

Long-term trends in zooplankton of Dorset, Ontario, lakes: the probable interactive effects of changes in pH, total phosphorus, dissolved organic carbon, and predators¹

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Abstract: Time trends in abundance, body size, species richness, and species composition indicate that crustacean zooplankton communities of southern Canadian Shield lakes changed between 1980 and 2003. Total abundance did not decline despite reductions in total phosphorus, but all other metrics changed. Species richness declined in Harp Lake (Ontario, Canada) following its *Bythotrephes* invasion, but richness increased in three other lakes. Average cladoceran body length increased from 0.6 to 1.0 mm in seven of the lakes, as larger-bodied taxa replaced smaller ones. Correlations with water quality and fish metrics suggest that cladoceran size increases were attributable to many factors: a decline in food availability following declining phosphorus levels increasing the competitive advantage of larger herbivores, a decline in acidity favouring the larger, acid-sensitive daphniids, and reduced risk of planktivory linked to a rise in dissolved organic carbon levels and changes in predation regimes. Zooplankton communities on the Canadian Shield are changing, and these changes are best viewed in a multiple-stressor context. Key anthropogenic stressors have also changed and may do so again if Ca concentrations continue to decline.

Résumé : Les tendances temporelles de l'abondance, de la taille corporelle, de la richesse spécifique et de la composition en espèces indiquent que les communautés de crustacés zooplanctoniques dans les lacs du sud du Bouclier laurentien ont changé entre 1980 et 2003. L'abondance totale n'a pas diminué malgré les réductions du phosphore total, mais toutes les autres métriques ont été modifiées. La richesse spécifique au lac Harp (Ontario, Canada) a décliné après l'invasion de *Bythotrephes*, mais la richesse a augmenté dans trois autres lacs. La longueur corporelle moyenne des cladocères s'est accrue de 0,6 à 1,0 mm dans sept des lacs, car des taxons à corps plus grand ont remplacé les taxons à taille plus petite. Les corrélations avec la qualité de l'eau et les métriques des poissons indiquent que l'augmentation de taille des cladocères s'explique par plusieurs facteurs : une baisse de la disponibilité de la nourriture à cause du déclin des concentrations de phosphore, ce qui a accru l'avantage compétitif des herbivores plus grands, une baisse de l'acidité qui a favorisé les daphniidés sensibles à l'acidité qui sont de plus grande taille, ainsi qu'une diminution du risque de planctonophagie reliée à l'accroissement des concentrations de carbone organique dissous et à des modifications des régimes de prédation. Les communautés zooplanctoniques sur le Bouclier laurentien sont en train de changer et ces modifications s'expliquent mieux dans le contexte d'agents multiples de stress. Les sources anthropiques majeures de stress ont aussi changé et peuvent encore le faire si les concentrations de Ca continuent à décliner.

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Introduction

Aquatic ecologists have long been interested in the zooplankton of temperate soft-water lakes such as those of the Canadian Precambrian Shield (Klugh 1921; Adamstone 1928). Given the extent of past work, one might think that we understand the regulators of these zooplankton communities. Certainly, many of the natural regulators are known. At the largest spatial scale, latitude, glacial history, and regional bedrock geology are each important (Pinel-Alloul et al. 1979), given their respective effects on lake thermal regimes (Patalas 1990), community assembly (Carter et al. 1980; Stemberger 1995), and water chemistry (Tessier and Horwitz 1990; Hessen et al. 1995; Wærvagen et al. 2002). Smaller-scale, landscape patterns are also important. Larger lakes, with their greater probability of colonist introduction and greater habitat diversity, support more taxa (Dodson 1992; Keller and Conlon 1994). Landscape position influences water chemistry (Quinlan et al. 2003) and connections to colonist, competitor, and predator sources (Cottenie et al. 2001; Beisner et al. 2006). Watershed features also influence the supply of macronutrients (eg. N, P, and C) to lakes, and this nutrient supply influences both total (Yan 1986) or specific size fractions (Finlay et al. 2007) of zooplankton biomass and the competitive interactions of species with different absolute (Gliwicz 1990) and relative nutrient requirements (Sterner et al. 1997; Elser et al. 1998). The dissolved organic fraction of the carbon supply (DOC) affects the reactive distance of visual predators (Carter et al. 1983; Wissel et al. 2003), lake acidity, and microbial food availability (Moore et al. 1994). Finally, among the natural regulators, zooplankton may be influenced by the size, shape, and biochemical composition of their algal prey (Park et al. 2002; Ghadouani et al. 2003; Hampton et al. 2006), by competition with other zooplankton (Allan 1973), by parasites (Yan and Larsson 1988; Ebert 2005), and by both vertebrate and invertebrate predators (e.g., Magnan 1988; Yan et al. 2001a).

In addition to these natural regulators, many anthropogenic stressors have also influenced Canadian Shield zooplankton. Historically, the common stressors were local ones, i.e., land clearing, agriculture, and forestry (Patoine et al. 2002), shoreline development (Dillon and Molot 1996), water level regulation (Quinlan and Smol 2001), and fish introductions (St. Jacques et al. 2005). More recently, anthropogenic stressors have regional or even larger-scale signatures. For example, increased ultraviolet (UV) irradiance affects the behaviour, distribution, and perhaps the composition of zooplankton communities in clear-water lakes (Williamson et al. 2001; Persaud and Yan 2003; Leech et al. 2005), but the majority of Shield lakes are probably not UV-transparent enough to be much affected (Molot et al. 2004). In contrast, acid rain has disturbed zooplankton in thousands of lakes in eastern Canada (e.g., Carter et al. 1986; Pinel Alloul et al. 1990; Havens et al. 1993), and near smelters, the damage has been compounded by metal toxicity (Yan and Strus 1980). Regionally coherent, annual fluctuations in their abundance indicate that Canadian Shield zooplankton are also responding to a changing climate (Rusak et al. 1999). Finally, Canadian Shield zooplankton are also now affected by the redistribution of native predators (Vander Zanden et al. 2004b) and the introduction of

nonnative ones (Yan et al. 2002). Despite this body of past understanding, built on both large (e.g., Carter et al. 1980; Keller and Pitblado 1989; Patalas 1990) and more regional synoptic surveys (e.g., Carter 1971; Patalas 1971; Pinel-Alloul et al. 1990), long-term observational studies (e.g., Yan and Pawson 1997; Keller et al. 2002; Olden et al. 2006), and whole-lake experiments (Keller et al. 1992; Elser et al. 1998; Yan et al. 2001a), it is again time to examine long-term trends in the crustacean zooplankton fauna of the Shield, because zooplankton are now facing both new stressors with unknown effects (e.g., Ca decline, Jeziorski and Yan 2006) and, more importantly, combinations of abiotic and biotic stressors that are unique in their postglacial experience (e.g., Strecker and Arnott 2005). Long-term data sets may be quite useful for teasing out multiple-stressor interactions (Hampton et al. 2006) and for comparing the magnitude of interlake and interannual variability (Olden et al. 2006). Here, we examine the 1980 to 2003 crustacean zooplankton records from the eight, long-term study lakes (Table 1) of the Ontario Ministry of the Environment's Dorset Environmental Science Centre (DESC) in south-central Ontario, Canada, to determine (i) if the magnitude of interannual variability in the communities differs among lakes, (ii) if there are long-term trends in community abundance, species richness, composition, and (or) size structure, (iii) if key changes are lake-specific or regional in scale, and (iv) which water quality changes, or combinations of changes, are correlated with the key observed trends. We focus on water quality correlations because climate drivers are considered elsewhere (Rusak et al. 1999).

Given that ice-free season length (Futter 2003; Keller 2007), water quality (Dillon et al. 2007), and predator assemblages (Boudreau and Yan 2003; Vander Zanden et al. 2004a) have all changed for many lakes on the south-central Shield and given that each may alter zooplankton communities (Chen and Folt 2002; Yan et al. 2002; Olden et al. 2006), we expected that the zooplankton communities of all of our long-term study lakes would have changed. Total phosphorus (TP) levels declined appreciably and pH rose in all but one of the lakes (Table 2). Because the magnitude of interannual variability in water quality differed among lakes, we predicted that the magnitude of interannual variability in the zooplankton metrics (objective 1) would also differ. We predicted a decrease in total zooplankton abundance, given the declining TP trends (Table 2) and the positive correlation between nutrients and zooplankton standing stocks observed in spatial surveys in the region (Yan 1986). Except for Harp Lake, with its *Bythotrephes* invasion (Yan and Pawson 1997), we predicted an increase over time in species richness, given the reduction in acidity in the lakes (Table 2) and the commonly observed, positive correlation between pH and crustacean species richness (Locke 1992). We predicted increases over time in the relative abundances of larger vs. smaller cladoceran species, leading to an increase in mean body size of the cladoceran assemblage, for a number of reasons. TP levels are falling, and larger herbivorous zooplankton should outcompete smaller ones as food resources fall (Gliwicz 1990). Chromophoric DOC levels have increased over time in several of the lakes (Keller et al. 2008), decreasing water clarity and lowering the relative risk of the larger taxa to visual predators. Acidity has also declined, fa-

Table 1. Lake area (A_o , in ha), mean depth (z_{mean} , in m), maximum depth (z_{max} , in m), lake order (LO), index of strength of summer stratification (stratification, as strong (S), weak (W), or normally absent (A)), the number of occupied shoreline dwellings (dwellings, from Dillon and Molot 1996), and presumed lake stressors during the study period (stress, including acidification (A), significant proportion of phosphorus supply predicted to come from shoreline development (P), and introduction of nonindigenous species (NIS)) for the eight study lakes.^a

	BC	CB	CN	DE	HP	HY	PC	RCm
A_o	52.4	34.4	56.7	93.6	71.4	21.4	32.1	44.1
z_{mean}	8.5	8.9	9.2	5.0	13.3	3.3	7.9	16.7
z_{max}	23	27	25	12	37.5	5.8	16.3	38
LO	1	1	1	1	1	1	1	2
Stratification	S	S	S	W	S	A	S	S
Dwellings	11	11	1	125	83	1	0	3
Stress		A	A	A, P	P, NIS	A	A	

^aLakes: Blue Chalk (BC), Chub (CB), Crosson (CN), Dickie (DE), Harp (HP), Heney (HY), Plastic (PC), and Red Chalk – main basin (RCm). See Yan et al. (2008) for lake locations. BC and RCm lakes are considered reference systems for both acidification and shoreline development studies.

Table 2. Comparison of 1980 and 2003 ice-free season averages of pH, TP ($\mu\text{g}\cdot\text{L}^{-1}$), DOC ($\text{mg}\cdot\text{L}^{-1}$), and Ca ($\text{mg}\cdot\text{L}^{-1}$) in the eight study lakes, along with the percentage change (Δ , in bold) from 1980 to 2003.

Lake	Ca			DOC			pH			TP		
	1980	2003	Δ (%)	1980	2003	Δ (%)	1980	2003	Δ (%)	1980	2003	Δ (%)
BC	2.75	2.45	-10.9	1.95	2.50	28.2	6.62	6.74	1.8	7.03	5.85	-16.8
CB	2.54	1.99	-21.7	5.38	6.05	12.5	5.53	5.76	4.2	12.6	9.24	-26.7
CN	2.26	1.85	-18.1	4.59	4.55	-0.9	5.53	5.72	3.4	11.4	8.17	-28.3
DE	2.52	3.15	25.0	5.71	5.46	-4.4	5.70	6.21	8.9	13.1	8.89	-32.1
HP	3.02	2.87	-5.0	4.02	3.92	-2.5	6.21	6.42	3.4	9.02	6.35	-29.6
HY	2.06	1.63	-20.9	3.21	3.77	17.4	5.64	5.91	4.8	8.44	5.51	-34.7
PC	2.04	1.54	-25.0	2.85	2.25	-21.1	5.80	5.77	-0.5	8.15	4.51	-44.7
RCm	2.79	2.25	-19.4	2.62	3.23	23.3	6.28	6.45	2.7	5.84	4.65	-20.4

Note: Lake abbreviations are provided in Table 1. DOC, dissolved organic carbon; TP, total phosphorus.

vouring the acid-sensitive daphniids (Havens et al. 1993), which, excluding *Daphnia ambigua*, are among the larger pelagic Cladocera. Smallmouth bass (*Micropterus dolomieu*; Vander Zanden et al. 2004a) and *Bythotrephes longimanus* (Yan and Pawson 1997) are appearing in area lakes, and both introductions commonly lead to increases in mean cladoceran body size (Yan and Pawson 1997; Yan et al. 2001a). Fish are particularly important regulators of zooplankton community size structure in low productivity lakes such as these (Finlay et al. 2007). Finally, although Ca levels are falling in most of the lakes, we do not believe they have declined enough as yet to harm the larger, more Ca-rich daphniids (Jeziorski and Yan 2006; Ashforth and Yan 2008).

