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REPORT

Recovery of copepod, but not cladoceran, zooplankton from severe and chronic effects of multiple stressors

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Abstract

In the mid-twentieth century, many lakes near Sudbury, Canada, were severely contaminated by acid and metal emissions from local smelters. For example, in the early 1970s, Middle Lake had pH of 4.2, and Cu and Ni levels both >0.5 mg L^{-1} . To determine if crustacean zooplankton could recover from such severe and chronic damage, Middle Lake was neutralized in 1973. A comparison of its zooplankton with that of 22 reference (pH > 6) lakes indicates that the planktonic Copepoda completely recovered by 2001. In contrast, the cladoceran assemblage improved but did not recover. Colonist sources existed – Cladocera and Copepoda occurred with equal frequency in area lakes – but six separate colonizations by cladoceran species failed. We argue that local factors, metal toxicity and predation by yellow perch, have, to date, prevented cladoceran recovery. Nonetheless, the complete copepod recovery is encouraging, given the severity and duration of pre-neutralization stress.

Keywords

Acid rain, colonization, Copepoda, copper, dispersal, multiple stressors, nickel, recovery, Sudbury, zooplankton.

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INTRODUCTION

The probability that biota will recover from disturbance is greatly reduced when the damage has been severe and chronic, and it is attributable to multiple classes of stressors, e.g. altered physical and chemical regimes plus altered food web structure (Niemi *et al.* 1990; Hughes & Connell 1999). With severe and long-lasting damage, local species extinctions are common, nearby colonist sources are often depleted, and habitat conditions that fostered the pre-disturbance community are often incompletely re-generated, even when the stressors are removed. Unfortunately, examples of such disturbance are now common. For example, of 181 species listed as threatened or at risk of extinction in the USA, two-thirds face three or more different classes of threats, half of which are defined as both chronic and severe (Lawler *et al.* 2002).

Many populations of aquatic biota currently face just such severe and long-lasting damage attributable to multiple stresses. For example, several thousand lakes in the vicinity of Sudbury, Ontario, Canada, were acidified by historical sulphur emissions. While damage attributable to acidification is evident at pH 6 (Keller *et al.* 1990; Holt *et al.* 2003), many Sudbury lakes were severely acidified, with pH levels near 4 (Beamish & Harvey 1972; Conroy *et al.* 1976; Keller & Pitblado 1986), and lakes close to the smelters were frequently also metal-contaminated (Keller & Pitblado 1986). This damage was chronic, reaching back at least until the 1950s (Gorham & Gordon 1960), if not much earlier (Dillon & Smith 1984; Dixit *et al.* 1992). Biota in

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these lakes also faced multiple stressors, indirectly related to the lakes' acidity and metal-contamination. For example, dissolved organic carbon (DOC) concentrations were much reduced (Yan *et al.* 1996a); and DOC is both the principal attenuator of subsurface UV radiation (Scully & Lean 1995), and the principal determinant of mixing depths in small temperate lakes (Pérez-Fuentetaja *et al.* 1999). Hence, damaging UV radiation penetrated deeply into these lakes (Yan *et al.* 1996a; Gunn *et al.* 2001), and summer thermoclines were unusually deep (Yan 1983). In extreme cases, the profundal cold-water habitat that is essential for many species (Moore *et al.* 1996) disappeared (Yan & Miller 1984). As a further consequence of the chemical and physical alterations, normal predator-prey interactions were altered by the elimination of fish (Gunn *et al.* 1988), the frequent explosion of pelagic macroinvertebrate predators (Stenson & Eriksson 1989; Yan *et al.* 1991), and great reductions in species richness (Scheider *et al.* 1975; Dillon *et al.* 1979; Yan & Miller 1984). Given the severity and duration of such alterations in lake physics, chemistry and food web structure, we would predict a slow rate of recovery of zooplankton should all stressors be removed. In fact complete recovery of Sudbury zooplankton from disturbances of these magnitudes has not as yet been observed (Keller & Yan 1991; Yan *et al.* 1996a,b,c; Keller *et al.* 2002).

