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A water level drawdown index for aquatic macrophytes in Nordic lakes

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Abstract Many northern lakes are regulated to enhance hydropower production and flood protection. This bears hydromorphological pressures which are important factors causing lowered ecological status. Water level fluctuation triggers erosion on the shoreline and, depending on fluctuation range, also affects species composition or disappearance of sensitive aquatic macrophytes. We developed a water level-drawdown index (WI_c) for Nordic lakes using macrophyte data from 73 lakes with varying water level fluctuation in Finland, Norway and Sweden. The index is based on the ratio between sensitive and tolerant macrophyte species. The sensitive and tolerant species are identified based on a percentile approach, analysing the presence or absence of species along the winter drawdown range. The index correlates well with winter drawdown in Finnish and Norwegian lakes with strongest correlations with winter drawdown in storage lakes (lakes regulated for hydroelectric power and with a considerable winter drawdown). The WI_c-index is applicable in low alkalinity, oligotrophic and ice-covered lakes, and is suggested to be a useful tool to identify and designate heavily modified water bodies in Nordic lakes according to the European Water Framework Directive.

Keywords Winter drawdown · Ice effect · Sensitive and tolerant species · Low alkalinity · Oligotrophic lakes · Ecological potential

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Introduction

Hydromorphological pressures in lakes are related to the human need to control water levels of lakes and flows of rivers for the production of hydropower, flood prevention, recreation, navigation and the supply of water for agricultural or human consumption (Kampa & Hansen, 2004). Regulation practices vary among systems and countries and depend on the objectives of regulation (Wantzen et al., 2008). Generation of hydro-electric power (HEP) is one of the most important pressures in water courses in Nordic lakes (Marttunen et al., 2006).

Rørslett (1988) defined a hydrolake as a water body where water levels are operated for generating HEP. He also suggested a classification of hydrolakes and natural lakes into five groups: (H1)—oscillating hydrolakes with very short residence time and high winter water level; (H2)—intermediate reservoirs with short residence time, small to medium water level fluctuation (<2–4 m) and high winter water level; and (H3)—storage reservoirs with a long residence time, high water level fluctuation (>4 m) and considerable winter drawdown. Further, he divided natural lakes into (N1)—river-run lakes with short residence time; and (N2)—other natural lakes with long residence time.

Aquatic macrophytes growing in the littoral zone are sensitive to changes in the water level fluctuation regime (Wantzen et al., 2008). Effects are enhanced in lakes covered by ice because the effects of down-dwelling ice are especially harmful for plants sensitive to freezing (e.g. Rørslett, 1984; Hellsten, 2001). Reports on the decline of large-sized isoetids such as *Isoetes lacustris* L. and *Lobelia dortmanna* L. have been published from northern Scandinavia (Quennerstedt, 1958; Rørslett, 1984; Rintanen, 1996; Hellsten, 2002) and Scotland (Smith et al., 1987; Murphy et al., 1990). Additional to the effect of freezing, changes in sediment quality also significantly affect their distribution (Murphy, 2002). These damages on the biology in the littoral zone make water level drawdown a successful management method in controlling aquatic plants, when so desired (Cooke et al., 2005).

The direct response of *I. lacustris* to ice-scour enables its littoral distribution to be used for classification purposes (Rørslett, 1989; Rørslett & Johansen, 1996; Hellsten, 2002). The deepest growing areas of *I. lacustris* are also sharply limited by reduced light conditions and therefore its growing niche can be predicted (Rørslett, 1988). The distribution of other large isoetids such as *Isoetes echinospora* Durieu, *L. dortmanna* and *Littorella uniflora* (L.) Aschers can also be used for classification purposes because they are all relatively sensitive to ice erosion and changes in sediment structure (Rørslett, 1989; Murphy, 2002).

Hellsten & Mjelde (2009) suggested a water level index (WI_c) using macrophytes to describe the ecological status or ecological potential for regulated lakes. The preliminary WI_c-index showed promising results; however, it was based on a Finnish-only classification system identifying increasing or decreasing species (Hellsten, 2002) in regulated lakes. In addition, water level data for some of the lakes, especially the Norwegian ones, were at that time insufficient.

The aim of the current study is twofold. First, we develop an objective classification based on data from Finland, Norway and Sweden to distinguish between species sensitive or tolerant to winter drawdown. Second, we upgrade the preliminary WI_c-index for evaluating the effects of winter drawdown in Nordic lakes using macrophyte data and improved hydrological data from all three countries.

Materials and methods

Analysed lakes

A total of 73 lakes from Finland, Norway and Sweden were used to develop the new water level index (Table 1). The lakes in our study are separated into three lake groups: storage reservoirs (H3), intermediate reservoirs (H2) and natural lakes (N2). The definitions follow Rørslett (1988), where the storage lakes (H3) only include storage reservoirs regulated for HEP. The intermediate reservoirs (H2) include all other types of regulation, i.e. drinking water reservoirs, reservoirs in rivers and lakes with stabilised water level for other reasons. The natural lakes (N2) also include semi-natural lakes (sN2) with minor effects of water level's regulation. Natural lakes show a distinct spring flood with high inter-annual variation in water level (Fig. 1). The hydrological regime of drinking water reservoirs is characterised by frequent inter- and intra-annual changes in water level (Fig. 1). Storage lakes are characterised by small inter-annual changes, but with a distinct decline in water level during winter followed by a significant increase in spring and almost stable water level during summer and autumn (Fig. 1).

