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Water level regulation in winter triggers fouling of fishing nets by the diatom *Aulacoseira islandica* in a boreal lake

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Water level regulation related to hydroelectric power production and flood prevention is an important hydro-morphological pressure on many watercourses around the world. Fouling of fishing nets in autumn during the open water period and in winter under the ice is a common phenomenon in large Finnish lakes where the water level is regulated. This fouling of fishing nets can sometimes be so extensive that fishing has to be stopped. Based on the practical experiences of fishermen, the main cause for the under-ice fouling has been proposed to be the winter draw-down of water causing low water level and stronger currents in lakes, but no conclusive relationship between fouling and water level regulation has yet been demonstrated. Here we show, using long-term winter data from a boreal lake and short-term netting experiments, that fouling of fishing nets results from increased water draw-down during winter (January–March). Our results also show that fouling of fishing nets takes place only if the high water flow rates are accompanied by an intensive lowering of the water level. We also discuss the relevance of our results to other regulated lakes with ice cover.

Introduction

Many lakes in Fennoscandia, Scotland and Austria are subject to water level regulation related to hydroelectric power production and flood prevention (e.g. Marttunen *et al*. 2006). In such lakes, the amplitude of regulation or winter draw-down varies from 0.1 to 35 metres, although in Finland the range of variation in water level is typically only a few metres (< 10.5 m; Marttunen *et al*. 2006, Hellsten 1997). Changes in water level can cause considerable geomorphological changes and erosion in the littoral region of lakes (Hellsten 1997), with negative effects on littoral flora (Hellsten 2001) and fauna (e.g. Palomäki 1994, Palomäki and Koskenniemi 1993, Aroviita and Hämäläinen 2008) as well as on reproduction of spawning fish (Cott *et al*. 2008, Sutela and Vehanen 2008, Gertzen *et al*. 2012). Water level regulation has also often been suggested

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to lead to fouling of stationary fishing gear and hence to impede professional and occupational fishing. However, no conclusive relationship between water level regulation and fouling of fishing nets has yet been established.

Fouling of fishing nets is often one of the first signs of deteriorating water quality (e.g. Heinonen *et al*. 1984, Willén 2001). The most common microorganisms causing fouling or clogging of fishing nets are planktonic diatoms of the genera *Aulacoseira*, *Melosira*, *Fragilaria*, *Tabellaria* and *Asterionella* forming filaments or star-like colonies, and cyanobacteria such as *Aphanizomenon* and *Dolichospermum* (*Anabaena*) forming long filaments. In clear water lakes, a filamentous green alga, *Hyalotheca dissiliens*, may attach to fishing nets during summer and cause fouling. In humic lakes, the raphidophyte, *Gonyostomum semen* (Lepistö 1992), is most often the species causing problems. Suspended organic and inorganic material and water plants may also cause fouling of fishing nets.

Microorganisms causing fouling are often most abundant during summer (e.g. Lepistö 1992), but fouling of fishing nets can also occur during winter. Under-ice fouling is most commonly caused by diatoms which have a thick and sticky organic coating (Willén 1991). From November to March, the centric diatom *Aulacoseira* (*Melosira*) *islandica* is known to be dominant in many large, deep and well mixed lakes, such as Lakes Erie and Ontario (Reavie & Barbiero 2013), Lake Baikal (species originally named as *A. baicalensis*; Edgar & Theriot 2004), Lake Como (Scheffler & Morabito 2003), Lake Iseo (Garibaldi *et al*. 2003). In the large Swedish lakes, Vänern, Vättern, Mälaren and Hjälmaren, *A. islandica* has been known to stick to fishing nets to such an extent that fishermen had to stop fishing (Willén 2001).

According to observations made by fishermen, fouling of fishing nets under winter ice cover is also a common phenomenon in large regulated lakes in Finland. Under-ice fouling of fishing nets in lakes in southern Finland has been reported for Pyhäjärvi (S. Moilanen and H. Nieminen unpubl. data) and Lakes Konnivesi and Ruotsalainen (Anttila-Huhtinen and Manninen 1997, Raunio 2005). Under-ice fouling in regulated lakes has been suggested to be caused by winter draw-down which leads to a lower water level and stronger currents. However, no causal relationship between fouling of fishing nets and winter draw-down has yet been demonstrated. Fouling of fishing nets does not necessarily occur every year and it seems not to be directly proportional to the amount of release of water (e.g. Anttila-Huhtinen and Manninen 1997). The situation is further complicated by the fact that fouling of fishing nets also occurs in lakes where the water level is not regulated (Leminen 2007; S. Moilanen and H. Nieminen, unpubl. data). Comprehensive studies are lacking, and the preliminary reports (Anttila-Huhtinen and Manninen 1997, Raunio 2005, S. Moilanen and H. Nieminen unpubl. data) have not been able to conclusively establish the primary reason for the fouling of fishing nets.

In this study, we focused on the fouling of fishing nets in Pyhäjärvi (southern Finland), which often experiences two major periods of fouling of fishing nets. The first fouling period starts in autumn when the water temperature falls below 8–10 °C. The second fouling period takes place under the ice in January–March during winter draw-down, at the time of stronger currents promoting resuspension of sedimented organic and inorganic material. This resuspended matter, in turn, has been suggested to cause fouling of fishing nets and to reduce fishing potential. We tested the hypothesis that winter draw-down causes the fouling of fishing nets in Pyhäjärvi using two approaches. First, we related the ranked remarks on the state of fishing nets, as described in the catch account books of fishermen, to the amount of water released, water level, and other physical and chemical variables. Second, we performed winter netting experiments to study the composition of the material causing the fouling of fishing nets. By these approaches we were able to confirm for the first time a relationship between fouling of fishing nets and increased water draw-down during winter.

