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WATER-LEVEL FLUCTUATIONS

Natural lake level fluctuation and associated concordance with water quality and aquatic communities within small lakes of the Laurentian Great Lakes region

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Abstract Long-term ($\sim$20 year) data on water level, water quality and aquatic biota from four remote research areas in the Laurentian Great Lakes region were compiled to reveal patterns of natural water-level fluctuation (WLF) and associated effects on water quality and aquatic communities. Of the 16 natural lakes (no dam impoundment and lowest possible anthropogenic disturbance) yearly amplitude in water level did not exceed 1.27 m ($\bar{x} = 0.26 \pm 0.15$ m) and yearly average water levels did not deviate greater than 0.75 m ($\bar{x} = 0.10 \pm 0.11$ m) from the long-term mean. Linear and waveform regression analyses revealed a significant ($P \leq 0.05$) decreasing trend in water levels and a 10-year oscillation in WLFs. Similarly, linear regression analysis demonstrated a significant reduction in yearly amplitude WLF over time. Correlation analyses revealed significant correlations with water quality parameters (DOC, Ca^{2+}, Conductivity, pH, $SO_4{}^{2-}$) and WLFs in Boreal Shield research areas. Of the long-term biotic information available (periphyton, macrophytes, macroinvertebrates and fish) only macroinvertebrates demonstrated a significant relationship with natural WLFs. Species richness followed a unimodal response ($P = 0.002$, $r^2 = 0.66$) with richness decreasing in years when water levels were either higher or lower than the long-term mean. The novel results of this study demonstrate patterns in natural WLF and associated correlations with water quality and biota across multiple lakes within the Laurentian Great Lakes region. The results are congruent with the intermediate disturbance hypothesis and have direct implications for reservoir management and climate change modeling.

Keywords Water-level fluctuations · Intermediate disturbance hypothesis · Macroinvertebrates · Climate change · Water quality · Lentic systems

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Ecological Effects of Water-Level Fluctuations in Lakes.

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Introduction

The regulation of aquatic systems for anthropogenic purposes (e.g., drinking water supply, agriculture, shipping channels, and hydroelectric power) is becoming common place across the world (Pimentel et al., 2004). Despite a rapid increase in water level regulation, there is limited data concerning the role of water-level fluctuations (WLFs), both within (intra-annual) and between (inter-annual) years, in structuring aquatic communities and influencing water quality. Congruent with anthropogenic disturbance, climate change is also expected to alter lake hydrology (Loaiciga et al., 1996; Magnuson et al., 1997). It is imperative that the linkages between current natural (unregulated) WLFs and lacustrine ecosystems be elucidated before these systems are forever altered.

Although lacustrine systems have been studied extensively, the relationship between WLFs and ecosystem response is poorly understood (Coops et al., 2003). Natural WLFs are controlled largely by local and regional climatic conditions that span in time frame from immediate precipitation events to decadal (and longer) climate change trends. WLFs are extremely complex and are often simplified when analyzing with biological data. WLFs can be measured both inter-annually and intra-annually; however, most studies focus on intra-annual fluctuations due to time constraints. The timing of WLFs can also be extremely important in determining community structure, especially in the aquatic-terrestrial ecotone, as has been shown with macrophytes (Riis & Hawes, 2002). The majority of the literature, and our understanding of WLFs, stems from detailed comparisons of macrophytes in reservoir systems of varying intra-annual amplitudes (Furey et al., 2004; Hill et al., 1998; Wilcox & Meeker, 1991). Similarly, controlled whole lake manipulations have revealed decreases in macrophyte diversity and biomass with WLFs (Turner et al., 2005; Wagner & Falter, 2002). Although the majority of published research has focused on macrophytes, WLFs are known to affect fish (Fisher & Öhl, 2005), macroinvertebrates (Grimås, 1961), waterfowl (McIntyre, 1994) and abiotic factors such as littoral nutrients, sediments, and thermal stratification (Furey et al., 2004; Weston et al., 2004). While these studies have been instrumental in evaluating and understanding the impacts of WLFs, there exists a paucity of data concerning ‘natural’ systems and in particular, how inter-annual fluctuations may affect water quality and biota. This knowledge gap may be attributed to stable inter-annual reservoir WLFs and a lack in long-term WLF information from natural systems. There is an intrinsic understanding that the functioning of lacustrine ecosystems is controlled, in part, by the quantity and periodicity of the water resource, which is directly related to WLFs (Coops et al., 2003). It is essential that we understand, in detail, how natural WLFs affect the water quality, community structure and biodiversity of lake ecosystems.