Materials and methods

The study lakes

Blue Chalk, Chub, Crosson, Dickie, Harp, Heney, Plastic, and Red Chalk lakes are the focus of this study. The lakes were selected to vary widely in sensitivity to acid inputs and in proportion of the theoretical total phosphorus load that was attributed to inputs from shoreline dwellings (Dillon and Molot 1996). The early 1990s introduction of the non-indigenous zooplanktivore *Bythotrephes longimanus* to Harp Lake (Yan and Pawson 1997) added an unplanned stressor to

the planned pH and TP gradients of the lakes (see Table 1) and left only Blue Chalk and Red Chalk lakes as reference systems, i.e., as clear-water, dimictic lakes that were selected to be unaffected by shoreline development, acid rain, or introduced zooplanktivores.

The water quality of the lakes has changed significantly over the 24-year study period. Levels of Ca declined in seven of the eight lakes (Table 2; Watmough and Aherne 2008), increasing only in Dickie Lake, likely associated with dust control treatment of roads in its watershed (Table 2). Levels of pH increased in all but one of the lakes over the entire study period in response to reductions in acid deposition (Table 2; Dillon et al. 2007). In Red Chalk, Blue Chalk, and Harp lakes, levels of pH were always >6 , i.e., above the commonly accepted threshold for zooplankton damage (Havens et al. 1993; Holt and Yan 2003). Levels of TP declined substantially in all the lakes over time (Table 2), and algal composition also changed, with colonial chrysophytes replacing diatoms as the dominant taxa in several of the lakes (Paterson et al. 2008).

Zooplankton sampling and analysis

Between 1980 and 2003, 1635 samples were collected and enumerated from the lakes. Animals were collected between 0800 and 1600 as a single bathymetrically weighted, composite sample from a station located over the point of maxi-

imum depth in each lake. The composite was formed by combining the contents of four to seven vertical hauls taken from predetermined depths to the surface using a 12.5 cm diameter, 80 μm mesh, high efficiency (McQueen and Yan 1993), metered, tow net. The lengths and numbers of hauls were set so that lake depth strata contributed to the composite sample in approximate proportion to their volumes. Samples were preserved immediately after collection with a buffered sucrose formalin solution. Except for Harp, Plastic, and Dickie lakes, all lakes were sampled on a monthly basis during the ice-free season after 1980. Harp and Plastic lakes were sampled on a fortnightly basis. Dickie Lake was sampled monthly until 1988, then fortnightly thereafter. Such differences in sampling frequency have very minor effects on ice-free season averages of zooplankton community metrics (Yan 1986; J. Rusak, personal observation).

In the laboratory, all animals were identified and enumerated by either Bill or Dee Geiling (Limnoservices Inc., Lansdowne, Ontario, Canada). A minimum of 250 individuals were identified and enumerated in each sample, and body lengths of video images of all counted animals were measured (Allen et al. 1994) from the top of the head to the base of the tail spine or mucron in Cladocera or to the base of caudal ramus in Copepoda. Cladocera and adult Copepoda were identified to the species level, while immature copepods were identified to the level of suborder. To execute the counts, sequential subsamples were produced with a Folsom plankton splitter and enumerated in such a way as to ensure that no single counting category (species or copepod life stage) contributed more than 20% to the total count. With this standardized counting protocol, the number of animals identified and counted each year in each lake was mainly a function of sampling frequency. Roughly 1700 and 3250 animals, respectively, were identified and counted each year in each lake with monthly vs. fortnightly sampling frequencies.

Data analysis

Zooplankton data generated on a fortnightly or monthly basis from a single deep station provide reliable estimates of ice-free season averages for the pelagic zone in our lakes, i.e., ice-free season means that are very close to those generated from weekly samples (Yan 1986). We analyze only ice-free season averages herein, and given the regularity of sampling, these were computed as simple arithmetic averages of the data from each sampling date. We acknowledge that this decision prevents us from detecting potentially interesting differences in seasonality, especially among years with differing weather patterns (e.g., Straile and Adrian 2000; Winder and Schindler 2004), but detecting such changes was not our current purpose.

Long-term changes in aquatic invertebrate communities are best examined with multiple metrics (Bowman et al. 2006). Environmental covariations with, and sensitivity to, particular stressors differ among zooplankton metrics (Yan et al. 1996a). Here we report long-term trends in five crustacean zooplankton metrics: (1) species richness (species-standard count⁻¹ of a composite sample, excluding the invading *Bythotrephes* in Harp Lake); (2) total crustacean abundance (animals-L⁻¹, accounting for lake bathymetry given the compositing collection technique); (3) mean cladoceran body size (length in mm,

correcting for the differences in subsample volumes examined for rare and common species); and (4) and (5) the scores of the first two axes of a correspondence analysis of log_{x+1}-transformed abundances of all common species to quantify changes in the species composition of the community.

We excluded several other possible metrics from consideration. Biomass was an obvious choice, but we had not determined it directly; hence, we would have had to have calculated it from abundances and body weights. Individual body weights of zooplankton are influenced by many factors in addition to body length (Yan and Mackie 1987), and without species-specific models incorporating these important factors, we would not have been able to quantify the accuracy and precision of biomass estimates. In addition, we do not report community-level functional metrics based on feeding patterns, e.g., herbivore biomass, given the probability that many taxa are facultative omnivores.

We selected correspondence analysis (CA) as our multivariate technique for reasons detailed elsewhere (Yan et al. 1996a). The one weakness of CA is its sensitivity to sparse input matrices. Consequently, we removed rare taxa from the input matrices. Over 403 000 animals, representing 49 species, were counted in the 1980 to 2003 samples. Of this total, 25 species, representing a total of only 174 individuals (0.04% of the total count), were each observed 25 or fewer times across the eight lakes and at an obvious breakpoint in a plot (not shown) of the log-transformed numbers of individuals counted per identification category vs. the category rank. All but four of these 25 species were littoral Cladocera, the populations of which we undoubtedly had sampled poorly in offshore waters (Walseng et al. 2003). Distinguishing littoral from pelagic components of the microcrustacean community is an ongoing dilemma (Walseng et al. 2006), but we deleted these 25 species from the input data to the CA, leaving us with 31 pelagic species and immature copepod categories that were encountered more than 73 times in the lakes. With this number of taxa retained in the analyses, interpretation of species loadings on axis scores can be problematic. We ran the analysis in Statistica (StatSoft Inc., Tulsa, Oklahoma) and used its index named "quality", which quantifies the proportion of the total variance (0–1) for each species that is accounted for in the solution of the selected dimensionality. Thus we focused our presentation of the CA results on those species with a quality index of >0.5 in our selected two-dimensional ordination.

Statistical methods

To determine if the magnitude of interannual variability differed among lakes for each of the five metrics (objective 1), we used a Levene's test for the homogeneity of variance (Levene 1960). This was implemented as a one-way analysis of variance (ANOVA) *F* test among lakes of absolute deviations of each year's mean from the 24-year mean for that lake. Total abundances were log-transformed prior to running the Levene's tests. To test for the presence of monotonic time trends (objective 2), we employed the *S* statistic of the Mann-Kendall (M-K) trend test (Yue et al. 2002) as operationalized by one of us (KS) in Microsoft Excel. We performed these time trend tests individually on the data series from each of the study lakes, thereby increasing the risk of falsely ascribing some nonsignificant trends as signifi-

Table 3. Summary statistics of the Mann–Kendall (M-K) trend tests on the five zooplankton metrics from the eight study lakes from 1980 to 2003.

	Lakes							
	BC	CB	CN	DE	HP	HY	PC	RCm
Total abundance								
M-K test	0.248	-1.538	-1.488	-0.496	-0.149	-1.042	2.084	0
Slope (no.·L ⁻¹ ·year ⁻¹)	0.104	-0.501	-0.591	-0.391	-0.017	-0.711	0.826	0.036
Percent change	5.7	-28.3	-44.2	-18.8	-2.3	-23.8	87.0	4.1
Species richness								
M-K test	2.63*	-0.45	0.25	-1.89	-3.57*	2.48*	1.64	3.08*
Slope (taxa·year ⁻¹)	0.071	-0.025	0.017	-0.036	-0.128	0.094	0.054	0.08
Percent change	16.9	-6.7	4.0	-9.0	-27.6	28.8	15.7	14.6
Cladoceran length								
M-K test	2.480*	2.588*	2.324*	4.120*	5.110*	4.991*	3.473*	-0.248
Slope (mm·year ⁻¹)	0.007	0.013	0.013	0.021	0.03	0.011	0.01	0
Percent change	14.3	46.7	34.8	51.9	192	46.9	49.3	0.0
CA axis I scores								
M-K test	-0.645	-2.63*	-0.298	-1.488	-2.73*	0.546	-0.298	1.885
Slope	-0.002	-0.008	0	-0.008	-0.006	0.002	0	0.005
CA axis II scores								
M-K test	1.637	3.175*	2.133*	2.679*	3.076*	-2.18*	-1.339	4.564*
Slope	0.003	0.012	0.011	0.016	0.022	-0.008	-0.006	0.011

Note: Trends that were significant at $P < 0.05$ and after false discovery rate corrections are printed in bold and with an asterisk (*), respectively. The percent change over the 24 years was calculated for abundance, richness, and Cladoceran body length using the Sen's slope (slope) with respect to the 1980 mean (1981 for Cladoceran length in CB, CN, DE, and HY lakes). Lake abbreviations are provided in Table 1.

cant. As we considered these M-K trend tests to provide our key results, we corrected for the potential false discovery rate (FDR) employing Benjamini and Hochberg's (1995) procedure, for reasons identical to those given in Barnett and Beisner (2007). To make the FDR correction, we ranked the observed P values of the M-K trend test for the metric (e.g., richness for the eight lakes, body size for 15 cladoceran species, etc.) from lowest to highest, computing $P_{FDRi} = (i/n)\alpha$, where P_{FDRi} is the critical value controlling for the FDR, i is the rank of the P value, n is the number of trends examined (e.g., $n = 8$ for the 8 lakes, one trend per lake) for $\alpha = 0.05$. Then we compared the observed P_i with P_{FDRi} to decide on rejecting the null hypothesis of no significant time trend. Recognizing that there is a range of opinions on such corrections, we report both the P_i and P_{FDRi} results for the trend tests. To determine if key trends were lake-specific, or common across the region (objective 3), we performed multi-group M-K tests (Van Belle and Hughes 1984; Yue et al. 2002). Finally, to develop hypotheses to help explain the key time trends in the zooplankton metrics in our Discussion, again correcting for the FDR, we examined Pearson correlations of the zooplankton metrics with several physical and meteorological metrics assembled by one of us (KS), with TP, pH, DOC, and Ca levels from the lakes and selected fish metrics provided by G. Morgan and J. Gunn (unpublished data). With so many changes in climate, water quality, food base composition, and predator assemblages in the lakes, we adopted this correlation approach as the logical first step in constructing hypotheses of factors that could be responsible for the observed changes in the zooplankton communities. Testing of these hypotheses will require additional, more focused research and a consideration of higher-

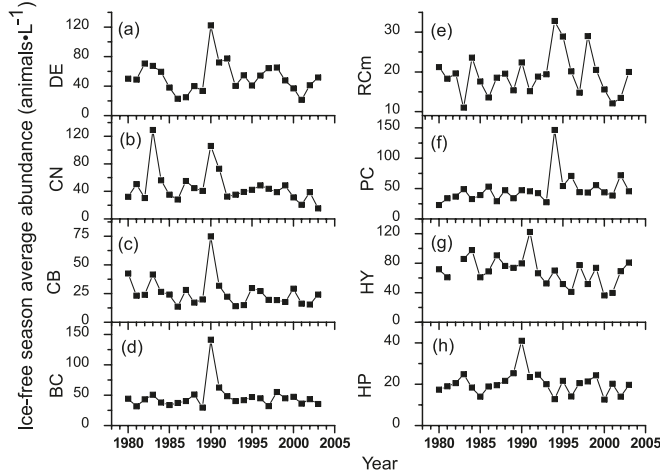
order individual effects, lagged responses, nonmonotonic effects, and stressor interactions, all of which are possible.