Material and methods

Study area

Pyhäjärvi is a lake in southern Finland (Fig. 1)

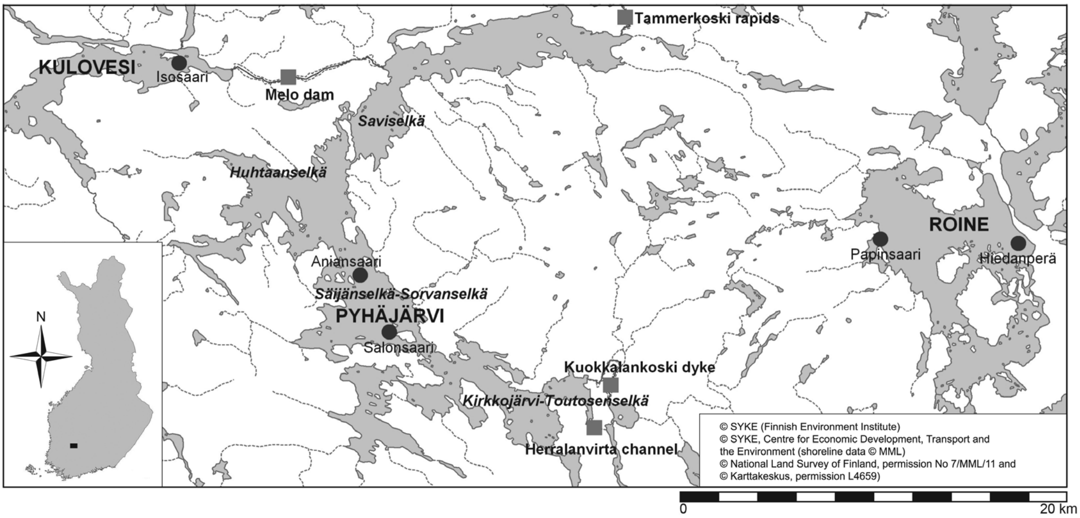

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Fig. 1. Map of the study area showing the studied sub-basins of Pyhäjärvi (Saviselkä, Säijänselkä–Sorvanselkä and Kirkkojärvi–Toutosenselkä), the areas where the netting experiments were conducted (Aniansaari and Salonsaari in Pyhäjärvi, Isosaari in Lake Kulovesi and Papinsaari and Hiedanperä in Lake Roine), and the locations of the Melo dam, the Herralanvirta channel, the Kuokkalankoski dyke, and the Tammerkoski rapids.

whose area is 121.6 km^2, mean depth 5.5 m, maximum depth 50 m, volume 0.67 km^3, and catchment area 17073 km^2. Water enters the lake from Vanajavesi through the Herralanvirta and Lempäälä channels in the south, and through the Tammerkoski rapids in the north. Water from the lake drains eastwards through the Nokianvirta into Lake Kulovesi and thence through a series of lake systems into the Kokemäenjoki and ultimately into the Bothnian Bay in the northern Baltic Sea.

During the last century, the lake has experienced considerable spring flooding. In 1899, a record-breaking flood increased the water level by 2.6 m. Since 1962 the water level of the lake has been regulated, primarily for hydroelectric power generation. The water level regulation is implemented by diurnal regulation at the Melo dam (Fig. 1) which causes short-term fluctuations of water level near the dam. The highest permitted water level fluctuation is 1.55 meters during winter draw-down but, the average yearly amplitude of water level fluctuation is only ca. 1.0 metres. The lake water level is also regulated in the south by the Kuokkalankoski dyke in the Herralanvirta channel, but the effect on the water level is minor compared to that of the Melo dam.

Fouling of fishing nets reported in catch accounting

Fishermen in Pyhäjärvi have agreed to keep accounts of their catches. These notes include information about fish species caught, and the number and biomass of each fish species in the catch. Many fishermen also make other notes, including the state of their fishing nets. We used these notes to characterize the occurrence of fouling events. We examined 177 catch notebooks kept by 28 fishermen during the years 1989–2010. We took into account all remarks made from September to April, the time encompassing the two periods of fouling in the lake.

For the study, Pyhäjärvi was divided into sub-basins (Fig. 1) representing the principal fishing areas. Three of the sub-basins, Kirkkojärvi-Toutosenselkä, Säijänselkä–Sorvanselkä and Saviselkä, are situated in the area of stronger currents. The sub-basin Huhtaanselkä, outside the influence of the stronger currents, was used as a control area.

The catch account data had some limitations. First, the number of fishermen in the sub-basins varied from 1 to 11 (Table 1). Second, the book keeping of catches is voluntary, and some fishermen did not return their notebooks every year. Third, as the reporting of the state of the fishing nets was not requested, the state of fishing nets was not always systematically reported. On average our data covered 85% of the fouling period (73%–97% depending on the basin). When only the beginning and end of the fouling period was recorded, we interpreted fouling of fishing nets to have happened throughout the intervening time. In some cases, observations about the state of the fishing nets were contradictory among fishermen fishing in the same sub-basin. For all these, we did not classify the severity of fouling of the fishing nets. For the statistical analysis the notes were normalized into monthly values: 1 = fouling and 0 = non-fouling.

Netting experiments

We studied the quantity and quality of the matter fouling the nets by performing four consecutive netting experiments. The netting areas in Pyhäjärvi were selected inside and outside the areas of the stronger currents. Experiments were also done in two neighbouring non-regulated lakes: Lake Kulovesi (Isosaari) and Roine (Papinsaari and Hiedanperä). The experiments were carried out between October 2011 and February/March 2012. Experiments in Pyhäjärvi, were conducted in two areas (Aniansaari and Salonsaari) situated in the Säijänselkä–Sorvanselkä sub-basin, inside the area of stronger currents. The third area (Riihiniemi) is situated in the Huhtaanselkä sub-basin, outside the main current area (Fig. 1).

The experiments were done according to Heinonen *et al.* (1984) and Herve and Heinonen (2004). Fish, especially roach, may attack the nets disturbing them. Therefore, to ensure three replicate nettings for the statistical analysis, four replicate nets were incubated. The nets (webbing 0.15 mm, mesh 20 mm) were attached to a frame of 50 × 50 cm. Prior to the experiment, the nets were washed with distilled water and dried at 60 °C for two hours and weighed after cooling in a desiccator. The lower edge of the net frame was anchored 1 m above the bottom of the lake facing the current and the nets were incubated for 14 days.

After incubation, the nets were lifted carefully, detached from the frames, put into plastic containers and transported to the laboratory. Nets were omitted from analysis if they had become detached from their frames or had caught several fish. The nets were rinsed with 2.0 l of distilled water. Half of the water was used for determination of chlorophyll *a* (SFS 5772:1993) and the other half for determination of total and organic solids (SFS-EN 872:2005).

For microscopic counting, 2 ml of the rinsing water was pooled to a composite sample of 6 ml, representing each incubation site. A subsample of 0.5 ml of each composite sample was then diluted with 2.5 ml of distilled water, stirred carefully and settled in 3 ml Utermöhl counting chambers for 4 hours. Samples were analyzed using inverted microscopy, applying a semi-quantitative method at a scale from 1 (solitary specimens in the sample) to 5 (several specimens in every field of view) from 10–30 fields of view with 260× magnification (Järvinen *et al.* 2011).

Table 1. Information on catch account notebooks kept by fishermen for Pyhäjärvi. The number of participating fishermen, years with accounts and total number of remarks of non-fouling and fouling events in Pyhäjärvi from September to April in 1989–2010.

