Multispecies crayfish declines in lakes: implications for species distributions and richness

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Abstract. Aquatic communities are highly threatened by anthropogenic and climate change. However, despite their importance in these communities, information regarding temporal changes in populations and assemblages of North American crayfish is scarce. Long-term monitoring of crayfish populations in south-central Ontario, Canada, indicates that the populations are in a significant state of decline. We sought to determine whether these population declines are spatially and taxonomically broad, and if so, what factors might be associated with the declines. We sampled crayfish abundance (catch per unit effort) in 100 lakes, and compared current abundances to survey results from the early 1990s. Abundances of all species (natives and nonnatives) declined significantly during this interval. Declines were both severe (63–96% loss of abundance) and geographically widespread for all species. Previous studies have documented native species declines caused by the invasive crayfish *Orconectes rusticus*, but this species was absent from almost all lakes and was not a factor in the declines. We hypothesize that the introduction of predatory smallmouth bass (*Micropterus dolomieui*), increases in Al concentrations, and reduced Ca concentrations in these lakes are negatively affecting crayfish populations.

Key words: crayfish, *Cambarus*, *Orconectes*, abundance, population declines, inland lakes, calcium decline, Canadian Shield, south-central Ontario.

Aquatic ecosystems are severely threatened by environmental change and loss of biodiversity. In North America, the number of aquatic taxa in need of conservation or monitoring vastly outnumbers the number of terrestrial taxa of the same status (Master 1991). Literature on the status of North American freshwater fishes (e.g., Williams et al. 1989, Jelks et al. 2008) and amphibians (reviewed in Stuart et al. 2004) has mounted during the past 20 y, but North American crayfish have received less attention (Taylor et al. 1996, 2007) despite their importance in aquatic ecosystems (Momot et al. 1978). Information on the status of crayfish in Canada is even more limited (Hamr 1998, 2006).

Ontario has the richest crayfish biodiversity in Canada and is home to 9 of the 11 species that can be found in the country. These species include natives (*Fallicambarus fodiens*, *Cambarus diogenes*, *Cambarus bartonii*, *Cambarus robustus*, *Orconectes immunis*, *Orconectes propinquus*, and *Orconectes virilis*) and nonnatives (*Orconectes obscurus* and *Orconectes rusticus*). Work has begun on determining the status of crayfish in southern Ontario, particularly in relation to the burrowing crayfishes *C. diogenes* and *F. fodiens* (Hamr 2006, Guiasu 2007), but crayfish status elsewhere in Canada has not been directly evaluated. The most recent status report of the Canadian Endangered Species Conservation Council (CESCC 2006; www.wildspecies.ca) lists no native species as "At Risk" or "May be At Risk." The burrowing crayfishes *C. diogenes* and *F. fodiens* are listed as "Sensitive," whereas the remaining native species are listed as

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"Secure." However, this ranking has been based on very sparse monitoring efforts, particularly in central and northern Ontario. In fact, several native populations in lakes in south-central Ontario appear to have experienced significant declines (David et al. 1994) that might indicate broader ecological issues.

The general consensus is that 4 major causes of aquatic imperilment exist: 1) loss or degradation of appropriate habitat, 2) various forms of chemical pollution, 3) introductions of nonnative species, and 4) overexploitation for human uses (Allan and Flecker 1993, Wilcove et al. 1998). In the case of crayfish, overexploitation for human uses is not a likely factor. Reason exists to hypothesize that any of the other 3 factors might be affecting crayfish, but to date, no studies have examined the broader status of crayfish populations and communities. In general, crayfish community structure is not well understood, and few data exist with which to assess particular trends in crayfish communities.

Crayfish are the largest freshwater crustaceans in North America and where present, they often comprise a large portion of the total biomass in the ecosystem (Momot et al. 1978). Crayfish are omnivores, and can act as primary consumers, carnivores, and decomposers (Momot 1995, Dorn and Wojdak 2004). Thus, they are an important component of aquatic food webs and transfer energy from lower to higher trophic levels when they are consumed by predatory fishes, mammals, and birds. Systems without crayfish have diminished energy cycling, community productivity, and food availability at the top of the food chain. Thus, crayfish might be keystone species where they are present (Momot 1995). Crayfish are ecosystem engineers. They modify the physical environments in which they live and alter breakdown and availability of basal food sources (Creed and Reed 2004). Thus, changes to crayfish communities could have broad effects in aquatic ecosystems.

Our objective was to determine the current status of crayfish populations across south-central Ontario ($>22,000$ km^2), and if changes were detected, to determine whether particular environmental factors might be contributing to these changes. We compared crayfish abundances and water chemistry data from 100 lakes to survey results from the early 1990s (David et al. 1997, Ontario Ministry of Environment [MOE], unpublished data) to assess changes. We evaluated the community-level and distributional implications of any population changes detected and determined environmental factors that might be related to the patterns observed in the abundances of crayfish in these lakes.
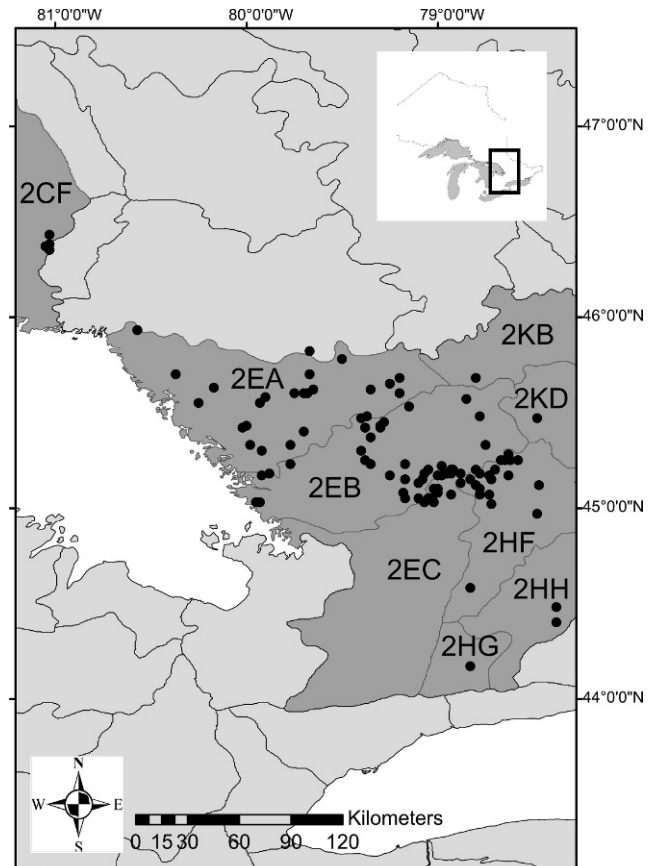

Fig. 1. Study region in Ontario, Canada, showing 100 lakes surveyed. Tertiary watershed delineations and codes: 2EA = Georgian Bay tributaries, 2EB = Moon and Go Home rivers, 2EC = Severn River, 2HF = Cameron Lake drainage, 2CF = Sudbury Region, 2KD = Upper Madawaska River, 2KB = Deep River, 2HH = Kawartha Lakes region, 2HG = Scugog River.

Study Lakes and Study Region

Our survey included 100 inland lakes from 9 tertiary watersheds across south-central Ontario (Fig. 1), based on the availability of historical records for crayfish and water chemistry. The lakes range in longitude from 78°23′W (Kawartha region) to 81°03′W (Georgian Bay region), range in latitude from 44°10′N (Scugog region) to 46°26′N (Sudbury area), and cover a wide geographical range (minimum convex polygon area of 22,300 km^2).

Most of the lakes were in 4 tertiary watersheds: Georgian Bay Tributaries (2EA), Moon and Go Home rivers (2EB), Severn River (2EC), and the Cameron Lake Drainage (2HF). The geology of this region is typical of the Canadian Shield, with a predominance of granitic bedrock and pockets of thin, acidic, and nutrient-limited soils (Jeffries and Snyder 1983, Chapman and Putnam 1984). Secondary-growth

mixed forest covers much of the study area, with patches of coniferous- and deciduous-dominated stands distributed throughout the forest (David et al. 1997). These watersheds are characterized by different intensities of cottage development and recreational use and include a number of small communities.