Results

Despite differences among lakes in morphometry, landscape position, thermal stratification patterns, water chemistry, and anthropogenic stressors (Table 1) and despite long-term changes in several key water quality parameters (Table 2), there was no difference among lakes in the magnitude of interannual variability in total crustacean zooplankton abundance (Levene's test, $F = 1.08$, $P = 0.376$). Further, the time trend in total abundance was significant ($P < 0.05$) only for Plastic Lake, but after the false discovery rate (FDR) correction, there were no significant trends over time in total zooplankton abundance in any of the study lakes (Table 3). Thus, our first prediction was not supported: total zooplankton abundance did not decline over time with declining TP. If anything, it may have increased in Plastic Lake. There did, however, appear to be at least one unusual year in the record: 1990 witnessed unusually high total zooplankton abundance in five of the lakes — Blue Chalk, Chub, Crosson, Dickie, and Harp (Fig. 1).

Given the differences in changes in pH among the eight lakes (Table 2), we might have expected interlake differences in the magnitude of interannual variability in mean species richness. The observed differences did approach significance (Levene's test, $F = 1.85$, $P = 0.08$). Richness changed over time in four of the eight lakes (Table 3). It increased significantly in Blue Chalk and Red Chalk lakes, our two nonacidic reference lakes (Fig. 2). The Sen's slope (the median rate of change of all possible pairs of years) was 0.071 and 0.080 species-collection⁻¹·year⁻¹ in Blue Chalk

Fig. 1. Long-term changes in ice-free season averages of total abundance of the crustacean zooplankton assemblage, 1980–2003. Note that Heney Lake was not sampled in 2002 and that y axes differ among subpanels. Lake abbreviations: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; HY, Heney; PC, Plastic; RCm, Red Chalk – main basin.



and Red Chalk lakes, respectively (Table 3). Thus we found roughly 1.7 more species per collection at the end than at the beginning of the time series. Richness also increased significantly over time in Heney Lake (Fig. 2) at a rate of 0.094 species-collection⁻¹·year⁻¹, or 2.2 species over the record. This change was the largest proportional increase in richness observed in the lakes (Table 3), given that Heney Lake supported the fewest species (6–8-standard count⁻¹) among the lakes at the start of the record (Fig. 2). Given these stable or increasing richness trends in seven of the lakes, the large decline in richness in Harp Lake is particularly striking (Fig. 2). With a Sen’s slope of –0.128 species-collection⁻¹·year⁻¹ (Table 3), there were three fewer species per collection on average in 2003 than in 1980 in Harp Lake, a loss of more than one-quarter of the native zooplankton biodiversity. These losses were mainly to the small Cladocera and occurred after *Bythotrephes* colonized the lake in the early 1990s (Yan et al. 2001b). We had predicted an increase in richness associated with increases in pH, and although pH increased from 1980 to 2003 in all but one of the lakes (Table 2), richness increased significantly in only three of the lakes, and two of these (Blue Chalk and Red Chalk) weren’t particularly acidic at the start of the record.

Unlike both richness and total abundance, the magnitude of interannual variability of mean cladoceran body size clearly differed among lakes (Levene’s test, $F = 7.43$, $P < 0.001$). There was little interannual variability in cladoceran length (Fig. 3) in Blue Chalk and Red Chalk lakes, for example (coefficients of variation (CVs) of 10.5% and 10.9%, respectively, calculated from the annual means), relative to the amount of variability in Chub, Crosson, Dickie, Harp, Heney, and Plastic lakes, with their CVs of 18%, 26%, 20%, 37%, 17%, and 17%, respectively. We observed significant positive trends over time in mean cladoceran body size in seven of the study lakes (Table 3), and in several cases, the increases were dramatic. For example, in Harp Lake, mean cladoceran body size calculated from the Sen’s slope of

Fig. 2. Long-term changes in ice-free season averages of mean species richness of crustacean zooplankton (in species-collection⁻¹·year⁻¹), 1980–2003. Asterisks indicate that the Mann–Kendall trend test was significant after correcting for the false discovery rate ($P < 0.05$). Note that Heney Lake was not sampled in 2002 and that y axes differ among subpanels. Lake abbreviations: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; HY, Heney; PC, Plastic; RCm, Red Chalk – main basin.

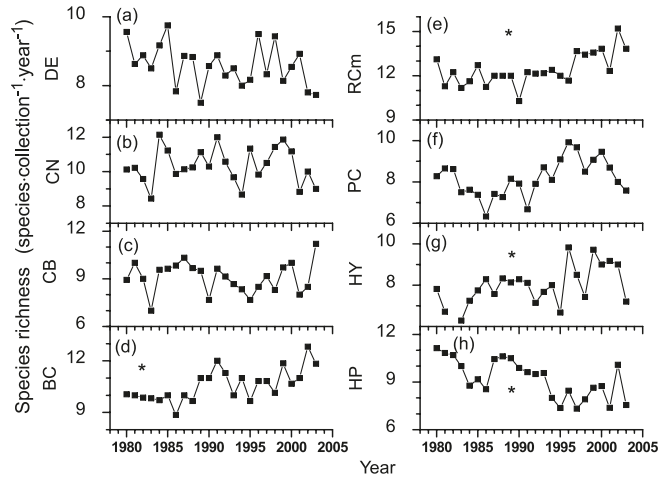
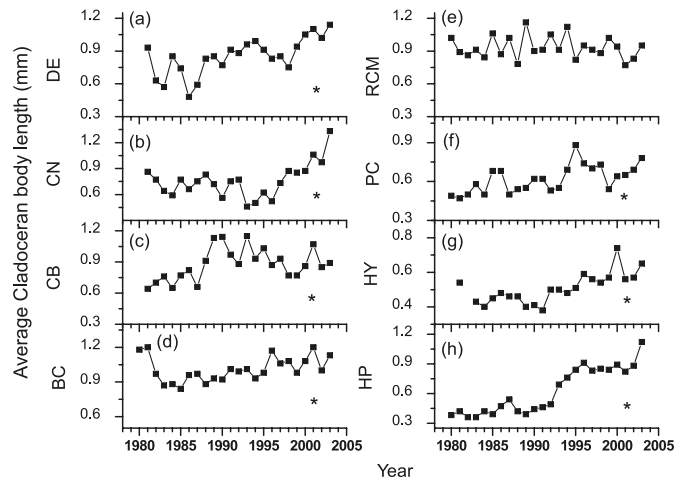


Fig. 3. Long-term changes in ice-free season averages of mean Cladoceran body size (length in mm), 1980–2003. Asterisks indicate that the Mann–Kendall trend test was significant after correcting for the false discovery rate ($P < 0.05$). Note that Cladocera were not measured in Chub, Crosson, Dickie, and Heney lakes in 1980, Heney Lake was not sampled in 2002, and the y axes of subpanels d and g differ from those of the other lakes. Lake abbreviations: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; HY, Heney; PC, Plastic; RCm, Red Chalk – main basin.



0.03 mm·year⁻¹ increased by almost 200% over the study period (Table 3). However, considering only the 2003 and 1980 mean body lengths (1.12 mm vs. 0.38 mm, respectively) yields a tripling of mean cladoceran body length from the first to the last year of the record.

The multiple-group M-K test (objective 3) detected both lake-specific effects and a regional trend in mean cladoceran

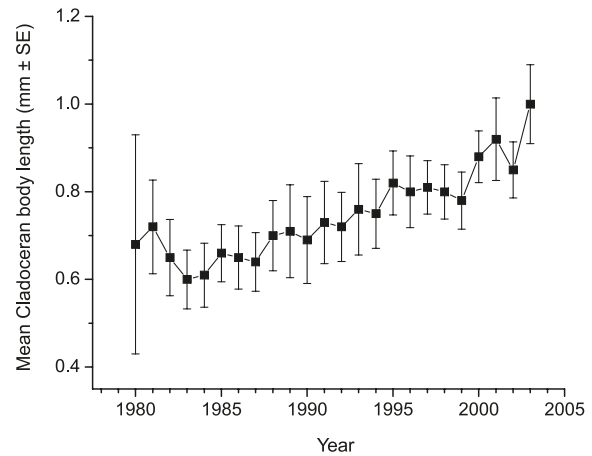
Table 4. Summary of results of a multigroup Mann–Kendall trend test to determine if there were consistent regional trends in abundance-weighted mean Cladoceran body size for (a) all eight lakes and (b) all lakes except Red Chalk Lake.

Effect	χ^2	df	<i>P</i>
(a) All eight lakes			
Lakes	15.62	7	0.029
Trend	58.91	1	<0.001
Total	74.54	8	
(b) All lakes, except Red Chalk			
Lakes	7.21	6	0.3
Trend	67.33	1	< 0.001
Total	74.54	7	

body size when all eight lakes were included in the analysis; however, when Red Chalk Lake was excluded, differences among lakes disappeared, leaving a common, seven-lake, significant trend (Table 4). For these seven lakes, mean cladoceran body size increased from an average of 0.6–0.7 mm in the early 1980s to 1.0 mm in 2003, a 55% change (Fig. 4). Such an increase could be attributed to shifts in the cladoceran assemblage from small- to large-bodied species, to increases in mean body size of individual species, or to some combination of the two. Here, a long-term shift from small- to large-bodied taxa was the more important explanation. Of the 15 common cladoceran taxa that were measured routinely, Sen’s slopes indicated that slight increases and decreases in body size over time were equally likely (Table 5). Significant increases ($P < 0.05$) in body size over time were observed for *Bosmina freyi/liederi*, *Daphnia ambigua*, *D. longiremus*, the *Daphnia pulex* group, *Eubosmina tubicen*, and *Holopedium gibberum*; however, body size trends over time that approached significance ($0.05 < P < 0.1$) were also common but were negative in all cases (Table 5). Mean body size did not differ among taxa with increasing vs. decreasing trends over time (Student’s *t* test, $t = 0.41$, $P > 0.05$). Only *Daphnia ambigua* grew in size over time across the eight lakes after FDR correction (Table 5).

The CA proved that initial differences in species composition among the lakes were largely preserved over the 24-year record, but that some time trends in composition had also occurred. We performed two ordinations, with and without Harp Lake. The first CA revealed large differences in composition among the lakes and, more interestingly, changes in composition over time, but this CA was dominated by Harp Lake. All lakes except Harp Lake had low scores on axis II and were distributed along the first CA axis (Fig. 5a), with the reference lakes Blue Chalk and Red Chalk defining its negative end. Species particularly characterizing Blue and Red Chalk lakes, taxa for which the two-dimensional solution was robust (with quality indices > 0.5), included *Skistodiaptomus oregonensis*, *Diacyclops bicuspidatus thomasi*, *Daphnia mendotae*, and *Cyclops scutifer* (Fig. 5b). The remaining five lakes were distributed along axis I to the right of Blue and Red Chalk lakes, and all had pH levels < 6 at the start of the record. Further, their depths (Table 1) declined with increasingly positive scores along axis I, with the shallowest lakes, Dickie and Heney, having the most

Fig. 4. Long-term trend in mean Cladoceran body length in the seven-lake set that excludes Red Chalk Lake. The standard error is large in 1980, as Cladocera were measured in only four lakes that year but in all lakes every other year.



positive CA I scores. Among taxa for which the two-dimensional solution was of high quality, *Daphnia retrocurva* best characterized the positive end of this gradient, being particularly common in Heney Lake (Fig. 5b). The generality of this ordination (Fig. 5a) was affected by the fact that axis II distinguished Harp Lake from all of the other lakes. The unique zooplankton composition of Harp Lake was attributable not to the presence of the invading *Bythotrephes*, which was excluded from this analysis, but to the richness of the lake’s hypolimnetic calanoid copepod fauna, especially to the abundance of *Leptodiaptomus sicilis* and *Senecella calanoides* (Fig. 5b). The arrival of *Bythotrephes* in the early 1990s simply increased Harp Lake’s uniqueness (Fig. 5a), as the abundance of *L. sicilis* increased after 1993 and abundances of many small Cladocera declined dramatically (Yan et al. 2001b). Because the descriptive power of this analysis was reduced by the inclusion of Harp Lake, we repeated the analysis without Harp Lake.