	Number of		Years with catch accounting	Fouling of fishing nets		Total number of catch remarks
	fishermen	account books		no	yes	
Pyhäjärvi	29	177	1989–2010	214	215	429
Sub-basins						
Kirkkojärvi–Toutosenselkä	7	52	1993–2009	62	66	128
Säijänselkä–Sorvanselkä	11	65	1989–2010	54	75	129
Saviselkä	10	54	1991–2008	63	62	125
Huhtaanselkä	1	6	2001–2006	35	12	47

During the netting experiments, ambient phytoplankton composition and physical and chemical properties of the lake water were also monitored (water temperature, chlorophyll-*a* concentration, alkalinity, Secchi depth visibility, dissolved oxygen concentration and oxygen saturation, turbidity, conductivity, pH, water colour, total nutrient (P_{tot} and N_{tot}) concentrations, and ammonium nitrogen (NH_4-N) and sum of nitrate and nitrite nitrogen (NO_2 + NO_3-N) concentrations). Analyses were performed according to standard methods (e.g. APHA 1998)

Statistical analysis

We analysed the catch accounting data by modelling the relationship between the fouling of fishing nets and the measured environmental variables. Because the fouling of fishing nets (the dependent variable in the model) is dichotomous (0 = non-fouling, 1 = fouling), we used a stepwise binary logistic regression model. The logistic regression model is a special case of regression models for categorical (binary or multinomial) outcomes. The explanatory variables can be either continuous or categorical. With the logistic regression model, we were able to study the probability of a fouling event and how the predictor variables influenced this probability. The logistic regression model is expressed as $P = 1/[1 + \exp(-Z)]$, where P is the probability that the observations belong to group 1 (fouling). In the model: $Z = b_0 + b_1X_1 + \ldots + b_pX_p$. The regression coefficients $b_0, b_1, \ldots, b_p$ were estimated by iterations according to the highest probability. $X_1, \ldots, X_p$ were the variables explaining the fouling of fishing nets. We used a forward likelihood ratio test method to determine the order in which the variables were added one by one into the regression model. Prior to analysis, we checked that the normality, equality of variances and uncollinearity requirements of the test were met.

Our data contained 429 observations of fouling. Only the data for monthly discharge, water level and meteorological variables covered the whole study period. The physical and chemical properties of water are routinely monitored only during summer months and many data were missing. Variables with missing values could not be included in the binary logistic regression. Therefore, we also performed a non-parametric Kruskal-Wallis test to study if the distributions of the measured chemical and physical variables were similar when fouling or non-fouling was reported.

We used a non-parametric Kruskal-Wallis ANOVA to test the effect of measured environmental variables on the fouling of the experimental nettings, because the netting experiment data did not meet the requirements of parametric statistical tests. The statistical analyses were done using SPSS 15.0 and 20.0 (SPSS Inc.) and R 2.15.1 (R Core Team 2012).

Results

Biological, chemical and physical properties of the water

Pyhäjärvi has been monitored since 1963. Most physical and chemical data represent the open-water period (most often the summer months from July to September). Winter data are mainly available from March. Based on the chemical properties of the water, the lake can be considered mesotrophic (Table 2).

Phytoplankton sampling has been infrequent and mostly in summer (June–August). Only a few isolated data for quantitative phytoplankton composition and biomass were available for the study period. In March 1986, the centric diatom *Aulacoseira* comprised 70%–90% of the total phytoplankton biomass. In September 1986, the most abundant phytoplankton were the cyanobacterium *Aphanizomenon* and cryptomonads. In November 1986, *Aulacoseira* was again dominant, comprising 90% of the total biomass. From November 1996, the database of the Finnish Environment Institute (SYKE) has one notification of fouling of fishing nets by *Aulacoseira*.

With only a few exceptions (February 1997, and April 1995 and 1997), the minimum water level was reached in March (Fig. 2). During the years 1989–2010 the minimum water level was 0.31–0.81 m below the long-term average (1989–2010). The maximum monthly release of water (31–197 $m^3 s^{-1}$) was most often in February (Fig. 3), but varied between years from Janu-

Table 2. Secchi depth and concentrations of oxygen, chlorophyll *a*, and total nutrients in Pyhäjärvi during September–April 1989–2010. Values are mean ± SD (number of observations, *n*, in parentheses). Surface = 1 m depth, bottom = 1 m above sediment surface.

	Secchi depth (m)	Oxygen conc. (mg l^{-1})		Chl *a* 0–2 m ($\mu g\ l^{-1}$)	Total phosphorus ($\mu g\ l^{-1}$)		Total nitrogen ($\mu g\ l^{-1}$)	
		surface	bottom		surface	bottom	surface	bottom
Pyhäjärvi	1.9 ± 0.6 (n = 183)	10.4 ± 1.2 (n = 178)	7.7 ± 3.6 (n = 179)	12 ± 5.8 (n = 52)	26 ± 5.4 (n = 184)	88 ± 230 (n = 179)	771 ± 206 (n = 183)	894 ± 390 (n = 179)
Sub-basins								
Kirkkojärvi–Toutosenselkä	1.5 ± 0.5 (n = 44)	10.3 ± 1.2 (n = 44)	5.8 ± 4.8 (n = 44)	13 ± 6.4 (n = 20)	28 ± 6.4 (n = 44)	246 ± 427 (n = 44)	774 ± 180 (n = 44)	1096 ± 606 (n = 44)
Säijänselkä–Sorvanselkä	1.9 ± 0.7 (n = 69)	10.4 ± 1.4 (n = 66)	8.5 ± 1.8 (n = 67)	9 ± 4.2 (n = 22)	25 ± 4.1 (n = 70)	29 ± 6 (n = 67)	764 ± 231 (n = 69)	760 ± 186 (n = 67)
Saviselkä	2.0 ± 0.5 (n = 50)	10.4 ± 1.1 (n = 49)	8.6 ± 3.5 (n = 49)	14 ± 5.2 (n = 6)	26 ± 5.3 (n = 50)	41 ± 40 (n = 49)	768 ± 204 (n = 50)	861 ± 289 (n = 49)
Huhtaanselkä	2.1 ± 0.6 (n = 20)	10.6 ± 0.9 (n = 19)	7.4 ± 4.3 (n = 19)	17 ± 4.1 (n = 4)	26 ± 5.4 (n = 20)	54 ± 55 (n = 19)	796 ± 19 (n = 20)	981 ± 320 (n = 19)

ary to December and no significant correlation was found between minimum water level and maximum water discharge.