Using long-term data (20 years) from four research areas, we describe inter-annual patterns and relationships of natural (i.e. no dam control structure) WLFs among sixteen lakes of the Laurentian Great Lakes region and relates these patterns to water quality and aquatic communities. Inter-annual WLFs were evaluated using two indices; change in yearly amplitude and the yearly difference from long-term mean water levels. Water quality parameters included; pH, SO_4^{2-}, conductivity, Ca^{2+}, dissolved organic carbon (DOC), NO_3^- and NO_2^-. Macrophyte, fish and macroinvertebrate species richness data was utilized in analyses. The underlying assumption and hypothesis of this study is that natural WLFs act as an intermediate disturbance (Hutchinson, 1953), which structures the physical, chemical, and biotic components of lacustrine ecosystems. Therefore, we predict that natural WLFs will demonstrate significant concordance with water quality parameters and species richness.

Materials and methods

Data sources

The four research areas are all located in the Laurentian Great Lakes watershed and include: (1) the Experimental Lakes Area (ELA) in northwestern Ontario, (2) the Long-term Ecological Research (LTER) area in northern Wisconsin, (3) the Turkey Lakes Watershed Study (TLWS) in northeastern Ontario and (4) the Dorset Research Centre (DRC) in central Ontario (Fig. 1). All four research areas were able to provide long-term data on water fluctuation and water quality parameters; however, only the LTER site was able to provide consistently sampled biotic information appropriate for WLF analyses. In total, sixteen lakes ($A_o = 12.1 - 1607.9$ ha, $\bar{x} = 174.8$ ha) were included in this

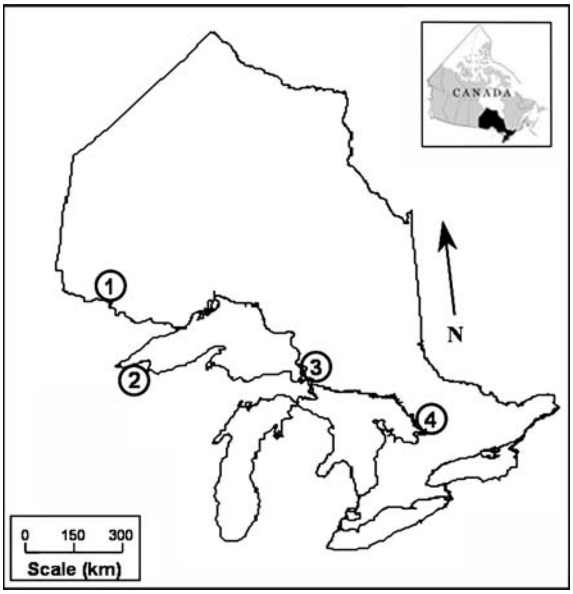

Fig. 1 Map of Ontario depicting approximate locations of long-term research areas; 1—Experimental Lakes Area (ELA), 2—Long-term Ecological Research area (LTER-Wisconsin), 3—Turkey Lakes Watershed Study (TLWS), 4—Dorset Research Center (DRC)

study, their names and associated research areas are as follows: L239 and L114 (ELA); Trout, Sparkling, Allequash, Crystal, and Big Muskellunge (LTER); Turkey and Little Turkey (TLWS); Blue Chalk, Chub, Crosson, Dickie, Harp, Plastic, and Red Chalk (DRC).

Although each research area is unique, the three research areas located in Ontario (ELA, TLWS, DRC) are very similar: all are situated on the Boreal Shield, and thus, have similar topography, geology and vegetation. The LTER site is situated on glacial till which increases the amount of ground water recharge its lakes receive compared to the other three research areas. A complete description of each area is given in: ELA (Department of Fisheries and Oceans, 2005), LTER (University of Wisconsin, 2004), TLWS (Government of Canada, 2005) and DRC (Molot & Dillon, 1991, 1993).

