

Response of fish communities in five north temperate lakes to exotic species and climate

Theodore V. Willis¹ and John J. Magnuson

Center for Limnology, University of Wisconsin-Madison, 680 N Park Street, Madison, Wisconsin 53706

Abstract

Exotic species invasions and climatic variation that occurred in north central Wisconsin provided the opportunity to contrast influences of climate and invasive species in shaping fish community dynamics in five Wisconsin lakes from 1981 to 2001. Year (passage of time) was positively correlated ($r > 0.9$) with invasive species. Year, invasive species, and climatic variables were the principal determinants of fish community dynamics according to redundancy analysis (RDA). The same invasive species negatively affected the same general group of species in different lakes; benthic invertivores declined in lakes invaded by crayfish, *Orconectes* spp., and pelagic zooplanktivores declined in lakes invaded by rainbow smelt, *Osmerus mordax*. *Micropterus dolomieu*, *Pimephales notatus*, and *Notropis volucellus* increased in abundance in lakes invaded by crayfish. When year was included in RDAs as a covariable (partial RDA), fish community changes in three lakes did not differ significantly from ordinations of Monte Carlo simulated data; for two lakes, growing season length and lake productivity were significant explanatory variables under the reduced model. The resulting shifts in the fish community might represent declines in those species that used resources similar to the invading crayfish and smelt or were eaten by the invading smelt. Subsequent community compensation might have occurred, with other species increasing in response to the declines in species affected directly by the invasive species.

Sala et al. (2000) identified climatic variation and biotic exchange as two of the most pervasive threats to biodiversity in freshwater lakes over the next century. However, until recently, documenting the ecological effects of biotic exchange has been far more tractable than documenting ecological effects of climate change. Predation, competition, and loss of habitat are often and readily documented effects of invasive species. For fish, classic case studies can be found in Lake Victoria, Africa, the Laurentian Great Lakes, and Panama (Zaret and Paine 1973; Gitay et al. 2001; Vanderploeg et al. 2002). Invasive species introduced either by accident or through fisheries management (Rahel 2002) often radically change the functioning of aquatic ecosystems; ripple effects created by the extirpation of native fish fauna include reduced ecosystem goods and services that affect resource users economically and culturally (Gitay et al. 2001).

Bridging the relationships between climatic variation and fish and fisheries has become more tenable in the last decade with the emergence of more long-term records and techniques. Long-term records of both climate and fisheries landings are the most readily available data combinations that demonstrate a response of fish to changing climate (Krovnin et al. 2001). Records for centuries of climate variation developed from lake core paleolimnology indicate that natural climate variation is a strong actor on lake productivity (Rusak et al. 2004; Smol et al. 2005) and fish life history (Finney et al. 2000). Evolving data sets from long established ecological programs in freshwater systems (e.g., Experimental Lakes Area, the English Lake District, Lake Washington, etc.) have made it possible to look across decades and consider multiple fish taxa when estimating how climate, invasive species, and anthropogenic influences affect the functions of freshwater ecosystems.

It is possible that the combination of climatic variation, now widely regarded as climate change, and invasive species will interact to exacerbate changes in fish species composition in freshwater lakes, especially in temperate and northern regions. The resulting marriage of novel invaders and climate could push lake ecosystems and fish communities in unexpected directions. Habitats in northern regions will become more susceptible to invaders as seasonal temperatures that prevented establishment of less cold adapted species become more moderate (Magnuson et al. 1997; Gitay et al. 2001). Warming could benefit native fishes, provided sufficient food resources exist to satisfy the energetic needs of natives and the additional demands that invaders place on ecosystems (Gitay et al. 2001). However, unexpected interactions between lake ecosystems and climate (e.g., higher water temperatures affecting composition and quality of primary producers, which ripples up the food web [Beisner et al. 1997]) might change the nature of competitive interactions between native and invasive fish

¹To whom correspondence should be addressed. Present address: Aquatic Systems Group, University of Southern Maine, 350 Commercial Street, Portland, Maine 04101 (theowillis06@aim.com).

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Table 1. Long-term summer (June, July, August) average physical and limnological characteristics of the NTL-LTER lakes calculated for the period 1981 and 2001. Values in parentheses are standard deviations.