In autumn, before freezing, the predominant winds blow from the southwest, south or southeast, following the longest fetch of the main basins and causing wind-induced mixing. At the beginning of September, water temperature usually falls below 8–10 °C and the lake freezes over by the end of the year. In 1992, the lake froze over already in November, but in 2006–2007, and 2007–2008 the lake did not freeze over until the end of January. Ice-out occurs around the beginning of May, hence the duration of the ice-covered period varies from three to five months. The average thickness of the ice is from 0.27 to 0.77 m.

Catch accounting notes

Altogether, the catch account books contained 607 notes of the state of fishing nets. The notes deviated between basins, although most of the remarks (68%) concerned fouling rather than non-fouling of fishing nets. After the results were normalized into monthly values, 215 notes concerned fouling and 214 non-fouling (clean or almost clean fishing nets) (Table 1). Only in the Huhtaanselkä control area, outside the main current area, did most notes (74%) concern clean/non-fouling of fishing nets.

Fouling of fishing nets impeded fishing especially in autumn/winter 2002/2003 and 2004/2005. The timing of fouling events varied between the sub-basins. In the Säijänselkä–Sorvanselkä and Saviselkä sub-basins the first fouling period took place in autumn (October-November) and the second under the ice in January–March. In the Kirkkojärvi–Toutosenselkä sub-basin, there was only one fouling period under the ice (Fig. 4). No significant fouling was observed in the Huhtaanselkä control area.

The stepwise binary logistic regression models applied to Pyhäjärvi data showed higher predictive power for the non-fouling than fouling events (80%). The model result was significant ($p < 0.001$) when the deviation of monthly water level from the long-term yearly average (1996–2010) water level was used as the only

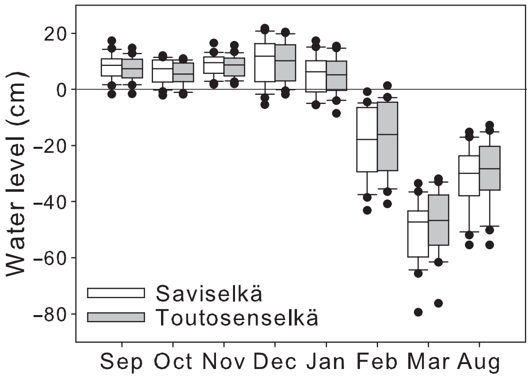

Fig. 2. Deviation of monthly water level from the long-term mean (1989–2010) in the Saviselkä and Toutosenselkä sub-basins of Pyhäjärvi. The box plot shows median, 25th and 75th percentiles (box boundaries), 10th and 90th percentiles (error bars) and outlying values (black circles).

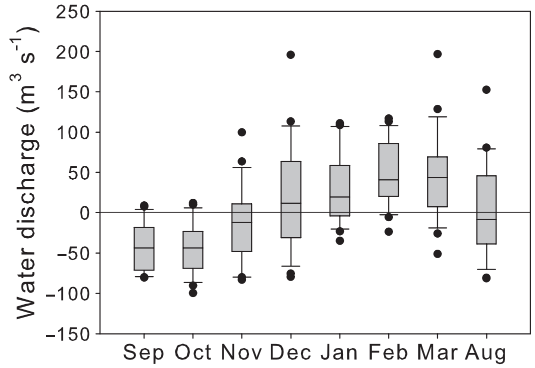

Fig. 3. Deviation of monthly water discharge from the long-term mean (1989-2010) at the Melo dam (*see* Fig. 1). The box plot shows median, 25th and 75th percentiles (box boundaries), 10th and 90th percentiles (error bars) and outlying values (black circles).

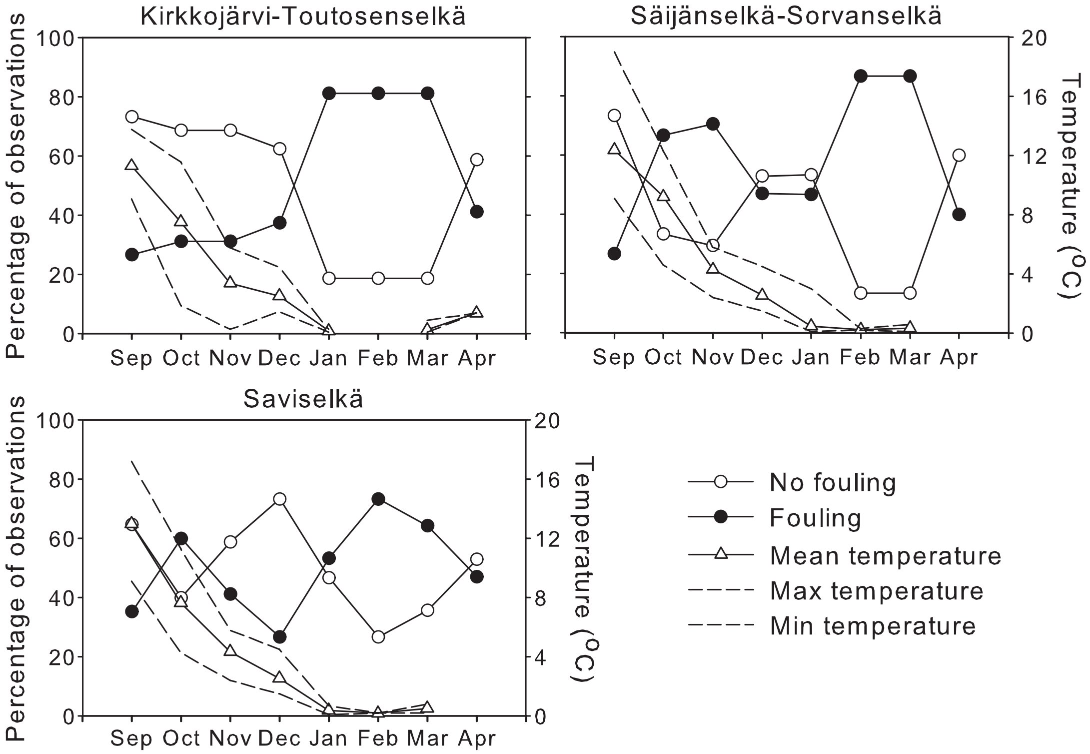

Fig. 4. Number of remarks in fishermen's account books concerning fouling of fishing nets [as normalized into monthly values] (1 = fouling, 0 = non-fouling) in the sub-basins of Pyhäjärvi and mean, min and max water temperature in September–August.

explanatory variable (Fig. 5). The model was also significant ($p = 0.045$) after the deviation of monthly release of water at the Melo dam from the long-term yearly average was added into the model. The model output shows that when the release of water is higher than average and the water level is lower than average the probability of fouling is high (Fig. 6); however, the