WLFs indices

In describing inter-annual WLFs two indices were chosen: amplitude and difference from the long-term mean (DLTM). Yearly amplitude was calculated as the difference between the maximum and minimum open water (May 1–Nov 31) water level. DLTM was calculated by determining the mean water level from 1980 to 2003 for each lake and then subtracting that mean value (across years) from the mean value for each particular year. These calculations result in positive and negative values indicating the mean water level for a particular year relative to the lake's overall long-term mean. It is important to note that the frequency of water level measurements differed between research areas: bi-weekly (LTER), weekly (DRC), and daily (ELA and TLWS).

Water quality parameters

The following water quality parameters were measured at the four research areas and were included in our analyses: pH, SO_4^{2-}, conductivity, and Ca^{2+}. DOC, NO_3^- and NO_2^- are also included in this analysis but were not measured across all research areas. Samples for water quality data were obtained at varying frequencies between the research areas: monthly (LTER and ELA) and weekly (DRC and TLWS).

Biological data

The only research area with available, consistently sampled, long-term biological data was the LTER site. At this area, data were available for fish, macrophytes and benthic macroinvertebrates for Trout and Sparkling Lakes. Benthic macroinvertebrates were sampled in triplicate using Hester-Dendy samplers placed 3 m apart in 1 m depth of water in nearshore areas. The Hester-Dendy samplers were deployed in mid-August and retrieved 4 weeks later. The family level of taxonomic resolution was used in analyses to maintain consistency among years. No significant results were found in this study for fish or macrophytes; therefore, their sampling methodology is not presented. For detailed sampling protocols please refer to the North Temperate lakes LTER program (University of Wisconsin, 2004).

Statistical analyses

In order to assess lake and site similarity, principal components analysis (PCA) was conducted with PC-ORD© (McCune & Mefford, 1999) using the five commonly sampled water parameters: conductivity,

Ca^{2+}, pH, SO_4^{2-} and amplitude. PCA is an acceptable ordination technique given the linear nature of the environmental variables used in this analysis. Regression techniques were employed to better understand the nature of WLFs in small lakes of the Laurentian Great Lakes region. Regression analyses, both linear and a waveform sine distribution, were preformed in SigmaPlot© (SPSS, 2000) to determine patterns in WLFs over time. WLFs (DLTM and Amplitude) concordance with water quality parameters (pH, SO_4^{2-}, conductivity, Ca^{2+}, DOC, NO_3^- and NO_2^-) was assessed with SAS© (SAS, 2001) through correlation analyses using Pearson's correlation coefficients. These analyses were conducted both on a site-by-site basis and across all sites. Data that was not normally distributed was transformed to meet the assumptions of normality necessary for both Pearson's and regression analyses. Regression analyses were used to determine whether species richness responded to WLFs. Both linear regression and Gaussian distributions (non-linear) were used in SigmaPlot© to determine the influence of WLFs on species richness. Since a Gaussian distribution follows a unimodal pattern, it was hypothesized that species richness has an optimum level, after which, either higher or lower water levels will decrease species richness.

Results

Lake characterization

The results of PCA ordination show a clear separation between the LTER lakes (located on glacial till) and the lakes of the other three research areas which are located on the boreal shield (Fig. 2). Of the five axes extracted in the PCA only axis 1 and 2 are presented as they explain the majority of the extracted variance, 90.8% in total, 74.4% and 16.4%, respectively. The LTER lakes ordinated in the upper left of the ordination biplot and are characterized as having high conductivity values and Ca^{2+} concentrations, while the boreal shield lakes ordinated to the lower right and are characterized by having higher yearly amplitude and SO_4^{2-} concentrations. Interestingly, pH was not a strong descriptor in lake partitioning when utilizing the first two axes.

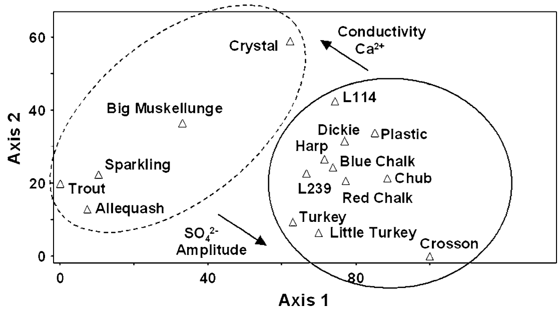

Fig. 2 PCA analyses of the 16 lakes used to characterize water-level fluctuation. The dashed ellipse encompasses lakes located on glacial till at the LTER area in Wisconsin, while the solid ellipse encompasses Ontario lakes located on the boreal shield. Lakes in the upper left corner are characterized by having higher conductivity and Ca^{2+} values while lakes in the lower right corner demonstrate higher SO_4^{2-} levels and increased within year water-level fluctuations (Amplitude)