The Finnish dataset included low alkalinity, both clear and humic, lakes. Annual water level fluctuation varied between 0.1 and 6.8 m. The Norwegian dataset consisted mainly of clear water, low alkalinity lakes with annual water level fluctuations between 0.1 and 5.7 m. The Swedish dataset sampled by Wallsten (2010) included low alkalinity lakes with wide range of humic substances, all located in the county of

Table 1 Number of lakes used for developing the water level drawdown index (A) and for the definition of sensitive and tolerant species (B)

	Storage lakes (H3)		Other regulated lakes (H2)		Natural/seminatural lakes (N2 + sN2)		Total	
	A	B	A	B	A	B	A	B
Finland	16	17	3	3	9	9	28	29
Norway	13	7	12	9	10	9	35	25
Sweden	4	6	3	3	3	3	10	13

The lake classification follows Rørslett (1988)

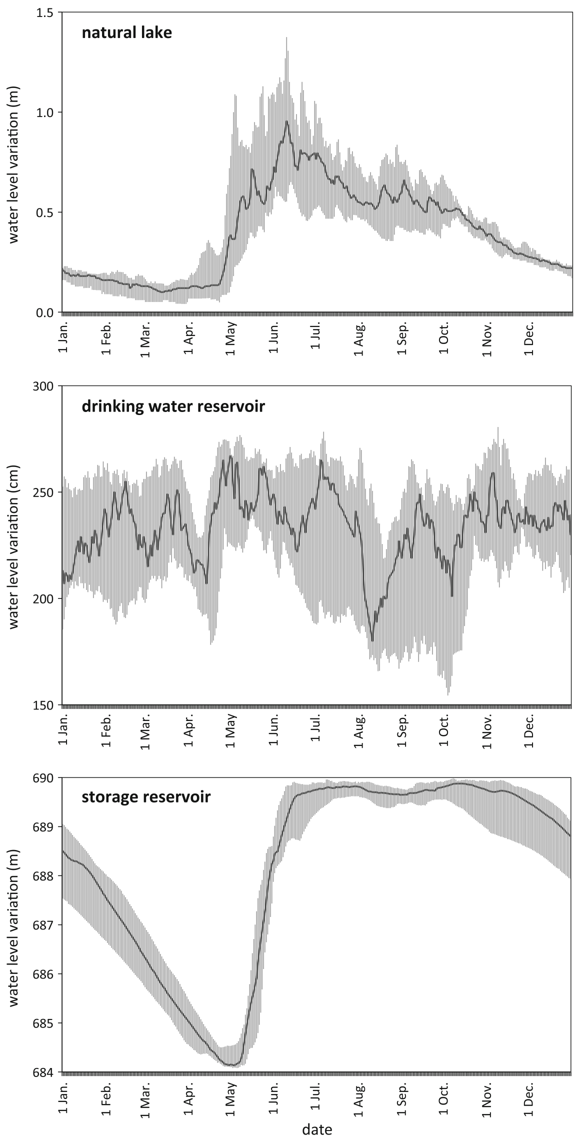

Fig. 1 Typical water level variations in a natural lake (Lake Atnasjøen, Norway, *top*), drinking water reservoir (Lake Maridalsvatn, Norway, *middle*) and a storage reservoir (Lake Aursunden, Norway, *bottom*). Median, 10th and 90th percentiles. Notice different scales. Data provided by NVE, Norway

Värmland. All lakes in the dataset are oligotrophic to slightly mesotrophic lakes, expecting eutrophication effects on macrophytes to be negligible.

Lakes were further classified according to the typology used in European intercalibration for the implementation of the Water Framework Directive (WFD) (Poikane et al., 2011); low alkalinity clear water lakes, low alkalinity humic lakes and medium alkalinity clear water lakes. Low alkalinity implies less than 0.2 meq l^{-1} and medium alkalinity implies between 0.2 and 1.0 meq l^{-1}. Clear water lakes have colour less than 30 and humic lakes more than 30 mg Pt l^{-1}.

Water level fluctuation analysis

Rørslett (1988) pointed out that lake levels can be extremely variable, even for non-manipulated lakes, indicating that annual mean ranges are poor descriptive statistics concerning water level fluctuations. We have therefore used water level medians, computed for 5, 10 or 20 years periods before macrophyte survey.

The daily water level data were collected from the Hertta database (SYKE) in Finland, the NVE database in Norway and the Fortum database in Sweden, excluding natural lakes with values modelled by the Swedish Meteorological and Hydrological Institute (SMHI). In Finland, water level data from 1980 to 1999 were used for all lakes, whereas Norwegian data included the last 5 or 10 years before the macrophyte survey. Water level data from Sweden comprised 10 years before the macrophyte survey.

We used winter drawdown as an indicator of water level regulation amplitude (see Hellsten, 2001; Keto et al., 2006, 2008). Winter drawdown was calculated as the average difference between the highest water level during the period October–December and the lowest level during the following period April–May.

Aquatic macrophyte data

Aquatic macrophytes in Finland were surveyed by the main belt transect method (Keto et al., 2006) between 1996 and 2004. The surveys in Norway took place from 1976 to 2003 by means of the standard method, i.e. by boat with aquascope and rake (Mjelde, 1997) or with the underwater photo method (Rørslett et al., 1978). In addition, old literature data from 1940 to 1941 (Tesaker, 1942), surveyed by means of the standard method, were included in the Norwegian dataset. In Sweden, a virtual transect method (zone analysis) similar to the Swedish standard was used (Wallsten, 2010). The method is based on virtual transects of 0.5 × 0.5 m plots along a depth gradient with 0.5-m intervals, giving a minimum of five plots per transect.

