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WATER-LEVEL FLUCTUATIONS

Effects of water-level regulation on the nearshore fish community in boreal lakes

Tapio Sutela · Teppo Vehanen

Abstract The fish community in the littoral areas of eight regulated lakes and five reference lakes in Finland was sampled by electrofishing. No significant effect of winter drawdown on species richness was recorded across lakes. Total fish density for stony bottoms of the regulated and reference lakes averaged 19.3 and 32.7 individuals per 100 m^2, respectively, but this difference was not statistically significant. The combined proportion of littoral fish species, including minnow (*Phoxinus phoxinus*), bullhead (*Cottus gobio*), alpine bullhead (*Cottus poecilopus*), nine-spined stickleback (*Pungitius pungitius*), and stone loach (*Barbatula barbatula*), supplemented with zoobenthos feeders ruffe (*Gymnocephalus cernuus*) and young burbot (*Lota lota*), was much lower in the regulated lakes than in the reference lakes. Besides winter drawdown, other variables, such as nutrient level and lake size, affected the fish community.

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Ecological Effects of Water-Level Fluctuations in Lakes

T. Sutela (✉)
Finnish Environment Institute, P.O. Box 140,
00251 Helsinki, Finland
e-mail: tapio.sutela@rktl.fi

T. Vehanen
Finnish Game and Fisheries Research Institute,
Oulu Game and Fisheries Research, Tutkijantie 2 E,
90570 Oulu, Finland

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Introduction

The water level of about 220 lakes (area > 1 km^2) in Finland is regulated, mainly for hydroelectric purposes (Alasaarela et al., 1989). The water level is lowered 0.5–7 m by increasing discharge in winter, when the consumption of electricity is highest. Finnish lakes are typically shallow with a considerable proportion of the bottom area falling dry and partly freezing during the winter. Ice of about 0.5–1 m in thickness descends on the littoral zone and presses the bottom, thus extending the impact of winter drawdown still deeper. In the spring, snow melts refilling the lakes with the aid of the reduced discharge. Spring flooding does not exist, and the water level is usually kept quite constant over the summer until late autumn.

Water-level regulation via a winter drawdown has been documented to affect littoral geomorphology (Hellsten, 1997), vegetation (Hellsten & Riihimäki, 1996), zoobenthos (Palomäki & Koskenniemi, 1993), and fish fauna (Gaboury & Patalas, 1984; Paller, 1997). The impact of abnormal water fluctuation is generally most evident in the littoral zone exposed to temporal falling dry. This pattern suggests that littoral fish species are especially vulnerable to winter drawdown. Littoral fish are forced to leave their habitat temporarily to avoid falling dry in winter. Fish species may have different strategies in responding to limited habitat availability in the low-water-level period (Fischer & Öhl, 2005). Breeding of fish species that spawn in shallow littoral waters may be disturbed by water-level fluctuation (Gafny et al., 1992). Available food resources for fish may diminish following the reduction in zoobenthos biomass in the littoral areas of the regulated boreal lakes (Grimås, 1961, Palomäki & Koskenniemi, 1993, Koskenniemi, 1994). Thus, littoral and zoobenthivore fish species may be especially vulnerable to winter drawdown. In this study, we sampled littoral fish assemblages in regulated and non-regulated lakes in order to examine differences between them and to evaluate possible impact mechanisms of winter drawdown.

Materials and methods

Lakes studied

Five natural reference lakes with normal water-level fluctuation and eight regulated lakes in Northern Finland were studied (Table 1). The magnitude of water-level fluctuation is expressed as winter drawdown, which denotes the difference in water level between freeze-up in late autumn and the annual minimum of late winter. The range of the average winter drawdown in the regulated lakes was 1.54–6.75 m, whereas in the reference lakes the natural winter drawdown was less than 0.4 m. Lake size ranged from 12 to 887 km^2, while mean depth varied between 4.2 and 9.7 m. The lakes can be classified as oligotrophic or mesotrophic on the basis of their total phosphorus content (Forsberg & Ryding, 1980). Brown colour reflects the effect of organic compounds originating from boggy catchment. Nutrient loading from agriculture and forestry has caused deterioration in water quality on a small scale in all the lakes.