WLF characterization

Of the 16 lakes studied, yearly amplitude did not exceed 1.27 m ($\bar{x} = 0.26$, $\sigma = 0.15$) and yearly average water levels did not deviate greater than 0.75 m ($\bar{x} = 0.10$, $\sigma = 0.11$) from the long-term mean. Linear regression analysis revealed a significant ($P = 0.0012$) negative relationship with mean water levels decreasing over time ($r^2 = 0.03$), while the waveform, Sine (3 parameter), equation $y = a*\sin(2*\pi*x/b + c)$ similarly revealed a significant result ($P < 0.0001$, $r^2 = 0.18$) (Fig. 3). Linear regression analysis also revealed a significant

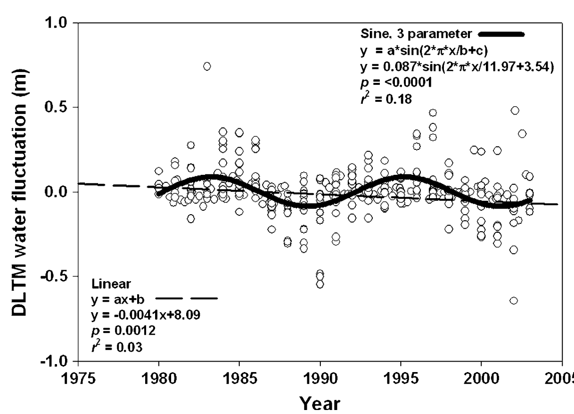

Fig. 3 Linear and waveform regression of mean water levels, expressed as difference from the long-term mean (DLTM), over time (1980–2003) for the 16 study lakes. The negative trend suggests that water levels are lowering over time; however, a 10-year periodicity (oscillation) is present

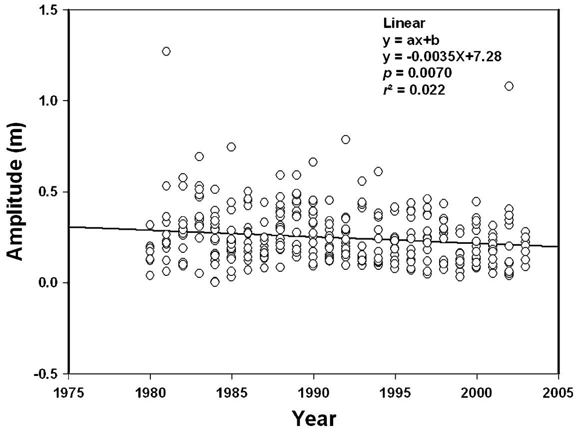

Fig. 4 Linear regression of yearly amplitude over time (1980–2003) for the 16 study lakes. The negative trend suggests that yearly amplitude has been decreasing steadily since 1980

($P = 0.007$) negative relationship with yearly amplitude decreasing over time ($r^2 = 0.022$) (Fig. 4). Although the r^2 values of the linear regressions are extremely low, due to heterogeneity between lakes and research areas, power analyses for linear regressions were high for DLTM and amplitude, 0.91 and 0.77, respectfully. Although all lakes demonstrated similar magnitudes in yearly amplitude, there was not a consistent pattern between lakes. Conversely, all lakes showed a consistent waveform pattern between lakes and across years.

WLF concordance with water quality

Pearson's correlation coefficients (r) and significance values are presented in Table 1 for DLTM and water quality parameters, and in Table 2 for yearly amplitude and water quality parameters. Significant concordance was found at the $P \leq 0.05$ level for five water quality parameters in three research areas. DOC ranged from 1.53 to 10.11 mg/l across all lakes and demonstrated a positive relationship with increasing mean water levels at the ELA site. Interestingly, DOC also showed positive concordance with DLTM and negative concordance with yearly amplitude at the DRC area; however, both were only marginally significant ($0.05 < P \leq 0.10$). DOC data were unavailable for the TLWS and no relationship was found at the LTER site. The range of pH values was 5.51–8.47 across the 16 lakes. We found a negative correlation between pH and yearly amplitude at the TLWS; however, no other significant correlations were found. Sulphate, measured as SO_4^{2-}, was found at concentrations of 1.40–8.53 mg/l across the study lakes and only one significant correlation was found. Sulphate levels were positively correlated at the DRC site with increasing yearly amplitude. Ca^{2+} ranged from 0.98 to 12.94 mg/l across all lakes and demonstrated a positive correlation with DLTM at the DRC research area. Conductivity values ranged from 12.0 to 99.5 μS/cm across the study lakes. Interestingly, conductivity demonstrated significant concordance at both the TLWS and DRC sites; however, TLWS showed negative concordance ($r = -0.36$) while DRC showed positive concordance ($r = 0.16$). These contrasting trends within similar geologic and climatic conditions demonstrate that water quality concordance with WLFs is area specific. Nitrogen was measured as NO_3^- at the ELA and TLWS and as