Eliminating Harp Lake from the ordination did not change the ordering of the remaining lakes along CA axis I (Fig. 6a). The communities of Blue Chalk and Red Chalk lakes often overlapped in composition, and Red Chalk Lake also frequently overlapped with Crosson Lake. The communities of Chub, Plastic, and Dickie lakes could not be readily distinguished in most years in terms of their dominant compositional patterns, and Heney Lake clearly had a different community than the other lakes, perhaps no surprise given that it is the only unstratified lake of the group (Table 1). The unique community composition of Heney Lake was particularly attributable to relatively high abundances of *Alona* sp., *Daphnia retrocurva*, and *Leptodora kindtii*, species for which this analysis was of high quality (Fig. 6b). We have recently found that 12% of 101 *Leptodora* populations in south-central Ontario are in lakes with maximum depths of 5 m or less (E. Weisz and N.D. Yan, unpublished data), so its importance in Heney Lake is unusual but not unprecedented. The remaining six lakes were distributed roughly around a 45° diagonal in the plot (Fig. 6a) from the clear-water, nonacidic Blue Chalk and Red Chalk lakes with higher abundance of *Daphnia dubia*, *Skistodiaptomus orego-*

Table 5. Summary of results of Mann-Kendall tests for trends in body length of common Cladocera in the eight study lakes.

Species	Mean length (mm)	Mann-Kendall	Sen's slope ($\mu\text{m}\cdot\text{year}^{-1}$)	<i>P</i>	<i>P</i> _{FDR}
<i>Alona</i> sp.	0.34 (0.069)	-0.367	-0.28	0.714	0.05
<i>Bosmina freyi/liederi</i>	0.33 (0.024)	2.084	1.26	0.037	0.0167
<i>Chydorus sphaericus</i>	0.29 (0.026)	0.794	0.18	0.427	0.047
<i>Daphnia ambigua</i>	0.91 (0.114)	3.721	12.57	<0.001	0.0033
<i>D. dubia</i>	1.24 (0.112)	-1.885	-5.68	0.059	0.023
<i>D. mendotae</i>	1.26 (0.086)	-1.736	-4.03	0.083	0.037
<i>D. longiremus</i>	0.85 (0.035)	2.480	3.03	0.013	0.01
<i>D. pulicaria, pulex, and catawba</i>	1.38 (0.134)	2.430	8.95	0.015	0.013
<i>D. retrocurva</i>	0.88 (0.092)	-1.836	-5.17	0.066	0.03
<i>Eubosmina tubicen</i>	0.40 (0.024)	1.984	1.85	0.047	0.02
<i>Holopedium gibberum</i>	0.85 (0.06)	2.530	3.99	0.011	0.0067
<i>Polyphemus pediculus</i>	0.60 (0.102)	-1.796	-5.54	0.073	0.033
<i>Sida crystallina</i>	1.51 (0.281)	-1.637	-9.91	0.102	0.043
<i>Eubosmina longispina</i>	0.41 (0.039)	-1.885	-2.47	0.059	0.027
<i>Diaphanosoma birgei</i>	0.65 (0.037)	1.687	1.55	0.092	0.04

Note: The mean length (with standard deviation (SD) in parentheses, in mm) is reported, calculated from 22–24 annual means in all eight lakes. The bold values indicate significance ($P < P_{\text{FDR}}$) after false discovery rate correction.

nensis, *D. bicuspidatus thomasi*, and *Daphnia mendotae*, in particular, to the initially more acidic lakes (Table 1) with higher abundances of *Holopedium gibberum*, *C. scutifer*, and *D. ambigua*, in particular (Fig. 6b). Several other common species, e.g., *L. minutus* and *M. edax*, while of high quality in the ordination, had axis scores near 0.0 (Fig. 6b), suggesting they are ubiquitous in the lakes.

In this seven-lake analysis, there were significant differences between lakes in the magnitude of interannual variability (Levene's test: CA I, $F = 3.22$, $P = 0.005$; CA II, $F = 2.62$, $P = 0.012$), consistent with our prediction. The spread of annual scores in the ordination demonstrate the large amount of interannual variability in Dickie, Chub, and Heney lakes, for example, in comparison with several of the other lakes. Axis I scores could clearly distinguish some lakes, e.g., Red Chalk and Blue Chalk vs. Chub, Plastic, and Dickie vs. Heney Lake (Fig. 6a), but they were less useful in revealing trends over time (not illustrated). For CA I, we detected significant time trends for only Harp Lake, with its *Bythotrephes* invasion, and Chub Lake (Table 3). In contrast, CA II scores changed significantly in six of the eight lakes (Table 3), with changes being positive for Red Chalk, Dickie, Crosson, and Chub lakes in the second ordination and Harp Lake in the initial ordination. Hence, the main compositional pattern in the 31 taxa \times 24 years \times 8 lake data set was a consistent difference among lakes summarized by CA I scores, accounting for 20% of the variance. However, there were also significant time trends in six of the lakes captured mainly by CA II scores, accounting for a further 18% of the total variance.

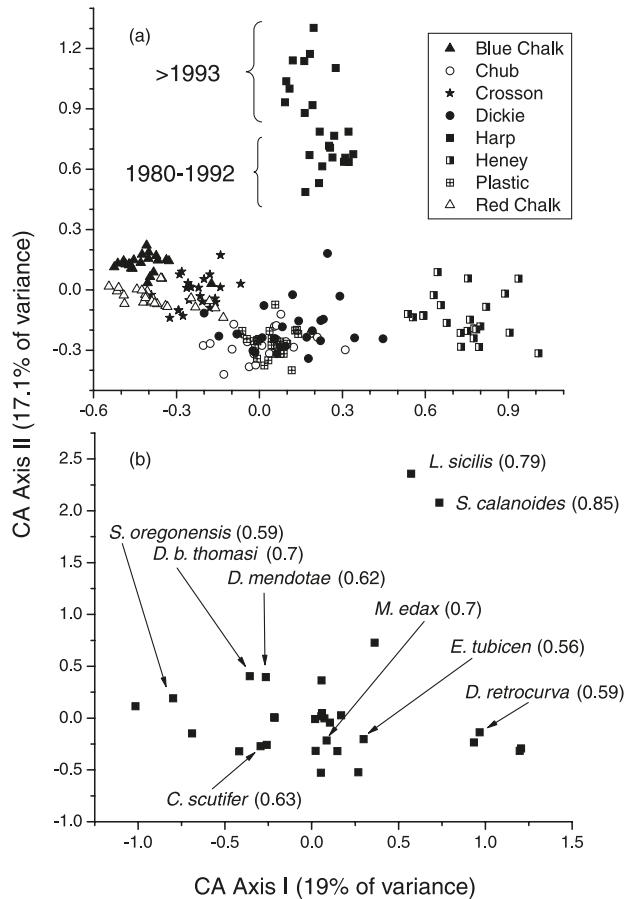
Discussion

Biological communities can change in monotonic, curvilinear, or more complex ways, but even in restricting our attention to monotonic trends, it is clear that change has been the only constant for the crustacean zooplankton communi-

ties in our study lakes over the last quarter century. A simple tally (vote count) of the numbers of FDR-corrected significant time trends in the metrics indicates that the zooplankton community of every lake has changed during our period of observation (Table 6). If a count of these FDR-corrected trends reflects the number of ways that a community has changed, then Harp Lake has changed in the largest number of ways, i.e., every metric except total abundance has changed significantly over the 24-year record. Perhaps surprisingly, it is not the clear-water, nonacidic, undeveloped, "reference" lakes (Blue and Red Chalk) that have changed in the fewest number of ways. That mantle falls on the Plastic Lake community, where only cladoceran body size has changed. Interestingly, the phytoplankton community of Plastic Lake also exhibited very little compositional change at the algal group level in comparison with the other lakes (Paterson et al. 2008). If we compare the signs and magnitudes of the trends, it is clear that the changes occurring in Harp Lake are the most unique in the data set. It is only in Harp Lake that richness has fallen, and only in Harp and Chub lakes that the assemblage of taxa represented by CA I scores has changed. It is worth repeating that Harp Lake is the only lake in this study that has been invaded by *Bythotrephes*, but the changes that we have seen in Harp Lake are not unique in Canada. They are, in fact, quite typical consequences of *Bythotrephes* invasions in the Laurentian Great Lakes (Barbiero and Tuchman 2004) and in inland lakes in Ontario (Boudreau and Yan 2003; Strecker et al. 2006).

Not all metrics reflect the community changes that are occurring. Tallying the results for each metric produces zero, two, four, six, and seven significant trends, respectively, for total zooplankton abundance, CA I scores, richness, CA II scores, and mean cladoceran body size after correcting for the false discovery rate (Table 6). As in severely acidified and metal-contaminated lakes (Yan et al. 1996a), total zooplankton abundance is not a sensitive metric to quantify changes in crustacean zooplankton communities in Canadian

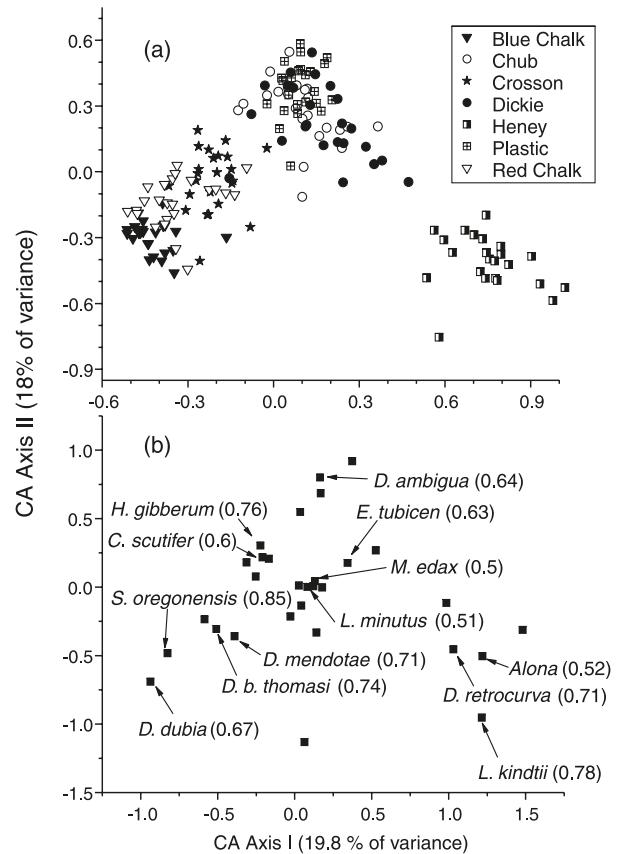
Fig. 5. (a) Scattergram of lake-year scores from the correspondence analysis (CA) on log abundances of 31 species and immature copepod identity categories. Points are year scores for each lake from 1980 to 2003. (b) Scattergram of the axis scores for the 31 taxa included in the CA. Taxa are identified when the quality of the two-dimensional solution (percent of variance explained for the taxon) was >0.5 for that taxon. Quality scores are provided for these taxa in parentheses. Note that the scales of the two panels differ.