Eight more northern Shield lakes were from the Sudbury region (2CF) and from Algonquin Park (Upper Madawaska River [2KD] and Deep [2KB] watersheds and the northeastern corner of the Moon and Go Home River watershed [2EB]). The Sudbury region is sparsely vegetated with secondary-growth mixed forest (Girard et al. 2006). This area of Algonquin Park is dominated by coniferous forest and is completely undeveloped (except for walking trails and camp sites) where our study lakes were situated.

Four lakes were south of the Canadian Shield and enabled us to compare and contrast crayfish populations and physicochemical variables between the 2 geological regions. The 4 off-Shield lakes (1 in the southern tip of tertiary watershed 2HF and 3 in watersheds 2HH and 2HG) are in heavily urbanized and deforested areas, experience high levels of recreational use year-round, and are hard-water lakes that are rich in Ca. Collectively, the Shield lakes and the southerly off-Shield lakes represented a long gradient of anthropogenic impacts, including atmospheric acidification and metal deposition, and human development intensity.

Methods

Site selection and crayfish sampling

Site selection and sampling methods were developed by the MOE (David et al. 1994). Recently molted individuals, berried females, or females carrying young rarely enter traps (Somers and Green 1993, Richards et al. 1996). Moreover, crayfish are most active, and thus, most likely to enter traps, when surface water temperatures are >20°C (Somers and Green 1993, Richards et al. 1996, Hein et al. 2007). Therefore, each lake was sampled once between late June and the end of August to coincide with the period of highest crayfish catchability when both cambarid and orconectid crayfishes should be in an intermolt stage, females should not be carrying young (Crocker and Barr 1968, Somers and Green 1993, David et al. 1994, Richards et al. 1996, but see Hamr and Berrill 1985), and when water temperatures had reached 20°C. This limited catchability window constrained sampling such that most lakes were sampled over 3 summers (2005–2007). Five lakes were part of MOE's regular crayfish population monitoring program and had been sampled in 2002 to 2004 (MOE, unpublished data). The historical data were collected over 6 summers (1989–1992, 1994, 1995).

Crayfish were collected with standard, commercially available, wire-mesh Gee minnow traps. Each trap was baited with a single perforated plastic film canister filled with fish-flavored canned cat food. Funnel entrances were enlarged to ~3.5-cm diameter to accommodate larger crayfish. Traps were set and then retrieved the following day (18–26 h) so that traps were out at night when crayfish are most active.

Three site types (rock, macrophyte, or woody debris dominated) were sampled in each lake because species vary in terms of their preferred habitats (Crocker and Barr 1968, Nystrom et al. 2006). Fifty-four traps were set in each lake (18 traps at each of the 3 site types). Three trap lines, each consisting of 6 traps secured at 3-m intervals, were set perpendicular to the shore 2 to 5 m apart at locations with a minimum depth of 0.5 m for the first trap in a line and a place on the shoreline where the line could be tied. Trap depths ranged from 0.5 to 8 m depending on the slope of the littoral zone. This design is similar to that used to collect the historical data, in which trap depths ranged from 1 to 6 m in depth at 1-m depth intervals (David et al. 1997). Single baited traps effectively sample a radius of 4.2 m (56.3 m^2). Therefore, the total area sampled by the historical and current sampling designs is equivalent. Crayfish were identified using the taxonomic keys in Crocker and Barr (1968). The number of crayfish/species in each trap was used to calculate a catch per unit effort (CPUE) estimate of relative abundance.

Chemistry sampling

Water chemistry was sampled in the same year that crayfish were sampled in early spring before lakes became stratified. Epilimnetic water was collected using a 5-m vertical composite sampler (Girard et al. 2007). Access to a small number of lakes was difficult in spring because of road washouts, so samples from these lakes were collected with the same apparatus but in summer when crayfish were sampled. In deeper lakes, this sampling approach represents the chemical conditions of only the epilimnion, but this approach is appropriate because it matches that method used by David et al. (1997) and because crayfish preferentially inhabit this depth (Jones and Momot 1981).

A total of 18 chemical variables (pH, alkalinity [mg/L], conductivity [μS/cm], Al and Mg [mg/L], Mn and Fe [μg/L], dissolved inorganic and organic C [DIC and DOC, respectively; mg/L], Ca, K, Na, Cl,

TABLE 1. Results of the Model II regression analyses comparing current and historical relative abundances (catch per unit effort [CPUE]) for all lakes in which a species was found. n = the number of lakes in which a species was found, p = probability associated with the difference from the null expectation (1:1), % historical = the percentage of lakes in which the species occurred historically that have current populations of the species.

Species	n	r	SE	Slope	p	% historical
Orconectes virilis	57	0.61	0.044	0.28	$\ll 0.001$	28
Orconectes propinquus	39	0.74	0.013	0.09	$\ll 0.001$	9
Orconectes obscurus	9	0.76	0.115	0.32	< 0.001	32
Orconectes immunis	7	0.36	0.239	0.37	< 0.05	37
Orconectes rusticus	3	0.71	0.085	0.09	< 0.05	9
Cambarus bartonii	33	0.79	0.013	0.10	$\ll 0.001$	9
Cambarus robustus	12	0.27	0.041	0.04	$\ll 0.001$	4

and SO_4 [mg/L], and NH_4, NO_3, total Kjeldahl N, and total P [µg/L]) were analyzed from these samples using standard analytical methods (Anonymous 1983).

Accidental freezing in the laboratory resulted in the loss of 35 DIC samples in the current survey, and 6 DIC samples were lost for unreported reasons in the historical study. These losses reduced the number of lakes for which the comparison of DIC was possible to 60 (Scugog Lake was the only off-Shield lake retained). A linear regression model relating Cl to Na was used to estimate the historical Na concentration for Scugog Lake.

Data analysis

Model II major axis regression was used to examine the congruence between current and historical CPUE for each species. Model II regressions are appropriate when both variables are subject to error (from natural inherent variability or measurement error; Chen and Jackson 2000), and allowed us to determine the slope and y-intercept of the interrelationship between 2 variables when we were not interested in the independent and dependent (i.e., predictor and response) relationship between them (Sokal and Rohlf 1995). If no changes had occurred between the 2 survey periods, one would expect a strong regression relationship with slope = 1. This expectation was evaluated with t-tests to determine whether the modeled slopes differed significantly from the null expectation of a 1:1 relationship. The t-tests were based on the formula, $t = (b_1 - 1)/SE_{b1}$, where b_1 is the slope of the major (Model II) axis and SE_{b1} is its standard error (see Yang et al. 2004).

To evaluate changes at the community level, a frequency distribution of the number of lakes with 0, 1, 2, 3, and 4 species was generated for both the historical and current data sets. Fisher's exact test was used to determine whether these species richness

relationships had changed significantly between the 2 survey periods.

Paired t-tests were used to screen chemical variables for significant changes between current and historical conditions in all lakes and then in only Shield lakes. Tests were corrected for multiple comparisons with the False Discovery Rate approach (Benjamini and Hochberg 1995). This correction technique is particularly appropriate when conducting exploratory analyses or when the variables under consideration covary (reviewed in de Castro and Singer 2006). Each variable that showed a significant change was further analyzed with Model II regression to obtain a visual assessment of the trends between the 2 surveys, again with the 1:1 line as the baseline expectation.

Results

Crayfish

Abundance.—Seven crayfish species (*O. immunis*, *O. obscurus*, *O. propinquus*, *O. rusticus*, *O. virilis*, *C. bartonii*, and *C. robustus*) were encountered during both studies. Crayfish were not found in 25 lakes during the historical survey and in 33 lakes during our survey. Where crayfish were found, total crayfish abundance (as CPUE) including all species present ranged from 0.01 to 12.8 in the historical survey and from 0.02 (in 8 lakes) to 2.89 in our survey.