Table 1 Pearson's correlation coefficients (r) and P values for long-term research areas with selected water quality parameters and difference from long-term mean water levels

Research area		DOC (mg/l)	PH	SO_4^{2-} (mg/l)	Ca^{2+} (mg/l)	Cond (μS/cm)	NO_3^- (μg/l)	$NO_3^- + NO_2^-$ (μg/l)
ELA	r	0.42**	−0.16	−0.29	−0.19	−0.24	0.10	NA
(2 lakes)	P	0.01**	0.29	0.06	0.21	0.12	0.51	
TLWS	r	NA	−0.19	0.06	−0.04	−0.36**	−0.05	NA
(2 lakes)	P		0.22	0.72	0.80	0.02**	0.77	
DRC	r	0.15*	−0.01	0.07	0.17**	0.16**	NA	NA
(7 lakes)	P	0.07*	0.94	0.42	0.05**	0.05**		
LTER	r	−0.05	−0.08	−0.22	−0.11	−0.15	NA	0.07
(5 lakes)	P	0.67	0.48	0.84	0.29	0.16		0.49
All	r	NA	−0.06	0.00	0.05	−0.06	NA	NA
(16 lakes)	P		0.34	0.99	0.35	0.26		

Values with ** highlight significant concordance ($P \leq 0.05$), while values with * highlight potential concordance ($0.05 < P < 0.10$)

Table 2 Pearson's correlation coefficients (r) and P values for long-term research areas with selected water quality parameters and yearly water amplitude

Research area		DOC (mg/l)	PH	SO_4^{2-} (mg/l)	Ca^{2+} (mg/l)	Cond (μS/cm)	NO_3^- (μg/l)	$NO_3^- + NO_2^-$ (μg/l)
ELA	r	0.10	0.02	0.01	0.16	0.17	0.13	NA
(2 lakes)	P	0.52	0.90	0.95	0.30	0.27	0.41	
TLWS	r	NA	−0.32**	0.15	−0.06	−0.16	0.09	NA
(2 lakes)	P		0.04**	0.36	0.71	0.30	0.55	
DRC	r	−0.16*	−0.13	0.18**	−0.00	0.05	NA	NA
(7 lakes)	P	0.07*	0.11	0.04**	0.99	0.55		
LTER	r	−0.04	−0.11	0.02	−0.10	−0.03	NA	−0.07
(5 lakes)	P	0.72	0.32	0.88	0.35	0.82		0.50
All	r	NA	−0.05	0.10*	−0.02	0.02	NA	NA
(16 lakes)	P		0.39	0.08*	0.77	0.75		

Values with ** highlight significant concordance ($P \leq 0.05$), while values with * highlight potential concordance ($0.05 < P < 0.10$)

$NO_3^- + NO_2^-$ at the DRC and LTER and ranged from 1.4 to 367.7 μg/l and 0.3–27.0 μg/l, respectively. There was no concordance between nitrogen and WLFs at any of the research areas.

WLF relationships with biota

As stated in the methodology, Trout and Sparkling Lakes were the only lakes from the available long-term data with appropriate biological data for analyses. We did not find significant relationships with either fish or macrophyte species richness and yearly amplitude. The macroinvertebrate data did show a significant unimodal response to DLTM in Sparkling Lake (Fig. 5). The Gaussian, 4-parameter equation $y = 14.89 + 6.35{*}\exp(-0.5{*}((x - 0.04)/0.14)^2)$ yielded a significant ($P = 0.002$) relationship ($r^2 = 0.66$) between macroinvertebrate richness and DLTM. Richness was highest in years closest to the long-term mean and decreased with either increasing or decreasing water levels. Although the same response was not evident with macroinvertebrate richness in Trout Lake this could likely be due to the lower WLFs experienced in Trout Lake (−0.13 m to +0.22 m) compared to Sparkling Lake (−0.50 m to +0.38 m). Similarly, macrophyte richness appeared to be responding to DLTM with the same unimodal pattern in Trout Lake; however, a greater magnitude in WLF was likely needed to show statistical significance (data not shown).