Electrofishing

In August of 2003–2005, a total of 256 electrofishings were conducted in the five reference lakes and eight regulated lakes (Table 2). Only the deepest, non-wadable rocky shores were excluded from the randomised site selection. The mean number of electrofishings per lake was 20, with large lakes usually having higher numbers. Average depth in the sampled 100-m^2 areas was 30 cm. Fish were captured with Hans Grassl GmbH ELT 6011 GI Honda GXV50 electrofishing gear using pulsed (50-Hz) DC current with a voltage of 800–1000 V. Each area was fished once by two waders, one using the anode and an assistant collecting the stunned fish with a dip-net. Escape nets were used only with some exceptional sand bottoms having no stones or vegetation, which could offer a hiding place for the fish.

Table 1 Characteristics of the lakes studied

Lake	Water-level fluctuation	Winter drawdown (m)	Surface area (km^2)	Mean depth (m)	Total phosphorus (µg/l)	Brown colour (mg Pt/l)	pH
Simojärvi	Natural	0.22	90	5.0	9	33	6.8
Pesiöjärvi	Natural	0.27	13	4.2	12	50	6.5
Änättijärvi	Natural	0.32	24	9.7	9	60	6.6
Lentua	Natural	0.40	78	7.4	9	50	6.6
Kellojärvi	Natural	0.43	22	5.0	16	80	6.7
Oulujärvi	Regulated	1.54	887	8.4	14	57	6.7
Koitere	Regulated	1.76	164	8.2	11	70	6.5
Kiantajärvi	Regulated	3.12	169	7.6	11	60	6.5
Iso-Pyhäntä	Regulated	3.50	12	6.9	16	85	5.7
Ontojärvi	Regulated	3.51	105	5.7	15	60	6.6
Kostonjärvi	Regulated	4.02	44	5.1	11	40	7.0
Vuokkijärvi	Regulated	4.71	51	5.0	18	70	6.4
Kemijärvi	Regulated	6.75	206	5.5	16	80	6.8

Table 2 Sampling dates and characteristics of the sampled areas (reference lakes in italics)

	Sampling year	Sampling date	Electro-fishings (N)	Water temp. (°C)	Mean depth (cm)	Stony bottom (N)
Simojärvi	2005	10–11 Aug.	21	18.6	29	19
Pesiöjärvi	2004	19 Aug.	12	16.7	24	8
Änättijärvi	2003	18–21 Aug.	20	17.2	31	17
Lentua	2003	11–22 Aug.	23	17.9	35	15
Kellojärvi	2005	1–2 Aug.	16	19.1	27	9
Oulujärvi	2004	4–8 Aug.	22	21.5	31	15
Koitere	2005	3–4 Aug.	20	20.1	27	15
Kiantajärvi	2004	16–18 Aug.	18	16.5	30	13
Iso-Pyhäntä	2004	2–5 Aug.	18	19.7	40	3
Ontojärvi	2003	25–28 Aug.	20	15.9	29	12
Kostonjärvi	2005	8–9 Aug.	20	18.2	27	17
Vuokkijärvi	2004	9–12 Aug.	20	19.4	27	14
Kemijärvi	2004	23–27 Aug.	26	14.1	29	20
Mean			20	18.1	30	13.6

Environmental conditions, including water temperature, mean and maximum depth over the area, bottom quality, and percentage coverage of vegetation, were recorded. Bottom quality was assessed as percentages of the area in the classes organic bottom, sand bottom (particle size of 0–2 cm in diameter), and stony bottom (particle size > 2 cm). Stony bottoms dominated in our material (Table 2).

Statistical methods

Canonical correspondence analysis (CCA) (ter Braak, 1986, ter Braak & Verdonschot, 1995) was used to analyse species/environment relationships with the program PC-ORD (McCune & Mefford, 1999). The significance of the patterns detected was tested with Monte Carlo permutations (100 permutations). ANOVA and ANCOVA were used to compare average species richness in the regulated and reference lakes, and Mann–Whitney for fish densities. In addition, Pearson and Spearman correlation analyses were applied on different occasions.