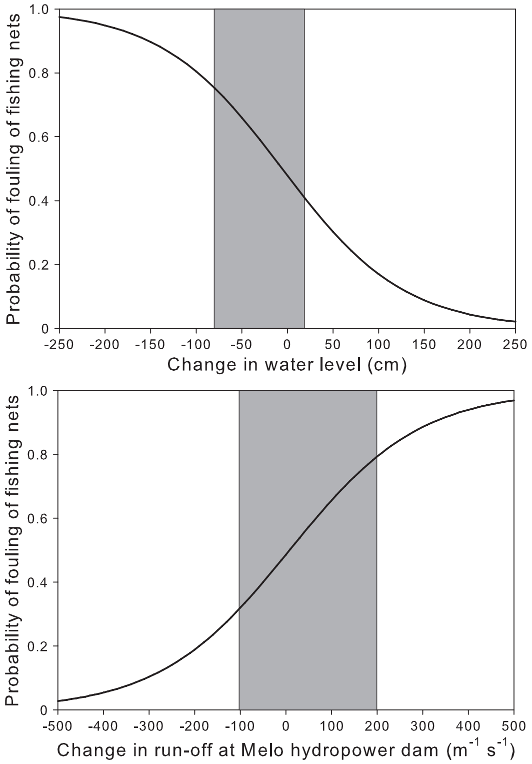

Fig. 5. Probability of fouling of fishing nets in Pyhäjärvi as a function of the change in the water level (upper panel) and as a function of the change in discharge at the Melo hydropower dam (lower panel). Grey area shows the range of change observed in the lake.

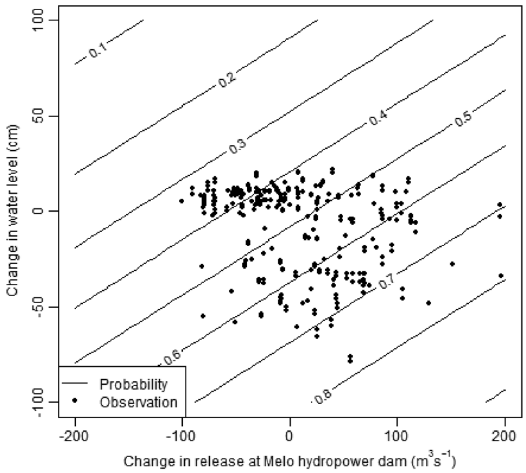

Fig. 6. Probability of fouling of fishing nets as a function of changes in water level and run-off in Pyhäjärvi. Observed combinations of the change in water level and run-off are shown as dots. The contour lines represent the probabilities of fouling in different situations.

coefficient of determination was only 3.0%–18.4% (Table 3). The predictive power of the models was generally rather low (51.1%–56.6%) and decreased in the models for individual sub-basins. The predictive power was highest for the Säijänselkä–Sorvanselkä sub-basin data and the model better explained the fouling than non-fouling events.

Results from the Kruskal-Wallis test were consistent with the results from the binary logistic regression model (Table 4). The deviation of monthly water level from the long-term yearly average was significantly different in the groups of fouling and non-fouling of fishing nets in Pyhäjärvi ($\chi^2_1 = 20.47$, $p < 0.001$), and also in the Kirkkojärvi–Toutosenselkä sub-basin ($\chi^2_1 = 10.86$, $p \leq 0.001$). Moreover, depth of snow ($\chi^2_1 = 19.37$, $p \leq 0.001$), depth and presence of ice cover ($\chi^2_1 = 18.85$, $p \leq 0.001$; and $\chi^2_1 = 10.75$, $p = 0.001$; respectively), mean wind speed ($\chi^2_1 = 9.90$, $p = 0.002$), maximum wind speed ($\chi^2_1 = 11.79$, $p = 0.001$), and direction of wind ($\chi^2_1 = 11.41$, $p = 0.001$), were observed to be different when fouling was detected or when the nets were clear in Pyhäjärvi (corresponding χ^2_1 values 20.57, 13.47, 16.67, 20.97, 20.15 and 20.75, $p \leq 0.001$, *see* Table 4), and in the Kirkkojärvi–Toutosenselkä sub-basin). In the Säijänselkä–Sorvanselkä sub-basin, the mean deviation of water level from the long-term yearly average was different for fouling and non-fouling events ($\chi^2_1 = 9.25$, $p = 0.002$). Instead, in the Saviselkä sub-basin the mean deviation of yearly release of water at the Melo dam from the long-term yearly average differed significantly depending on when fouling was reported or not ($\chi^2_1 = 4.04$, $p = 0.044$).

Netting experiments

Fouling of nets declined from November 2011 to February 2012. In November, fouling was most pronounced in Aniansaari and Salonsaari, both situated in the Säijänselkä–Sorvanselkä sub-basin (Fig. 7). Deposition of organic (maximum deposition 18–22 mg g^{-1} day^{-1}) and inorganic (maximum deposition 36–49 mg g^{-1} day^{-1}) matter was also considerably higher in Aniansaari and Salonsaari than in Riihiniemi (maximum deposition 1 and 14 mg g^{-1} day^{-1}, respectively). In Lake Kulovesi, fouling was most pronounced in December. In Lake Roine the fouling was minor throughout the netting experiment.

Accumulation of organic and inorganic matter differed significantly between the study areas (Kruskal-Wallis test: $\chi^2_2 = 14.336$, $p < 0.001$; and $\chi^2_2 = 16.219$, $p < 0.001$; respectively). In November, at the beginning of the netting experiments, the diatom *Aulacoseira islandica* comprised more than 90% of the ambient phytoplankton biomass in Pyhäjärvi (Fig. 8). It was also the most important contributor to the fouling of nets in Aniansaari and Salonsaari. In the Riihiniemi and Isosaari areas of Lake Kulovesi fouling was mainly caused by a filamentous cyanobacterium of the genus *Phormidium* and by *Aulacoseira*. In Lake Roine, fouling was caused by *Aulacoseira*, but chlorophyll-*a* concentration was significantly lower than in Pyhäjärvi. *Aulacoseira* was present in the ambient phytoplankton of Lake Roine. However, *Phormidium* was not found in the phytoplankton samples collected simultaneously at the end of each netting experiment in Lake Roine (Fig. 8). Detritus was most abundant on nets in Lake Kulovesi.