Each lake was visited once between July and September at maximum abundance of aquatic macrophytes. All countries included species composition, frequency and abundance in their analysis; but, due to different field methodology and abundance estimates, we decided to use the presence-absence data for the percentile analysis.

Only full aquatic macrophytes (isoetids, elodeids, nymphaeids, lemnids and charophytes) were included in further analysis. Helophytes were not included in the field survey in all countries, and were therefore excluded from the analysis.

Identifying sensitive and tolerant species

In general, sensitive species are defined as species preferring relatively unimpacted or reference lakes, and show low frequency and abundance if water level fluctuations increase. These species are often absent when winter drawdown exceeds 2.5–3 m. Tolerant species increase in frequency and abundance if water level fluctuations increase and are less frequent in reference lakes.

To distinguish between sensitive and tolerant taxa, we used the 75th percentiles combined with expert knowledge about well-known species (e.g. Hellsten, 2001). The 75th percentile represents the drawdown value below which 75% of the lakes where a certain species occur fall. Rare species may occur occasionally in some lakes and represent no indication value. Therefore, only species with occurrence in at least four lakes were included in the analyses. To avoid any eutrophication effects, only oligotrophic or slightly mesotrophic lakes were included. In addition, we extracted only low alkalinity lakes (alkalinity less than 0.2 meq l^{-1}, see above) from the original dataset because most of the large-sized isoetids prefer soft waters (e.g. Murphy, 2002). A total of 67 lakes were used for the percentile analysis: 29 Finnish lakes, 25 Norwegian lakes and 13 Swedish lakes (Table 1).

Defining the water level drawdown index

The equation for the water level drawdown index (WI_c) is the same as for the preliminary index (Hellsten & Mjelde, 2009):

$$WI_c = \frac{N_S - N_T}{N} \times 100$$

where WI_c is the winter drawdown index, N_S is the number of sensitive species, N_T is the number of tolerant species and N is the total number of species in the lake.

The index produces one value for each lake. The value can vary between +100, where all species in the lake are sensitive, and −100, where all species are tolerant.

Ecological status boundaries

The primary aim of the WFD (EC, 2000) is to achieve at least good ecological status for all surface waters and groundwater bodies, or good ecological potential for heavily modified water bodies. Five ecological status groups are defined: high, good, moderate, bad and poor status. Management is required in water bodies with less than good status. For boundaries suggestion in the WI_c index, we decided to use the change in abundance for *I. lacustris*, the best macrophyte indicator for regulation effects (Hellsten, 2002). We recalculated the different abundance estimates for *I. lacustris* to the semi-quantitative scale 1–5 (where 1 = rare, 2 = scattered, 3 = common, 4 = locally dominant and 5 = dominant). *I. lacustris* is the dominant species in these lakes and we expect that its presence and abundance are given particular attention. Despite different methodology we assume the abundance estimates for this species to be reliable enough for this purpose.

Setting boundaries based on almost linear gradients implies uncertainty close to the threshold. Such classification problems will appear regardless of which border we use, and will need some expert judgement when assessing the ecological status. One way to avoid this is to use only the most obvious sensitive and tolerant species, i.e. species on the two ends of the scale. For regulation effects, we chose this approach to define the most tolerant and most sensitive species.

Statistical analysis

Spearman Rank Correlation (Zar, 2009) was used in most cases when a quantitative relationship was sought between variables. However, index validation was carried out with a parametric linear regression analysis using average winter drawdown (m) as the independent and WI_c as the dependent variable to allow for a finer analysis. Though data were likely not normally distributed, such regressions used original, untransformed data due to technique robustness and reliability when non-normality is not extreme (Zar, 2009). Slope and regression strength (quantified by the correlation coefficient r, with $r = \sqrt{r^2}$) were compared for the statistically significant (i.e., those with $P < 0.05$) regressions for Norway and Finland: slopes were compared with the modified two-tailed t test in Zar (2009), and regression strength was compared by means of the Z-test after Fisher z transformation of r values (Zar, 2009). Such differences were considered significant for $P < 0.05$. Spearman rank correlations are identified by the use of r_s and parametric correlation by the use of r or r^2 as the correlation/regression coefficient, respectively.

Results

Species composition and species number

In total, 69 species of aquatic macrophytes were recorded in the lakes, 49 species in the storage reservoirs, 59 in other regulated lakes and 56 in natural lakes.

The dominating aquatic macrophytes were the isoetids *Ranunculus reptans* L., *I. echinospora*, *Eleocharis acicularis* (L.) R. & S., *I. lacustris*, *Subularia aquatica* L., *L. dortmanna*, the nymphaeid *Nuphar lutea* (L.) Sibth. & Sm., and the two elodeids *Juncus bulbosus* L. and *Myriophyllum alterniflorum* DC. The species composition indicates low alkalinity, oligotrophic lakes.