Here we report 30 years of change in the crustacean zooplankton community in Middle Lake, following its 1973 neutralization (Scheider & Dillon 1976). Planktonic Cladocera have not yet recovered. We do not believe regional factors explain the cladoceran time series, as we documented several cladoceran colonizations in the lake. Rather, as six such colonizations failed we believe local factors are responsible, specifically, continuing metal toxicity and/or predation from a very abundant population of yellow perch (*Perca flavescens*). In contrast, the recovery of the copepod assemblage is now complete, with six species of copepod colonists founding large, stable populations in the lake. The copepod recovery in this severely disturbed lake augurs well for the future of zooplankton currently damaged by the severe and chronic effects of multiple stressors. For example, should S emission reductions be followed by widespread chemical and physical normalization in the world's acidified lake districts (Stoddard *et al.* 1999), we predict the planktonic Copepoda at least will recover, and Copepoda are major components of the freshwater zooplankton.

STUDY LAKE DESCRIPTION AND METHODS

Thirty years ago, Middle Lake (46°26′N, 81°02′W) was acidic (pH 4.2), and contaminated with both Cu (0.5 mg L^{-1}) and Ni (1 mg L^{-1}, Scheider *et al.* 1976). It had extremely clear waters (Secchi depth = 12 m), and it did not stratify in the summer – an aberrant situation for a lake of its small size (area = 28 ha) and maximum depth (15 m). All fish had disappeared from the lake, and biodiversity was reduced at all levels of the food web (Scheider *et al.* 1976; Yan & Strus 1980; Yan & Miller 1984). Predictably, the crustacean zooplankton community was highly disturbed. On average, mid-lake, vertical plankton hauls captured only two to three species, and a single small cladoceran, *Bosmina longirostris*, comprised 99% of crustacean standing stocks (Yan & Strus 1980).

To determine if severely contaminated Sudbury lakes could recover, slurries of $CaCO_3$ and $Ca(OH)_2$ were added to Middle Lake and the nearby Lohi and Hannah lakes between 1973 and 1975 (Scheider *et al.* 1976). Small amounts of phosphoric acid were also added to Middle Lake from 1975 to 1978 in order to stimulate production, but the fertilization effects were modest and short-lived (Yan & Lafrance 1984). Base additions raised lake pH from the 4.2 to >6, and reduced metal concentrations many-fold (Scheider & Dillon 1976). Phytoplankton community composition recovered fairly quickly when assessed at the divisional taxonomic level (Yan & Dillon 1984); however, with the exception of the acid-sensitive, *Daphnia mendotae* (Keller *et al.* 1990; Yan *et al.* 1996c), there was no evidence of recovery of crustacean zooplankton in Middle Lake by 1989, when the data were last examined (Yan *et al.* 1996b).

Since 1980, Middle Lake has been sampled on roughly a monthly basis during the ice-free season for water quality, thermal profiles and zooplankton composition. Yan & Strus (1980) describe the pre-1980 sampling methods. Since 1980, volume-weighted composite zooplankton samples have been prepared by combining the contents of mid-lake, 76-μm mesh, vertical hauls from 3, 6, 10 and 13 m (Yan *et al.* 1996b). Animals were preserved in a 4% sugar formalin solution, and counted as described by Yan *et al.* (2001). The body lengths of all counted animals were measured and recorded (Allen *et al.* 1994).

There are no pre-disturbance data that can be used to assess recovery of zooplankton in Middle Lake. It acidified more than 50 years ago. Instead, we assess recovery by comparing its fauna with that of 22 non-acidic reference lakes located far from the smelters but in the same zoogeographic region for zooplankton (Yan *et al.* 1996b). Zooplankton methods employed in these reference lakes were similar to those employed in Middle Lake after 1980.

Yan *et al.* (1996b) determined that the best two metrics to assess recovery of zooplankton from acidification were species richness (ice-free season averages of numbers of species found in standard counts of fortnightly or monthly samples), and a multivariate metric based on the scores of a correspondence analysis (CA) ordination run using the log-transformed, species abundance matrix. Here we employ these two metrics to assess recovery in Middle Lake, constructing recovery targets from the 22 non-acidic lakes. We use the mean ± 2 SD as our target for richness (Yan *et al.* 1996b; Kilgour *et al.* 1998). It has a value of eight to 12 species per standardized count (Yan *et al.* 2002). To assess recovery of cladoceran and copepod assemblages we employ graphical analysis, asking simply if the Middle Lake zooplankton trajectory has returned within the grouping of CA axis I and II scores of the 22 non-acidic lakes, i.e. if the numbers and relative abundances of its species are now similar to that of the reference lakes, for the two dominant inter-species covariance patterns.