Chlorophyll-*a* deposition on the nets also decreased during late winter incubations (Fig. 9). During the experiments, the mean lake chlorophyll-*a* concentration was highest in Pyhäjärvi (ca. 34 μg l^{-1}), and lower in Lake Kulovesi (16 μg l^{-1}) and Lake Roine (5 μg l^{-1}). Accordingly, the minimum Secchi depth was only 1.0 m in Pyhäjärvi, 1.3 m in Lake Kulovesi, and 2.5 m in Lake Roine. In Pyhäjärvi the mean P_{tot} and N_{tot} concentrations were 30 μg l^{-1} and 750 μg l^{-1}, respectively. In Lake Kulovesi, P_{tot} was ~13 μg l^{-1} and in Lake Roine ~22 μg l^{-1}. The corresponding N_{tot} concentrations were < 400 μg l^{-1} in Lake Kulovesi and ~830 μg l^{-1} in Lake Roine. At the beginning of the first netting experiment water temperature was around 8 °C and declined by about 2 °C during each experiment, being close to 0 °C during the last experiment.

Table 3. Results of the stepwise binary logistic regression model, including explanatory rate, predictive power for the whole model and for fouling and non-fouling events, significance of explanatory variable (X_1 and X_2) and regression coefficients (b_0, b_1 and b_2).

Area	Step	*n*	Explanatory rate (%)	Predictive power (%)			Significance (*p*)			Coefficients		
				Model	fouling	non-fouling	Model	X_1	X_2	b_0	b_1	b_2
Pyhäjärvi	1	429	3.0	55.5	80.0	30.9	< 0.001	< 0.001[a]		–0.107	–0.016	
	2	429	4.8	52.7	67.3	38.2	0.045	0.006[b]	0.003[a]	–0.113	0.005	–0.014
Kirkkojärvi–Toutosenselkä	1	128	15.9	51.1	44.4	57.8	0.727	< 0.001[c]		0.775	–0.019	
	2	128	18.4	51.1	43.5	58.8	0.902	0.054[b]	< 0.001[c]	0.661	0.007	–0.017
Säijänselkä–Sorvanselkä	1	129	8.7	56.6	38.6	76.4	0.073	0.007[a]		0.204	–0.029	
Saviselkä	1	125	3.3	55.1	62.1	48.1	0.442	0.046[b]		–0.055	0.007	

[a] model includes deviation of water level from long-term yearly average water level.
[b] model includes deviation of release of water from long term yearly average water discharge at the Melo dam
[c] model includes sum of wind speed for the preceding month.

Discussion

The filament-forming centric diatom *A. islandica*

Table 4. Results of a non-parametric Kruskal-Wallis test (χ^2 is the test value, p is the asymptotic statistical significance). p values indicating statistically highly significant results ($p \leq 0.001$) are in boldface and significant results ($0.001 < p \leq 0.05$) are underlined.

Variable	Pyhäjärvi		Kirkkojärvi–Toutosenselkä		Säijänselkä–Sorvanselkä		Saviselkä	
	χ^2_1	p	χ^2_1	p	χ^2_1	p	χ^2_1	p
Monthly discharge/yearly mean discharge ratio ($m^3 s^{-1}$)	15.60	**< 0.001**	12.38	**< 0.001**	1.75	0.186	4.04	0.044
Monthly water level/yearly mean water level ratio (cm)	20.47	**< 0.001**	10.86	**0.001**	9.25	0.002	2.53	0.112
Snow depth (cm)	19.37	**< 0.001**	20.57	**< 0.001**	1.41	0.236	2.16	0.142
Depth of ice cover (cm)	18.85	**< 0.001**	13.47	**< 0.001**	4.09	0.043	1.56	0.212
Presence of ice cover (+/–)	10.75	**0.001**	16.67	**< 0.001**	0.12	0.726	0.69	0.405
Wind speed ($m s^{-1}$)	9.90	0.002	20.97	**< 0.001**	0.00	0.979	0.26	0.608
Maximum wind speed ($m s^{-1}$)	11.79	**0.001**	20.15	**< 0.001**	0.09	0.771	0.60	0.439
Sum of wind speed of preceding month ($m s^{-1}$)	9.84	0.002	21.02	**< 0.001**	0.00	0.996	0.28	0.596
Average wind direction	11.41	**0.001**	20.75	**< 0.001**	0.03	0.861	0.33	0.566
Sum of precipitation of preceding month (mm)	0.72	0.396	1.92	0.166	1.23	0.267	0.35	0.552
Secchi depth (m)	3.93	0.047	0.15	0.698	0.13	0.719	1.03	0.309
Chlorophyll *a* ($\mu g\ l^{-1}$, 1 m)	0.26	0.610	5.10	0.024	0.00	1.000	0.00	1.000
Total phosphorus ($\mu g\ l^{-1}$, 1 m)	4.55	0.033	4.57	0.032	2.99	0.084	0.38	0.537
Oxygen concentration ($mg\ l^{-1}$, 1 m above bottom)	5.88	0.015	6.32	0.012	1.06	0.303	0.02	0.902
Turbidity (FNU, 1 m above bottom)	4.40	0.036	3.26	0.071	0.85	0.358	1.37	0.242