	Allequash	Big Muskellunge	Crystal	Sparkling	Trout
Area (km ²)	1.68	3.96	0.37	.64	16.1
Mean depth (m)	2.9	7.5	10.4	10.9	14.6
Max depth (m)	8	21.3	20.4	20	35.7
Fish diversity with/without rare species	38/30	30/23	24/16	28/22	40/35
Epilimnetic temp (°C)	21.0(1.0)	20.7(0.9)	20.5(1.0)	20.6(0.9)	19.7(1.1)
Avg Secchi depth (m)	3.6(0.5)	7.8(1.1)	8.7(1.0)	7.1(0.9)	5.4(0.6)
No. of days ice free	212(15)	220(17)	222(15)	224(15)	226(16)
Chl <i>a</i> (µg L ⁻¹)	11.7(4.5)	2.7(0.9)	2.5(0.9)	3.8(1.3)	2.9(0.6)
NO ₃ NO ₂ (µg L ⁻¹)	3.0(2.2)	10.0(5.8)	2.9(1.9)	5.7(6.4)	34.6(15.5)
Total P (µg L ⁻¹)	19.7(9.8)	10.1(4.5)	3.1(1.8)	6.1(3.2)	4.5(2.6)
Alkalinity (µeq L ⁻¹)	917(77)	410(26)	26(12)	625(37)	838(30)

temp, Temperature; avg, average.

species. Outcomes of novel invasive introductions are generally unpredictable, but additional factors unrelated to internal (intrinsic) lake processes, like climatic variation (extrinsic process), could even alter the established effects of known invaders.

Multidecadal data sets collected over several generations of variation for most species provide new opportunities to observe changes in diversity and species composition lagged over generations. Long-term studies have taken advantage of natural variability, climatic variability, anthropogenic perturbations, and environmental manipulations to advance our understanding of ecology (Greenland and Kittel 2002; Kratz et al. 2003). The North Temperate Lakes Long-Term Ecological Research project (NTL-LTER) is focused on seven northern Wisconsin and four southern Wisconsin lakes and their surrounding landscapes (Magnuson et al. 2006a). The charge of the program is to address how biophysical setting, climate, and changing land use and cover interact to shape lake characteristics and dynamics over time. Our objective was to explore coherent changes in the fish communities of five north temperate lakes against a background of fish invasions, crayfish invasions, and fluctuating lake temperatures. In particular, we examined the benthic invertebrate guild for evidence of species compensation (i.e., changes in species composition) to maintain ecosystem properties such as production or biomass (Ernest and Brown 2001).

We expected that:

1. Fish community composition of invaded lakes would change significantly through time.
2. Fish communities in invaded lakes would respond to changes in invasive species abundance, whereas fish communities in lakes that were not invaded would respond more strongly to climatic variability, including, in this time series, drought and the Mt. Pinatubo eruption. Presumably, fish community response in invaded lakes would provide evidence through correlations for the influence of ecological processes associated with the invaders, such as competition, predation, and habitat modification.

3. Benthic fish species documented to be negatively influenced by *Orconectes* spp. would decline, and species with less resource overlap with crayfish would increase.

Material and methods

Database—The NTL-LTER program began in 1981 (Magnuson et al. 2006a). The five lakes we studied are primary research lakes of the NTL-LTER program and are located within 6 km of each other in Vilas County, Wisconsin (centered at 46.01823°N, 89.67918°W). The lakes are embedded in a glacial outwash plain of granitic sand, poor in calcium. Thus, those lakes high in the groundwater flow system have low alkalinity, nutrient, and chlorophyll levels. Two of the primary lakes are dystrophic and are not included in this study because each contains only one fish species. The other five lakes range from mesotrophic (Trout, Allequash) to oligotrophic (Crystal), with average summer Secchi depths from 4 to 9 m. Trout Lake is the largest at 16.1 km² and 14.6 m mean depth, and Crystal Lake is the smallest with an area of 0.37 km² and 10.4 m mean depth (Table 1). All five are thermally stratified in summer and ice covered in winter. The average open water period is about 220 d.

Fish in the NTL-LTER lakes are sampled once per year in July or August on the same date (± 1 week). Fish are collected with six gear types over a 2-d period per lake. On each of the two sampling days, three 33-m beach seine hauls (12 m long, 3.2 mm stretch mesh) were made at three sites (changed to two hauls per site after 1996); five modified wire mesh minnow traps (6.4 mm mesh and 7.6 cm opening, baited with 120 g of beef liver) were set for crayfish at three sites (changed to three traps per site after 1996); one fyke net (7 mm delta stretch mesh nylon) was set in 1 m of water at three sites; one trammel net was set at one site on the bottom and extended across the thermocline; and seven vertical monofilament gillnets (19, 25, 32, 38, 51, 64, and 81 mm stretched mesh) were set from surface to bottom at the deepest location in the lake. In addition, four ~ 300 -m, 30-min electroshock transects (changed to a total of three transects per lake after 1996)

were made. Starting in 1997, sampling effort was decreased to reduce operating costs of the fish sampling program. Before making this change, the existing data were analyzed for recurring bias on central tendencies with and without the proposed changes to the existing data. Variability increased, but no directional biases in central tendency were detected (B. Benson pers. comm.). For more information on sampling methods, gear specifications, and protocols, see Willis (2003) and the fish sampling section of the NTL-LTER website (<http://lterquery.limnology.wisc.edu>).