Shield lakes. Individual species certainly come and go or slip below our detection threshold (Arnott et al. 1999), but total abundance remains relatively unchanged. Jeppesen et al. (2002) similarly observed that total zooplankton standing stocks were stable in Danish lakes with falling TP levels, even though phytoplankton and fish standing stocks fell. It may require extreme circumstances for total zooplankton abundance to change. Such circumstances could include major increases in the nutrient base, which might increase zooplankton standing stocks (Stemberger and Lazorchak 1994; Finlay et al. 2007), or the establishment of generalized predators with growth rates approximating those of their prey (Yan et al. 1991). In such circumstances, zooplankton could not outgrow their predators, and if they could not avoid them, zooplankton abundance would fall.

In contrast to total abundance, species richness changed significantly in half of the lakes. The decline in richness in Harp Lake needs no explanation beyond the direct and indirect effects of the *Bythotrephes* invasion (Yan et al. 2002; Pangle and Peacor 2006). We had predicted an increase in

Fig. 6. (a) Scattergram of lake-year scores from the correspondence analysis (CA) on log abundances of the 31 taxa in seven lakes, all lakes except Harp Lake. Points are year scores for each lake from 1980 to 2003. (b) Scattergram of the axis scores for the 31 taxa included in the CA. Taxa are identified when the quality of the two-dimensional solution (percent of variance explained for the taxon) was >0.5 . Quality scores are provided for these taxa in parentheses. Note that the scales of the two panels differ.



richness in lakes that were recovering from acidification. Such ecological recovery has been reported elsewhere, for example, near Sudbury, Ontario (Keller et al. 2002; Holt and Yan 2003). Interestingly, pH has increased (Sen's slopes for pH are positive) in the three lakes with increasing zooplankton richness, i.e., Blue Chalk, Red Chalk, and Heney, but among these, only Heney Lake was considered acid-stressed (i.e., pH < 6 ; Havens et al. 1993) early in the record. As the pH of Heney Lake rose to above 5.9 between 1987 and 1989 and then remained >5.9 in every year after 1993, an adequate time for recovery of zooplankton from modest acidification (Yan et al. 1996a; Frost et al. 2006), the simplest explanation for its positive trend in richness is recovery from acidification. Daphniids are the most acid-sensitive of the Cladocera, but the total abundance of daphniids has not increased over time in the lake (M-K, $S = 0.79$, $P = 0.42$). In contrast, the number of species of *Daphnia* has increased significantly (M-K, $S = 2.48$, $P = 0.013$; Sen's slope = 0.083 species-year $^{-1}$). On average, there were two more daphniid species in the collections at the end of the Heney Lake record than at the beginning, and this increase in daphniid richness accounts for 90% of the increase in total species

Table 6. Summary of the Mann–Kendall trend tests for the five zooplankton community metrics in the eight lakes.

Metric	BC	CB	CN	DE	HP	HY	PC	RCm
Abundance								
Richness	+				–	+		+
Cladoceran size	+	+	+	+	+	+	+	
CA I ^a		–			–			
CA II ^a		+	+	+	+	–		+

Note: A plus sign (+) indicates a significant positive trend; a minus sign (–) indicates a significant negative trend, after false discovery rate (FDR) correction. Blank cells indicate no significant trend after FDR correction. $P < 0.05$ for abundance in Plastic Lake, but the Mann–Kendall S statistic was not significant after FDR correction. Lake abbreviation codes are provided in Table 1.

^aHP Lake results are from eight-lake CA, all others are from seven-lake CA.

richness in the lake. Given the acid sensitivity of daphniids, the simplest explanation for this pattern is recovery from acidification. Supporting this suggestion, a regression of number of species of *Daphnia* recorded in our Heney Lake counts each year (Daphniid richness) with yearly lake pH is significant and positive (daphniid richness = $-12.5 + 2.53 \cdot \text{pH}$, $F = 4.74$, $P = 0.04$, $r^2 = 0.18$). Arnott et al. (1999) reported close to a 20% annual apparent species turnover rate in Heney Lake based on 1978 to 1989 data; hence, we should not be surprised that species richness can change rapidly over time in our lakes, especially in Heney Lake.

Richness did not increase significantly over time in Chub, Crosson, Dickie, or Plastic lakes. This was no surprise in Chub and Crosson lakes, as the most recent pH levels were still below 6; in fact, average ice-free season pH never rose above 5.8 in either lake during the record. The lack of increase in richness in Plastic Lake is also not surprising, as its pH did not rise significantly over time (M-K, S for pH = -1.12 , $P = 0.26$). Indeed, it was only in Plastic Lake among all lakes that the Sen's slope for pH was negative ($-0.0024 \cdot \text{year}^{-1}$ between 1980 and 2003). The one surprise was Dickie Lake. Its pH was over 6.0 in seven years: 1987, 1995–1999, and 2003. There was, however, a drought-induced re-acidification event in the late 1990s (Dillon et al. 2007) that lowered average lake pH to 5.7 in 2001. Shield lake zooplankton communities are actually quite resistant to colonist establishment (Forrest and Arnott 2006), and modest acidification events equivalent to those observed in Dickie Lake in 2001 can dramatically reduce the establishment success of acid-sensitive colonists (Binks et al. 2005), especially at low nutrient levels (Forrest and Arnott 2006). A comparison of the multilake patterns in richness suggests to us that sustained pH recovery, such as that observed in Heney Lake, is a requirement for increases in zooplankton species richness to occur.

Perhaps the most interesting change that we detected, given its consistency among the lakes, was the switch in composition from small- to large-bodied cladoceran assemblages over time, resulting in a substantial increase in mean cladoceran body size in seven of the lakes. No such increase was detected in Red Chalk Lake, but it was already dominated by large-bodied species at the beginning of the record. Abundances of *Daphnia*, particularly the large *D. pulicaria*,

increased significantly in all the lakes, whereas abundances of the equally large *Holopedium* increased in three lakes. Abundances of the mid-sized *Diaphanosoma* increased significantly in four lakes, but decreased in two others. In contrast, abundances of the bosminids, the smallest common Cladocera, decreased in five of the lakes, and no significant increases in its abundance were observed (A. Jeziorski and N.D. Yan, unpublished data).

In theory, many factors could have led to an increase in mean cladoceran body size. The most obvious possibilities include (i) reductions in temperature leading to slower growth but larger size at maturity (Atkinson 1994; Moore et al. 1996); (ii) reductions in food concentrations as TP and chlorophyll levels fall, favouring larger Cladocera with their lower limiting food thresholds, i.e., food concentrations at which all net metabolic costs are just met and above which growth is possible (Gliwicz 1990); (iii) reductions in acidity favouring the acid-sensitive daphniids, which are the largest common Cladocera, *Holopedium* excepted (Dillon et al. 1984; Havens et al. 1993); (iv) earlier springs or warmer summers giving daphniids a “leg-up” on larval *Chaoborus* (Neill 1981), a principal invertebrate predator in our lakes (Ramcharan et al. 2001); (v) increases in chromophoric DOC due to climatic change or reductions in acidity (Keller et al. 2008) leading to reductions in the risk from visual predators (Brooks and Dodson 1965); (vi) reductions in abundance of planktivorous fish (Carpenter et al. 1985), perhaps attributable to the spread of bass (*Micropterus* spp.) across the region (Whittier et al. 1997; MacRae and Jackson 2001); (vii) the appearance in Harp Lake of *Bythotrephes*, which appears to selectively consume the smaller Cladocera in nature (Yan et al. 2001b), despite its preference for larger prey in the lab (Schulz and Yurista 1999); (viii) long-term increases in Ca levels from below to above levels of about $1.5 \text{ mg} \cdot \text{L}^{-1}$, a threshold hypothesized to limit the larger, Ca-rich daphniids (Jeziorski and Yan 2006; Ashforth and Yan 2008); (ix) shifts to higher quality prey assemblages favoured by larger species (Hampton et al. 2006), and finally, (x) interactions of any of these factors. Many possible interactive effects are possible. For example, stoichiometric considerations suggest that reductions in light penetration from rising chromophoric DOC should favour daphniids over other Cladocera, whereas reductions in TP levels should have the opposite effect (Sterner et al. 1997). Such DOC and TP changes have occurred in our lakes. With such a large number of possible explanations and with the additional complication of possible lagged effects, nonmonotonic trends, and nonlinear cause–effect linkages (e.g., Carpenter 2003), in addition to factor interactions, we must be cautious in our consideration of possible explanations of the increase in mean body size across the lakes. Hence, we restrict ourselves to erecting hypotheses.

We do not believe that the increase in mean cladoceran body size is a direct reflection of regional climatic change. The mean cladoceran body size in the seven lakes with increasing trends was not significantly correlated with mean annual air temperature ($r = 0.07$) or total precipitation ($r = -0.23$), with the number of ice-free ($r = 0.38$) or ice-covered ($r = -0.20$) days, or with the actual ice-off date ($r = -0.05$), nor was it correlated with average epilimnetic temperature ($r = -0.09$), nor with several global climate change indicators. Specifically, correlations

Table 7. Pearson's correlation coefficients of ice-free season mean Cladoceran body length in the eight study lakes with ice-free season means of variables reflecting the principal water quality changes in the lakes, i.e., increased salinity (Na), oligotrophication (TP), rising colour (DOC and Secchi), recovery from acidification (pH and alkalinity), and Ca decline (Ca).

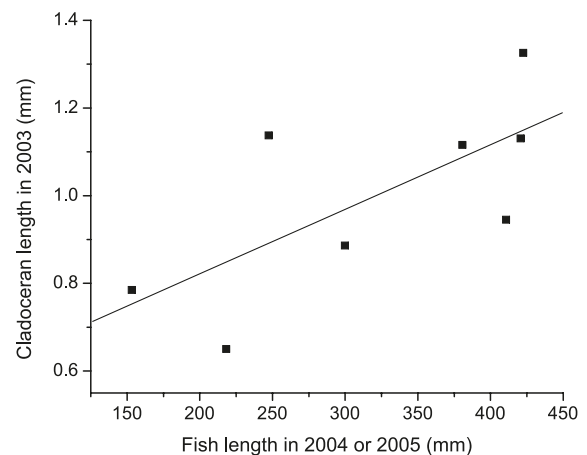
	BC	CB	CN	DE	HP	HY	PC	RCm
Alkalinity	0.014	0.26	-0.051	0.37	0.58**	0.48*	-0.12	-0.27
Ca	-0.36	-0.081	-0.35	0.72**	-0.49*	-0.59**	-0.58**	0.345
DOC	0.59**	0.41	0.078	0.58**	0.35	0.69**	-0.24	-0.080
Na	-0.024	0.45*	0.20	0.77**	0.92**	0.47*	0.074	0.20
pH	0.47*	0.028	0.67**	0.13	0.71**	0.45*	0.06	-0.25
TP	0.10	-0.36	-0.50*	-0.50*	-0.75**	-0.25	-0.54**	0.22
Secchi	-0.078	-0.18	0.59**	0.038	0.52**	-0.081	0.21	-0.024

Note: Bold values with single and double asterisks indicate $P < 0.05$ and 0.01 , respectively. Underlined values were significant at $P = 0.05$, after false discovery rate correction. Sample size was 22 to 24, depending on the lake, as body length was not measured in all lakes until 1981. Lake abbreviations are provided in Table 1.

of mean cladoceran length with the Southern Oscillation Index (SOI), Pacific Decadal Index (PDI), North Atlantic Oscillation Index (NAOI), and the Arctic Oscillation Index (AOI) (assembled by K.M. Somers, unpublished data) were all < 0.3 and not significant. There were, however, significant ($P < 0.05$) negative correlations of mean cladoceran length with the previous year's PDI ($r = -0.453$) and the duration of the ice-cover season ($r = -0.43$), but these lag correlations were not significant after FDR correction.