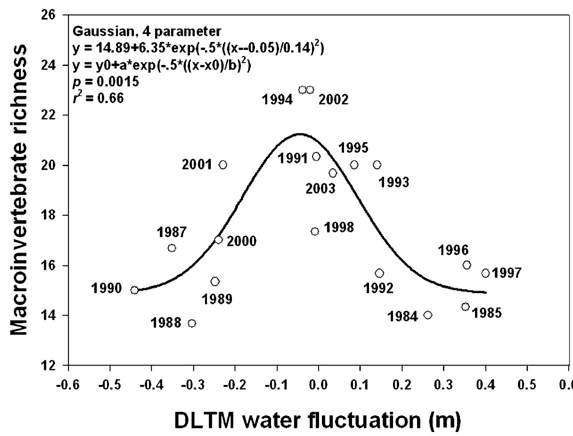

Fig. 5 Regression analysis demonstrating unimodal response of macroinvertebrate species richness (Family level taxonomic resolution) with DLTM over a 20 year period for Sparkling lake at LTER-Wisconsin

Discussion

A typical intra-annual (yearly) hydrograph for unregulated 'natural' inland lakes of the Laurentian Great Lakes region consists of a pulse of water in the spring during snowmelt (April–May) and a subsidiary pulse again in the fall (October–November). This results in a ~75 cm increase in spring water levels and a ~25 cm increase in fall water levels demonstrating a bimodal pattern and 'flashy' (Boreal Shield lakes) response due to the impermeable bedrock (Fig. 6). Limnologists have long recognized this intra-annual pattern in WLFs, but what was not evident was how inter-annual WLFs change over time, and just as importantly, the magnitude and patterns that exist across multiple lake systems. A clear oscillation, or periodicity, ($\sim$10 years) is evident across the 16 lakes, whether this pattern will persist or was present before the 20 years of available data is unknown. Interestingly, the oscillation is consistent between lakes, presumably due to the overriding effect of similar climatic conditions within the Laurentian Great Lakes watershed. This pattern in WLF could not be related to the North Atlantic Oscillation (NAO) as was found in Lake Võrtsjärv (Nõges et al., 2003) or the Southern Oscillation Index (SOI), but it is likely associated with periodicity in precipitation events driven by global climatic factors. The same concordance among lakes was not found with amplitude and analyses on a lake-by-lake basis revealed that amplitude does vary greatly between years showing no continuity within a single lake (data not shown).

The waveform response in DLTM across multiple lakes suggests that it is largely regulated by broad-scale ecoregion climatic conditions. Conversely, the minute concordance of amplitude among lakes and indiscernible scatter within and between lakes (data not shown) suggest that it is influenced by local, small-scale, ecodistrict effects. The negative slope of both linear regressions (DLTM, amplitude) across time suggests that mean water levels and amplitude intensities have been decreasing in the Laurentian Great Lakes region over the last 20 years. This pattern supports many climate change scenarios

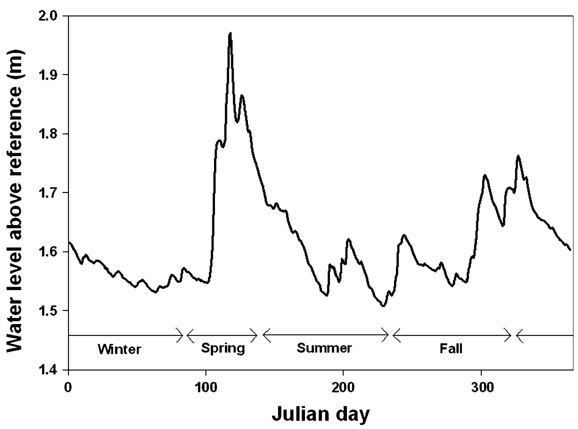

Fig. 6 Typical intra-annual hydrograph for Turkey Lake, 1994 (TLWS)

(Blenckner, 2005; Giorgi et al., 2001; Magnuson et al., 1997; Suffling & Scott, 2002), as temperate regions increase in annual temperature evaporation rates increase and rainfall becomes more consistent throughout the year.