For the CA we assembled a data matrix composed of the three decades of ice-free season average zooplankton abundances ($\log_{x+1}$ transformed) in Middle Lake and in single years from the 22 reference lakes. Nauplii were excluded from the analysis because they were not identified to sub-order in the early years; however, calanoid and cyclopoid copepodids were included as separate taxa. All stage VI copepodids (i.e. adults) were identified to species. Species encountered in only one of the 22 reference lakes were excluded, as were the principally littoral taxa which our offshore protocols poorly sampled (Yan *et al.* 1996b). Hence, the CA-input matrix was composed of 25 taxa in single years for the 22 reference lakes, and each year from 1973 to 2002 in Middle Lake, excepting 1980, when the lake was not sampled.

We employed a separate 1990 synoptic zooplankton survey data set to determine the frequency of occurrence of planktonic Copepoda and Cladocera in lakes in the city of Sudbury. We employ this data set to determine if there was an equal frequency of potential Cladocera and copepod colonist sources in the region. We sampled these 32 lakes using single, mid-summer, mid-lake, vertical hauls from 1 m above bottom to the surface with a 30 cm diameter, 80 μm mesh net. As the lakes were sampled only once, our estimate of colonist availability is probably conservative.

RESULTS

The chemical and physical conditions of Middle Lake were substantially improved by the initial planned neutralization (Fig. 1). These benefits were prolonged by municipal land re-greening programmes in the late 1980s, programmes that included soil liming (Lautenbach 1987), and by reductions in S and metal emissions from local smelters (Keller *et al.* 2003). In consequence, the pH of Middle Lake has remained above 6.5 since 1974 (Fig. 1a). Concentrations of Cu and Ni (Fig. 1b), and many other metals were reduced by additions of base (Yan & Dillon 1984), and have continued to fall since the mid-1970s. The lake waters of Middle Lake were very transparent in 1973 (Fig. 1c), and the lake did not stratify, i.e. bottom temperatures did not differ from surface temperatures even at the time of maximum summer heat content (Fig. 1d). The liming and modest fertilization lowered transparency in the mid-1970s, but since that time average Secchi transparency has ranged from 4 to 6 m, typical levels for small Shield lakes (Fig. 1c). The lake has stratified each year since 1974, and bottom waters have slowly cooled (Fig. 1d). Hence the lake now has both the profundal cold-water habitat and dimictic thermal regimes that are typical of small temperate lakes.

We assume that it was acidification and metal-contamination that eliminated all fish from the lake (Scheider *et al.* 1975). *In-situ* experiments confirmed that metal levels prevented their re-establishment shortly after base additions (Yan & Dillon 1984). However, yellow perch (*Perca flavescens*) established a large population in the lake in the mid-1980s,

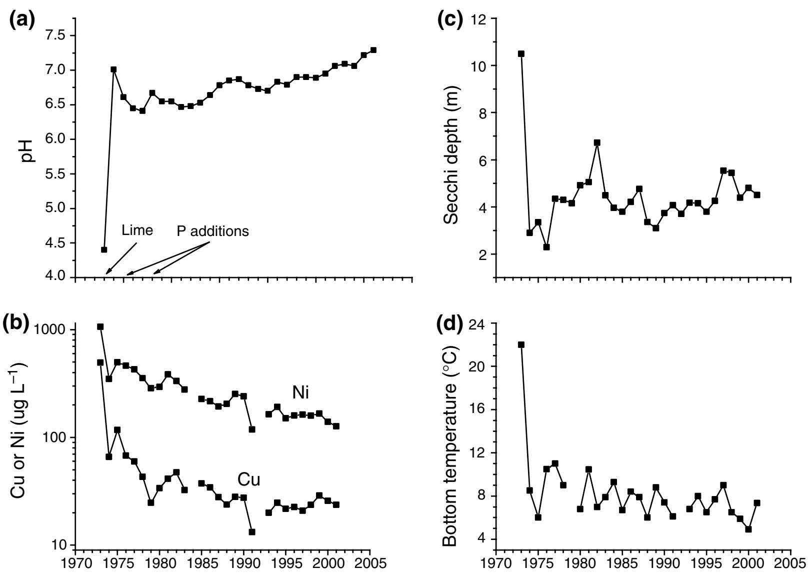

Figure 1 Long-term changes in ice-free season averages of pH (a), total Cu and Ni concentrations (b), Secchi transparency (c), and mid-summer bottom water temperatures (d) in Middle Lake. Metal concentrations and pH were assessed on at least a monthly basis in volume-weighted samples through all depths. The lake was not stratified in 1973. Dates of experimental neutralization and phosphorus additions are indicated. Base was also added to the lake's watershed in the late 1980s.