Here we present the NTL-LTER fish data as time series of index values. The index values are calculated as the sum of the average catch per set (or haul for night beach seines) from each of the six gear types used in any lake. The time series of index values, or annual catch per unit effort (CPUE), represents change through time in the abundance of a species relative to other years in that lake. All of the individual species index values taken together are a description of the fish community in that year. Index values were $\log(y + 1)$ transformed. "Rare" species were defined as those occurring in only 1 yr between 1981 and 2001, and they were omitted from the analysis. Although gear manufacturer and materials occasionally changed over the 21 yr of sampling, we made no additional corrections to account for these variations.

We combined the six gear types to obtain a robust annual estimate of species composition in the NTL-LTER lakes. The suite of gear chosen was designed to sample all major fish habitats and all life stages (sizes) of fish. Weaver et al. (1993) and Jackson and Harvey (1997) both indicated that a wide variety of gear types improved the characterization of the fish community. Replicate sets of the same gear were built into the protocol to compensate for the high variability in species and abundance observed between sets and sites (Benson and Magnuson 1992). Benson and Magnuson (1992) found significant and meaningful differences among sets at a site, sites in a lake, and lakes.

Environmental variables—The NTL-LTER collected a rich array of data on physical, chemical, and biotic variables (Magnuson et al. 2006a). For our study, we considered the number of ice-free days (open), Secchi depth (secchi, m), filtered total P (P, $\mu\text{g L}^{-1}$), NO_2NO_3 (N, $\mu\text{g L}^{-1}$), and the average annual summer (days of the year 151–243) oxygen stress temperature (temp, $^{\circ}\text{C}$) as potential explanatory variables. Oxygen stress temperature is the temperature at the depth in the water column where dissolved oxygen falls below 4 mg L^{-1} saturation; below this depth, some fish species would begin to experience oxygen stress. If the oxygen stress temperature is higher (i.e., O_2 saturation falls below 4 mg L^{-1} at a shallower depth), less habitat should be available to cold water species such as lake trout, cisco, and rainbow smelt. Environmental variables were transformed to best approximate normality if necessary; environmental variables were evaluated by lake and included untransformed (Secchi, open, year, temp), square root (N, P, secchi, open), cube root (smelt, crayfish), natural log (N, P), and log (N, P, smelt) data.

We included the abundances of *Orconectes* crayfish and rainbow smelt (*Osmerus mordax*) as the environmental variables for invaders. All lakes, except Crystal, initially contained the native crayfish *Osmerus virilis*. The crayfish *Osmerus propinquus* arrived in the Trout Lake region ca. 1950, possibly as a range expansion from southern Wisconsin (Horns and Magnuson 1981). *Osmerus rusticus*, a widespread invasive crayfish native to the Ohio valley (Lodge et al. 2000), was first detected in Trout Lake in 1979 (Lodge et al. 1986). *O. rusticus* first appeared in the NTL-LTER fish sampling in 1982 (Fig. 1a) and in 1988 became the most abundant crayfish in Trout Lake. Sparkling Lake has had consistently detectable populations of *O. rusticus*, *O. propinquus*, and *O. virilis* since 1981, with *O. rusticus* as the numerical dominant (Fig. 1b). *O. rusticus* are not present in Big Muskellunge Lake, but *O. propinquus* has been present in the lake for the duration of our records and became numerically dominant over *O. virilis* in 1991 (Fig. 1c). Allequash Lake, which has been dominated by *O. propinquus* since the start of NTL-LTER record, has a small population of crayfish relative to the other lakes (Fig. 1d). We combined *O. rusticus* and *O. propinquus* relative abundance into a single metric of invasive crayfish CPUE. The invasive crayfish CPUE consists entirely of *O. propinquus* for Big Muskellunge and Allequash Lakes and almost entirely of *O. rusticus* in Trout Lake since about 1990.