Due to the varying frequencies that water level measurements were taken between research areas, it was not feasible to assess the effect of fine scaled intra-annual differences in WLFs (timing of min and max water levels and rates of increase or decrease) with biota or water quality parameters. However, we found that inter-annual WLFs demonstrated significant concordance with water quality parameters as has been suggested by other studies. Webster et al. (1996, 2000) demonstrated that Wisconsin lakes of various landscape positions responded differently to increases in calcium and magnesium concentrations after a 2-year drought. Temperate lakes also have demonstrated concordance with DOC concentrations in relation to landscape characteristics (Rasmussen et al., 1989; Xenopoulos et al., 2003) and nitrate concentrations with winter climate conditions (George et al., 2004). Similarly, in an investigation of Boreal Plain lakes of northern Alberta, inorganic and organic nutrients were correlated with land use, soil properties and vegetation communities (Prepas et al., 2001). We show that all boreal shield research areas, but not the LTER area, exhibited concordance with WLFs (DLTM or amplitude). The lack of concordance with the LTER lakes can be explained by the porous glacial soil and resultant dominant groundwater inputs to the LTER lakes compared to the impervious bedrock found at the other three research areas. This translates to boreal lakes receiving direct surface water runoff exposed to nutrient leaching during precipitation events. The LTER-Wisconsin lakes are fed by groundwater sources that are homogenous in nutrient and elemental compositions and are less influenced by precipitation events due to percolation of surface runoff through the substratum into groundwater recharge areas. Lake separation through PCA analysis also supports the characteristically discriminant LTER-Wisconsin lakes. The demonstrated concordance of water quality with WLFs is not unexpected as water levels are directly controlled by hydrological inputs that are driven by drought and precipitation events. An increase or decrease in water level indicates a shift in a lakes hydrologic budget. The concordance of water quality with WLFs results from the multifarious interaction of landscape controls (Dillon & Molot, 2005), internal lake nutrient cycling (Hanson et al., 2003), and biotic relationships (Wagner & Falter, 2002).

Species response to WLFs has been well documented in riverine systems and relationships of macroinvertebrate community structure to riverine WLFs has been demonstrated often (Ogbeibu & Oribhabor, 2002; Wood & Armitage, 2004). Lentic systems, and in particular temperate systems, have received much less attention. This is due presumably to the subordinate magnitude of WLFs in temperate lentic systems when compared to riverine systems. Since the biota inhabiting these systems have evolved with distinctive WLFs, deviations from these regimes may dramatically alter community composition and biotic richness, particularly in littoral areas. Recently, aquatic ecologists have started to recognize the importance of WLFs in temperate lentic ecosystems through research geared toward evaluating the impacts of regulated WLFs in reservoirs. These studies have focused mainly on the effect of yearly amplitude on macrophyte diversity. All studies suggest that a fluctuation between 1.5 and 2.0 m is the optimal level at which the highest macrophyte diversity is attained (Hill et al., 1998; Wagner & Falter, 2002; Wilcox & Meeker, 1991). A New Zealand study focusing on the low growing mixed macrophyte community along lake margins of 21 lakes yielded similar results, suggesting that a 1.1-m fluctuation yielded highest species richness in this zone (Riis & Hawes, 2002). The same study also conjectured that inter-annual WLFs were just as important as intra-annual WLFs in establishing high levels of species richness.

While these studies concerning macrophytes in regulated systems provide enormous insight into the confounding influences of WLFs, the results are limited as they are short-term (2 years max), evaluate yearly amplitude only, focus on macrophytes and often do not incorporate pristine reference conditions. They do not assimilate the dynamic patterns of WLFs across multiple years, or account for the fact that amplitudes are not consistent between years in any natural lake system.

Macrophyte diversity did not show a significant response with changes in WLFs in this study; however, the data obtained from Trout lake suggest that macrophytes near the lower limit of the photic zone ($\sim$4 m) begin to demonstrate decreased diversity in years experiencing maximum amplitudes ($\sim$25 cm) events (data not shown). This is not surprising as aquatic plants inhabiting these depths are likely Photosynthetically Active Radiation (PAR) limited in the spring during the start of the growing season when amplitudes would be at their highest. Similarly, macrophyte richness attained its highest numbers in years closest to the long-term mean (data not shown). This suggests that macrophyte diversity may be responding to WLFs but a significant pattern is not discernable at current natural WLFs. Changes to the current pattern of natural WLFs (i.e., climate change) may elicit a response in macrophyte richness.