and by the early 1990s, yellow perch contributed >99% of fish caught in multiple trap net sets (J.M. Gunn, unpublished data). In summary, the physical, chemical and food web regimes of the lake have dramatically improved, in the sense that they are now more typical of non-acidified lakes. There are however two key exceptions. First, Cu and Ni levels, while greatly reduced are still elevated in comparison with remote lakes (LaZerte 1986). Secondly, most northern Ontario lakes have fish, but a community formed essentially solely of planktivorous (i.e. stunted) yellow perch is highly unusual.

In comparison with the 22 non-acidic lakes, the zooplankton community of Middle Lake has improved steadily over the last 30 years, but the entire community has not yet recovered. Ice-free season average crustacean species richness has increased from 2.6 species per standard count in 1973 to an average of six to eight species after 2000 (Fig. 2). While the pattern of improvement is clear, the target of 8–12 species per count per year (Yan *et al.* 2002) has not yet been reached.

Copepoda and Cladocera are the principal groups in the crustacean zooplankton community. The copepod assemblage of Middle Lake has completely recovered, while recovery of Cladocera stalled about 1990. These two patterns are clear in the CA ordinations. The copepod CA (Fig. 3) reflects inter-lake and year-to-year variation in abundances of immature calanoid and cyclopoid copepodids, and in adults of three calanoid species (*Leptodiaptomus minutus*, *Epischura lacustris* and *Skistodiaptomus oregonensis*), and six cyclopoid species (*Cyclops bicuspidatus thomasi*, *Acanthocyclops vernalis*, *C. scutifer*, *Mesocylops edax*, *Tropocyclops extensus*, and *Orthocyclops modestus*). Although the copepod fauna of Middle Lake differed substantially from the 22 reference lakes in the early years, it has not been distinguishable from the reference communities since 1996 (Fig. 3a). By our definition, the copepod fauna of Middle Lake has recovered. Taxa scores of the CA (Table 1, Fig. 3b) indicate that this recovery reflects the early disappearance of *A. vernalis* and

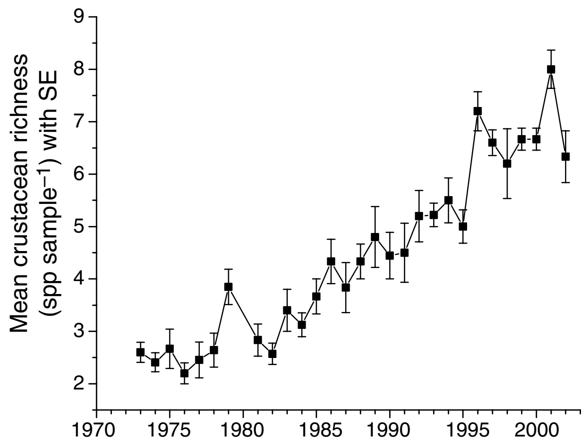

Figure 2 Long-term changes in ice-free season average crustacean zooplankton species richness identified in standard counts of monthly samples. Only individuals identified to the species level are included. The SE calculated from monthly richness estimates is indicated.