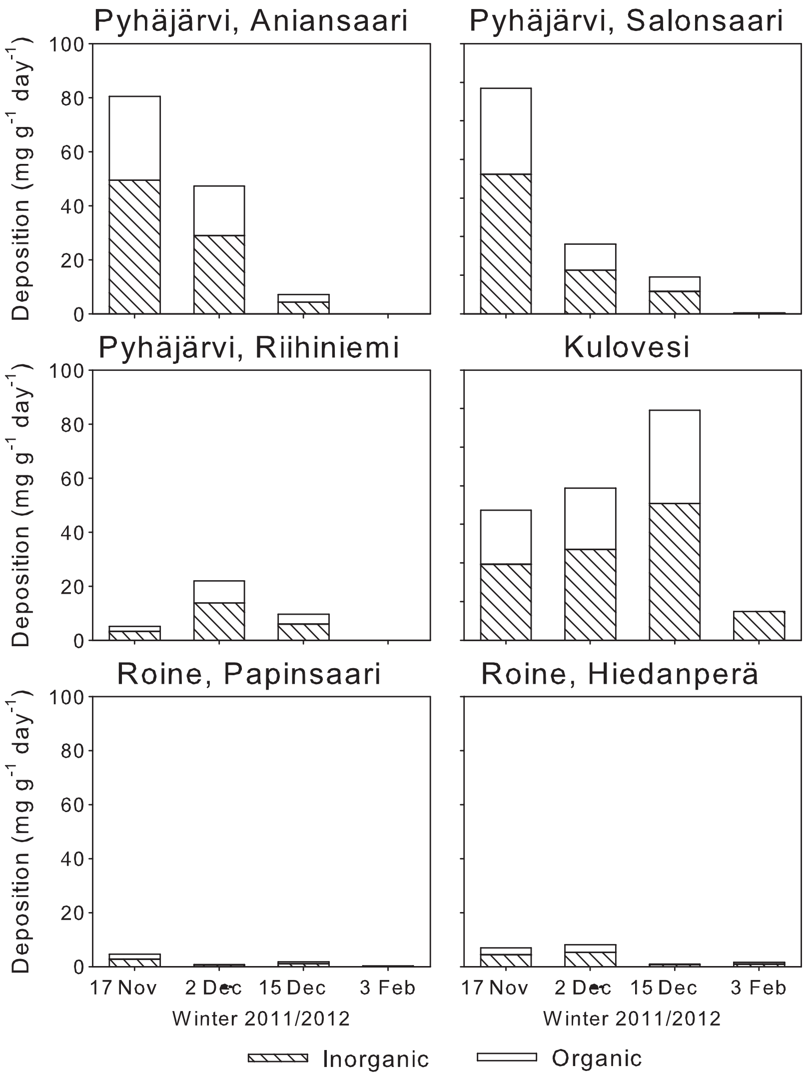

Fig. 7. Deposition of organic and inorganic matter during the netting experiments in Pyhäjärvi.

was the main reason for the fouling of fishing nets in Pyhäjärvi. Other organic and inorganic matter had only a minor role in fouling. *Aulacoseira* has been reported to have slimed/fouled/clogged fishing nets in Ringsjön in Sweden already in the 1880s and 1890s (Lung-Almestrand 1954), and it is still typically the primary cause of the clogging of fishing nets in large lakes in Sweden (Willén 2001).

According to the catch account notebooks of the fishermen, Pyhäjärvi experiences two periods of fouling of fishing nets. The first period of fouling takes place at the end of the open water season, in October–November. Autumn fouling of fishing nets is most pronounced in the Saviselkä and Säijänselkä–Sorvanselkä sub-basins and takes place when the water temperature drops below ca. 10 °C. *Aulacoseira islandica* is known to occur abundantly in water temperatures below 10–12 °C, with an optimum temperature for growth at ~6 °C (Cleve-Euler 1951, Lund-Almestrand 1954, Willén 1962, Stoermer *et al*. 1981). However, the autumn peak is mostly absent in the Kirkkojärvi–Toutosenselkä sub-basin, where, particularly during windy periods, fragments of water plants were found attached to fishing nets, which may have masked any fouling by diatoms.

Pyhäjärvi can be considered mesotrophic based on the total phosphorus concentration of

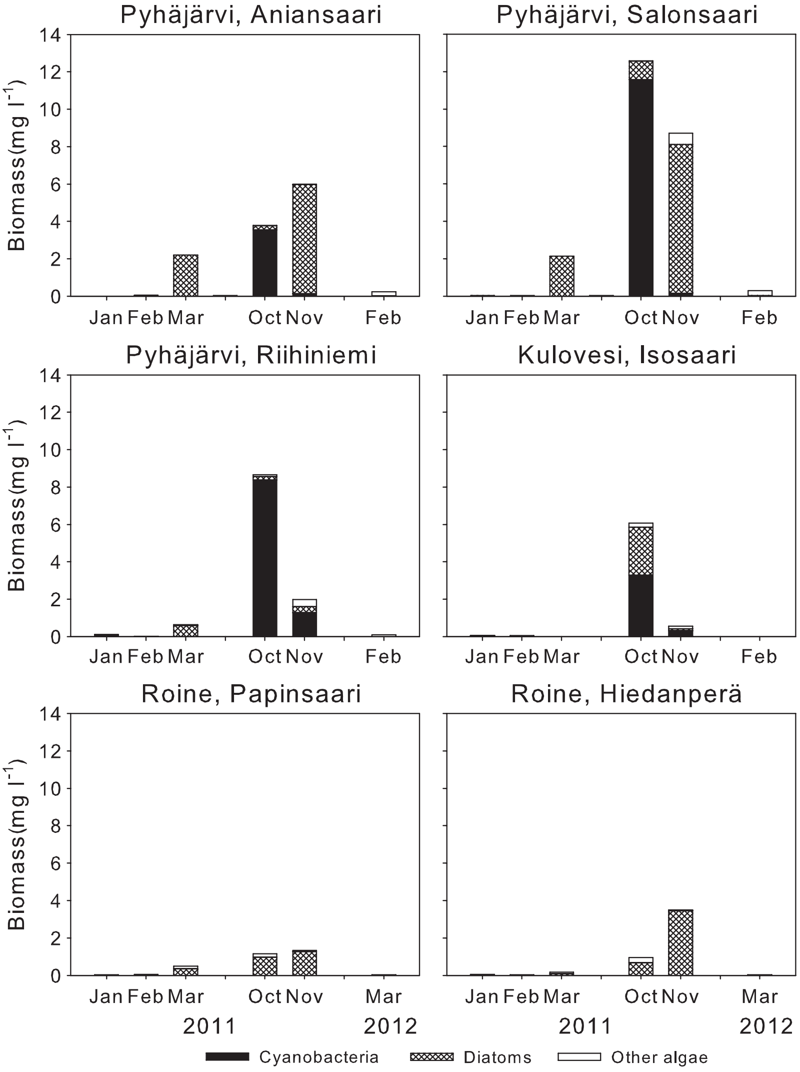

Fig. 8. Ambient phytoplankton biomass and composition of the most abundant phytoplankton groups (cyanobacteria and diatoms) during the netting experiments in Pyhäjärvi, Kulovesi and Roine.

20–30 μg l^{-1}. *Aulacoseira islandica* is most often found in oligo- and slightly mesotrophic lakes, but it may benefit from eutrophication. In the Laurentian Great Lakes it was found to be abundant in littoral areas where nutrient concentrations were higher (Stoermer *et al*. 1981). It has also been reported to form under-ice mass occurrences in highly eutrophic lakes (Ventelä *et al*. 1998, Blank *et al*. 2009).