Rainbow smelt are native to the eastern seaboard of North America, where they exist in both land-locked and anadromous populations (Franzin et al. 1994). As early as 1912, rainbow smelt were purposefully introduced into Crystal Lake, Michigan, and soon spread from there into the upper Laurentian Great Lakes. They have since spread to many inland lakes (Evans and Loftus 1987). Rainbow smelt were first detected in Sparkling Lake in 1982 (Fig. 1e) and replaced cisco as the numerically dominant zooplanktivore by 1985 (Hrabik et al. 1998). Rainbow smelt were first detected in Crystal Lake in 1985 (Fig. 1f).

Multivariate fish community analyses—The unconstrained variation in each species \times year matrix was estimated with principal components analysis (PCA); the constrained variation was estimated with redundancy analysis. Each lake was considered a separate data set; years constituted samples or sites. Redundancy analysis (RDA) is the equivalent of a canonical correspondence analysis (CCA) but is specifically designed for data sets believed to have linear relationships between the species \times site and environmental matrices. An RDA is similar to a CCA in that the ordination is constrained by the environmental variables and addresses the question of how sites and species separate on gradients of environmental variables; the appropriateness of the environmental variables chosen determines to a large degree how much variation can be explained by the ordination. An RDA is more appropriate for a data set if the standard deviation of species turnover (SD units) on the first axis of a detrended correspondence analysis (DCA) is <2 . Gradient lengths for our data of 1.1–1.9 indicated that RDA was appropriate (Gauch 1982). We used Canoco 4 for DCA, PCA, and RDA analyses (Ter Brakk 1998).

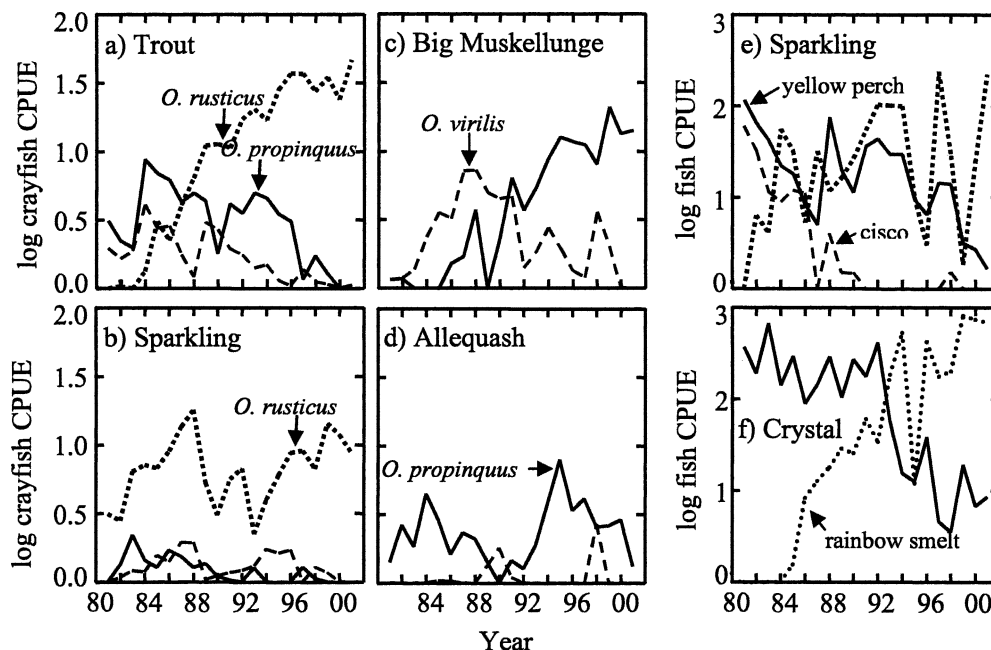


Fig. 1. (a–d) Time series between 1981 and 2001 of abundance of invading rusty crayfish *O. rusticus* (dotted line) and (e–f) invading rainbow smelt (dotted line) in five NTL-LTER research lakes. Graphs also show changes in the abundance of *O. virilis* (dashed line, panels a–d), *O. propinquus* (solid line, panels a–d), cisco (dashed line, panel e), and yellow perch (solid line, panels e–f).

Environmental and species gradients were represented in RDA triplot figures as vectors; vector length is proportional to the strength of the gradient (i.e., the correlation between species abundance and environmental variables and years). By projecting species onto a vector representing an environmental variable, those species can be ranked on that quantitative environmental gradient (Legendre and Legendre 1998). Thus, species or years on the same side of a plot as a gradient vector had high(er) values for that environmental variable, whereas species or years perpendicular to a gradient vector had weaker values. Environmental vector lengths are calculated as $\text{vector} = (a^2 + b^2)^{1/2}$, where a is an environmental variable score of RDA axis 1 and b is an environmental variable score of RDA axis 2. To provide a cut-off value to establish the stronger relationships, we considered a vector length >0.34 significant at $p < 0.05$ ($n = 21$); this value equals $(0.24^2 + 0.24^2)^{1/2}$, where 0.24 is the single-axis RDA score equivalent to a significant Pearson correlation coefficient.