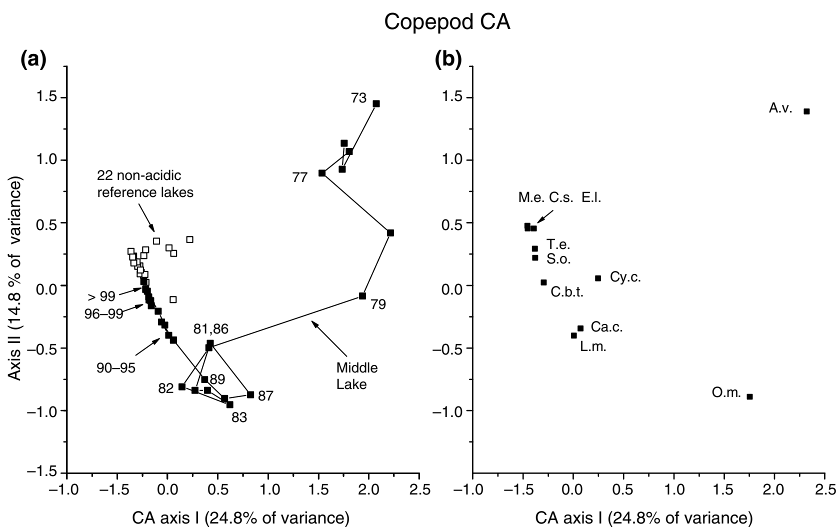

Figure 3 Scattergram of lake-year (a) and taxa (b) scores of the first two axes of the Correspondence Analysis ordination run on the $\log_{x+1}$ transformed ice-free season mean abundances of Copepoda in the 22 non-acidic reference lakes and Middle Lake. Each point in the Middle Lake trajectory represents a year. By the mid-1990s, the Middle Lake trajectory was within the envelope of the reference lakes. Scores of the Middle Lake taxa on the two CA axes are provided in Table 1. Taxa included in the ordination (see b) include *Acanthocyclops vernalis* (A.v.), *Cyclops bicuspidatus thomasi* (C.b.t.), *Cyclops scutifer* (C.s.), *Epischura lacustris* (E.l.), *Leptodiaptomus minutus* (L.m.), *Mesocyclops edax* (M.e.), *Orthocyclops modestus* (O.m.), *Skistodiaptomus oregonensis* (S.o.), *Tropocyclops extensus* (T.e.), and calanoid (Ca.c.), and cyclopoid (Cy.c.) copepodids.

Table 1 Ice-free season average abundances (animals per m^3) of all zooplankton taxa recorded in two or more years in Middle Lake*

	Cladocera†						Copepoda‡								
	S. sp	C. s.	B. l.	D. b.	D. m.	H. g.	A. v.	O. m.	Cy. c.	Ca. c.	L. m.	C.b.t.	S. o.	T. e.	M. e.
CA1	2.32	1.13	0.58	0.25	0.08	−0.72	2.32	1.75	0.25	0.07	0.01	−0.29	−0.38	−0.38	−0.39
CA2	3.63	0.54	−0.15	−0.64	−0.46	0.18	1.39	−0.89	0.06	−0.34	−0.4	0.02	0.22	0.29	0.46
1973		329	48647				17		112						
1974		37	1071				157		48	248		0.7			
1975	0.2	394	122				10		47	1	0.1	0.1		0.2	
1976		17192	113				26		86	8					
1977	19.9	3707	18				118		4574	4	5.3		0.7		
1978	8.9	1265	5				64	51	7767						
1979§	7.8	555	1066				75	293	1242	40	6.7				
1981		26	6994				3		98	18883	2843				
1982	5.1	194	219						18	85137	4249				
1983		174	6412					45	108	110614	4124				
1984		164	9517					3.8	75	25898	1513				
1985	0.5	21	176					1.1	23	14826	1992				
1986		27	257	9	10		2		188	11216	1393				
1987		379	12668		18		0.5	110	430	16674	1131				
1988		406	25936	23	77			19	129	24798	2171				
1989	0.7	39	62892	105	25	1		11	265	39223	4415	28			
1990		22	33678	70	521				11881	32066	1504	1469			
1991		65	67997	3352	272				12914	13776	3018	1248			
1992		18	32094	646	3822				2701	24605	2025	1227			
1993		22	17859	366	1699				6273	22391	1971	895	6		
1994		93	45584	5565	1920				14077	12716	1078	2460	32		
1995		21	68681	4247	499				6340	6615	410	745	9	93	
1996		41	106931	6233	2071				14678	20442	959	924	1094	442	
1997			31551	12730	2817				4988	27941	1082	941	1025	109	
1998		15	47695	10770	2721				12827	31363	1018	593	832	838	
1999		83	25764	7033	1573				7686	22427	1150	1001	903	946	
2000		155	49714	3155	3255				8748	18868	311	1513	785	737	
2001		44	4256	933	1196	12			6234	6199	644	486	770	150	13
2002		8	4684	829	3343				6231	8396	570	332	598	328	216

Cladoceran and copepod species are separately sorted based on the ranks of taxa scores on the first CA axis of their respective ordinations (see Figs 3 and 4). CA axis I and II scores of the taxa are provided.