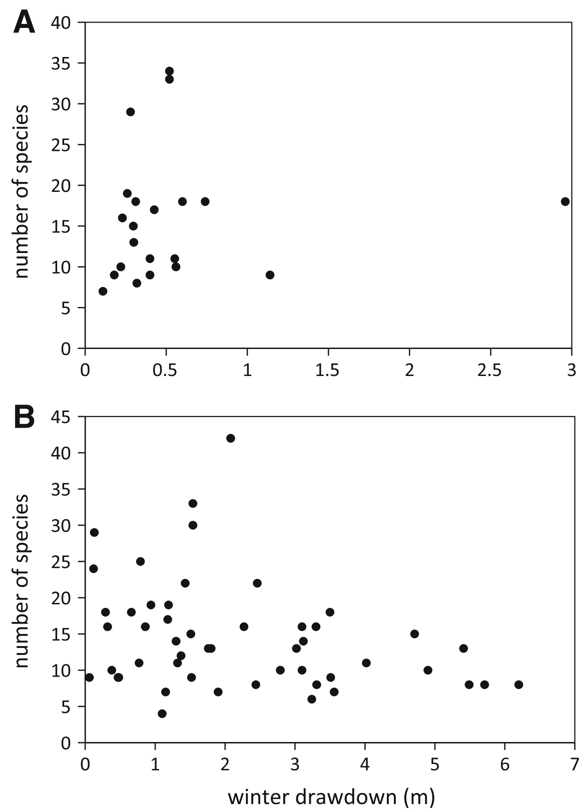

Fig. 2 Relation between the number of species and winter drawdown in natural and seminatural lakes (**A**) and storage and other regulated lakes (**B**)

In natural (N2) and semi-natural lakes (sN2), there was a trend for a positive correlation between winter drawdown and the number of aquatic macrophytes species ($r_s = -0.36$, $n = 22$, $P < 0.05$) (Fig. 2A). In contrast, in storage and other regulated lakes, the total number of species was negatively correlated with winter drawdown ($r_s = -0.34$, $n = 44$, $P < 0.05$) (Fig. 2B).

Sensitive and tolerant species

We identified sensitive species as species with 75th percentiles <1.6 m winter drawdown, while the most tolerant species were the species with 75th percentiles >2.6 m winter drawdown (Fig. 3).

Based on the percentile analysis, 46% of the aquatic macrophytes could be characterised as sensitive, while 25% were tolerant (Table 2). Twenty-nine percent of the species were not characterised. According to this

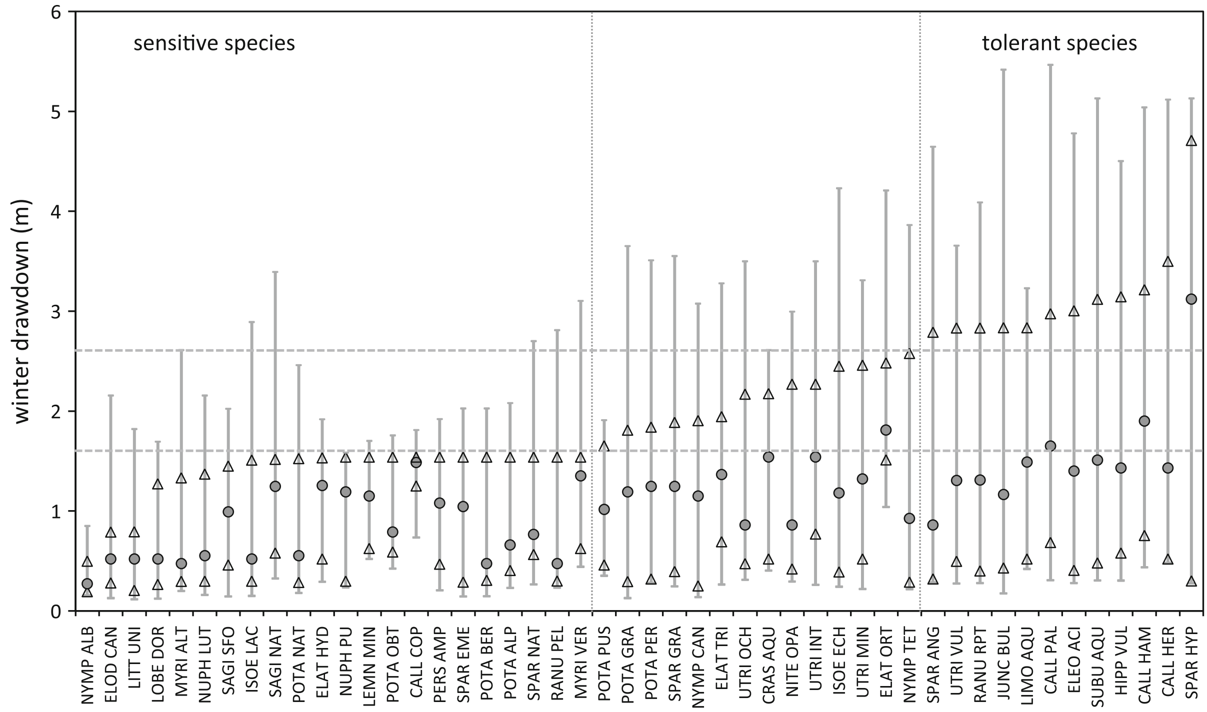

Fig. 3 Distribution of sensitive and tolerant species along a gradient of winter drawdown, based on Finnish, Swedish and Norwegian lakes. The graph includes 10, 25, 50, 75 and 90th percentiles. Species occurring in less than four lakes were excluded. The species were sorted by the 75th percentile. The thresholds for the sensitive and tolerant taxa, corresponding to winter drawdown values at 1.6 and 2.6 m, are indicated

classification, for example *I. lacustris* was classified as a sensitive and *J. bulbosus* as a tolerant species.

The water level drawdown index

The correlation between WI_c and winter drawdown for the natural and the slightly regulated lakes was weak and not significant ($r^2 = 0.091$, $n = 18$, $P = 0.223$) and the analysis was limited to storage reservoirs.