Increases in mean cladoceran body size are often, indeed normally, attributed to reductions in predation from fish (Brooks and Dodson 1965; Mills et al. 1987), and whole-lake piscivore addition and removal experiments prove that mean cladoceran body length can be influenced by planktivorous fish predation on the Canadian Shield (e.g., Yan et al. 2001a). Unfortunately, we do not have a long-term record of planktivorous fish abundance in our lakes, but G. Morgan and J. Gunn (personal observations) did describe the fish communities in the lakes in 2004 and 2005 using a netting technique that was implemented in a manner that provides quantitative data. To determine if fish predation might account for the recent interlake differences in mean cladoceran body size, we examined correlations of the 2003 mean cladoceran body size with several fish community metrics taken from G. Morgan and J. Gunn (unpublished data). The correlations between cladoceran body size and the biomass of littoral ($r = -0.43$, $n = 8$, $P > 0.1$) or pelagic ($r = 0.37$) fish species were weak. However, when mean fish length was calculated in a biomass-weighted fashion, i.e., (Σ fish biomass in 1 cm length increments \times mean length of increment) / Σ biomass), there was a relationship between mean fish length and mean cladoceran length that was positive and too close to significant to ignore, i.e., mean cladoceran size (mm) = $0.00147(\text{fish size (in mm)}) + 0.527$, $r^2 = 0.49$, $P = 0.054$ (Fig. 7). This is the relationship that we would expect if fish predation does influence zooplankton size structure, as the larger fish are more often piscivores and, when abundant, could reduce the abundance of planktivores. Whether changes in fish predation have produced the temporal increases in cladoceran body size, we can not say as we do not have an historical fish record. However, as DOC has increased over time in Blue Chalk, Crosson, and Red Chalk lakes (Keller et al. 2008), we can say that the risk of large Cladocera to individual fish en-

Fig. 7. Scattergram of the relationship between mean Cladoceran body length in each study lake in 2003, with biomass-weighted mean fish length in each lake determined by Morgan and Gunn (unpublished data) in 2004 or 2005. Each point represents one of the A lakes. The equation of the regression line is $y = 0.00147x + 0.52$ ($r^2 = 0.49$, $P = 0.054$).



counters should have declined in these lakes, and the correlation of recent fish with cladoceran lengths indicates that fish predation may currently be influencing the relative abundances of large and small Cladocera in our lakes. A similar influence has certainly been detected in other unproductive Canadian lakes (e.g., Finlay et al. 2007).

The dominant water quality changes that have occurred in the lakes include decreases in acidity and TP, declines in Ca in all the lakes except Dickie Lake, where a sudden recent increase is likely attributable to dust control on summer roads, and increases in salt levels in Dickie and Harp lakes due to de-icing of winter roads within their watersheds. Ice-free season mean Na levels were correlated with ice-free season mean cladoceran body sizes in Dickie and Harp lakes after FDR correction (Table 7), but we do not believe there is a causal link between Na levels and cladoceran body size. Na levels in the lakes are well above required minima but still orders of magnitude below toxic thresholds (Biesinger and Christensen 1972). We also do not believe that the correlations of body size with Ca in Dickie, Harp, Heney, and Plastic lakes have a causal foundation. In Dickie Lake, Ca

levels are rising for reasons given above, but they were never $<1.5 \text{ mg}\cdot\text{L}^{-1}$, the threshold that we believe limits daphniid population growth (Ashforth and Yan 2008). In Harp, Heney, and Plastic lakes, Ca levels have been falling while daphniid abundances and mean cladoceran body sizes have been rising (Table 7), but Ca levels are still above what we currently believe to be the critical Ca threshold. On the other hand, long-term changes in DOC, TP, and acidity may individually, or in combination, explain the rising mean cladoceran body size. If DOC was responsible for the increase because it protects larger animals from predation, then we would expect positive correlations of DOC with mean cladoceran body size. This is what we see in Blue Chalk, Dickie, and Heney lakes (Table 7), all of which have large perch (*Perca flavescens*) populations (G. Morgan and J. Gunn, unpublished data). If herbivorous zooplankton are in competition for limiting resources, then falling TP levels should favour larger herbivores (Gliwicz 1990), given their greater starvation resistance. Consistent with this hypothesis, TP is negatively correlated with mean cladoceran body size in Crosson, Dickie, Harp, and Plastic lakes. Finally, if recovery from acidification permits the blossoming of acid-sensitive daphniid populations, we might expect to see positive correlations of pH or alkalinity with cladoceran body size, and this is what we see in Crosson and Harp lakes. Even small increases in pH might be important in lakes with pH near 6.0, given that LC_{50} s for pH for several daphniid taxa are in the range of or just under 6.0 (Havens et al. 1993). Further, there are no significant correlations of cladoceran body size with pH, DOC, or TP, which have a sign that is inconsistent with these explanations. Thus we hypothesize that the increase in mean cladoceran body size in the lakes is attributable to a combination of recovery from acidification, falling TP levels, a *Bythotrephes* invasion in the case of Harp Lake, and rising DOC, which reduces risk to planktivorous fish. With the exception of Plastic Lake, all the lakes support large- and (or) small-mouth bass (*M. salmoides* and *M. dolomieu*, respectively) populations (G. Morgan and J. Gunn, personal observation), both of which are known to reduce abundances of planktivorous fish (MacRae and Jackson 2001). We do not think that the falling levels of Ca are having negative effects on zooplankton in the lakes now, but we believe that this is a transitory situation. If Ca levels continue to fall, because of net losses of exchangeable Ca from surface soils in the watersheds (Watmough et al. 2005), then Ca concentrations may soon limit at least the daphniid assemblages in the lakes, i.e., the Ca-rich component (Jeziorski and Yan 2006), and this limitation may become more severe as the climate warms (Ashforth and Yan 2008).

Implications

There are several implications of these changes in zooplankton communities. First, we believe it is time to seriously consider the likelihood that interactions of multiple anthropogenic stressors now contribute to the regulation of zooplankton communities in north-temperate lakes. Complex interactions among natural plankton drivers (e.g., nutrients and predators) have long been the subject of intense study in northern lakes (e.g., Neill 1988), but there are growing arguments to adopt a multiple, anthropogenic stressor viewpoint

for aquatic community regulation (Vinebrooke et al. 2004; Christensen et al. 2006) based on the common recent co-occurrences of multiple anthropogenic stressors in nature (e.g., Schindler et al. 1996; Yan et al. 1996b). This multiple-stressor view of Shield ecosystem regulation is not as yet the norm for zooplankton.

Secondly, if the results from our eight lakes prove to be typical, it appears that the dominant anthropogenic influences on crustacean zooplankton composition of the past half century may be changing for the southern Precambrian Shield. The pervasive influence of acidification so important over the last 30 years does appear, thankfully, to be on the wane for most of our study lakes. With rising DOC levels, the influence of UV irradiance on zooplankton is likely also in general decline. However, climatic variability is emerging as a regional synchronizer of the abundance of common zooplankton species in our lakes (Rusak et al. 2008), as it is for other North American (Winder and Schindler 2004) and European lakes (Straile and Adrian 2000). A climate change influence on zooplankton in temperate lakes now appears to be a reality for the northern hemisphere. Oligotrophication, i.e., TP decline and resultant limnological changes, is also a new emerging reality in our region, at least over the last three decades. The effects of increasing phosphorus levels on zooplankton are well understood, but impacts of declining TP levels (Manca and Ruggiu 1998; Jeppesen et al. 2002) from levels that were already quite low warrant additional research. Given that the fecundity of daphniids in our lakes is normally at least an order of magnitude lower than their potential fecundity, it is likely that declining nutrients will alter competitive interactions within the zooplankton community; however, the nonlinear responses of zooplankton communities to changes in nutrients levels (Neill 1988) complicates prediction. There is also little doubt that the introduction and spread of nonindigenous species, such as *Bythotrephes*, and the spread of native predators, such as bass, are already having significant effects on zooplankton. The 30% decline in species richness in Harp Lake linked to the *Bythotrephes* invasion (Yan et al. 2002), coupled with the rapid spread of *Bythotrephes* in Ontario (Muirhead and MacIsaac 2005) and beyond (Branstrator et al. 2006), suggests that *Bythotrephes* may soon have an enormous negative impact on native zooplankton biodiversity across the Canadian Shield.

Thirdly, the changes that we observed make it clear that reference data, e.g., the data that we collected from Blue Chalk and Red Chalk lakes, must be updated at regular intervals if they are to be used to create targets for environmental decision making. As change appears to be the only reality for our, and other (Olden et al. 2006), temperate lakes, older zooplankton data may not provide a sound footing for contemporary decision making if we assume that these data reflect today's minimally impacted sites. Indeed, our recent uses of these older data for target setting (e.g., Yan et al. 2002, 2004) should perhaps be re-examined when contemporary spatial data sets become available. We might first assume that our reference lakes are changing mainly because of regional changes in climate (e.g., Rusak et al. 1999), but these reference lakes are located in a meta-community landscape across which many changes may occur. If lakes are hydrologically connected in the landscape (Michels et al. 2001), for example, Blue Chalk Lake upstream of Red Chalk

Lake, then intermixing of faunas will certainly occur. Zooplankton propagules can also move among regional lakes that are not hydrologically connected (e.g., Proctor 1964), and daphniid colonists, in particular, may not be effectively suppressed by the resident community (Binks et al. 2005), even though local habitat conditions can certainly lead to establishment failure (Yan et al. 2004). Thus, meta-community connections, not just regional climatic variations, could lead to changes in reference lake communities over time.

Finally, we hypothesize that the changes we have reported here, especially the recent switch to large-bodied, daphniid-dominated cladoceran assemblages, do not reflect a new, long-term steady state for zooplankton on the south-central Shield. We hypothesize that daphniid populations have been on the rise in the lakes in response to a combination of falling acidity and TP levels coupled with reduced threats from planktivores, this reduced threat linked to the spread of bass and rising DOC levels. However, if Ca levels continue to fall (Watmough and Aherne 2008) and the climate continues to warm, both of which seem likely, thresholds will be reached that will be very detrimental initially to the daphniid fauna among the zooplankton, given their high Ca demands, and then likely to other taxa of the lakes. As a society, we are making progress with environmental threats such as acid rain and enhanced nutrient loading and are likely also doing so with UV radiation; however, the interactive effects of the spread of invaders, Ca decline, and climate warming are important emerging issues for applied zooplankton ecologists to explore.