*Additional species recorded in just a single year in Middle Lake were *Daphnia dubia* in 1985, *Eubosmina tubicen* in 1986, *Daphnia longiremus*, *Daphnia pulex* and *Daphnia retrocurva* in 1990, *Epischura lacustris* in 1992, and *Cyclops scutifer* in 1996. Additional species found only in the reference lakes that were included in the analyses were the Cladocera: *Daphnia ambigua*, *Polyphemus pediculus* and *Eubosmina longispina*.

†These Cladocera are *Simocephalus* sp. (S. sp), *Chydorus sphaericus* (C.s.), *Bosmina longirostris* (B.l.), *Diaphanosoma birgei* (D.b.), *Daphnia mendotae* (D.m.) and *Holopedium gibberum* (H.g.).

‡These Copepoda are *Acanthocyclops vernalis* (A.v.), *Orthocyclops modestus* (O.m.), cyclopoid copepodid (cy.c.), calanoid copepodid (ca.c.), *Leptodiaptomus minutus* (L.m.), *Cyclops bicuspidatus thomasi* (C.b.t.), *Skistodiaptomus oregonensis* (S.o.), *Tropocyclops extensus* (T.e.), and *Mesocyclops edax* (M.e.)

§The lake was not sampled in 1980.

O. modestus, the appearance of *L. minutus* and *S. oregonensis*, the two most common calanoid copepods in Ontario (Rigler & Langford 1967), and the appearance of stable populations of three other common cyclopoid copepods, *C. bicuspidatus thomasi*, *T. extensus* and *M. edax* (Table 1). On average the number of copepod species in the Middle Lake assemblage increased from one in 1973 to five in 2002, accounting for the majority of the increase in zooplankton species richness (Fig. 2).

In contrast to the copepods, the cladoceran trajectory was promising, but recovery has stalled (Fig. 4a). The acid- and metal-tolerant *Bosmina longirostris* and *Chydorus sphaericus* remain dominant members of the assemblage (Table 1). The 1986 appearances of *Diaphanosoma birgei* and *Daphnia*

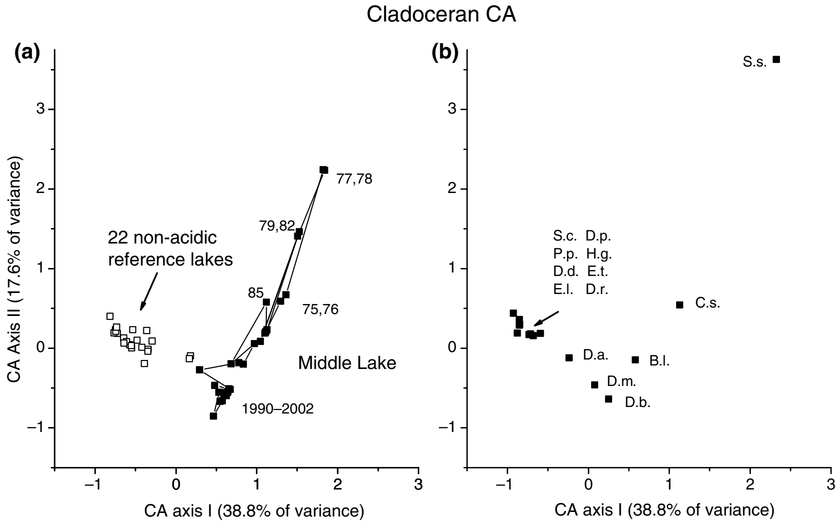

Figure 4 Scattergram of lake-year (a) and taxa (b) scores of the first two axes of the Correspondence Analysis run on the log(x + 1)-transformed ice-free season mean abundances of Cladocera in the 22 non-acidic reference lakes and in Middle Lake. Each point in the Middle Lake trajectory represents a year. Note that the assemblage of Middle Lake was very stable after 1990, but outside the envelope of the reference lakes. Taxa scores for the Middle Lake Cladocera are provided in Table 1. Taxa included in the ordination (see b) were *Bosmina longirostris* (B.l.) (now termed *Bosmina freyi* in Middle Lake), *Chydorus sphaericus* (C.s.), *Daphnia ambigua* (D.a.), *Daphnia dubia* (D.d.), *Daphnia mendotae* (D.m.), *Daphnia pulex* (D.p.), *Daphnia retrocurva* (D.r.), *Diaphanosoma birgei* (D.b.), *Eubosmina tubicen* (E.t.), *Simocephalus serrulatus* (S.s.), *Eubosmina longispina* (E.l.), *Polyphemus pediculus* (P.p.), and *Sida crystallina* (S.c.).