Abundances of all species decreased between the 2 surveys. Slopes of all lines generated by Model II regression analyses were significantly <1 (Table 1, Fig. 2A–F). The decline was most striking for *C. robustus* (to ~4% of historical values; r = 0.27, slope = 0.04, $p \ll 0.001$; Fig. 2F), closely followed by *O. propinquus* (to ~9%; r = 0.74, slope = 0.09, $p \ll 0.001$; Fig. 2B), *O. rusticus* (to ~9%, r = 0.71, slope = 0.09, $p < 0.05$; graph not shown because *O. rusticus* is associated only with 3 sites), and *C. bartonii* (to ~10%; r = 0.79; slope = 0.10, $p \ll 0.001$; Fig. 2E).
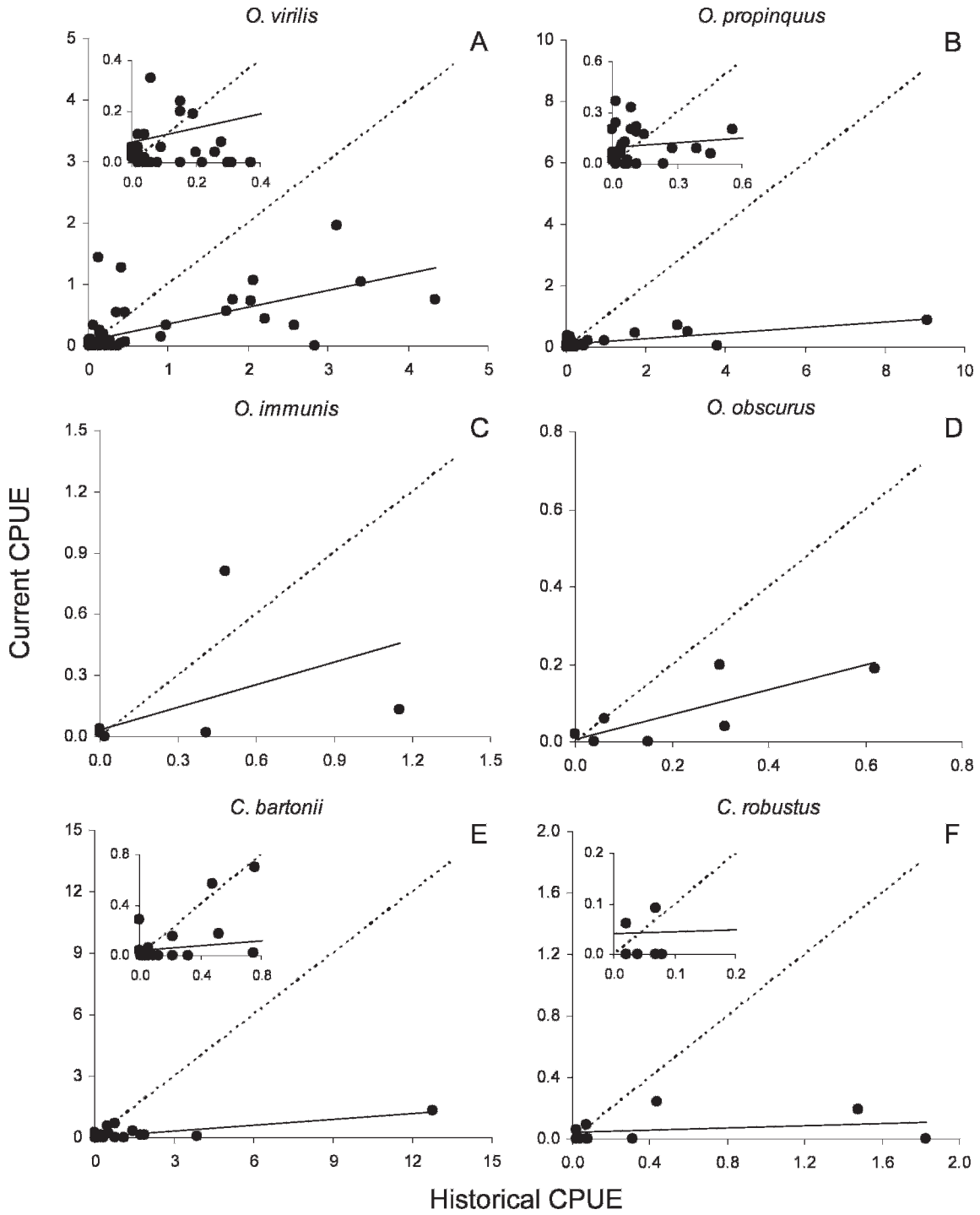
FIG. 2.   Model II regression plots for current vs historical abundance (as catch per unit effort [CPUE]) of *Orconectes virilis* (A), *Orconectes propinquus* (B), *Orconectes immunis* (C), *Orconectes obscurus* (D), *Cambarus bartonii* (E), and *Cambarus robustus* (F) in relation to the 1:1 null expectation (dashed line). Insets show details for species with many low abundances.

Less extreme declines were observed for *O. virilis* (to ~30%; $r = 0.61$, slope = 0.28, $p \ll 0.001$; Fig. 2A) and *O. obscurus* (to ~32%; $r = 0.76$, slope = 0.32, $p < 0.001$; Fig. 2D). The species with the least severe declines

was *O. immunis* (to ~37%; $r = 0.36$, slope = 0.37, $p < 0.05$; Fig. 2C), but a large increase in the abundance of a single population strongly influenced this regression. In absolute terms, the disparity between the
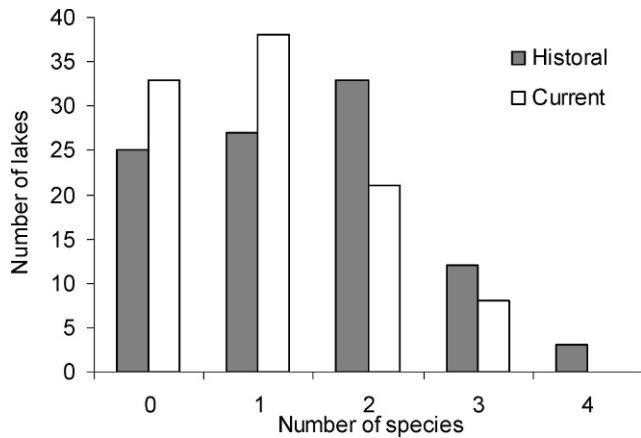
Fig. 3. Frequency distributions of crayfish species richness in the historical and current surveys.

Fig. 4. Changes in the number of lakes with populations of *Orconectes virilis* (*O.v.*), *Orconectes propinquus* (*O.p.*), *Orconectes immunis* (*O.i.*), *Orconectes obscurus* (*O.o.*), *Orconectes rusticus* (*O.r.*), *Cambarus bartonii* (*C.b.*), and *Cambarus robustus* (*C.r.*) between the historical and current surveys in relation to the 1:1 null expectation (dashed line).

historical and current estimates of abundance was greatest for populations with historically higher abundances. However, one can interpret the Model II regression line as providing the general trend for a species across populations. The general trend across populations was that abundances in our survey were lower than abundances in the historical survey, regardless of historical abundance. A few populations were more abundant in our survey than in the historical survey; e.g., populations of *O. virilis* with low abundances (Fig. 2A inset) and 1 population of *O. immunis* (Fig. 2C). Variability associated with each model and the significance of the relationships described vary by species (Table 1) because of inherent variability in the data and because species have different incidence rates, e.g., *O. virilis* occurs in more lakes than does *O. immunis*.

Species richness.—Species richness was distinctly lower in our survey than in the historical survey, but the shift was not statistically significant (Fisher's exact test, $p = 0.069$; Fig. 3). The percentage of lakes with no crayfish increased from 25 to 33%, and the modal species richness decreased from 2 (32% of lakes) to 1 (38% of lakes) (Fig. 3). In the historical survey, 53% of lakes contained ≤1 species and numerous lakes contained 3 or 4 species, whereas in our survey, 71% of lakes contained ≤1 species and none were found to continue supporting 4 species.