Results

Species richness

In total, 11 fish species were recorded in the littoral electrofishings (Table 3). The number of fish species recorded for a single lake varied between 3 and 9, averaging 5.6 in the reference lakes and 6.8 in the regulated lakes. As a biasing factor, the size of the lake correlated with the number of species recorded (Pearson correlation, $R^2 = 0.63$, $P < 0.01$, area of the lake ln-transformed). The mean area of the regulated lakes was greater than that of the reference lakes. Secondly, the number of electrofishings tended to increase with lake area. When we harmonised the data by counting the number of species recorded after 16 electrofishings and excluded Pesiöjärvi lake (number of electrofishings: 12), we still had higher average species richness for regulated lakes (6.4) than in reference lakes (5.5). This difference was not statistically significant, whether or not we took lake area (ln-transformed) as a covariate (ANCOVA and ANOVA, $P > 0.05$ in both cases).

Stone loach (*Barbatula barbatula*), nine-spined stickleback (*Pungitius pungitius*), and dace (*Leuciscus leuciscus*) were recorded only in regulated lakes. None of the fish species emerged as an evident indicator species for lake regulation in terms of its existence or non-existence in the reference and regulated lakes.

Fish densities

Total fish density and species composition varied considerably among the lakes (Fig. 1). Total fish density averaged 18.3 individuals per 100 m^2 (SD

Table 3 Fish species identified in the electrofishing catch of the five reference lakes with natural water-level fluctuation (in italics) and the eight regulated lakes

	Minnow	Nine-spined stickleback	Bullhead	Alpine bullhead	Stone loach	Perch	Ruffe	Pike	Burbot	Roach	Dace	Number of species
Simojärvi			x			x	x	x	x			5
Pesiöjärvi	x							x	x			3
Änättijärvi	x		x	x		x	x	x	x	x		8
Lentua	x		x			x	x	x	x	x		7
Kellojärvi			x			x	x	x	x			5
Oulujärvi		x	x		x	x	x	x	x	x	x	9
Koitere	x			x		x	x	x	x	x	x	8
Kiantajärvi	x	x		x		x	x	x	x			7
Iso-Pyhäntä						x	x	x	x			4
Ontojärvi	x		x			x	x	x	x	x		7
Kostonjärvi	x		x			x	x		x			5
Vuokkijärvi						x	x	x	x	x	x	6
Kemijärvi		x	x			x	x	x	x	x	x	8

13.3) in the regulated lakes and 23.7 per 100 m^2 (SD 9.9) in the reference lakes, but this difference was not statistically significant (Mann–Whitney, $P > 0.05$). For stony bottoms of regulated and reference lakes, total fish density averaged 19.3 and 32.6 ind./100 m^2, respectively, but even this difference was not statistically significant (Mann–Whitney, $P > 0.05$).

The most abundant fish species were minnow (*Phoxinus phoxinus*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernuus*), and bullhead (*Cottus gobio*). Perch density was high in regulated lakes, with the exception of the two lakes with the greatest winter drawdown (Fig. 1). The high density of 0+ cyprinid fish in the lake Oulujärvi was based on one electrofishing catch of about 400 small individuals that could not be identified as to species.

Five of the fish species caught—minnow, bullhead, alpine bullhead (*Cottus poecilopus*), stone loach, and nine-spined stickleback—were classified as littoral species because they spend their entire life in littoral areas and were thus caught also as adults. The individual size in these species is small, usually below 10 cm in total length (TL). With other fish species—namely, perch, ruffe, pike (*Esox lucius*),