In this study, macroinvertebrates demonstrated a classical unimodal response to DLTM and WLFs. Maximum species richness was attained in years closest to the mean water level and decreased as mean water levels deviated (+ or −) from the long-term mean. It can be postulated that this is a result of mean DLTM community structures containing species which favor both high and low water levels. The sensitivity of macroinvertebrates to WLFs compared to macrophytes and fish in this study is not surprising. Macroinvertebrate communities have long been considered paramount in biomonitoring projects due to their inherent characteristics; diverse functional feeding groups, importance in food webs, sensitivity to water quality, confined to specific area, and they are easy to sample (Mackie, 2001). These same properties result in their highly responsive nature to WLFs and appropriateness in assessing associated impacts to aquatic systems. Previous research concerning macroinvertebrates and WLFs in lentic systems has focused on ephemeral and permanent flooding of wetlands (Hillman & Quinn, 2002; Neckles et al., 1990; Whiles & Goldowitz, 2005). The effect on boreal lakes (where species are not adapted to extreme WLFs) is largely unknown. The few studies that have been conducted in lentic Boreal systems involve anthropogenic changes in amplitude with increasing amplitudes resulting in decreased species diversity (Grimås, 1961) and extirpation of important taxa, including amphipods and isopods (Hunt & Jones, 1972) and *Hexagenia* sp. and *Oecetis* sp. (Cooper, 1980). Although these studies were conducted on regulated systems they do demonstrate the highly responsive nature of macroinvertebrates to WLFs.

The stimulation of species diversity associated with the intermediate disturbance hypothesis has been demonstrated in many habitats (Bertrand et al., 2004; Johst & Huth, 2005; Valdivia et al., 2005; Wilcox & Meeker, 1991). This study demonstrates that the amount of disturbance created by natural WLFs in the Laurentian Great Lakes watershed stimulates diversity in biotic communities. Nevertheless, the plasticity of these systems to uncharacteristic increases or alterations to natural WLFs due to anthropogenic effects (climate change and water regulation) is uncertain. Much of our current understanding of WLFs in temperate lentic systems stems from detailed studies of regulated systems. The majority of this research focuses on changes in yearly amplitude and suggests that $\sim$2 m yearly fluctuation results in the highest macrophyte diversity. This study demonstrates that DLTM should also be considered when making management decisions as has been suggested by Riis & Hawes (2002). Furthermore, macroinvertebrates should be utilized also due to their higher sensitivity to WLFs compared to macrophytes. More importantly, community structure and abundances need to be considered as many invertebrate species are important food sources for birds, fish and amphibians, which ultimately has unforeseen consequences for many species throughout the food web. Lastly, as is evident in Fig. 6, future studies in lentic systems should quantify other properties of hydrographs that are commonly characterized in riverine systems, such as, number of pulse events, durations of higher water level, rate of increase and decrease, and timing of pulse events to determine how these characteristics may influence lentic systems.

In conclusion, water quality responds immediately to natural WLFs in the Boreal Shield ecozone. Macro-biota appear to be less sensitive (have a delayed response) to natural WLFs; however, macroinvertebrates did show a significant unimodal response (possibly due to their higher mobility) while slight alterations to the sessile macrophyte community were noted. This study emphasizes the need for aquatic ecologists, reservoir managers and climate change modelers to assimilate the dynamic ways in which WLFs change across time, both within and between years. The role of natural WLFs are of paramount importance in structuring aquatic communities, especially in littoral habitats, and alterations to these patterns (climate change and water regulation) may result in severe consequences to water quality, biodiversity and the health of lake ecosystems. The data presented in this study, acquired from renowned lacustrine research areas, supports the hypothesis that natural WLFs act as an intermediate disturbance that structures the physical, chemical, and biotic components of lacustrine ecosystems. The incorporation of long-term data in aquatic ecosystem assessments cannot be understated (Kratz et al., 2003). It is only with long-term monitoring programs that we can truly comprehend the complex way in which communities interact with their stochastic environments.

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