	675	0	0	1239
	2002	401	280	0	1882
0–4 p.m.	2001	916	779	201	3224
	2002	168	84	24	259
Total, g	2001	4367	2200	235	6995
	2002	2200	2035	106	5624

sunset. Whereas juvenile pike got entrapped in shallow waters either in the dark or in the morning, mature pike foraged on roach in the afternoon at a depth of 4 m. In the littoral zone, fish were the most frequent at noon and the scarcest long before sunset, when the nearby

Table 2. The abundances of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in lake Verevi at explored depths over a 24-h period in 2001 and 2002

Time	Pelagic zone				Littoral zone			
	2001		2002		2001		2002	
	Roach	Perch	Roach	Perch	Roach	Perch	Roach	Perch
0–4 p.m.	33	14	9	6	20	26	7	24
4–8 p.m.	14	9	30	4	6	25	17	45
8–12 p.m.	22	–	14	2	24	–	48	29
0–4 a.m	10	3	16	–	17	13	22	11
4–8 a.m.	18	5	7	10	27	16	16	26
8–12 a.m.	10	7	9	9	7	42	3	14
In 24 h	107	38	85	31	101	122	113	149
Both species	145		116		223		262	

forest overshadowed the station. Tench was active in the littoral zone in the afternoon, whereas juvenile tench was captured in the pelagial zone at sunset.

Discussion

Among the local fish species, roach is the most abundant planktivore in Estonian small lakes where it is followed by piscivorous perch (Pihu, 1993). While perch prefers and is more numerous in clear-water lakes (Diehl, 1988), cyprinids including roach, are known to thrive under eutrophic and turbid conditions (Helminen et al., 2000; Jeppesen et al., 2000; Jacobsen et al., 2002a, 2002b). In our study on Lake Verevi, roach and perch were co-dominants, the roach slightly outnumbering but clearly overweighing perch. A similar composition of fish is characteristic of mesotrophic lakes in southern Finland (Olin et al., 2002). In highly eutrophic lakes, the proportion of other cyprinids and percids, such as bream, white bream (*Blicca bjoerkna*) and ruff, increased (Michelsen et al., 1994; Olin et al., 2002). During the past years L. Verevi, especially its epilimnion, has changed from hypertrophic to mesotrophic with oligotrophic features (Ott et al., 2005) while bream and ruffe have disappeared by now.

Compared with other small Estonian lakes explored in summer, the catch per unit effort (CPUE) of multi-mesh gillnet calculated in kilograms per night (12 h) reached only the average of the littoral zone, and three times lower of the pelagial (Krause et al., 2001). The length of juvenile roach corresponded to that backcalculated for Estonian small lakes (Eesti järved, 1968) and for Finnish lakes (Horppila & Nyberg, 1999) and its length frequency distributions was similar to that in the eutrophic lake Frederiksborg Slotssø (Michelsen et al., 1994). Age composition showed a similar scarceness of 2- to 3-year-aged roach both in the pelagic and littoral zones, being obviously catchable as a refugee in reeds (Herzig et al., 2002), the biotope not explored in lake Verevi.

On a daily basis, the migration of roach depends mostly on temperature (Krause et al., 1998), and on the need to escape or forage (Ekloev & Perrson, 1995, 1996; Jachner, 2001). According to our investigation, juvenile roach (TW less than 10 g) was active in the dark and early in the morning in the pelagic zone. At this time, juvenile pike was foraging in the littoral zone. Roach, with TW over 30 g, was active over a 24-h period, and catchable conditioned by light. Roach inhabited the upper layer of the pelagial in the dark and descended in the daylight, contrary to the previously described pattern based on the movement of zooplankters (Rowe, 1994; Dörner et al., 1999; Lauridsen et al., 1999; Romare et al., 1999; Burks et al., 2002).

In Lake Verevi, the abundance and biomass of large copepods was the highest in the lower layer of the metalimnion (Kübar et al., 2005) avoided by fish. Although the highest biomass of planktivores was located in the topmost epilimnion, decreasing sharply with each next metre in depth, the biomass of *Daphnia cucullata* remained unchanged up to a depth of 5 m, where fish occurred extremely rarely. This might indicate strong predation on juvenile perch that consumes predominantly cyclopoid copepods in the absence of predators and macroinvertebrates in the presence of predators (Persson & Ekloev, 1995). Juvenile roach feeds on phytoplankton, then switches to rotifers and microcrustaceans, maintaining the capacity to feed on blue-green algae and higher plants (Hofer & Wiezer, 1987; Persson, 1987). Roach remains among the vegetation in the presence of perch, while both roach and perch remain in the vegetation in the presence of pike (Ekloev & Persson, 1996). Roach is reported to move vertically in turbid lakes – ascending in the daylight and descending at night, contrary to the mainly horizontal movement between the pelagic and littoral zones described in a clearwater lake (Jacobsen et al., 2002b).