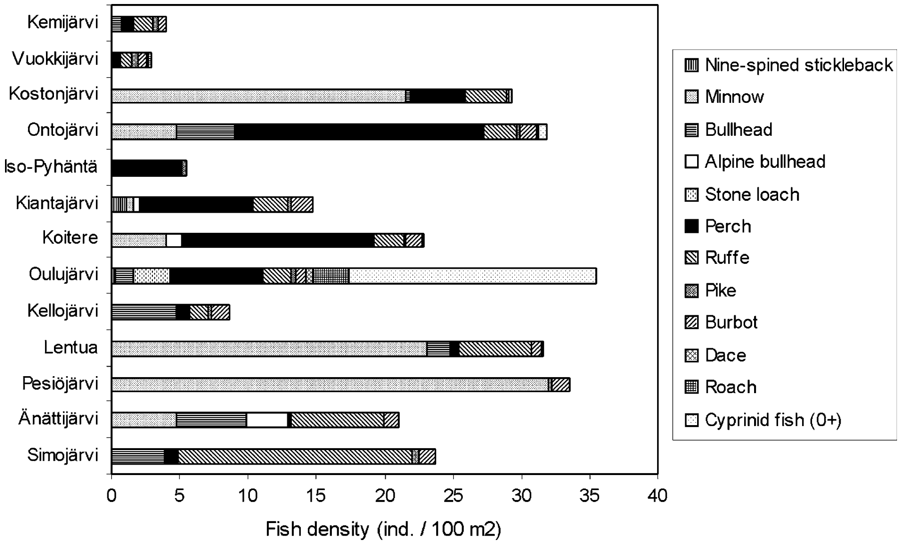


Fig. 1 Average fish densities in the five reference lakes (Simojärvi–Kellojärvi) and in the eight regulated lakes (Oulujärvi–Kemijärvi), based on a single electrofishing run

burbot (*Lota lota*), roach (*Rutilus rutilus*), and dace—young individuals in 0+ and 1+ age classes dominated in our catch. The majority of these individuals were below 15 cm in TL.

According to our preconception, littoral and zoobenthivore fish species were considered especially vulnerable to winter drawdown because of the possible impact in over-winter predation mortality, reproductive success, and food availability. Winter drawdown explained 62% of the variance ($P < 0.01$) in the combined proportion of littoral species and zoobenthos feeder (juvenile burbot and ruffe) biomass for stony shores of the lakes (Fig. 2). Lake Iso-Pyhäntä was omitted from this figure because of its small amount of stony shores (Table 2). Judged from the figure, there may be a threshold value for winter drawdown at about one metre, after which the increase in winter drawdown elevates the response no further. The average percentages of littoral species plus zoobenthos feeders in the regulated and reference lakes were 55.6 and 91.9 %, respectively. This difference was statistically significant (Mann-Whitney, $P < 0.001$).

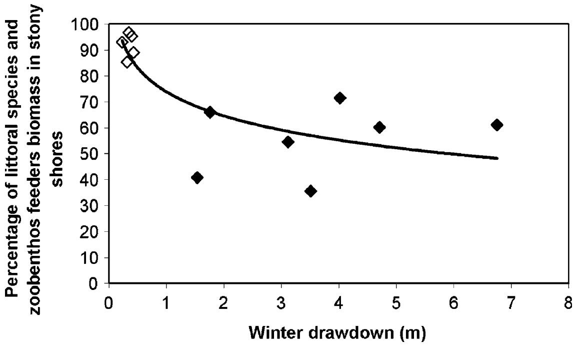


Fig. 2 Combined percentage of littoral species (minnow, bullhead, alpine bullhead, stone loach, and nine-spined stickleback) and zoobenthos feeder (young burbot and ruffe) biomass for stony shores (%) in relation to winter drawdown (m) in the regulated lakes (*filled diamonds*) and reference lakes (*open diamonds*). The curve follows the equation $y = -13.51 \ln(x) + 73.94$, $R^2 = 0.62$