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References

- Adamstone, F.B. 1928. The Cladocera of Lake Muskoka in Ontario, Canada. *Trans. Am. Microsc. Soc.* **47**: 460–463.
- Allan, J.D. 1973. Competition and the relative abundances of two cladocerans. *Ecology*, **54**: 484–498.
- Allen, G., Yan, N.D., and Geiling, W. 1994. ZEBRA2 — zooplankton enumeration and biomass routines for APIOS: a semi-automated sample processing system for zooplankton ecologists. Ontario Ministry of the Environment Report, Dorset, Ontario.
- Arnott, S.E., Yan, N.D., Magnuson, J.J., and Frost, T.M. 1999. Interannual variability of biodiversity: species turnover of zooplankton in lakes. *Can. J. Fish. Aquat. Sci.* **56**: 162–172.
- Ashforth, D., and Yan, N.D. 2008. The interactive effects of Ca concentration and temperature on the survival and reproduction of *Daphnia pulex* at high and low food concentrations. *Limnol. Oceanogr.* **53**: 420–432.
- Atkinson, D. 1994. Temperature and organism size — a biological law for ectotherms. *Adv. Ecol. Res.* **25**: 1–58.
- Barbiero, R.P., and Tuchman, M.L. 2004. Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*. *Can. J. Fish. Aquat. Sci.* **61**: 2111–2125.
- Barnett, A., and Beisner, B.E. 2007. Zooplankton biodiversity and lake trophic state: explanations invoking resource abundance and distribution. *Ecology*, **88**: 1675–1686.
- Beisner, B.E., Peres-Neto, P.D., Lindstorm, E.S., Barnett, A., and Longhi, M.L. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology*, **87**: 2985–2991.
- Benjamini, Y., and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. B Methodol.* **57**: 289–300.
- Biesinger, K.E., and Christensen, G.M. 1972. Effects of various metals on survival, growth, reproduction, and metabolism of *Daphnia magna*. *J. Fish. Res. Board Can.* **29**: 1691–1700.
- Binks, J.A., Arnott, S.E., and Sprules, W.G. 2005. Local factors and colonist dispersal influence crustacean zooplankton recovery from cultural acidification. *Ecol. Appl.* **15**: 2025–2036.
- Boudreau, S.A., and Yan, N.D. 2003. The differing crustacean zooplankton communities of Canadian Shield lakes with and without the nonindigenous zooplanktivore *Bythotrephes longimanus*. *Can. J. Fish. Aquat. Sci.* **60**: 1307–1313.
- Bowman, M.P., Somers, K.M., Reid, R.A., and Scott, L.D. 2006. Temporal response of stream benthic macroinvertebrate communities to the synergistic effects of anthropogenic acidification and natural drought events. *Freshw. Biol.* **51**: 768–782.
- Branstrator, D.K., Brown, M.E., Shannon, L.J., Thabes, M., and Heimgartner, K. 2006. Range expansion of *Bythotrephes longimanus* in North America: evaluating habitat characteristics in the spread of an exotic zooplankton. *Biol. Invasions*, **8**: 1367–1379.
- Brooks, J.L., and Dodson, S.I. 1965. Predation, body size, and composition of plankton. *Science (Washington, D.C.)*, **150**: 28–35.
- Carpenter, S.R. 2003. Regime shifts in lake ecosystems: pattern and variation. *In Excellence in ecology*. No. 15. *Edited by O. Kinne*. International Ecology Institute, Nordbunte 23, 21385 Oldendorf/Luhe, Germany.
- Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. *Bioscience*, **35**: 634–639.
- Carter, J.C.H. 1971. Distribution and abundance of planktonic Crustacea in ponds near Georgian Bay (Ontario, Canada) in relation to hydrography and water chemistry. *Arch. Hydrobiol.* **68**: 204–231.
- Carter, J.C.H., Dadswell, M.J., Roff, J.C., and Sprules, W.G. 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. *Can. J. Zool.* **58**: 1355–1387.
- Carter, J.C.H., Sprules, W.G., Dadswell, M.J., and Roff, J.C. 1983. Factors governing geographical variation in body size of *Diaptomus minutus* (Copepoda, Calanoida). *Can. J. Fish. Aquat. Sci.* **40**: 1303–1307.
- Carter, J.H.C., Taylor, W.D., Chengaleth, R., and Scruton, D.A. 1986. Limnetic zooplankton assemblages in Atlantic Canada with special reference to acidification. *Can. J. Fish. Aquat. Sci.* **43**: 444–456.
- Chen, C.Y., and Folt, C.L. 2002. Ecophysiological responses to warming events by two sympatric zooplankton species. *J. Plankton Res.* **24**: 579–589.
- Christensen, M.R., Graham, M.D.M., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J., and Turner, M.A. 2006. Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biol.* **12**: 1–7.
- Cottenie, K., Nuytten, N., Michels, E., and De Meester, L. 2001. Zooplankton community structure and environmental conditions in a set of interconnected ponds. *Hydrobiologia*, **442**: 339–350.
- Dillon, P.J., and Molot, L.A. 1996. Long-term phosphorus budgets and an examination of a steady-state mass balance model for central Ontario lakes. *Water Res.* **30**: 2273–2280.

- Dillon, P.J., Yan, N.D., and Harvey, H.H. 1984. Acidic deposition: effects on aquatic ecosystems. *CRC Crit. Rev. Environ. Control*, **13**: 167–194.
- Dillon, P.J., Watmough, S.A., Eimers, M.C., and Aherne, J. 2007. Long-term changes in boreal lake and stream chemistry: recovery from acid deposition and the role of climate. *In Acid in the environment: lessons learned and future prospects. Edited by G.R. Visgilio and D.M. Whitelow.* Springer, New York. pp. 59–75.
- Dodson, S.I. 1992. Predicting crustacean zooplankton species richness. *Limnol. Oceanogr.* **37**: 848–856.
- Ebert, D. 2005. Ecology, epidemiology and evolution of parasitism in *Daphnia*. National Library of Medicine (USA), Bethesda, Maryland.
- Elser, J.J., Chrzanowski, T.H., Sterner, R.W., and Mills, K.H. 1998. Stoichiometric constraints on food-web dynamics: a whole-lake experiment on the Canadian Shield. *Ecosystems*, **1**: 120–136.
- Finlay, K., Beisner, B.E., Patoine, A., and Pinel-Alloul, B. 2007. Regional ecosystem variability drives the relative importance of bottom-up and top-down factors for zooplankton size spectra. *Can. J. Fish. Aquat. Sci.* **64**: 516–529.
- Forrest, J., and Arnott, S.E. 2006. Immigration and zooplankton community responses to nutrient enrichment: a mesocosm experiment. *Oecologia*, **150**: 119–131.
- Frost, T.M., Fischer, J.M., Klug, J.L., Arnott, S.E., and Montz, P.K. 2006. Trajectories of zooplankton recovery in the Little Rock Lake whole-lake acidification experiment. *Ecol. Appl.* **16**: 353–367.
- Futter, M. 2003. Patterns and trends in southern Ontario lake ice phenology. *Environ. Monit. Assess.* **88**: 431–444.
- Ghadouani, A., Pinel-Alloul, B., and Prepas, E.E. 2003. Effects of experimentally induced cyanobacterial blooms on crustacean zooplankton communities. *Freshw. Biol.* **48**: 1–19.
- Gliwicz, Z.M. 1990. Food thresholds and body size in Cladocerans. *Nature (London)*, **343**: 638–640.
- Hampton, S.E., Scheuerell, M.D., and Schindler, D.E. 2006. Coalescence in the Lake Washington story: interaction strengths in a planktonic food web. *Limnol. Oceanogr.* **51**: 2042–2051.
- Havens, K.E., Yan, N.D., and Keller, W. 1993. Lake acidification: effects on crustacean zooplankton populations. *Environ. Sci. Technol.* **27**: 1621–1624.
- Hessen, D.O., Faafeng, B.A., and Andersen, T. 1995. Competition or niche segregation between *Holopedium* and *Daphnia*: empirical light on abiotic key parameters. *Hydrobiologia*, **307**: 253–261.
- Holt, C.A., and Yan, N.D. 2003. Recovery of zooplankton communities from acidification in Killarney Park, Ontario, 1972–2000: pH 6 as a recovery goal. *Ambio*, **32**: 203–207.
- Jeppesen, E., Jensen, J.P., and Sondergaard, M. 2002. Response of phytoplankton, zooplankton and fish to re-oligotrophication: an 11 year study of 23 Danish lakes. *Aquat. Ecosyst. Health Manag.* **5**: 31–43.
- Jeziorski, A., and Yan, N.D. 2006. Determinants of the calcium concentration of freshwater crustacean zooplankton. *Can. J. Fish. Aquat. Sci.* **63**: 1007–1013.
- Keller, W. 2007. Implications of climate warming for Boreal Shield lakes: a review and synthesis. *Environ. Rev.* **15**: 99–112.
- Keller, W., and Conlon, M. 1994. Crustacean zooplankton communities and lake morphometry in Precambrian Shield lakes. *Can. J. Fish. Aquat. Sci.* **51**: 2424–2434.
- Keller, W., and Pitblado, J.R. 1989. The distribution of crustacean zooplankton in northern Ontario, Canada. *J. Biogeogr.* **16**: 249–259.
- Keller, W., Paterson, A.M., Somers, K.M., Dillon, P.J., Heneberry, J., and Ford, A. 2008. Relationships between dissolved organic carbon concentrations, weather, and acidification in small Boreal Shield lakes. *Can. J. Fish. Aquat. Sci.* **65**: 786–795.
- Keller, W., Yan, N.D., Howell, T., Molot, L.A., and Taylor, W.D. 1992. Changes in zooplankton during the experimental neutralization and early re-acidification of Bowland Lake near Sudbury, Ontario. *Can. J. Fish. Aquat. Sci.* **49**(Suppl. 1): 52–62.
- Keller, W., Yan, N.D., Somers, K., and Heneberry, J. 2002. Crustacean zooplankton communities in lakes recovering from acidification. *Can. J. Fish. Aquat. Sci.* **59**: 726–735.
- Klugh, A.B. 1921. Notes on Canadian Entomostraca. *Can. Field-Nat.* **35**: 72–73.
- Leech, D.M., Padeletti, A., and Williamson, C.E. 2005. Zooplankton behavioral responses to solar UV radiation vary within and among lakes. *J. Plankton Res.* **27**: 461–471.
- Levene, H. 1960. Robust tests for equality of variances. *Contributions to probability and statistics. I. Olkin.* Stanford University Press, Palo Alto, Calif. pp. 278–292.
- Locke, A. 1992. Factors influencing community structure along stress gradients: zooplankton responses to acidification. *Ecology*, **73**: 903–909.
- MacRae, P.S.D., and Jackson, D.A. 2001. The influence of small-mouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. *Can. J. Fish. Aquat. Sci.* **58**: 342–351.
- Magnan, P. 1988. Interactions between brook charr, *Salvelinus fontinalis*, and nonsalmonid species: ecological shift, morphological shift, and their impact on zooplankton communities. *Can. J. Fish. Aquat. Sci.* **45**: 999–1009.
- Manca, M., and Ruggiu, D. 1998. Consequences of pelagic food-web changes during a long-term lake oligotrophication process. *Limnol. Oceanogr.* **43**: 1368–1373.
- McQueen, D.J., and Yan, N.D. 1993. Metering filtration efficiency of freshwater zooplankton hauls: reminders from the past. *J. Plank. Res.* **15**: 57–65.
- Michels, E., Cottenie, K., Neys, L., De Gelas, K., Coppin, P., and De Meester, L. 2001. Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modeling of the effective geographical distance. *Mol. Ecol.* **10**: 1929–1938.
- Mills, E.L., Green, D.M., and Schiavone, A., Jr. 1987. Use of zooplankton size to assess the community structure of fish populations in freshwater lakes. *N. Am. J. Fish. Manag.* **7**: 369–378.
- Molot, L.A., Keller, W., Leavitt, P.R., Robarts, R.D., Waiser, M.J., Arts, M.T., Clair, T.A., Pienitz, R., Yan, N.D., McNicol, D.K., Prairie, Y.T., Dillon, P.J., Macrae, M., Bello, R., Nordin, R.N., Curtis, P.J., Smol, J.P., and Douglas, M.S.V. 2004. Risk analysis of dissolved organic matter-mediated ultraviolet B exposure in Canadian inland waters. *Can. J. Fish. Aquat. Sci.* **61**: 2511–2521.
- Moore, M.V., Yan, N.D., and Pawson, T.W. 1994. Omnivory of the larval phantom midge (*Chaoborus* spp.) and its potential significance for freshwater planktonic food webs. *Can. J. Zool.* **72**: 2055–2065.
- Moore, M.V., Folt, C.L., and Stemberger, R.S. 1996. Consequences of elevated temperatures for zooplankton assemblages in temperate lakes. *Arch. Hydrobiol.* **135**: 289–319.
- Muirhead, J.R., and MacIsaac, H.J. 2005. Development of inland lakes as hubs in an invasion network. *J. Appl. Ecol.* **42**: 80–90.
- Neill, W.E. 1981. Impact of *Chaoborus* predation upon the structure and dynamics of a crustacean zooplankton community. *Oecologia (Berl.)*, **48**: 164–177.
- Neill, W.E. 1988. Complex interactions in oligotrophic lake food webs: responses of nutrient enrichment. *In Complex interactions*