mendotae, two common Shield lake species, were promising, but many daphniid species, in particular, are still missing (Fig. 4b), and the most common large cladoceran in Canadian Shield lakes, the metal-sensitive (Yan & Strus 1980) *Holopedium gibberum* has apparently twice failed to colonize the lake (Table 1). Five other cladoceran species briefly appeared in the assemblage, but did not persist. They included four *Daphnia* species (*D. dubia*, *D. longiremis*, *D. pulex*, *D. retrocurva*) and *Eubosmina tubicen* (Table 1). In summary there were at least six apparently unsuccessful colonizations of Middle Lake by cladoceran species that are common in many non-acidic lakes in Ontario.

DISCUSSION

Despite three decades of non-acidic conditions, the cladoceran assemblage of Middle Lake has not recovered. All daphniid species excepting *D. mendotae* are currently missing, and *H. gibberum*, generally the dominant cladoceran in Canadian Shield lakes (Yan *et al.* 1988), is very rare. Nonetheless, we are encouraged by the recovery of the Copepoda, and we suspect that the current delay of cladoceran recovery is largely a function of local rather than regional processes. In fact we believe the influence of such local processes may be extremely strong in metal-contaminated lakes, i.e. those near the smelters, or downstream of contaminated industrial discharges. Alternatively, the local conditions may be a function of the unusual predation regime in the lake. In this case, recovery of the Cladocera will only occur when a more 'typical' fish community is established.

The (re)-assembly of zooplankton communities after removal of historical stress that is severe enough to cause local extinctions, must follow a set generic sequence (Yan *et al.* 2003). Colonists must be supplied either from egg banks or from other lakes. These colonists must survive and reproduce, if nascent populations are to persist and grow. Both Calanoida and Cladocera produce long-lived resting stages that are commonly abundant in lake sediments (Hairston *et al.* 1990; Pollard *et al.* 2003). The two calanoid copepod species that colonized Middle Lake (*L. minutus* and *S. oregonensis*) first appeared in the mid-1970s, during lake fertilization. Their resting eggs produced at that time may have provided local colonists for the eventual establishment of large and persistent populations. In contrast, egg-banks cannot explain the recovery of cyclopoid copepods, given their lack of long-lived resting stages.

Cyclopoid copepods apparently colonize new habitats more rapidly than do Cladocera (Cáceres & Soluk 2002), but we do not believe that their greater vagility accounts for the copepod recovery in Middle Lake. In the first place, the number of local colonization sources did not differ between Copepoda and Cladocera. In 1990, cladoceran and copepod taxa had the same mean frequency of occurrence in the 32 local lakes, at 11.4 and 8.5 lakes per species, respectively, on average ($t = 0.72$, $P = 0.48$). Of more significance, many cladoceran colonists did clearly reach Middle Lake.

Five cladoceran species appeared in 1 year and failed to persist, while *Holopedium* colonization has apparently failed twice (Table 1). Hence, it would appear that recovery of Cladocera was not limited by regional processes, i.e. by the dispersal of colonists, rather the arriving colonists failed to start viable populations. Such local control of zooplankton colonization success may in fact be the norm, even in uncontaminated lakes (Lukaszewski *et al.* 1999; Shurin 2000).