Effects of environmental variables on fish assemblage

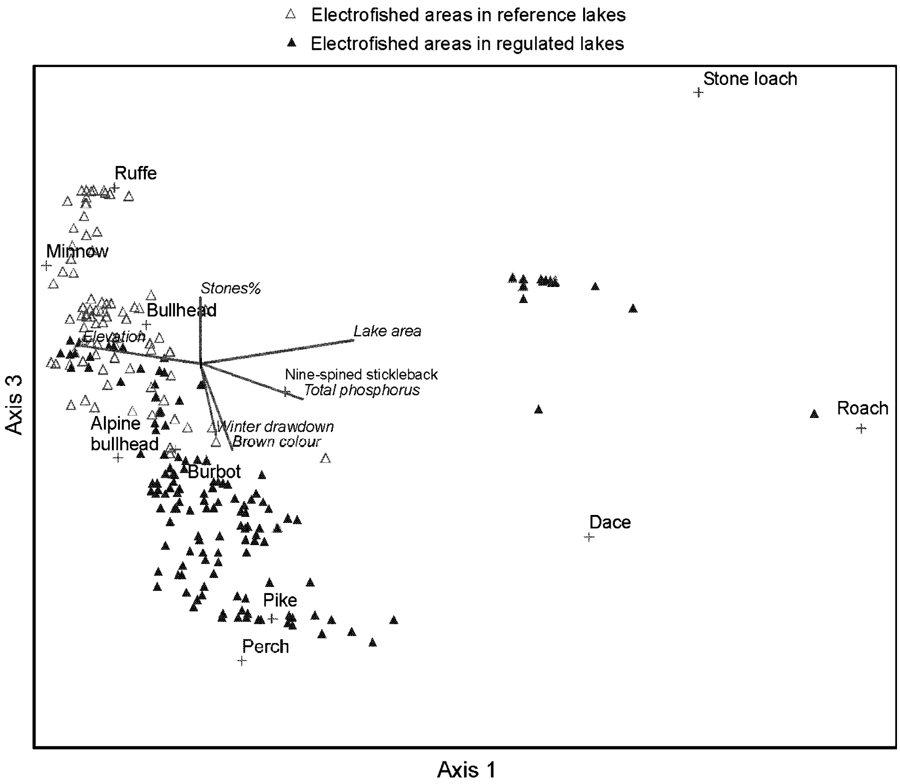
The three significant axes of CCA explained 24% of the variance in the density data of the fish species (Table 4). The first CCA axis was most strongly correlated with lake area and the second axis with coverage of macrophytes. The third axis was strongly correlated with water colour and winter drawdown. In the biplot of axes 1 and 3, the overlap of the electrofished areas in reference lakes and regulated lakes is limited to a small area (Fig. 3). The separate clump in the right section of the figure is formed from the electrofishing areas of lake Oulujärvi. The biplot

Table 4 Summary of the results from canonical correspondence analysis (CCA) relating the densities of all fish species in electrofished areas and lake-specific environmental factors

Total variance in the fish species abundance data = 5.26	Axis 1	Axis 2	Axis 3
Eigenvalues	0.658	0.328	0.268
Cumulative proportion (%) of variance explained	12.5	18.7	24.2
Monte Carlo test (*P*-value, 100 permutations)	0.01	0.01	0.01
Environment/fish species correlations*			
Winter drawdown	0.076	0.036	−0.608
Latitude	−0.226	−0.098	0.489
Elevation above sea level	−0.731	0.290	0.233
Lake area	0.957	−0.109	0.176
Total phosphorus	0.645	−0.148	−0.317
Colour of the water	0.186	−0.125	−0.809
Proportion of stony bottom in the electrofished area (%)	0.011	−0.280	0.558
Coverage of macrophytes (%)	0.415	0.737	−0.127
Maximum depth in the electrofished area	−0.074	−0.204	−0.086

* Intra-set correlations (ter Braak, 1986)

Fig. 3 Biplot of axes 1 and 3 of the canonical correspondence analysis (CCA) relating environmental variables and fish abundances. Open and filled triangles represent the electrofished areas in the reference and regulated lakes, respectively. Environmental variables are represented by lines that roughly point towards the factor direction of maximum variation. The length of the line corresponds to the importance of that variable in assemblage ordination



suggests that increasing water colour and winter drawdown favoured perch and pike but depressed minnow and ruffe.

Minnow were not caught in the five lakes where total phosphorus exceeded 14 µg/l. One of these five lakes was a reference lake (Fig. 4). In all other lakes with lower phosphorus content, minnow were recognised, with the exception of lake Simojärvi. Minnow density correlated negatively with phosphorus content (Spearman r −0.61, $P < 0.05$). Of the other fish species, ruffe also density correlated negatively with total phosphorus content (Spearman r −0.72, $P < 0.01$).