Year sampled (i.e., 1981–2001) was included as an environmental variable in the first ordination analysis and as a covariable in a second analysis. Crayfish and smelt environmental variables, in particular, correlated strongly with year. For lakes in which year was a significant factor, a partial RDA was run with year as a covariable or dummy variable. The resulting values were similar to detrending both the environmental and species time series. Graphically, including year as a covariable shortened the vector of an environmental or species gradient in proportion to the variation shared with the variable year (Ter Brakk and Smilauer 1998). Partial RDAs with nonsignificant Monte Carlo simulations ($p > 0.05$, $n = 9,999$) were not reported.

Within-lake community analysis: Kendall's W—We used Kendall's coefficient of community concordance (W) to test whether environmental gradients, species gradients, or fish communities were similar either across lakes or between years within a lake. W is calculated by comparing rankings of attributes (environmental variables or species abundances) between lakes or years. The W statistic ranges from 0 (no concordance) to 1 (perfect concordance). However, because Kendall's W is sensitive to the number of species included in the analysis (Grossman et al. 1990), we removed species that occurred in only 1 yr or made up $<5\%$ of the catch across all 21 yr.

Species compensation analysis: Variance ratio—We used variance ratios (Klug et al. 2000) to evaluate abundance relationships between species through time. If covariances between two species were 0 (the variance ratio = 1), species varied independently among years. If the variance ratio was <1 , species covaried negatively, and if their variance ratio was >1 , species covaried positively (Klug et al. 2000; Vinebrooke et al. 2003). Negative covariance between two species suggests that increases in species A compensates for declines in species B, provided those species are ecologically related, usually as prey and predator or as competitors (Frost et al. 1995). However, species with negative covariance could be responding to changes in environmental conditions or some other unmeasured occurrence (Klug et al. 2000).

We focused on compensatory dynamics within the benthic invertivore guild (organisms that eat benthic insects and other bottom-dwelling aquatic invertebrates) because increases in *Orconectes* spp. abundance occurred in several

lakes (i.e., Trout, Sparkling, and Big Muskellunge Lakes) and thus could be used to evaluate stability of this guild after addition of another member. Several studies have found that outside of their native range, rusty crayfish have strong negative effects on several families of benthic macroinvertebrates (for a review, see McCarthy et al. 2006); this includes two long-term studies from the NTL-LTER site (Wilson et al. 2004; McCarthy et al. 2006). A similar analysis was not done for the rainbow smelt invasions in Crystal and Sparkling Lakes and the zooplanktivore guild because the two lakes had only a few pelagic zooplanktivores and differed in species present and crayfish abundance. We chose the 10 species of benthic invertivore, both facultative and obligate, with the highest rank sum species scores—bluegill, bluntnose minnow, common shiner, mimic shiner, mottled sculpin, pumpkinseed, rock bass, smallmouth bass, and white sucker—for pairwise analysis of compensatory dynamics. These species were present and in many cases relatively common in these three lakes for some period of time (Willis 2003).

The variance ratios for species pairs were calculated from total CPUE (see Frost et al. 1995) within a lake rather than from biomass, as is often done in variance ratio analyses. The statistical significance of pairwise variance ratios was evaluated by Monte Carlo simulations of species abundance. Catches of individual species were randomized with replacement to simulate 999 time series for each species in each lake. Variance ratios were recalculated from these simulated data, and the distributions were used to determine whether the variance ratios calculated from real data were in the tails of the distribution ($95\% < x < 5\%$).

Results

Principal components analysis of each NTL-LTER lake's fish community explained 52% to 78% of the variation among years in the first two multivariate axes. Variation explained was 78% for Crystal Lake, 71% for Sparkling Lake, 64% for Big Muskellunge Lake, 54% for Allequash Lake, and 52% for Trout Lake. Redundancy analysis produced ordinations significantly different from random for all five lakes when year was included as a variable. The most variation was accounted for in Sparkling Lake (62%) and the least in Allequash Lake (39%). Partitioning out the effects of year by including year as a covariable in partial RDAs resulted in nonsignificant ordinations for Allequash, Crystal, and Sparkling Lakes, in part by removing the primary variation, lag-one autocorrelation, in some species and environmental variables. However, the partial RDAs for Trout and Big Muskellunge Lakes accounted for 22% and 28% of the variation in the first two axes, respectively, demonstrating additional variation underlying the variation identified by the full RDAs.