Distribution.—The number of lakes inhabited by each species has decreased for all species except *O. immunis* (Fig. 4). The orconectids tended to have fewer apparent losses and less serious declines than did the cambarids. *Orconectes immunis* appears to have been lost from 1 lake (14.3% of historical occurrences) and was newly detected in 3 lakes (42.9% of historical occurrences). *Orconectes propinquus* appears to have been lost from 10 lakes (25.6%)
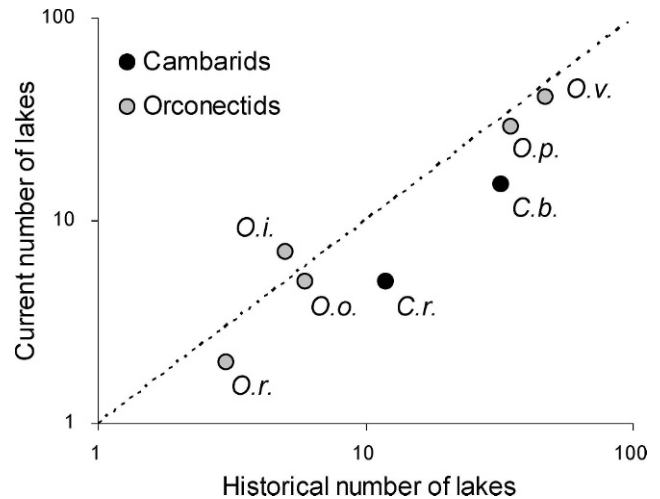
and has declined by ≥50% in 10 lakes (25.6%) (Fig. 5A). In total, 51.3% of *O. propinquus* populations are currently at risk or have been lost, but these losses were partially offset by 4 new detections (10%). No obvious spatial patterns in *O. propinquus* losses or detections were observed (Fig. 5A), although 3 losses occurred in the lakes in the Black River system at the northern tip of the Severn River Watershed (2EC). *Orconectes virilis* appears to have been lost from 15 lakes (26.3%) and has declined ≥50% in 15 lakes (26.3%) (Fig. 5B). In total, 52.6% of *O. virilis* populations are currently at risk or have been lost, but these losses were offset by 10 new detections (18%). A large number of *O. virilis* population losses or reductions occurred in one set of connected lakes in the Black River system, whereas *O. virilis* was newly detected in each of a string of 4 connected lakes in the northwestern portion of the Cameron Lake Drainage (2HF) (Fig. 5B).

The apparent loss of populations was most marked for the 2 cambarid species (Fig. 4). *Cambarus bartonii* appears to have been lost from 18 lakes (54.6%) and has declined by ≥50% in 7 lakes (21.2%) (Fig. 5C). In total, 75.7% of *C. bartonii* populations have been lost or are at risk, and these losses were offset by only 2 new detections (6.1%). *Cambarus bartonii* losses and declines have occurred across the northern and southern portions of its historical range, but a narrow band of currently stable populations was found across the center of the range. *Cambarus robustus* appears to have been lost from 7 lakes (58.3%) and has declined substantially in 1 lake (8%) (Fig. 5D). These results
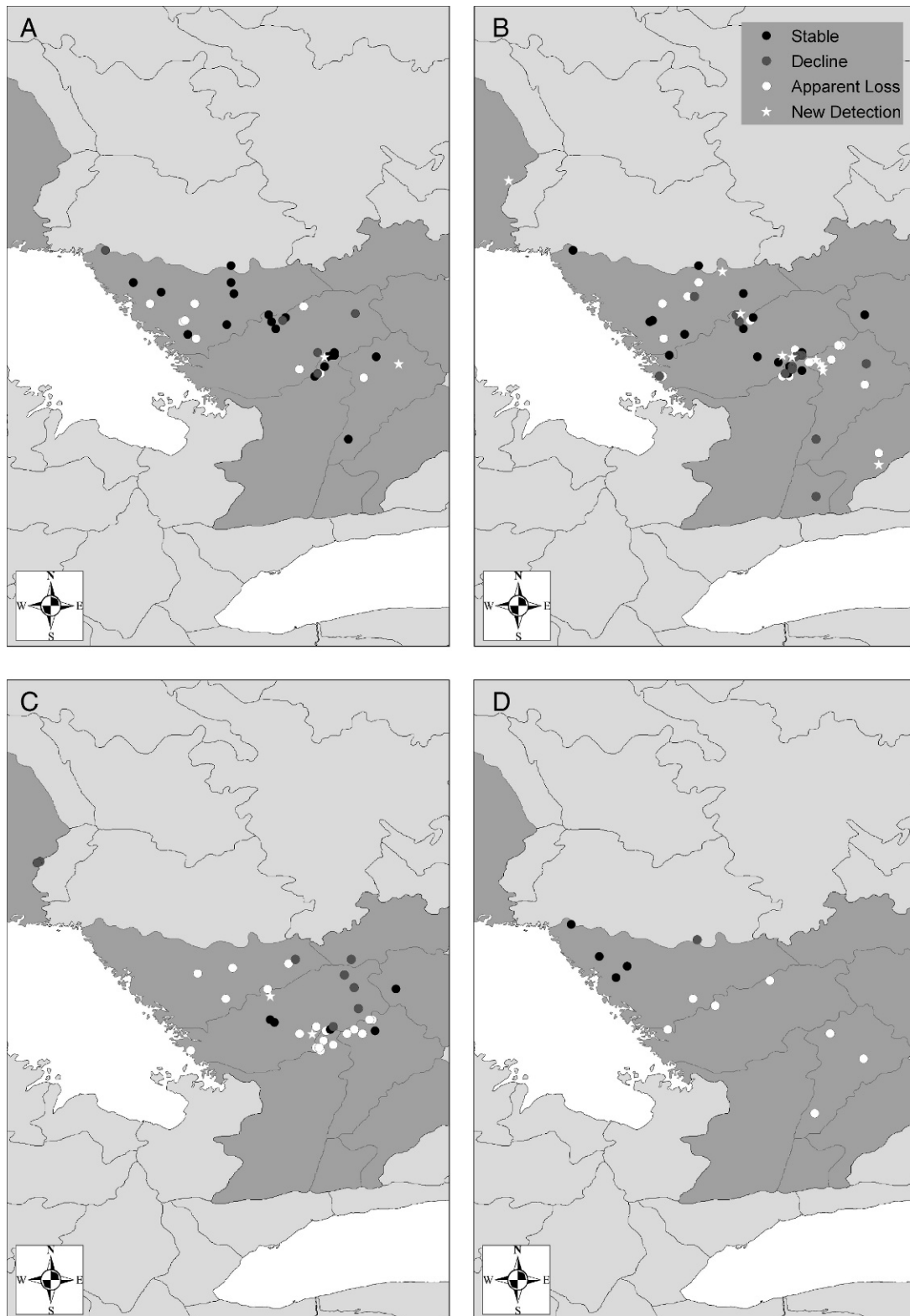
FIG. 5. Distributions of *Orconectes propinquus* (A), *Orconectes virilis* (B), *Cambarus bartonii* (C), and *Cambarus robustus* (D), indicating populations that appear stable, have declined by ≥50%, appear to have been lost, or newly detected.

Table 2. Chemical variables that changed significantly in all study lakes or in the Shield lakes between the historical survey and the current study. Δ = % change, Alkti = alkalinity, DIC = dissolved inorganic C. p = probability associated with paired t-tests comparing current and historical values, * indicates differences were significant only in Shield lakes and means and Δ apply only to Shield lakes, ns = not significant ($p > 0.05$).

Variable	Means			p	
	Current	Historical	Δ (%)	All lakes	Shield lakes
Alkti (mg/L)	8.22	7.09	16.03	0.0102	ns
Al (mg/L)	52.30	29.70	76.09	≪0.0001	≪0.0001
Ca* (mg/L)	3.08	3.41	−9.95	ns	0.0014
Cl (mg/L)	5.61	4.21	33.40	0.0013	0.0035
DIC* (mg/L)	1.46	1.25	16.80	ns	0.0018
Mg* (mg/L)	0.77	0.86	−10.43	ns	0.0008
Na (mg/L)	3.83	2.63	45.24	0.0045	0.0107
NO_3 (µg/L)	58.15	25.02	132.47	≪0.0001	≪0.0001
SO_4 (mg/L)	5.54	7.40	−25.05	≪0.0001	≪0.0001

indicate that 66.7% of *C. robustus* populations are currently at risk or have been lost, and these losses were not offset by new detections. *Cambarus robustus* appears to have been lost in all of its southern and eastern historical range and is now limited to a small segment of the northern tip of a single watershed, the Georgian Bay tributaries (2EA).

Water chemistry

Significant changes between the historical and current chemical conditions were detected for 9 variables (Table 2). Mean alkalinity, Al, Cl, Na, and NO_3 increased significantly (by ~16, 76, 33, 45, and 132%, respectively), whereas mean SO_4 decreased significantly (~25%) between surveys. However, alkalinity did not differ significantly between surveys when off-Shield lakes were omitted from the analysis. Temporal trends in the remaining variables differed between lakes on and off the Canadian Shield. Mean Ca and Mg decreased significantly (10%) between surveys in Shield lakes but increased in off-Shield lakes. In contrast, DIC increased significantly (16%) in most Shield lakes for which data were available but decreased in off-Shield Lake Scugog.