Piscivores, perch and pike, were inactive in the dark. Mature perch remains among the littoral vegetation overnight, avoiding shallow waters in the daylight. One-year-old perch changes its habitat due to predation risk in the morning, at mid-day, and in the evening, migrating from the pelagial into the macrophytes in the morning (Imbrock et al., 1996). In the lakes lacking pike, perch used both littoral and pelagial habitats of the lake. The relative number of adult perch and pike increases with depth, although in pike-lakes, perch occurs along the littoral zone but never below the thermocline (Persson et al., 1996). In lakes having low density of pike, as in L. Verevi, the abundance of perch was twice higher in the littoral zone.

According to Perrow et al. (1996), tench was generally active at night and almost completely inactive during daylight, resting in shoals among the littoral emergent plants, mostly *Typha angustifolia*. Conversely, in L. Verevi tench was active only in daytime.

Sharp gradients in the oxygen content, food availability and temperature in the metalimnion, evidently, determine the vertical distribution of fish in L Verevi.

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References

Burks, R. L., E. Jeppesen, D. M. Lodge & T. Lauridsen, 2002. Diel horizontal migration of zooplankton: costs and benefits of habitating littoral zones. Freshwater Biology 47: 343–365.

Davenport, J. & M. D. J. Sayer, 1993. Physiological determinants of distribution in fish. Journal of Fish Biology 43: 121–145.

Diehl, S., 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos 53: 207–214.

Dörner, H., A. Wagner & J. Benndorf, 1999. Predation by piscivorous fish on age-0 fish: spatial and temporal variability in a biomanipulated lake (Bautzer reservoir, Germany). Hydrobiologia 408/409: 39–46.

Dörner, H., H. Schultz, T. Mehner & J. Benndorf, 2001. Interaction between prey availability and feeding behaviour of age-2 and age-2 Perch (*Perca fluviatilis* L.) in a Biomanipulated Lake (Bautzen Reservoir, Germany). Limnologica 31: 11–16.

Ekloev, P. & L. Perrson, 1995. Species – species antipredator capacities and prey refuges: interactions between piscivorous perch (*Perca fluviatilis*) and juvenile roach (*Rutilus rutilus)*. Behavioral Ecology and Sociobiology 37: 169–178.

Ekloev, P., 1997. Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 54: 1520–1531.

Helminen, H., J. Karjalainen, M. Kurkilahti, M. Rask & J. Sarvala, 2000. Eutrophication and fish biodiversity in Finnish lakes. Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie 27: 194–199.

Herzig, A., J. Kubecka & G. Wolfram, 2002. Fish distribution in the open water and littoral of Neusiedler See (Austria): a matter of habitat structure and abiotic factors. In: International Conference on Limnology of Shallow Lakes, Balatonfüred, Hungary 25–30 May (2002), Abstracts, Veszprm University Press Vp, 309 pp.

Hofer, W. W. R. & W. Wieser, 1987. Diet spectra and resource partitioning in the larvae and juveniles of three species and six cohorts of cyprinids from a subalpine lake. Oecologia (Berlin) 71: 388–396.

Holmgren, K., 1999. Between-year variation in community structure and biomass-size distributions of benthic lake fish communities. Journal of Fish Biology 55: 535–552.

Holmgren, K. & A. Appelberg, 2000. Size structure of benthic freshwater fish communities in relation to environmental gradients. Journal of Fish Biology 57: 1312–1330.

Horppila, J., 1998. Effects of mass removal and variable recruitment on nutrient excretion by a planktivorous roach stock. Journal of Fish Biology 52: 951–961.

Horppila, J. & K. Nyberg, 1999. The validity of different methods in the backcalculation of the lengths of roach – a comparison between scales and cleithra. Journal of Fish Biology 54: 489–498.

Hölkner, F. & B. Breckling, 2002. Influence of activity in heterogeneous environment on dynamics of fish growth: an individual-based model of roach. Journal of Fish Biology 60: 1170–1189.

Imbrock, F., A. Appenzeller & R. Eckmann, 1996. Diel and seasonal distribution of perch in Lake Constance: a hydroacoustic study and *in situ* observations. Journal of Fish Biology 49: 1–13.

Jachner, A., 2001. Anti-predator behaviour of nave compared with experienced juvenile roach. Journal of Fish Biology 59: 1313–1322.