Environmental gradients—Year was the highest ranked variable for all ordinations (Table 2). Pearson correlations with the first RDA axis ranged from $r = 0.67$ to 0.93 . For Big Muskellunge, Crystal, and Trout Lakes, correlations between year and crayfish or smelt were high ($r > 0.9$). For

Allequash Lake, year correlated significantly with total phosphorous ($r = 0.56$, $p < 0.05$). The similarity in rank order of environmental variables between lakes was moderate to weak, but significant ($W = 0.44$, $p < 0.05$, $n = 7$; Table 2). When year was a covariable, similarity in environmental variable rank order was weak and nonsignificant ($W = 0.14$, $p > 0.05$, $n = 6$). Thus, when year was included as an environmental variable in the ordinations, it was the most important variable across lakes, followed by invasive species abundance and then the number of days open. Fish communities in each lake appeared to respond to different environmental actors, but most notably those representing invasive species abundances, nutrient levels, and the climatic variables. However, we cannot emphasize enough that what mathematically was lag-one autocorrelation was an important component of the trendlike changes in both native and invasive species. The rather steady increase in crayfish over the time series equaled fewer pumpkinseed, more minnows, and more smallmouth bass. These changes were real and became more pronounced through time; this suggests a suite of complex but related interactions.

Species gradients—Overall, fish communities within a lake were not independent among years; the W statistic was significant at $p < 0.01$ for all lakes. Community concordance among years was strong in Allequash Lake ($W = 0.79$); moderate in Big Muskellunge ($W = 0.66$), Trout ($W = 0.73$), and Sparkling Lakes ($W = 0.64$); and moderate to weak in Crystal Lake ($W = 0.43$).

Some fishes exhibited significant changes in abundance through time across all lakes, indicating responses to regional conditions affecting all lakes like climatic variability. Lake-specific factors like species invasion should only have influenced the invaded lakes. Bluntnose minnow, smallmouth bass, mimic shiner, and largemouth bass increased in at least four lakes, whereas white sucker declined in four lakes (Table 3). The RDA plot (year as a variable) for Big Muskellunge Lake did not indicate significant declines in white sucker abundance (Fig. 2a), despite a crayfish invasion in that lake by *O. propinquus* (not *O. rusticus*); white sucker did decline in Allequash Lake (Fig. 3), a lake we described as free of invasion.

Other fishes did not show a consistent response across multiple lakes and thus might have responded to changes in lake-specific conditions. Pumpkinseed increased in Sparkling Lake despite the invasion of *O. rusticus* but declined precipitously in Trout Lake. Yellow perch exhibited significant species gradients among years in all five lakes, but in Allequash (Fig. 3), Big Muskellunge (Fig. 2a), and Trout Lakes (Fig. 4a), they increased, whereas in Crystal (Fig. 5) and Sparkling Lakes (Fig. 6), they decreased. The two lakes with decreasing yellow perch both had rainbow smelt invasions (Table 3), whereas the three that exhibited increases in perch did not.

Overall, detrending the data with the use of a time dummy variable (year covariable) in a partial RDA was an effective procedure for evaluating the influence of temporal autocorrelation. However, even relatively obvious and informative patterns, like those in Crystal Lake, were lost

Table 2. Vector lengths for environmental variables from RDA and ranks of environmental variables for RDAs and partial RDAs (year covariable). Values in parentheses are vectors for the partial RDA. Lower panels are ranks of individual environmental variables ordered by rank sum across the five lakes ranging from 7 (strong correlation) to 1 (weak correlation). Kendall's coefficient of concordance (W) indicated that lakes were similarly influenced by the environmental variables when year was included in the full RDA; however, when year was treated as a covariable, lakes were not similarly influenced by the remaining environmental variables. Significant vectors at $p < 0.05$ are indicated with an asterisk.