Model II regression results (Fig. 6A–I) provide support for the differences detected by paired t-tests; however, 3 cases warrant cautious interpretation. Present and historical values of alkalinity were strongly correlated ($r = 0.91$; Fig 6A). However, values declined slightly in a large number of lakes and increased strongly in a few lakes with historically low concentrations. These few lakes with large increases might have influenced the results of the paired t-test. The increase in Al was well supported ($r = 0.63$; Fig. 6B), but Al decreased in a large number of lakes. NO_3 increased dramatically in many lakes, but

the pattern of increases was highly variable ($r = 0.25$; Fig. 6H) and the regression was driven by increases in lakes with historically low NO_3 concentrations.

Discussion

Crayfish trends

Population declines or apparent losses were observed for all 7 species, in most of our study lakes, and in all 9 watersheds. Our results indicate that the trends noted previously for a few lakes in watersheds 2EB and 2EC by David et al. (1994) were not isolated occurrences, but instead were the first indication of a broader phenomenon. Declines have been severe for all species and range from a loss of 63% (*O. immunis*) to 96% (*C. robustus*) of historical abundance. Native *O. virilis*, *O. propinquus*, and *C. bartonii* have declined by 72%, 91%, and 91%, respectively, and nonnative *O. obscurus* and *O. rusticus* have declined by 68% and 91%, respectively. Across the region, crayfish assemblages are less diverse than they were in the early 1990s. In the past, lakes commonly supported 2 to 4 species, whereas today most contain ≤1.

Severe declines (≥50% of historical abundance) or apparent losses were detected for all 7 species in each watershed that they had inhabited historically (except that *O. virilis* and *C. bartonii* still have stable populations in the single lake that was included from the 2KD watershed). *Orconectes propinquus*, and to a lesser extent *O. virilis*, have lost populations or experienced severe declines throughout their historical ranges. However, except for the large number of declines or losses in the Black River system (2EC), the changes follow no clear spatial pattern. Moreover, the lakes in the Black River system have no obvious distinguishing characteristics that would set them apart as lakes in which crayfish should be in a greater
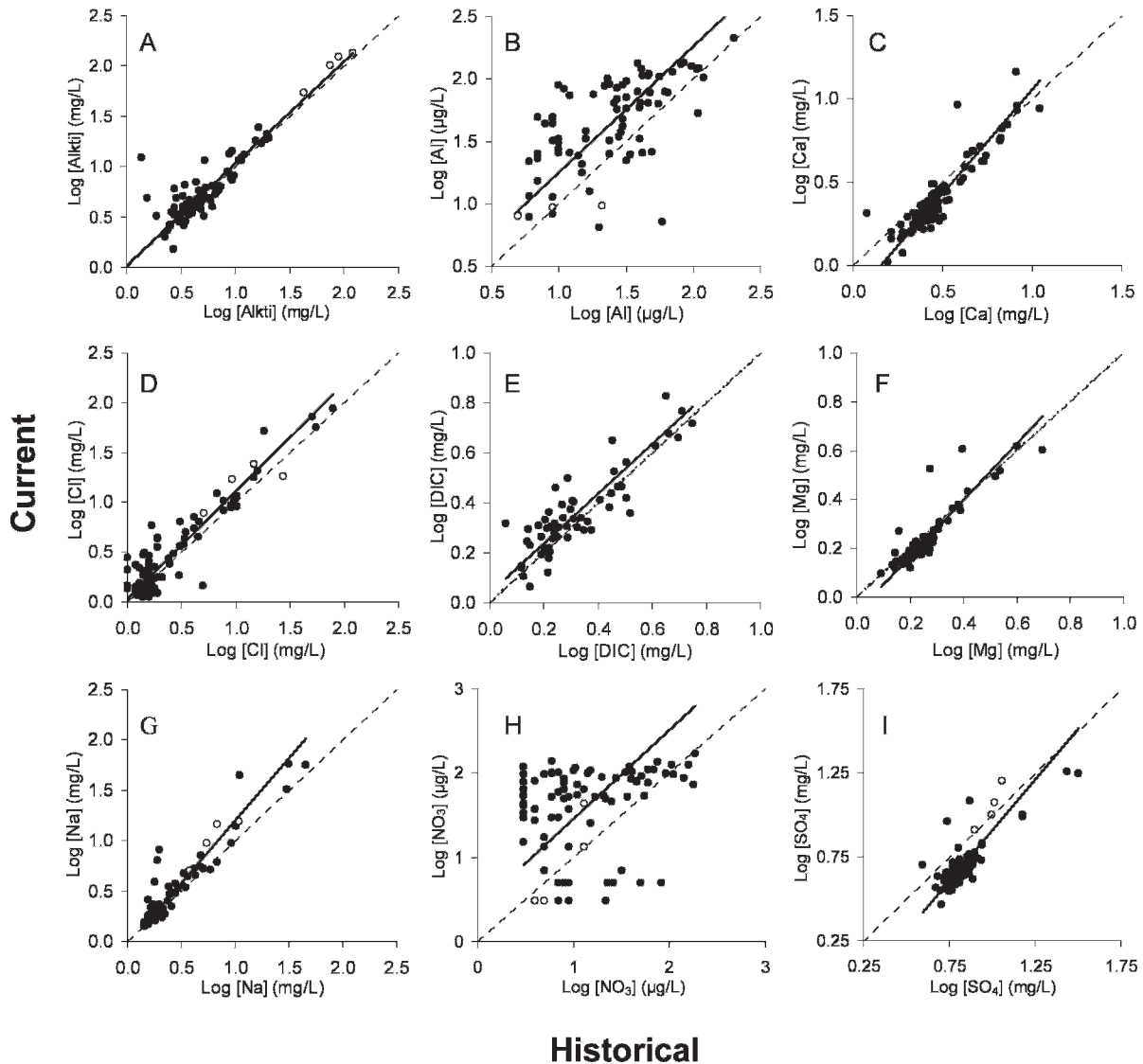
FIG. 6. Model II regression plots for log(x)-transformed current vs historical alkalinity (Alkti) (A), Al (B), Ca* (C), Cl (D), dissolved inorganic C (DIC*) (E), Mg* (F), Na (G), NO$_3$ (H), and SO$_4$ (I), in relation to the 1:1 null expectation (dashed line). Off-Shield lakes are designated by open circles. A constant of 1 (2 in the case of alkalinity) was added before transformation of Al, Cl, DIC, Mg, Na, and NO$_3$. * indicates differences were significant only in Shield lakes and so off-Shield lakes were excluded from analysis.

state of imperilment than elsewhere. The cumulative trend for these 2 orconectids is an increasingly fragmented spatial distribution. The remaining populations are separated by greater distances and potentially unsuitable connecting water bodies. These changes in spatial distribution could affect their long-term population viability.

The range of *C. robustus* was reported as increasing in Ontario (Guiasu et al. 1996), but our results show that its range might now be shrinking, at least in the region that we studied. More than half of the historical populations of this species have been lost,

and remaining populations are isolated within a single watershed (2EA). *Cambarus bartonii* also has lost >50% of its historical populations, and another 21% have declined drastically. The 5 remaining stable populations are contained within a narrow horizontal band. Our results indicate that cambarids are more vulnerable to population loss than are orconectids, and the rate of decline raises concerns regarding their overall viability in the larger geographic region.

A number of biological and physiological differences between *Cambarus* and *Orconectes* might account for the differences in imperilment between these

genera (Crocker and Barr 1968). South-central Ontario Shield populations of *Orconectes* spp. (*rusticus*, *propinquus*, *virilis*) extrude eggs in May and June, whereas *Cambarus* spp. (*bartonii* and *robustus*) tend to do so in August and September (Hamr and Berrill 1985, Somers and Green 1993). This difference in phenology means that orconectid juveniles have a head start on growth before molting ceases at the onset of decreased autumn/winter temperatures. Many cambarid females are unable to carry out their postbreeding molt until the following spring, which might delay or desynchronize subsequent reproductive cycles (Hamr and Berrill 1985, Somers and Green 1993) and account for previous reports of unrestricted timing of mating and reproduction (Crocker and Barr 1968). *Cambarus bartonii* and *C. robustus* reach sexual maturity at a larger size and at the end of their 3rd summer/growth season, whereas *O. rusticus*, *O. virilis*, and *O. propinquus* mature at smaller sizes in their 2nd season (Crocker and Barr 1968, Hamr and Berrill 1985, Holdich 2002). Limited information also indicates that these orconectids might produce greater numbers of smaller and potentially less costly eggs than do cambarids, particularly *C. bartonii* (Holdich 2002).