Jacobsen, L., S. Berg, M. Broberg, N. Jepsen & C. Skov, 2002a. Activity and food choice of piscivorous perch (*Perca fliviatilis*) in a eutrophic shallow lake, investigated by radiotelemetry. Freshwater Biology 47: 2370–2379.

Jacobsen, L., N. Jepsen & S. Berg, 2002b. Roach (Rutilus rutilus) behaviour by use of mini-radio transmitters: a comparative study of a clearwater and turbid lake. In: Shallow Lakes 2002, International Conference on Limnology of Shallow Lakes, Balatonfüred, Hungary 25–30 May 2002, Abstracts, Veszeprm University Press Vp, 309 pp.

Jeppesen, E., J. P. Jensen, M. Søndegaard, T. Lauridsen & F. Landkildehus, 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology 45: 201–218.

Jepsen, N., A. Koed & F. Økland, 1999. The movements of pikeperch in a shallow reservoir. Journal of Fish Biology 54: 1083–1093.

Jurvelius, J. & I. Sammalkorpi, 1995. Hyrdoacoustic monitoring of the distribution, density and the mass-removal of pelagic fish in a eutrophic lake. Hydrobiologia 316: 33–41.

Krause, J., G. Staaks & T. Mehner, 1998. Habitat choice in shoals of roach as a function of water temperature and feeding rate. Journal of Fish Biology 53: 377–386.

Krause, T., A. Palm & A. Järvalt, 2001. Eesti väikejärvede kalastik. Annual Report No 2-11-14/767, Min. Envir. Dep. Fish Res., Tartu, 41 pp. [Fish in small Estonian lakes. In Estonian].

Kübar, K., H. Agasild, T. Virro & I. Ott, 2005. Vertical distribution of zooplankton in a strongly stratified hypertrophic lake. Hydrobiologia 547: 151–162.

Lauridsen, T. L., E. Jeppesen, S. F. Mitchell, D. M. Lodge & R. L. Burks, 1999. Diel variation in horizontal distribution of *Daphnia* and *Ceriodaphnia* in oligotrophic and mesotrophic lakes with contrasting fish densities. Hydrobiologia 408/409: 241–250.

Michelsen, K., J. Pedersen, K. Christoffersen & F. Jensen, 1994. Ecological consequences of food portioning for the fish population structure in a eutrophic lake. Hydrobiologia 291: 35–45.

Moss, B., 1998. Ecology of fresh waters: man and medium, past to future. Blackwell Science, 531 pp.

Eesti järved. 1968. Tallinn, "Valgus". 532 pp. [Estonian lakes. In Estonian].

Mäemets, A., 1977. Eesti NSV järved ja nende kaitse. Valgus, Tallinn, 263 pp. (Lakes of the Estonian S.S.R. and their protection. In Estonian).

Olin, M., M. Rask, J. Ruuhijärvi, M. Kurkilahti, P. Ala-Opas & O. Ylönen, 2002. Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. Journal of Fish Biology 60: 593–612.

Ott, I., T. Kõiv, P. Nõges, A. Kisand, A. Järvalt & E. Kirt, 2005. General description of partly meromictic hypertrophic Lake Verevi, its ecological status, changes during the past eight decades and restoration problems. Hydrobiologia 547: 1–20.

Perrow, M. R., A. J. D. Jowitt & S. R. Johnson, 1996. Factors affecting the habitat selection of tench in a shallow eutrophic lake. Journal of Fish Biology 48/5: 859–870.

Persson, L., 1987. Effects of habitat and season on competitive interactions between roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*). Oecologia (Berlin) 73: 170–177.

Persson, L. & P. Ekloev, 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 76: 70–81.

Persson, L., J. Andersson, E. Wahlstroem & P. Ekloev, 1996. Size-specific interaction in lake systems: predator gape limitation and prey growth and mortality. Ecology 77: 900–911.

Pihu, E., 1993. Distribution of fish species in Estonian lakes. Proceedings of the Estonian Academy of Sciences Biology Ecology 3: 181–186.

Randall, R. G., C. K. Minns, V. W. Cairns & J. E. Moore, 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 53/1: 35–44.

Romare, P., E. Bergman & L.-A. Hansson, 1999. The impact of larval and juvenile fish on zooplankton and algal dynamics. Limnology and Oceanography 44(7): 1655–1666.

Rowe, K., 1994. Vertical segregation and seasonal changes in fish depth distributions between lakes of contrasting trophic status. Journal of Fish Biology 45: 787–800.

Ryder, R. A., S. R. Kerr, K. H. Loftus & H. A. Regier, 1974. The morphoedaphic index, a fish yield estimator – review and evaluation. Journal of the Fisheries Research Board of Canada 31: 663–688.