Vector	Allequash	Big Muskellunge	Crystal	Sparkling	Trout	Rank sum
Vector length						
Crayfish	0.37*	0.68*(0.18)	—	0.46*	0.62*(0.11)	
Days open	0.51*	0.35*(0.27)	0.36*	0.38*	0.26(0.40*)	
NO ₃ NO ₂	0.27	0.21(0.43*)	0.32	0.24	0.34*(0.38*)	
O ₂ stress temperature	0.36*	0.28(0.31)	0.51*	0.18	0.23(0.39*)	
Secchi	0.28	0.35*(0.37*)	0.25	0.38*	0.13(0.13)	
Smelt	—	—	0.72*	0.43*	—	
Year	0.64*	0.78*	0.76*	0.81*	0.64*	
Total P	0.40*	0.43*(0.20)	0.17	0.27	0.33(0.14)	
Rank of RDA ($W=0.44$; $p<0.05$)						
Year	7	7	7	7	7	35
Invaders	4	6	6	6	6	28
Days open	6	3	4	4	3	20
Total P	5	5	1	3	4	18
Secchi	2	4	2	5	1	14
O ₂ stress temperature	3	2	5	1	2	13
NO ₃ NO ₂	1	1	3	2	5	12
Rank of partial RDA, year covariable ($W=0.14$, $p>0.05$)						
Days open	5	3	4	5	6	23
NO ₃ NO ₂	1	6	5	4	4	20
Invaders	4	1	6	6	1	18
Secchi	6	5	1	2	2	16
O ₂ stress temperature	2	4	2	1	5	14
Total P	3	2	3	3	3	14

when variation associated with year was removed from the analysis. Environmental structure underlying the temporal changes in Big Muskellunge and Trout Lakes appeared significant. Removing the variation associated with year produced RDAs that accounted for only 29% of the 64% of explainable variation in fish communities in Big Muskellunge Lake and only 24% of the 52% in Trout Lake. Years were arranged on nutrient and productivity gradients in Big Muskellunge Lake (Table 2; Fig. 2b) and on climatic and nutrient gradients in Trout Lake (Table 2; Fig. 4b). In Big Muskellunge Lake, mimic shiner increased in years with higher nitrogen concentrations and yellow perch in years with larger phytoplankton blooms (low Secchi depths). Conversely, cisco increases occurred in less productive years. In Trout Lake, cisco and lake whitefish were more abundant when oxygen stress levels occurred deeper in the water column, whereas mimic shiner and bluntnose minnow were more abundant in years when less oxygenated habitat was available below the 4 mg L⁻¹ O₂ level. Smallmouth bass, pumpkinseed, and yellow perch were more abundant in years with high summer nitrogen and a longer ice-free season.

Species compensation—Variance ratios < 1 helped infer which fish species might be replacing other fishes that had declined in abundance through time. Five species pairs in Trout Lake and four species pairs in both Big Muskellunge and Sparkling Lakes had significant variance ratios < 1 ,

indicating the possibility of species compensation (Table 4). In Trout Lake, mimic shiner covaried negatively with declining bluegill, pumpkinseed, and rock bass populations; smallmouth bass covaried negatively with declining white sucker; and common shiner covaried negatively with declining pumpkinseed. In Big Muskellunge Lake, both bluntnose minnow and smallmouth bass covaried negatively with declining bluegill and pumpkinseed populations. In Sparkling Lake, a declining white sucker population covaried negatively with increasing pumpkinseed, smallmouth bass, and rock bass populations; smallmouth bass also covaried negatively with a declining yellow perch population.

Discussion

We asked whether fish community composition had changed significantly over two decades in a suite of LTER lakes in northern Wisconsin. Multivariate analysis indicated that one or more species that were common in the early 1980s became less common by 2001. Redundancy analysis produced statistically significant ordinations in which the passage of time and invasive species abundance, either rainbow smelt or *Orconectes* spp., produced the strongest gradients for Big Muskellunge, Crystal, Sparkling, and Trout Lakes. Allequash Lake, which we classified as “uninvaded,” also had significant year, days open, and *Orconectes* spp. gradients, but no fish species had

Table 3. Fish species vector length and rank sum table determined from RDA. Larger values indicate stronger species gradients in a lake's RDA plot and thus a stronger role that species might play in determining fish community dynamics. Values in parentheses are from a temporally detrended partial RDA (year sampled as a covariable); partial RDA results shown were significantly different from a distribution of randomly sorted solutions. A dash means the species was not present in that lake. Rank sum scores, calculated by ranking RDA vector lengths, provide an indication of a species' importance in determining the fish community dynamics of the lake set as a whole.