Some of the population losses or gains could indicate fluctuations around the detection level of our methods rather than extirpations and colonizations. However, our methods are sensitive to large changes in abundance. Thus, fluctuations in sparse populations are not likely to have influenced the overall trends observed in our study. In addition, some of the lakes in our study and additional lakes in the region are surveyed annually by MOE as part of a biomonitoring program, and most of these populations are decreasing (David et al. 1994, KMS, unpublished data). Year-to-year variation in crayfish abundance (CPUE) is generally low (David et al. 1994, Somers et al. 1996, KMS, unpublished data), particularly compared with the magnitude of declines reported here, and is thus, unlikely to have biased our findings.

The sampling method used in our survey was very similar to the method used by David et al. (1997), and sampling effort and efficiency were similar in both surveys. The original sampling locations in a few lakes were not recorded. However, new sites in those lakes were selected based on the same criteria as in the initial survey and included similar habitats for the detection of crayfish abundance. Therefore, any differences caused by use of new sampling sites should have provided equal opportunities to detect either population increases or decreases in any given lake rather than the systematic decreases that were observed.

Potential environmental links

Historical acidification and metal contamination related to long-range transport of airborne contaminants affected water chemistry throughout the inland Shield lakes of Ontario (Stoddard et al. 1999, Keller et al. 2003). Our water-chemistry data show clear signs of chemical recovery from historical acidification. The comparisons made here indicate that emission controls have resulted in a 16% increase in alkalinity and a 25% reduction in SO_4 concentrations. Despite evidence of recovery, the top-ranked threats to aquatic fauna, including physiochemical changes caused by loss or degradation of habitat and chemical pollution and introductions of nonnative species (Allan and Flecker 1993, Wilcove et al. 1998, Venter et al. 2006), have remained important across the region.

Physiochemical changes.—Physical habitat alteration and increased recreational development of some lakes in the region has been noted (e.g., Molot and Dillon 2008, Yan et al. 2008) but not directly quantified. Crayfish preferentially inhabit the near-shore littoral zone of lakes (Jones and Momot 1981). Depending on the species, crayfish use rocks, boulders, macrophyte beds, and coarse woody debris as refugia (Nystrom et al. 2006) and, in some cases, to construct depressions and burrows as long- or short-term dwellings (Crocker and Barr 1968). As the number of cottages and recreational homes around the lakes increase, natural shorelines are transformed, and undesired (by homeowners) substrates, plants, and materials are removed and often are replaced with sand. Such alterations result in less suitable habitat for crayfish and could lead to crowding and increased competition, cannibalism, and predation.

Climate change has caused water temperatures to increase and has resulted in longer ice-free seasons (Rusak et al. 2008). Both of these environmental changes could have implications for crayfish survival and reproduction. *Cambarus bartonii*, in particular, are sensitive to changes in temperature, which influence their reproductive cycle, growth, and behavior (Somers and Green 1993). Changes in seasonal patterns of molting and reproduction because of longer warm seasons could negatively affect overwintering and juvenile survival. Increased water temperatures make crayfish less tolerant of shifts in some chemical variables (DiStefano et al. 1991) and more susceptible to disease (Jiravanichpaisal et al. 2004).

Ca is an essential element for most biota. In addition to general physiological uses, crayfish must acquire Ca for the formation of exoskeletons and might experience increased metabolic costs in low-Ca

environments (Cairns and Yan 2009). Changes in Ca acquisition could make crayfish more vulnerable to predation, cannibalism, or competition, and impact their growth, survival, and reproductive success (Stein 1977, France 1987, Keller et al. 2001, Rukke 2002, Hammond et al. 2006, Cairns and Yan 2009). Ca concentrations have declined an average of 10% in our study lakes, a potentially significant change for organisms in many soft-water Shield lakes because historical Ca concentrations were very low. The reduction of major cations, including Ca, in the study lakes is a consequence of acidification recovery and reduced cation leaching from the surrounding soils, processes that have been well documented in the lakes of this region (Watmough and Dillon 2003, Molot and Dillon 2008, Watmough and Aherne 2008). Ca concentrations in watershed soil pools and surface waters are now well below preacidification levels (Stoddard et al. 1999, Watmough and Dillon 2003, Jeziorski et al. 2008), and concentrations are predicted to continue to drop 10 to 40% from their current levels (Watmough and Aherne 2008). Ca concentrations in many of Ontario's Shield lakes are now <2 mg/L (Jeziorski et al. 2008, MOE, unpublished data), which is lower than the lowest hypothesized habitat requirement for freshwater crayfish (2–10 mg/L; Greenaway 1974, France 1987, Hammond et al. 2006).

Al concentrations have increased an average of 76% in our study lakes and have decreased in only a few lakes, despite increases in pH. The distribution of *O. virilis* in the region is negatively correlated with Al concentration (David et al. 1997), and abundances (as CPUE) of *O. virilis*, *O. propinquus*, and *C. bartonii* are negatively correlated with Al concentrations (David et al. 1994, Somers et al. 1996). Al levels have not reached toxic concentrations, but concentrations of Al similar to those in our study lakes inhibit postmolt Ca acquisition in *O. virilis*, particularly when pH is <7, which is the case for >90% of the Shield lakes (Malley and Chang 1985). Thus, the increased levels of Al in the study lakes might be limiting the ability of crayfish to acquire Ca and enhancing the effects of low-Ca stress in these increasingly Ca-poor waters.

The observed increases in Na and Cl probably are associated with development and winter maintenance of roadways. Increases in lake salinities are directly linked to the 97% sand/3% salt deicing mixtures that have been applied on nearby roads (Molot and Dillon 2008). However, salinities high enough to cause chronic toxicity to invertebrates are unlikely in the near future (Molot and Dillon 2008).

Introduction of nonnative species.—Introductions of smallmouth bass (*Micropterus dolomieui*) have occurred across the study region, and the range of smallmouth bass is predicted to expand because of continued illegal angler introductions and climate change (MacRae and Jackson 2001,Vander Zanden et al. 2004, Sharma and Jackson 2008). Smallmouth bass are voracious predators of crayfish (Crocker and Barr 1968, Collins et al. 1983, Somers and Green 1993, Taylor et al. 2005). Crayfish abundance (as CPUE) often decreases in the presence of smallmouth bass because of predation-induced mortality or reduced catchability caused by predator-avoidance behavior (Collins et al. 1983, Hill and Lodge 1995, Nystrom et al. 2006). At the time of the historical survey, smallmouth bass were found in 55 of the lakes sampled (David et al. 1997, MOE, unpublished data). These lakes had significantly lower crayfish CPUE than did lakes without smallmouth bass (*t*-test, means = 0.42 with bass and 1.61 without bass, $p = 0.005$). The number of lakes inhabited by smallmouth bass probably increased between the historical and current surveys (Sharma and Jackson 2008, Kaufman et al. 2009), and thus, the presence of smallmouth bass might be related to the declines observed in our study.

We found no evidence to indicate that the presence of nonnative crayfish was related to the decline of native species. Abundances of native crayfish species might have declined when lakes were first invaded by the 2 nonnative crayfish species, *O. rusticus* and *O. obscurus*, particularly in lakes south of the Shield where *O. rusticus* was introduced (Berrill 1978, Wilson et al. 2004). However, crayfish can no longer be sold as bait or be transported between water bodies in Ontario because of concern that *O. rusticus* might invade new habitats. Moreover, water-chemistry issues, such as low Ca concentrations, might prevent the establishment of *O. rusticus* in the hundreds of thousands of lakes on the Canadian Shield. In fact, the ranges of the 2 nonnative crayfish species, *O. rusticus* and *O. obscurus*, have not expanded beyond the lakes that were historically documented as invaded (Berrill 1978, David et al. 1997), and both species have experienced declines similar to those experienced by native species.