We do not believe that the cladoceran failures were due to colonist starvation. The chlorophyll concentrations in Middle Lake were typical of Shield lakes after about 1985 (Girard *et al.* 2004). Further, the large and persistent *D. mendotae* population indicates that the seston is of a quality to support good daphniid growth (Sterner *et al.* 1997). The mortality of cladoceran colonists may be attributable to unusually heavy predation from yellow perch. Heavy fish predation has been cited as a cause for the slow recovery of Cladocera in Norwegian acidified lakes (Nilssen & Wærvagen 2002), and with no piscsivores, Middle Lake does have an unusually large, yellow perch population comprised of small-bodied individuals (J.M. Gunn, unpublished data). Further, cladoceran community composition is known to be much more vulnerable than is copepod composition to alterations in both vertebrate (Yan *et al.* 2001) and invertebrate (Boudreau & Yan 2003) predation. A comparison of body sizes of *D. mendotae* in Harp and the non-acidic reference lakes is consistent with this hypothesis. Cladoceran body size declines in the face of heavy fish predation (e.g. Yan *et al.* 2001), and *D. mendotae* were unusually small in Middle Lake in comparison with the non-acidic reference lakes (Fig. 5). It is at least equally likely that the cladoceran colonization failures are attributable to the greater sensitivity of Cladocera than Copepoda to metals. The timing of recovery of *D. mendotae* in Middle Lake and the neighbouring Hannah Lake has been unequivocally linked to metal toxicity (Yan *et al.* 1996c). When Ni, and especially Cu levels were low enough, *D. mendotae* colonized the lakes (Pollard *et al.* 2003) and subsequently established huge populations (Yan *et al.* 1996c). Copepods are more tolerant of Ni (48-h LC_{50} of 3.6–15 mg L^{-1}) than are Cladocera (48 h LC_{50} of 0.51–1.9 mg L^{-1}, reviewed in National Research Council Canada 1981), and the 20–30 μg L^{-1} of Cu remaining in Middle Lake after 1990 might very well pose a threat to the long-term survival of many species of *Daphnia* (Biesinger & Christensen 1972; Winner & Farrell 1976), if not to *D. mendotae*. Supporting the metal hypothesis are the correlations of axis scores with environmental variables. The Middle Lake Axis 1 and II scores for the cladoceran and copepod ordinations were much more strongly correlated with Ni concentrations (r = 0.51, 0.43, 0.72 and 0.66, respectively), than with pH, Cu, water transparency or water temperature.

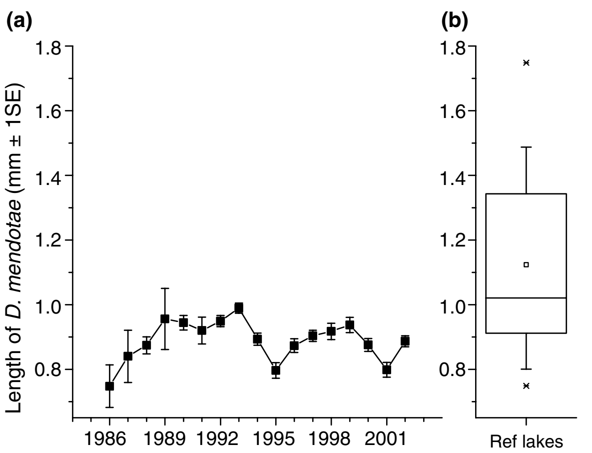

Figure 5 Long-term changes in ice-free season average body length of *Daphnia mendotae* in Middle Lake (a), in comparison with the distribution (box plot) of ice-free season mean lengths in the 19 non-acidic reference lakes with *D. mendotae* populations (b).

In summary, we believe that copepods have recovered in Middle Lake because founding individuals arrived into unsaturated food webs, at times when local conditions were suitable for their survival and growth. In contrast, we believe that the stalled recovery of Cladocera is not attributable to lack of colonists, or to inadequate food base availability or quality. Rather we believe it is attributable to unusual fish predation from the large yellow perch population and/or to continuing metal toxicity for the majority of large cladoceran species, including many daphniid taxa and *Holopedium*.

The complete recovery of the Middle Lake copepod fauna from severe and chronic impacts of chemical and physical disturbance and food web alteration bodes well for the recovery of planktonic Copepoda from multiple disturbances, and for their recovery from less severe disturbance once stressors are removed. As there are thousands of acidified lakes on the Canadian Shield, Middle Lake provides a hopeful case study for Copepoda (Doka *et al.* 2003). We must still await the future recovery of Cladocera in Middle Lake. We believe such recovery depends on continuing reductions in Cu and Ni levels, and perhaps also on the colonization of Middle Lake by piscivores that will reduce planktivorous fish population size.

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