- in lake communities. *Edited by S.R. Carpenter*. Springer Verlag, New York. pp. 31–44.
- Olden, J.D., Jensen, O.P., and Vander Zanden, M.J. 2006. Implications of long-term dynamics of fish and zooplankton communities for among-lake comparisons. *Can. J. Fish. Aquat. Sci.* **63**: 1812–1821.
- Pangle, K.L., and Peacor, S.D. 2006. Non-lethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia mendotae*. *Freshw. Biol.* **51**: 1070–1078.
- Park, S., Brett, M.T., Muller-Navarra, D.C., and Goldman, C.R. 2002. Essential fatty acid content and the phosphorus to carbon ratio in cultured algae as indicators of food quality for *Daphnia*. *Freshw. Biol.* **47**: 1377–1390.
- Patalas, K. 1971. Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, northwestern Ontario. *J. Fish. Res. Board Can.* **28**: 231–244.
- Patalas, K. 1990. Diversity of the zooplankton communities in Canadian lakes as a function of climate. *Verh. Int. Verein. Limnol.* **24**: 360–368.
- Paterson, A.M., Winter, J.G., Nicholls, K.H., Clark, B.J., Ramcharan, C.W., Yan, N.D., and Somers, K.M. 2008. Long-term changes in phytoplankton composition in seven Canadian Shield lakes in response to multiple anthropogenic stressors. *Can. J. Fish. Aquat. Sci.* **65**: 846–861.
- Patoine, A., Pinel-Alloul, B., and Prepas, E.E. 2002. Influence of catchment deforestation by logging and natural forest fires on crustacean community size structure in lakes of the eastern boreal Canadian forest. *J. Plankton Res.* **24**: 601–616.
- Persaud, A.D., and Yan, N.D. 2003. UVR sensitivity of *Chaoborus* larvae. *Ambio*, **32**: 219–224.
- Pinel-Alloul, B., Legendre, P., et Magnin, E. 1979. Zooplankton limnétique de 46 lacs et 17 rivières du territoire de la baie de James. *Can. J. Zool.* **57**: 1693–1709.
- Pinel-Alloul, B., Methot, G., Verreault, G., and Vigneault, Y. 1990. Zooplankton species associations in Quebec lakes: variation with abiotic factors, including natural and anthropogenic acidification. *Can. J. Fish. Aquat. Sci.* **47**: 110–121.
- Proctor, V.W. 1964. Viability of crustacean eggs recovered from ducks. *Ecology*, **46**: 728–729.
- Quinlan, R., and Smol, J.P. 2001. Chironomid-based inference models for estimating end-of-summer hypolimnetic oxygen from south-central Ontario shield lakes. *Freshw. Biol.* **46**: 1529–1551.
- Quinlan, R., Paterson, A.M., Hall, R.I., Dillon, P.J., Wilkinson, A.N., Cumming, B.F., Douglas, M.S.V., and Smol, J.P. 2003. A landscape approach to examining spatial patterns of limnological variables and long-term environmental change in a southern Canadian lake district. *Freshw. Biol.* **48**: 1676–1697.
- Ramcharan, C.W., McQueen, D.J., Pérez-Fuentetaja, A., Yan, N.D., Demers, E., and Rusak, J. 2001. Analyses of lake food webs using individual-based models to estimate *Chaoborus* production and consumption. *Arch. Hydrobiol. Spec. Issues Adv. Limnol. The Dorset Food Web Piscivore Manipulation Project*, **56**: 101–126.
- Rusak, J.A., Yan, N.D., Somers, K.M., and McQueen, D.J. 1999. The temporal coherence of zooplankton population abundances in neighbouring north-temperate lakes. *Am. Nat.* **153**: 46–58.
- Rusak, J.A., Yan, N.D., and Somers, K.M. 2008. Regional climatic drivers of synchronous zooplankton dynamics in north-temperate lakes. *Can. J. Fish. Aquat. Sci.* **65**: 878–889.
- Schindler, D.W., Curtis, P.J., Parker, B.R., and Stainton, M.P. 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature (London)*, **379**: 705–708.
- Schulz, K.L., and Yurista, P.M. 1999. Implications of an invertebrate predator's (*Bythotrephes cederstroemi*) atypical effects on a pelagic zooplankton community. *Hydrobiologia*, **380**: 179–193.
- Stemberger, R.S. 1995. Pleistocene refuge areas and postglacial dispersal of copepods of the northeastern United States. *Can. J. Fish. Aquat. Sci.* **52**: 2197–2210.
- Stemberger, R.S., and Lazorchak, J.M. 1994. Zooplankton assemblage responses to disturbance gradients. *Can. J. Fish. Aquat. Sci.* **51**: 2435–2447.
- Sterner, R.W., Elser, J.J., Fee, E.J., Guilford, S.J., and Chrzanowski, T.H. 1997. The light:nutrient ratio in lakes: the balance of energy and materials affects ecosystem structure and process. *Am. Nat.* **150**: 663–684.
- St. Jacques, J.M., Douglas, M.S.V., Price, N., Drakulic, N., and Gubala, C.P. 2005. The effect of fish introductions on the diatom and cladoceran communities of Lake Opeongo, Ontario, Canada. *Hydrobiologia*, **549**: 99–113.
- Straile, D., and Adrian, R. 2000. The North Atlantic Oscillation and plankton dynamics in two European lakes — two variations on a general theme. *Global Change Biol.* **6**: 663–670.
- Strecker, A.L., and Arnott, S.E. 2005. Impact of *Bythotrephes* invasion on zooplankton communities in acid-damaged and recovered lakes on the Boreal Shield. *Can. J. Fish. Aquat. Sci.* **62**: 2450–2462.
- Strecker, A.L., Arnott, S.E., Yan, N.D., and Girard, R. 2006. Variation in the response of crustacean zooplankton species richness and composition to the invasive predator *Bythotrephes*. *Can. J. Fish. Aquat. Sci.* **63**: 2126–2136.
- Tessier, A.J., and Horwitz, R.H. 1990. Influence of water chemistry on size structure of zooplankton assemblages. *Can. J. Fish. Aquat. Sci.* **47**: 1937–1943.
- Van Belle, G., and Hughes, J.P. 1984. Nonparametric tests for trend in water quality. *Water Resour. Res.* **20**: 127–136.
- Vander Zanden, M.J., Olden, J.D., Thorne, J.H., and Mandrak, N.E. 2004a. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. *Ecol. Appl.* **14**: 132–148.
- Vander Zanden, J., Wilson, K.A., Casselman, J.M., and Yan, N.D. 2004b. Species introductions and their impacts in North American Shield lakes. *In Boreal Shield watersheds: lake trout ecosystems in a changing environment. Edited by J.M. Gunn, R.J. Steedman, and R.A. Ryder*. Lewis Publishers, Boca Raton, Florida. pp. 229–263.
- Vinebrooke, R.D., Cottingham, K.L., Norberg, J., Scheffer, M., Dodson, S.I., Maberly, S.C., and Sommer, U. 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos*, **103**: 451–457.
- Wærvagen, S.B., Rukke, N.A., and Hessen, D.O. 2002. Calcium content of crustacean zooplankton and its potential role in species distribution. *Freshw. Biol.* **47**: 1866–1878.
- Walseng, B., Yan, N.D., and Schartau, A.-K. 2003. Identifying littoral microcrustacean (Cladocera and Copepoda) indicators of acidification in Canadian Shield lakes. *Ambio*, **32**: 208–213.
- Walseng, B., Hessen, D.O., Halvorsen, G., and Schartau, A.-K. 2006. Major contribution from littoral crustaceans to zooplankton richness in lakes. *Limnol. Oceanogr.* **51**: 2600–2606.
- Watmough, S.A., and Aherne, J. 2008. Estimating calcium weathering rates and future lake calcium concentrations in the Muskoka–Haliburton region of Ontario. *Can. J. Fish. Aquat. Sci.* **65**: 821–833.
- Watmough, S.A., Aherne, J., Alewell, C., Arp, P., Bailey, S., Clair, T., Dillon, P., Duschene, L., Eimers, C., Fernandez, I., Foster, N., Larssen, T., Miller, E.A., Mitchess, M., and Page, S. 2005. Sulphate, nitrogen and base cation budgets at 21 forested catch-

- ments in Canada, the United States and Europe. *Environ. Monit. Assess.* **109**: 1–36.
- Whittier, T.R., Halliwell, D.B., and Paulson, S.G. 1997. Cyprinid distributions in Northeast U.S.A. lakes: evidence of regional-scale minnow biodiversity losses. *Can. J. Fish. Aquat. Sci.* **54**: 1593–1607.
- Williamson, C.E., Neale, P.J., Grad, G., DeLange, H.J., and Hargreaves, B.R. 2001. Beneficial and detrimental effects of UV on aquatic organisms: implications of spectral variation. *Ecol. Appl.* **11**: 1843–1857.
- Winder, M., and Schindler, D.E. 2004. Climatic effects on the phenology of lake processes. *Global Change Biol.* **10**: 1844–1586.
- Wissel, B., Boeing, W.J., and Ramcharan, C.W. 2003. Effects of water color on predation regimes and zooplankton assemblages in freshwater lakes. *Limnol. Oceanogr.* **48**: 1965–1976.
- Yan, N.D. 1986. Empirical prediction of crustacean zooplankton biomass in nutrient poor Canadian Shield lakes. *Can. J. Fish. Aquat. Sci.* **43**: 788–796.
- Yan, N.D., and Larsson, J.I.R. 1988. Prevalence and inferred effects of microsporidia of *Holopedium gibberum* (Crustacea: Cladocera) in a Canadian Shield lake. *J. Plankton Res.* **10**: 875–886.
- Yan, N.D., and Mackie, G.L. 1987. Improved estimation of the dry weight of *Holopedium gibberum* (Crustacea, Cladocera) using clutch size, a body fat index, and lake-water total phosphorus concentrations. *Can. J. Fish. Aquat. Sci.* **44**: 382–389.
- Yan, N.D., and Pawson, T.W. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following the invasion by *Bythotrephes cederstroemi*. *Freshw. Biol.* **37**: 409–425.
- Yan, N.D., and Strus, R. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. *Can. J. Fish. Aquat. Sci.* **37**: 2282–2293.
- Yan, N.D., Keller, W., MacIsaac, H.J., and McEachern, L.J. 1991. Regulation of zooplankton community structure of an acidified lake by *Chaoborus*. *Ecol. Appl.* **1**: 52–65.
- Yan, N.D., Keller, W., Somers, K.M., Pawson, T.W., and Girard, R.E. 1996a. The recovery of crustacean zooplankton communities from acidification: comparing manipulated and reference lakes. *Can. J. Fish. Aquat. Sci.* **53**: 1301–1327.
- Yan, N.D., Keller, W., Scully, N.M., Lean, D.R.S., and Dillon, P.J. 1996b. Increased UV-B penetration in a lake owing to drought-induced acidification. *Nature (London)*, **381**: 141–143.
- Yan, N.D., Pérez-Fuentetaja, A., Ramcharan, C.W., McQueen, D.J., Demers, E., and Rusak, J.A. 2001a. Changes in the crustacean zooplankton communities of Mouse and Ranger Lakes — Part 6 of the Dorset Food Web Piscivore Manipulation Project. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **56**: 127–150.
- Yan, N.D., Blukacz, A., Sprules, W.G., Kindy, P.K., Hackett, D., Girard, R., and Clark, B.J. 2001b. Changes in the zooplankton and the phenology of the spiny water flea, *Bythotrephes*, following its invasion of Harp Lake, Ontario, Canada. *Can. J. Fish. Aquat. Sci.* **58**: 2341–2350.
- Yan, N.D., Girard, R., and Boudreau, S. 2002. An introduced predator (*Bythotrephes*) reduces zooplankton species richness. *Ecol. Lett.* **5**: 481–485.
- Yan, N.D., Girard, R., Heneberry, J.H., Keller, W., Gunn, J.M., and Dillon, P.J. 2004. Recovery of Copepod, but not Cladoceran, zooplankton from severe and chronic effects of multiple stressors. *Ecol. Lett.* **7**: 452–460.
- Yan, N.D., Paterson, A.M., Somers, K.M., and Scheider, W.A. 2008. An introduction to the Dorset special issue: transforming understanding of factors that regulate aquatic ecosystems on the southern Canadian Shield. *Can. J. Fish. Aquat. Sci.* **65**: 781–785.
- Yue, S., Pilon, P., and Cavadias, G. 2002. The power of the Mann–Kendall and Spearman’s rho tests for detecting monotonic trends in hydrological series. *J. Hydrol.* **259**: 254–271.