General implications

Conservation assessment and then local (state, provincial) or national protection is needed where endangered or threatened species of crayfish are identified (Taylor et al. 2007, Crandal and Buhay 2008). The longer a species is recognized as threatened or at risk, the greater its chances of recovery (Taylor et al. 2005). Although previous work indicated that abundances and frequencies of crayfish species in Canada have not changed in ways that might raise

concern (Hamr 1998, CESCC 2006), our results indicate that all species are in general decline over a relatively large geographic range. Notably, previously published work was based on limited monitoring efforts in lakes in distinct geographic areas that are characterized by high alkalinity and high levels of Ca and other nutrients, whereas our study involves primarily Shield lakes that are recovering from decades of acidification. Crayfish act as both keystone species and ecosystem engineers and physically and biologically modify the environments in which they live. Any significant changes in the abundance and community composition of crayfish in lakes are likely to have far-reaching effects on the rest of the ecosystem. How these effects might be manifested is unknown currently, but the declines we report, coupled with the concurrent changes in chemical conditions, are strong indicators of fundamental changes within vast numbers of aquatic ecosystems. These changes should be addressed.

Acknowledgements

Literature Cited

ALLAN, J. D., AND A. S. FLECKER. 1993. Biodiversity conservation in running waters. BioScience 43:32–43.

ANONYMOUS. 1983. Handbook of analytical methods for environmental samples. Volumes 1 and 2. Ontario Ministry of the Environment, Rexdale, Ontario.

BENJAMINI, Y., AND Y. HOCHBERG. 1995. Controlling the False Discovery Rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society B 57:289–300.

BERRILL, M. 1978. Distribution and ecology of crayfish in the Kawartha Lakes region of southern Ontario. Canadian Journal of Zoology 56:166–177.

CAIRNS, A., AND N. YAN. 2009. A review of the influence of low ambient calcium concentrations on freshwater daphniids, gammarids, and crayfish. Environmental Reviews 17:67–79.

CESCC (CANADIAN ENDANGERED SPECIES CONSERVATION COUNCIL). 2006. Wild species 2005: the general status of species in Canada. Minister of Public Works and Government Services Canada, Ottawa, Ontario. (Available from: www.wildspecies.ca)

CHAPMAN, L. J., AND D. F. PUTNAM. 1984. The physiography of Southern Ontario. Special Volume 2. Ontario Geological Survey, Sudbury, Ontario.

CHEN, Y., AND D. A. JACKSON. 2000. An empirical study on estimators for linear regression analyses in fisheries. Fisheries Research 49:193–206.

COLLINS, N. C., H. H. HARVEY, A. J. TIERNEY, AND D. W. DUNHAM. 1983. Influence of predatory fish density on trapability of crayfish in Ontario Lakes. Canadian Journal of Fisheries and Aquatic Sciences 40:1820–1828.

CRANDAL, K. A., AND J. E. BUHAY. 2008. Global diversity of crayfish (Astacidae, Cambaridae, and Parastacidae—Decapoda) in freshwater. Hydrobiologia 595:295–301.

CREED, R. P., AND J. M. REED. 2004. Ecosystem engineering by crayfish in a headwater stream community. Journal of the North American Benthological Society 23:224–236.

CROCKER, D. W., AND D. W. BARR. 1968. Handbook of the crayfishes of Ontario. University of Toronto Press, for the Ontario Ministry of the Environment, Toronto, Ontario.

DAVID, S. M., K. M. SOMERS, AND R. A. REID. 1994. Long-term trends in the relative abundance of crayfish from acid sensitive, softwater lakes in south central Ontario: a data summary for the first 5 years, 1988–1992. Ontario Ministry of the Environment, Dorset, Ontario.

DAVID, S. M., K. M. SOMERS, R. A. REID, AND R. I. INGRAM. 1997. Crayfish species assemblages in softwater lakes in seven tertiary watersheds in south-central Ontario. Ontario Ministry of the Environment, Dorset, Ontario.

DE CASTRO, M. C., AND B. H. SINGER. 2006. Controlling the False Discovery Rate: a new application to account for multiple and dependent tests in local statistics of spatial association. Geographical Analysis 38:180–208.

DISTEFANO, R. J., R. J. NEVES, L. A. HELFRICH, AND M. C. LEWIS. 1991. Response of the crayfish Cambarus bartonii bartonii to acid exposure in southern Appalachian streams. Canadian Journal of Zoology 96:1585–1591.

DORN, N. J., AND J. M. WOJDAK. 2004. The role of omnivorous crayfish in littoral communities. Oecologia (Berlin) 140:150–159.

FRANCE, R. L. 1987. Calcium and trace metal composition of crayfish (Orconectes virilis) in relation to experimental lake acidification. Canadian Journal of Fisheries and Aquatic Sciences 44:107–113.

GIRARD, R., N. D. YAN, J. HENEBERRY, AND W. B. KELLER. 2006. Physical and chemical data series from Clearwater, Lohi, Middle and Hannah lakes. Ontario Ministry of the Environment, Dorset, Ontario.

GIRARD, R. E., B. J. CLARK, N. D. YAN, R. A. REID, S. M. DAVID, R. INGRAM, AND J. D. FINDEIS. 2007. History of chemical, physiological and biological sampling methods, sampling locations and lake morphometry for the Dorset Environmental Science Centre (1973–2005). Technical Report Series 2006. Ontario Ministry of the Environment, Dorset, Ontario.

GREENAWAY, P. 1974. Total body calcium and haemolymph calcium concentrations in the crayfish *Austropotamobius pallipes* (Lereboullet). Journal of Experimental Biology 61:19–26.

GUIASU, R. C. 2007. Conservation and diversity of the crayfishes of the genus *Fallicambarus* Hobbs, 1969 (Decapoda, Cambaridae), with an emphasis on the status of *Fallicambarus foidens* (Cottle, 1863) in Canada. Crustaceana 80:207–223.

GUIASU, R. C., D. W. BARR, AND D. W. DUNHAM. 1996. Distribution and status of crayfishes of the genera *Cambarus* and *Fallicambarus* (Decapoda: Cambaridae) in Ontario, Canada. Journal of Crustacean Biology 16: 373–383.

HAMMOND, K. S., J. W. HOLLOWS, C. R. TOWNSEND, AND P. M. LOKMAN. 2006. Effects of temperature and water calcium concentration on growth, survival and moulting of freshwater crayfish, *Paranephrops zealandicus*. Aquaculture 251:271–279.

HAMR, P. 1998. Conservation status of Canadian freshwater crayfishes. World Wildlife Fund Canada, Toronto, Ontario.

HAMR, P. 2006. The distribution and conservation status of burrowing crayfishes *Fallicambarus fodiens* and *Cambarus diogenes* in Canada. Freshwater Crayfish 15:271–282.

HAMR, P., AND M. BERRILL. 1985. The life histories of north-temperate populations of the crayfish *Cambarus robustus* and *Cambarus bartonii*. Canadian Journal of Zoology 63: 2313–2322.

HEIN, C. L., M. J. VANDER ZANDEN, AND J. J. MAGNUSON. 2007. Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish. Freshwater Biology 52:1134–1146.

HILL, A. M., AND D. M. LODGE. 1995. Multitrophic-level impact of sublethal interactions between bass and omnivorous crayfish. Journal of the North American Benthological Society 14:306–314.

HOLDICH, D. M. (EDITOR). 2002. Biology of freshwater crayfish. Iowa State University Press, Ames, Iowa.

JEFFRIES, D. S., AND W. R. SNYDER. 1983. Geology and geochemistry of the Muskoka-Haliburton study area. Data Report DR 83/2. Ontario Ministry of Environment, Toronto, Ontario. (Available at: http://www.ene.gov.on.ca/en/contact/index.php)

JELKS, H. L., S. J. WALSH, N. M. BURKHEAD, S. CONTRERAS-BALDERAS, E. DIAZ-PARDO, D. A. HENDRICKSON, J. LYONS, N. E. MANDRAK, F. MCCORMICK, J. S. NELSON, S. P. PLATANIA, B. A. PORTER, C. B. RENAUD, J. J. SCHMITTER-SOTO, E. B. TAYLOR, AND M. L. WARREN. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 33(8):372–407.

JEZIORSKI, A., N. D. YAN, A. M. PATTERSON, A. M. DESELLAS, M. A. TURNER, D. S. JEFFRIES, B. KELLER, R. C. WEEBER, D. K. MCNICOL, M. E. PALMER, K. MCIVER, K. ARSENEAU, B. K. GINN, B. F. CUMMING, AND J. P. SMOL. 2008. The widespread threat of calcium decline in fresh waters. Science 322:1374–1377.