The WI_c index was negatively correlated with winter drawdown in the storage reservoirs in all countries (Fig. 4). The regressions were significant for Finland ($r^2 = 0.770$, $n = 16$, $P < 0.001$) and Norway ($r^2 = 0.670$, $n = 12$, $P < 0.01$), but not for Sweden ($r^2 = 0.730$, $n = 4$, $P = 0.143$), which was therefore excluded from further analysis.

The regressions for Finland and Norway had similar slopes ($t = 0.639$, $n_{FI} = 16$, $n_{NO} = 12$, $P = 0.529$) and similar strength (*Z*-test for correlation coefficients: $Z = 0.55315$, $P = 0.580$), allowing to pool the Finnish and Norwegian data together. The regression between WI_c and winter drawdown for Finnish and Norwegian storage reservoirs considered together (Fig. 4) was significant ($r^2 = 0.769$, $n = 28$, $P < 0.001$).

Defining class boundaries

Because of the different slope for the Swedish lakes, boundaries are only suggested for Finnish and Norwegian lakes.

As a reference value, we suggest that $WI_c = 29$ (Table 3). This represents the 75th percentile of the index values for natural and semi-natural lakes (Finnish and Norwegian lakes, only). Further, we suggest a high/good boundary $WI_c = 10$ (Table 3), which is the 25th percentile of the index values for natural and semi-natural lakes.

Stands of *I. lacustris* seem to disappear when winter drawdown exceed 3.4–3.5 m (Fig. 5). Therefore, we suggest a preliminary good/moderate boundary at $WI_c = -20$, which corresponds to these winter drawdown values.

Table 2 Aquatic macrophytes sensitive or tolerant to water level drawdown in Finnish, Swedish and Norwegian lakes

Group	Tolerant species	Sensitive species
ISOETIDS	*Eleocharis acicularis (ELEO ACI)*	*Elatine hydropiper (ELAT HYD)*
	Limosella aquatica (LIMO AQU)	*Isoetes lacustris (ISOE LAC)*
	Ranunculus reptans (RANU RPT)	*Littorella uniflora (LITT UNI)*
	Subularia aquatic (SUBU AQU)	*Lobelia dortmanna (LOBE DOR)*
ELODEIDS	*Callitriche hamulata (CALL HAM)*	*Callitriche cophocarpa (CALL COP)*
	Callitriche hermaphroditica (CALL HER)	*Elodea canadensis (ELOD CAN)*
	Callitriche palustris (CALL PAL)	*Myriophyllum alterniflorum (MYRI ALT)*
	Hippuris vulgaris (HIPP VUL)	*Myriophyllum verticillatum (MYRI VER)*
	Juncus bulbosus (JUNC BUL)	*Potamogeton alpinus (POTA ALP)*
	Utricularia vulgaris (UTRI VUL)	*Potamogeton berchtoldii (POTA BER)*
		Potamogeton obtusifolius (POTA OBT)
		Ranunculus peltatus (RANU PEL)
NYMPHAEIDS	*Sparganium angustifolium (SPAR ANG)*	*Nuphar lutea (NUPH LUT)*
	Sparganium hyperboreum (SPAR HYP)	*Nuphar pumila (NUPH PUM)*
		Nymphaea alba (NYMP ALB)
		Persicaria amphibian (PERS AMP)
		Potamogeton natans (POTA NAT)
		Sagittaria natans (SAGI NAT)
		Sagittaria sagittifolia (SAGI SFO)
		Sparganium emersum (SPAR EME)
		Sparganium natans (SPAR NAT)
LEMNIDS		*Lemna minor (LEMN MIN)*

Only species occurring in at least four lakes are included. Species abbreviations, used in Fig. 3, are shown in brackets. Species not listed in the table are indifferent to water level fluctuations in the three countries under study

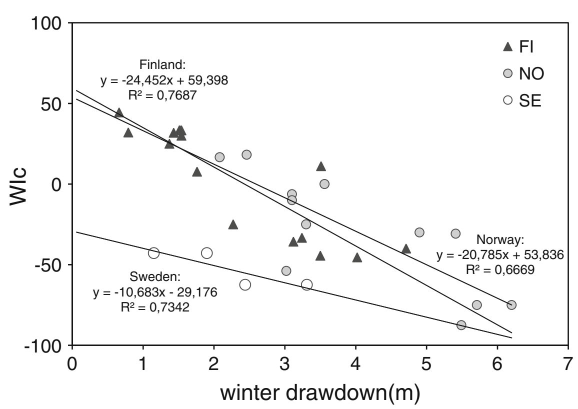

Fig. 4 Regression between winter drawdown and the water level index WI_c for the storage lakes. Regressions were calculated separately for the three Nordic countries. Lakes with a total species number <4 were excluded. In addition, Lake Kemijärvi, Finland, was excluded because of the large delta-area with fine substrate that remains unfrozen, despite the winter drawdown

Table 3 Water level drawdown index (WI_c) for Finnish and Norwegian storage lakes

Boundaries	WI_c value	Corresponding winter drawdown (m)
Reference value[a]	29	1.2
High/good	10	2.1
Good/moderate	−20	3.5
Moderate/poor	nc	nc
Poor/Bad	nc	nc

Preliminary reference value and boundary values for the different status classes are given; nc = not calculated

[a] The reference value is essential for counting the Ecological Quality Ratio (EQR) for the lakes (see EC, 2000)

Discussion

Our study showed a decreasing number of species number with increasing winter drawdown in regulated