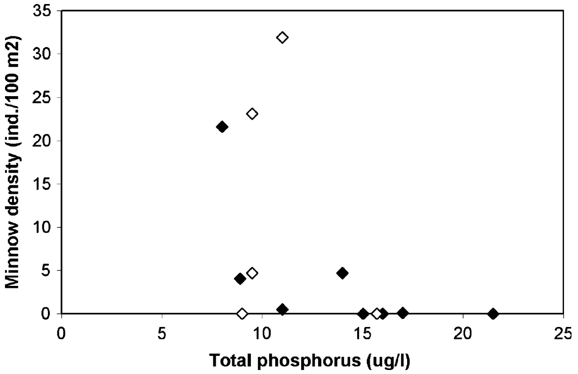


Fig. 4 Average minnow density in relation to total phosphorus (µg/l) in regulated lakes (*filled diamonds*) and reference lakes (*open diamonds*)

Discussion

Our results suggest that water-level fluctuation from man-made winter drawdown did not have clear response in terms of species richness or total fish density in the nearshore areas. Still, some changes probably affected by winter drawdown were seen in the relative abundance of certain fish groups. Also, other factors, such as lake area, had an impact on the littoral fish assemblages.

Our hypothesis that all littoral fish species are highly vulnerable to winter drawdown may be wrong. Nine-spined stickleback was recorded only in three large regulated lakes, including the most heavily regulated lake, Kemijärvi. Unlike all other littoral species, nine-spined stickleback did not seem to hide under stones; moreover, this species was often caught in the surface water. Benthic fish species, like stone loach and bullhead, favour stony habitat where they can hide within stone interstitials for shelter (Smyly, 1955; Sauvonsaari, 1971, Hyslop, 1982; Fischer & Eckmann, 1997). Besides predation effects, lack of sheltering stony habitat may substantially affect metabolism and somatic growth rates in benthic fish (Fischer, 2000). Winter drawdown may force fish to migrate to a much deeper zone with limited areas of stony bottom. Running dry of the stony littoral habitat may not harm nine-spined stickleback as much as benthic fish species.

Littoral fish species may move to deeper areas during winter even in non-regulated lakes. In Ovre Heimdalsvatn, southern Norway, minnows moved from very shallow water to deeper water of about 1 m, where they possibly remained throughout the period of ice cover (Lien, 1981). We lack knowledge concerning the habitat choice and preferred depth of littoral fish in winter. Littoral species favouring stony bottoms in the open-water period probably follow the same habitat choice in winter, if possible.

In the two highly regulated lakes Vuokkijärvi and Iso-Pyhäntä, no littoral species existed. These lakes showed some individual characteristics possibly coupled with the littoral fish assemblage. In the nearshore areas of Vuokkijärvi, we noted a specially clear pattern of stones being embedded in the sand in such a way that no hiding place remained under them for fish. The shores of lake Iso-Pyhäntä often had a narrow (1–2 m wide), stony, deeply sloping belt after which there started a gently sloping sandy bottom without stones. These special characteristics in the littoral morphology may arise from the degree by which the water level was raised at the start of their regulation (see Hellsten, 2000).

Besides this study, the positive impact of lake area on species richness has been documented in several other studies (e.g. Browne, 1981, Matuszek & Beggs, 1988). Stone loach was found only in Oulujärvi, which is a large, relatively southerly, and mildly regulated lake. The northernmost lake in our study, Kemijärvi, is outside the distribution range of stone loach (Koli, 1990).

Several studies have found minnow to be especially sensitive to eutrophication or other deterioration of water quality (Bagge & Hakkari, 1985, Rajasilta et al., 1999, Karels & Niemi, 2002). The results of this study support these findings. In our heterogeneous lake group, simultaneous responses to several coexistent environmental variables probably hindered clear identification of the effects of winter drawdown in fish species level. Still, after grouping of the fish species our results suggested an impact of water-level regulation on fish community level.

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