JIRAVANICHPAISAL, P., K. SODERHALL, AND I. SODERHALL. 2004. Effect of water temperature on the immune response and infectivity pattern of white spot syndrome virus (WWSV) in freshwater crayfish. Fish and Shellfish Immunology 17:265–275.

JONES, P. D., AND W. T. MOMOT. 1981. Crayfish productivity, allochthony and basin morphology. Canadian Journal of Fisheries and Aquatic Sciences 38:175–183.

KAUFMAN, S. D., E. SNUCINS, J. M. GUNN, AND W. SELINGER. 2009. Impacts of road access on lake trout (*Salvelinus namaycush*) populations: regional scale effects of over-exploitation and the introduction of smallmouth bass (*Micropterus dolomieu*). Canadian Journal of Fisheries and Aquatic Sciences 66:212–223.

KELLER, W., S. S. DIXIT, AND J. HENEBERRY. 2001. Calcium declines in northeastern Ontario lakes. Canadian Journal of Fisheries and Aquatic Sciences 58:2011–2020.

KELLER, W., J. H. HENEBERRY, AND S. S. DIXIT. 2003. Decreased acid deposition and the chemical recovery of Killarney, Ontario, lakes. Ambio 32:183–189.

MACRAE, P. S. D., AND D. A. JACKSON. 2001. The influence of smallmouth bass (*Micropterus dolomeiui*) predation and habitat complexity on the structure of littoral zone fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 58:342–351.

MALLEY, D. F., AND P. S. S. CHANG. 1985. Effects of aluminum and acid on calcium uptake by the crayfish *Orconectes virilis*. Archives of Environmental Contamination and Toxicology 14:739–747.

MASTER, L. L. 1991. Assessing threats and setting priorities for conservation. Conservation Biology 5:559–563.

MOLOT, L. A., AND P. J. DILLON. 2008. Long-term trends in catchment export and lake concentrations of base cations in the Dorset study area, central Ontario. Canadian Journal of Fisheries and Aquatic Sciences 65: 809–820.

MOMOT, W. T. 1995. Redefining the role of crayfish in aquatic ecosystems. Reviews in Fisheries Science 3:33–63.

MOMOT, W. T., H. GOWING, AND P. D. JONES. 1978. The dynamics of crayfish and their role in ecosystems. American Midland Naturalist 99:10–35.

NYSTROM, P., P. STENROTH, N. HOLMQVIST, O. BERGLUND, P. LARSSON, AND W. GRANELI. 2006. Crayfish in lakes and streams: individual and population responses to predation, productivity and substratum availability. Freshwater Biology 51:2096–2113.

RICHARDS, C., F. J. KUTKA, M. E. MCDONALD, G. W. MERRICK, AND P. W. DEVORE. 1996. Life history and temperature effects on catch of northern orconectid crayfish. Hydrobiology 319:111–118.

RUKKE, N. A. 2002. Effects of low calcium concentrations on two common freshwater crustaceans, *Gammarus lacustris* and *Astacus astacus*. Functional Ecology 16:357–366.

RUSAK, J. A., N. D. YAN, AND Y. M. SOMERS. 2008. Regional climatic drivers of synchronous zooplankton dynamics in north-temperate lakes. Canadian Journal of Fisheries and Aquatic Sciences 65:878–889.

SHARMA, S., AND D. A. JACKSON. 2008. Predicting smallmouth bass (*Micropterus dolomieu*) occurrence across North America under climate change: a comparison of

statistical approaches. Canadian Journal of Fisheries and Aquatic Sciences 65:471–481.

SOKAL, R., AND J. ROHLF. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Co., New York.

SOMERS, K. M., AND R. H. GREEN. 1993. Seasonal patterns in trap catches of the crayfish Cambarus bartonii and Orconectes virilis in six south-central Ontario lakes. Canadian Journal of Zoology 71:1136–1145.

SOMERS, K. M., R. A. REID, S. M. DAVID, AND R. I. INGRAM. 1996. Are the relative abundances of orconectid crayfish better indicators of water-quality changes than cambarid abundances? Freshwater Crayfish 11:249–265.

STEIN, R. 1977. Selective predation, optimal foraging, and the predator–prey interaction between fish and crayfish. Ecology 58:1237–1253.

STODDARD, J. L., D. S. JEFFRIES, A. LÜKEWILLE, T. A. CLAIR, P. J. DILLON, C. T. DRISCOLL, M. FORSIUS, M. JOHANNESSEN, J. S. KAHL, J. H. KELLOGG, A. KEMP, J. MANNIO, D. T. MONTEITH, P. S. MURDOCH, S. PATRICK, A. REBSDORF, B. L. SKJELKVÅLE, M. P. STAINTON, T. TRAAEN, H. VAN DAM, K. E. WEBSTER, J. WIETING, AND A. WILANDER. 1999. Regional trends in aquatic recovery from acidification in North America and Europe. Nature 401:575–578.

STUART, S. N., J. S. CHANSON, N. A. COX, B. E. YOUNG, A. S. L. RODRIGUES, D. L. FISCHMAN, AND R. W. WALLER. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

TAYLOR, C. A., G. A. SCHUSTER, J. E. COOPER, R. J. DISTEFANO, A. G. EVERSOLE, P. HAMR, H. H. HOBBS, H. W. ROBISON, C. E. SKELTON, AND R. F. THOMA. 2007. A reassessment of the conservation status of crayfishes of the United States and Canada after 10+ years of increased awareness. Fisheries 32(8):372–389.

TAYLOR, C. A., M. L. WARREN, J. F. FITZPATRICK, H. H. HOBBS, R. F. JEZERINAC, W. L. PFLIEGER, AND H. W. ROBISON. 1996. Conservation status of crayfishes of the United States and Canada. Fisheries 21(4):25–38.

TAYLOR, M. F. J., K. F. SUCKLING, AND J. J. RACHLINSKI. 2005. The effectiveness of the endangered species act: a quantitative analysis. BioScience 55:360–367.

TAYLOR, R. M., P. HAMR, AND A. KERSTAD. 2005. An illustrated guide to crayfishes. Chapter 10 in G. Winterton (editor). The comprehensive bait guide for eastern Canada, the Great Lakes region and northeastern United States. Bait Association of Ontario and Ontario Ministry of Natural Resources, University of Toronto Press, Toronto, Ontario.

VANDER ZANDEN, M. J., J. D. OLDEN, J. H. THORNE, AND N. E. MANDRAK. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecological Applications 14:132–148.

VENTER, O., N. N. BRODERU, L. NEMIROFF, B. BELLAND, I. J. DOLINSEK, AND J. W. A. GRANT. 2006. Threats to endangered species in Canada. BioScience 56:903–910.

WATMOUGH, S. A., AND J. AHERNE. 2008. Estimating calcium weathering rates and future lake calcium concentrations in the Muskoka-Haliburton region of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 65:821–833.

WATMOUGH, S. A., AND P. J. DILLON. 2003. Base cation and nitrogen budgets for seven forested catchments in central Ontario, 1983–1999. Forest Ecology and Management 177:155–177.

WILCOVE, D. S., D. ROTHSTEIN, J. DUBOW, A. PHILLIPS, AND E. LOSOS. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607–615.

WILLIAMS, J. E., J. E. JOHNSON, D. A. HENDRICKSON, W. CONTRERAS-BALDERAS, J. D. WILLIAMS, M. NAVARRO-MENDOZA, D. E. MCALLISTER, AND J. E. DEACON. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. Fisheries 14(6):2–20.

WILSON, K. A., J. J. MAGNUSON, D. M. LODGE, A. M. HILL, T. K. KRATZ, W. L. PERRY, AND T. V. WILLIS. 2004. A long-term rusty crayfish (Orconectes rusticus) invasion: dispersal patterns and community change in a north temperate lake. Canadian Journal of Fisheries and Aquatic Sciences 61:2255–2266.

YAN, N. D., A. M. PATERSON, K. M. SOMERS, AND W. A. SCHEIDER. 2008. An introduction to the Dorset special issue: transforming understanding of factors that regulate aquatic ecosystems on the southern Canadian Shield. Canadian Journal of Fisheries and Aquatic Sciences 65:781–785.

YANG, Y., R. A. MONSERUD, AND S. HUANG. 2004. An evaluation of diagnostic tests and their roles in validating forest biometric models. Canadian Journal of Forest Research 34:619–629.