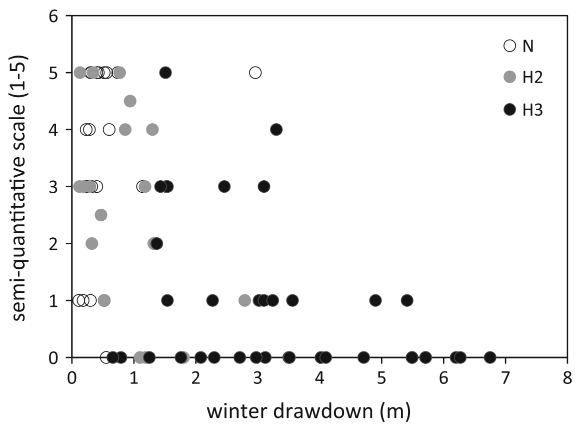

Fig. 5 Abundance of *Isoetes lacustris* compared to winter drawdown in Nordic natural and semi-natural lakes (N), storage lakes (H3) and other regulated lakes (H2). The abundance estimates are recalculated from different methods to a semi-quantitative scale 1–5 (where 1 = rare, 2 = scattered, 3 = common, 4 = locally dominant and 5 = dominant)

lakes. This agrees with earlier investigations, e.g. Rørslett, 1985, 1989; Nilsson et al., 1997; Hill et al., 1998; Hellsten, 2001, 2002, who found lower diversity of macrophytes in regulated lakes and river reservoirs compared to unregulated sites. However, a slight increase in disturbance could even create more suitable habitats for aquatic macrophytes (Murphy et al., 1990; Riis & Hawes, 2002) that is in accordance with the intermediate-disturbance hypothesis (Grime, 1974; Connell, 1978). Rørslett (1991) demonstrated that the regulation amplitude between 1 and 3 m supported the highest biological diversity. In the natural and semi-natural lakes studied here, species richness tended indeed to increase with winter drawdown.

The classification of tolerant and sensitive species agrees to a large extent with earlier knowledge and expert judgement (e.g. Rørslett, 1989; Hellsten, 2001; Hellsten & Mjelde, 2009). All tolerant species, except *Utricularia vulgaris* L., are either polymorphic (*J. bulbosus* L, *Hippuris vulgaris* L.) or amphiphytic, which enable them to withstand draining and erosion in the littoral zone. Especially, *J. bulbosus* can occur under a wide range of environmental conditions (Hinneri, 1976; Rørslett, 1989). However, our list of tolerant and sensitive species seems to deviate from some other classifications, e.g. Cooke et al. (2005). We believe that this is due to different lake types, different climate and/or some differences in water regulation procedures.

Natural and slightly regulated lakes show generally smaller water level fluctuations than storage lakes. In addition, hydrological regimes in slightly regulated lakes are very heterogeneous with different dynamics of the fluctuation depending on the regulation purpose. Owing to these facts, the correlations between WI_c and winter drawdown for slightly regulated lakes are weak; the index and the suggested boundaries are applicable only to storage reservoirs.

The WI_c index is based on the presence/absence data which give the same value independent of the abundance of the species. Sensitive species may still be present after winter drawdown is started to be implemented in a lake though with very low abundance (Nilsson & Keddy, 1988; Hellsten & Riihimäki, 1996). Due to this fact, abundance data may seem a better indicator for hydrological change than the presence/absence data, also indicated in earlier studies (Nilsson & Keddy, 1988; Coops and van der Velde, 1996; Hellsten et al., 1996; Hellsten, 2001). However, though typically preferable, abundance data may lead to underestimates of taxa with low abundance (Magurran & McGill, 2011). In addition, the most common approaches to identify the ecological status of aquatic macrophytes, according to the WFD (EC, 2000), comprise indices that use the relative number of sensitive versus tolerant species (e.g. Schaumburg et al., 2004; Stelzer et al., 2005; Poikane et al., 2011). The presence/absence data may be a more reliable basis for the purposes of the proposed index, both for conceptual and practical reasons.

The correlation between WI_c and winter drawdown for storage reservoirs was high for all three countries. The reason for the absence of statistical significance for Swedish lakes may be the low number of lakes. In addition, a low number of transect plots may have resulted in an incomplete species list in some of the lakes (Magurran & McGill, 2011). Until the number of Swedish lakes is increased, the index and suggested boundaries will be applicable to Finland and Norway only.

Highest diversity found in lakes with regulation amplitude between 1 and 3 m (e.g. Rørslett, 1991) indicates that storage lakes with winter drawdown less than 3 m have good ecological status/potential. Our good/moderate boundary at 3.4–3.5 m, based on the abundance of *I. lacutris*, corresponds well with Rørslett's (1991) rationale. However, the destruction of the stands with decreasing water level seems to happen

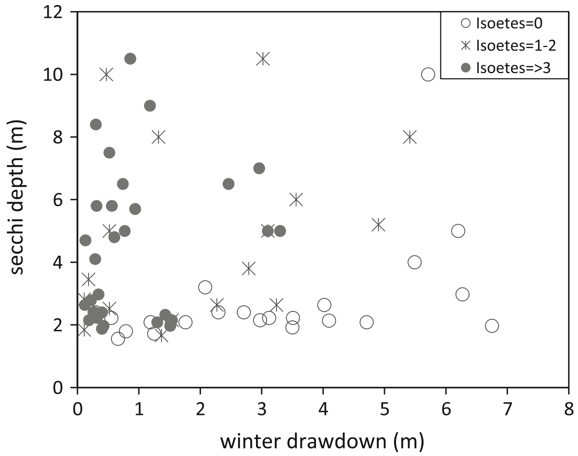

Fig. 6 The relationship between winter drawdown, Secchi depth and *Isoetes lacustris*. The presence of *I. lacutris* is based on a three-graded scale, where Isoetes = 0 means no *Isoetes* found (*open circles*), Isoetes = 1–2 means rare-scattered occurrence (stars) and Isoetes ≥ 3 means that the species is common in the lake or has small-large stands (*filled circles*)

quickly with even small changes in winter drawdown. Lakes with winter drawdown at 3.4–3.5 m seem to have healthy *I. lacustris* populations, while the latter are scant when winter drawdown exceeds 3.7–3.8 m. The analysis in Fig. 3 gives the same indication; 90th percentile for *I. lacustris* falls within the <3 m drawdown boundary, meaning that this species occurs in lakes with higher drawdown values only occasionally.