The second period of fouling of fishing nets took place under the ice in February–March. This peak coincided with winter draw-down to hinder spring flooding. Water circulation under the ice is usually negligible in unregulated lakes due to the exclusion of wind mixing which limits the possibilities for phytoplankton to stay suspended in the water. *Aulacoseira* filaments are reported to sink at a rate of 0.7–8.0 m day^{-1} (Titman and Kilham 1976, Sommer 1984, Kelley 1997). *Aulacoseira islandica* occurs temporarily in the water column only if there is enough turbulence in the water to keep the filaments planktonic (Kelley 1997). In our experiment, the nets were incubated 1 m above the bottom. The protoplasm of the *A. islandica* filaments found fouling the nets was somewhat condensed, which suggests that dormant cells formed dense populations in deeper water layers of Pyhäjärvi. In line with this, the main biomass of clogging *A. islandica* in the Swedish large lakes is from

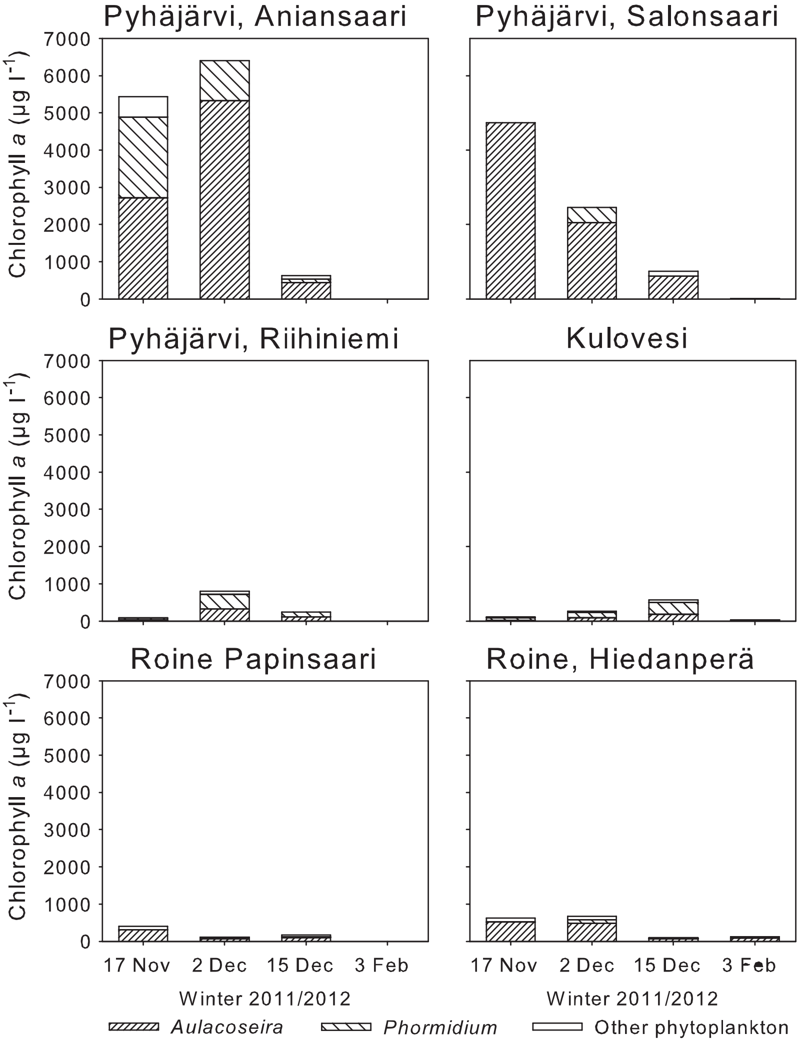

Fig. 9. Chlorophyll-*a* concentrations and the estimated contributions of phytoplankton groups to total chlorophyll *a* on the nets at the end of each experiment.

populations in a resting stage with condensed protoplast and a thicker organic coating (Willén 2001). Although the dormant cells may dominate the mass occurrences, during our last experiment in late February, fully formed parietal chloroplasts were found in *A. islandica* (data not shown). *Aulacoseira islandica* is considered a meroplanktic species occurring in deeper water layers in the hypolimnion (e.g. Bondarenko *et al.* 2006, Willén 1962), where it can also form mass occurrences (e.g. Willén 2001).

Under the ice in spring, horizontal convection driven by the heat flux from the sediment (e.g. Welch & Bergmann 1985) may cause advection from shallow to deeper areas and thus affect the occurrence of diatoms (Vehmaa and Salonen 2009). Moreover, vertical convective currents may circulate water sufficiently to keep heavy diatoms in suspension (Kelley 1997). Slow mixing of the whole water column may facilitate maintenance of diatoms in suspension and allow new recruitment from the sediment or hypolimnion to the epilimnion. However, this process is most pronounced during the last weeks of ice cover after the snow has melted from the ice (Likhoshway *et al.* 1996, Vehmaa and Salonen 2009). Under-ice convection currents are, therefore, unlikely to be the primary cause of fouling of fishing nets in Pyhäjärvi, where under-ice fouling of fishing nets usually starts in January–

February, clearly before the most likely period of under-ice convection in late March–early August.

Outside the main current area, fouling of fishing nets was much lower, supporting the assumption that the fouling is caused or strengthened by increasing water currents during the winter draw-down. Moreover, the fouling of fishing nets in Riihiniemi in the Huhtaanselkä sub-basin outside the main current area was mainly caused by the filamentous cyanobacterium *Phormidium*. Like *A. islandica*, *Phormidium* is also meroplanktic (e.g. Tang *et al*. 1997). In arctic areas, filaments of the genus *Phormidium* may form mats on the sediment surface and are adapted to low temperatures with an optimum temperature for growth of 10–15 °C, but are unable to grow at temperatures below 5 °C (Tang *et al*. 1997).

The autumn and winter/late-winter periods of fouling are not necessarily interrelated. In many years, there was a non-fouling period between the autumn fouling and the under-ice fouling. Moreover, autumn fouling is not always followed by an under-ice fouling period or vice versa. The fouling of fishing nets in Pyhäjärvi is not solely explained by the diurnal short-term regulation at the Melo dam, as fouling also occurs during periods of more and less intensive periods of discharge. Our results show that fouling of fishing nets takes place only if release of water is accompanied by intensive lowering of the water level.

The predictive power of the model for fouling events based on water level fluctuation in the Säijänselkä–Sorvanselkä sub-basin was 76%. The predictive power of the models, both for Pyhäjärvi and for each sub-basin, was rather low, being maximally 57%. There are several possible explanations for this. First reports of the state of fishing nets were not requested in the account books. Second, the remarks on fouling are rather subjective and fouling was more readily reported than non-fouling. Moreover, after consecutive years of fouling, slight fouling of the fishing nets might have been considered normal.

In conclusion, we showed for the first time how the fouling of fishing nets in regulated lakes is affected by release of water during the winter draw-down and the subsequent water level lowering. Although the primary cause of prolific fouling is increased nutrient levels promoting higher algal biomass, water level fluctuations trigger the visible problem, especially during the ice-covered period. Our results from a single boreal lake can likely be extrapolated to other regulated lakes with ice-cover in the boreal region, where the diatom *A. islandica* belongs to a characteristic winter phytoplankton composition of lakes.

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