When setting boundaries, it is important to take into account the clarity of the lake water. Rørslett (1989) discussed the relationship between erosion depth (similar to winter drawdown), Secchi depth and the presence/absence of *I. lacustris* in storage reservoirs. Similarly, the same relationship can be seen in the lakes analysed here (Fig. 6). *I. lacustris* was found in heavily regulated lakes as long as the Secchi depth was high. In contrast, if the Secchi depth is low, *I. lacustris* can disappear also in less regulated lakes. Based on Fig. 6, the good/moderate boundary requires a Secchi depth of at least 5–6 m. If the Secchi depth is lower, a winter drawdown less than 3.4–3.5 m can cause a loss of *I. lacustris*.

In general, there is a growing demand for water level-related indices (see, e.g. Wantzen et al., 2008). According to Annex V of the WFD (EC, 2000), the ecological status of a water body should be assessed from the status of biological elements and supporting hydromorphological and physico-chemical elements. Hydromorphological degradation is identified as one of the main pressures on lakes and rivers in Europe. In Norway, hydroelectric power developments affect approximately 1/3 of the total lake surface area, while 75% of the highest waterfalls are regulated (Schartau et al., 2010). In addition, several rivers are affected through different hydrological and morphological developments. Establishing reliable indices for the identification of hydromorphological pressure is essential. Our study contributes to an increased understanding of the effects of water level regulations on lake macrophytes. We also believe that the idea and structure of the index is applicable to other lake types, i.e. moderate or high alkalinity lakes. However, the macrophyte composition in these lake types will be different from our studied lakes and separate lists of sensitive and tolerant taxa have to be generated. On the other hand, the H2-lakes with smaller, but more frequent fluctuations, will affect the macrophytes' community in different ways than the hydroelectric regime in storage reservoirs. In fact, some of the H2 lakes may support nuisance vegetation (Rørslett, 1988; Mjelde et al., 1992). Therefore, a different approach and index development are needed for lakes with other regulation types (H2). In addition, other aspects, for example related to sampling methodology, abundance measures and lake typology, need to be further evaluated before implementing the suggested water level drawdown index at a European level.

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References

Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Cooke, G. D., E. B. Welch, S. A. Peterson & S. A. Nichols, 2005. Restoration and Management of Lakes and Reservoirs, 3rd ed. CRC Press, Taylor & Francis, Boca Raton, FL.

Coops, H. G. N. & G. van der Velde, 1996. Helophyte zonation in two regulated estuarine areas in the Netherlands: vegetation analysis and relationships with hydrodynamic factors. Estuaries 22: 657–668.

EC, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities L-327/1: 22.12.2000.

Grime, J. P., 1974. Vegetation classification by reference to strategies. Nature 250: 26–31.

Hellsten, S. 2001. Effects of lake water level regulation on aquatic macrophytes stands and options to predict these impacts under different conditions. Acta Botanica Fennica 171: 47 pp.

Hellsten, S., 2002. Aquatic macrophytes as indicators of water level regulation in northern Finland. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 28: 601–606.

Hellsten, S. & M. Mjelde, 2009. Macrophyte responses to water level fluctuation in Fennoscandinavian lakes – applying a common index. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 30: 765–769.

Hellsten, S. & J. Riihimäki, 1996. Effects of lake water level regulation on the dynamics of aquatic macrophytes in northern Finland. Hydrobiologia 340: 85–92.

Hellsten, S., M. Marttunen, R. Palomäki, J. Riihimäki & E. Alasaarela, 1996. Towards an ecologically-based regulation practice in Finnish hydroelectric lakes. Regulated Rivers: Research & Management 12: 535–545.

Hill, N. M., P. A. Keddy & I. C. Wisheu, 1998. A hydrological model for predicting the effects of dams on the shoreline vegetation of lakes and reservoirs. Environmental Management 22: 723–736.

Hinneri, S., 1976. On the ecology and phenotypic plasticity of vascular hydrophytes in a sulphaterich, acidotrophic freshwater reservoir, SW coast of Finland. Annales Botanici Fennici 13: 97–105.

Kampa, E. & W. Hansen, 2004. Heavily modified water bodies. Synthesis of 34 case studies in Europe. Springer, Berlin, Heidelberg, New York: 321 pp.

Keto, A., A. Tarvainen & S. Hellsten, 2006. The effect of water level regulation on species richness and abundance of aquatic macrophytes in Finnish Lakes. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 29: 2103–2108.

Keto, A., A. Tarvainen, M. Marttunen & S. Hellsten, 2008. Use of the water-level fluctuation analysis tool (Regcel) in hydrological status assessment of Finnish lakes. Hydrobiologia 613: 133–142.

Magurran, A. E. & B. J. McGill (eds), 2011. Biological Diversity – Frontiers in Measurement and Assessment. Oxford University Press, Oxford, UK.

Marttunen, M., S. Hellsten, B. Glover, A. Tarvainen, L. Klintwall, H. Olsson & T.-S. Pedersen, 2006. Heavily regulated lakes and the European Water Framework Directive – Comparisons from Finland, Norway, Sweden, Scotland and Austria. E-Water 2006(5): 1–22.

Mjelde, M., 1997. Virkninger av forurensning på biologisk mangfold: Vann og vassdrag i by- og tettstedsnære områder. Vannvegetasjon i innsjøer - effekter av eutrofiering. En kunnskapsstatus. NIVA-report 3755-97 (in Norwegian).

Mjelde, M., T. E. Brandrud, E.-A. Lindstrøm, 1992. Vannvegetasjonen i Hafslovatnet, Luster kommune. Vurdering av tilgroingssituasjonen. NIVA-report 2817 (in Norwegian).

Murphy, K., 2002. Plant communities and plant diversity in softwater lakes of northern Europe. Aquatic Botany 73: 287–324.

Murphy, K. J., B. Rørslett & I. Springuel, 1990. Strategy analysis of submerged lake macrophyte communities: an International example. Aquatic Botany 36: 303–323.

Nilsson, C. & P. A. Keddy, 1988. Predictability of change in shoreline vegetation in a hydroelectric reservoir, northern Sweden. Canadian Journal of Fisheries and Aquatic Sciences 45: 1896–1904.

Nilsson, C., R. Jansson & U. Zinko, 1997. Long-term responses of river-margin vegetation to water-level regulation. Science 276: 798–800.

Poikane, S., M. van den Berg, S. Hellsten, C. de Hoyos, J. Ortiz-Casas, K. Pall, R. Portielje, G. Phillips, A. Lyche Solheim, T. Deirdre, G. Wolfram & W. van de Bund, 2011. Lake ecological assessment systems and intercalibration for the European Water Framework Directive: aims, achievements and further challenges. Procedia Environmental Sciences 9: 153–168.

Quennerstedt, N., 1958. Effect of water level fluctuation on lake vegetation. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 13: 901–906.

Riis, T. & I. Hawes, 2002. Relationships between water level fluctuations and vegetation diversity in shallow water of New Zealand lakes. Aquatic Botany 74: 133–148.

Rintanen, T., 1996. Changes in the flora and vegetation of 113 Finnish lakes during 40 years. Annales Botanici Fennici 33: 101–122.

Rørslett, B., 1984. Environmental factors and aquatic macrophyte response in regulated lakes – a statistical approach. Aquatic Botany 19: 199–220.

Rørslett, B., 1985. Regulation impact on submerged macrophytes in the oligotrophic lakes of Setesdal, South Norway. Verhandlungen der Internationale Vereinigung für Theoretiche und Angewandte Limnologie 22: 2927–2936.

Rørslett, B., 1988. An integrated approach to hydropower impact assessment. I. Environmental features of some Norwegian hydro-electric lakes. Hydrobiologia 164: 39–66.

Rørslett, B., 1989. An integrated approach to hydropower impact assessment. II. Submerged macrophytes in some Norwegian hydro-electric lakes. Hydrobiologia 175: 65–82.

Rørslett, B., 1991. Principal determinants of aquatic macrophyte richness in northern European lakes. Aquatic Botany 39: 173–193.

Rørslett, B. & S. W. Johansen, 1996. Remedial measures connected with aquatic macrophytes in Norwegian regulated rivers and reservoirs. Regulated Rivers: Research & Management 12: 509–522.

Rørslett, B., N. W. Green & K. Kvalvågnaes, 1978. Stereophotography as a tool in aquatic biology. Aquatic Botany 4: 73–81.

Schartau, A. K., D. Dolmen, T. Hesthagen, M. Mjelde, B. Walseng, F. Ødegaard, J. Økland, K. A. Økland & T. Bongard, 2010. Freshwater. In Kålås, J. A., S. Henriksen, S. Skjelseth & Å. Viken (eds), Environmental Conditions

and Impacts for Red List Species. Norwegian Biodiversity Information Centre, Norway.
Schaumburg, J., C. Schranz, G. Hofmann, D. Stelzer, S. Schneider & U. Schmedtje, 2004. Macrophytes and phytobenthos as indicators of ecological status in German lakes – a contribution to the implementation of the Water Framework Directive. Limnologica 34: 302–314.
Smith, B. D., P. S. Maitland & S. M. Pennock, 1987. A comparative study of water level regimes and littoral benthic communities in Scottish lakes. Biological Conservation 39: 291–316.
Stelzer, D., S. Schneider & A. Melzer, 2005. Macrophyte based assessment of lakes – a contribution to the implementation of the European Water Framework Directive in Germany. International Review of Hydrobiology 90(2): 223–237.
Tesaker, H. 1942. Undersøkelse over makrovegetasjonen i en del vann i Oslo Nordmark. Unpublished Master Thesis, University of Oslo (in Norwegian).
Wallsten, M. 2010. Makrofyters respons på vattennivåförändringar i 13 Värmländska sjöar. En lämplig parameter för att bedöma ekologisk status i reglerade sjöar? Länsstyrelsen Värmland. Publ. nr: 2010/12: 1–20. ISSN: 0284-6845 (in Swedish).
Wantzen, K. M., K.-O. Rothhaupt, M. Mörtl, M. Cantonati, L. G.-Tóth & P. Fischer (eds), 2008. Ecological effects of water-level fluctuations in lakes. Developments in Hydrobiology 204: 21–31.
Zar, J. H., 2009. Biostatistical Analysis, 5th ed. Prentice Hall/ Pearson, Upper Saddle River, NJ.