Species	Species code	Allequash	Big Muskellunge	Crystal	Sparkling	Trout	Rank sum
Yellow perch	YP	1.09	2.62(2.72)	2.15	1.82	1.13(1.17)	112.0
Bluntnose minnow	BM	2.03	1.44(0.56)	0.28	0.55	1.71(0.68)	109.0
Bluegill	BG	0.64	1.62(0.49)	2.08	0.23	1.47(1.34)	97.0
Pumpkinseed	PS	0.25	1.87(0.38)	0.54	0.82	1.20(1.11)	95.0
Smallmouth bass	SMB	1.43	1.14(1.01)	0.16	1.65	0.46(0.73)	93.0
Mimic shiner	MS	0.40	1.65(1.85)	—	2.54	3.36(2.79)	92.5
Walleye	WI	1.65	0.76(0.83)	—	1.00	1.18(0.47)	90.5
Largemouth bass	LMB	1.09	0.54	2.30	0.51	0.42	86.0
Cisco	CI	—	0.86(1.59)	—	2.06	1.47(1.45)	77.5
White sucker	WS	0.56	0.26	0.41	1.22	0.35	76.0
Common shiner	CS	1.13	0.13	0.03	—	1.88(1.95)	72.0
Rock bass	RB	0.71	0.07	0.25	0.45	0.49(0.51)	67.0
Yellow bullhead	YB	0.98	1.36	0.82	—	0.04	67.0
Log perch	LP	0.45	0.69(0.43)	—	0.70	0.49(0.52)	66.5
Johnny darter	JD	1.22	0.21	—	0.10	0.53	62.5
Golden shiner	GS	1.65	0.25	—	0.20	0.34	61.5
Black crappie	BC	1.83	0.29	0.02	—	0.05	61.0
Blacknose shiner	BNS	0.43	0.28(0.35)	—	0.26	0.09	50.5
Northern pike	NP	1.09	0.40	—	0.04	0.03	50.5
Lake trout	LT	—	—	0.38	—	0.98(0.84)	46.5
Mottled sculpin	MTS	0.10	0.15	—	0.06	0.54(0.48)	45.5
Muskellunge	MY	0.47	0.10	—	0.13	0.05	42.5
Trout perch	TP	—	—	—	—	1.14(1.04)	36.0
Burbot	BT	—	0.34	—	0.06	—	35.5
Lake whitefish	LW	—	—	—	—	0.63(0.73)	33.0
Shorthead redhorse	SHR	0.40	—	—	—	0.21	29.0

statistically significant negative correlations with year or crayfish. Relatively common fish species responded to increasing invader abundance, but only in Crystal Lake were the resulting community changes significant according to Kendall's coefficient of concordance. However, at least one common species in each lake (yellow perch in Crystal Lake, cisco in Sparkling Lake, and bluegill in Trout and Big Muskellunge Lakes) declined and was related strongly to gradients of increasing invasive species and time. Increases in the abundance of other species (mimic shiner and bluntnose minnow in Big Muskellunge, Sparkling, and Trout Lakes and smallmouth bass in Sparkling and Big Muskellunge Lakes) correlated significantly and positively with invasive species abundances that increased through time.

An unexpected pattern in this dataset was the observation of cyprinid relative abundance increasing along with that of their predators. This pattern is counterintuitive because piscivores are well documented as a cause of local extinctions of cyprinids (Findlay et al. 2000; Jackson and Mandrak 2002). Several explanations could account for these patterns. First, increased refugia for prey can result in increased prey abundance, as has been observed, for example, in benthic communities associated with zebra mussel beds in the Laurentian Great Lakes (Mayer et al. 2002). However, refugia increases were not likely in our lakes. Crayfish-invaded lakes showed declines in macro-

phyte biomass and species richness (Wilson et al. 2004), and it is unlikely that coarse woody habitat, another source of prey fish refugia, increased during the study period (Schindler et al. 2000). Second, cyprinids might have experienced an increase in prey availability and subsequent population growth that offset predation. Declines in large-bodied benthic invertivorous fishes (bluegill, rock bass, and white sucker) could have increased the prey available to generalist cyprinids. However, increasing crayfish populations in Trout and Sparkling Lakes were associated with declining abundances of amphipods, trichopterans, and odonates during the same time period (Wilson et al. 2004; Mccarthy et al. 2006; Wilson and Hrabik 2006); presumably similar changes in the benthic invertebrate community happened in the other crayfish-invaded lakes. Third, and perhaps most likely, cyprinids might not have been a preferred prey item in lakes in which crayfish were abundant. When present, crayfish make up the majority of smallmouth bass and rock bass diets (Dorn and Mittelbach 1999; Hein et al. 2006), with small fish increasing in importance as crayfish become less available (Hein et al. 2006). In addition, overall predation pressure on cyprinids might have been reduced with the decline of small-gape centrarchids that consume larvae of these cyprinid species (Becker 1983).

Species compensation appears to have occurred within the benthic invertivore guild, with increased abundances of

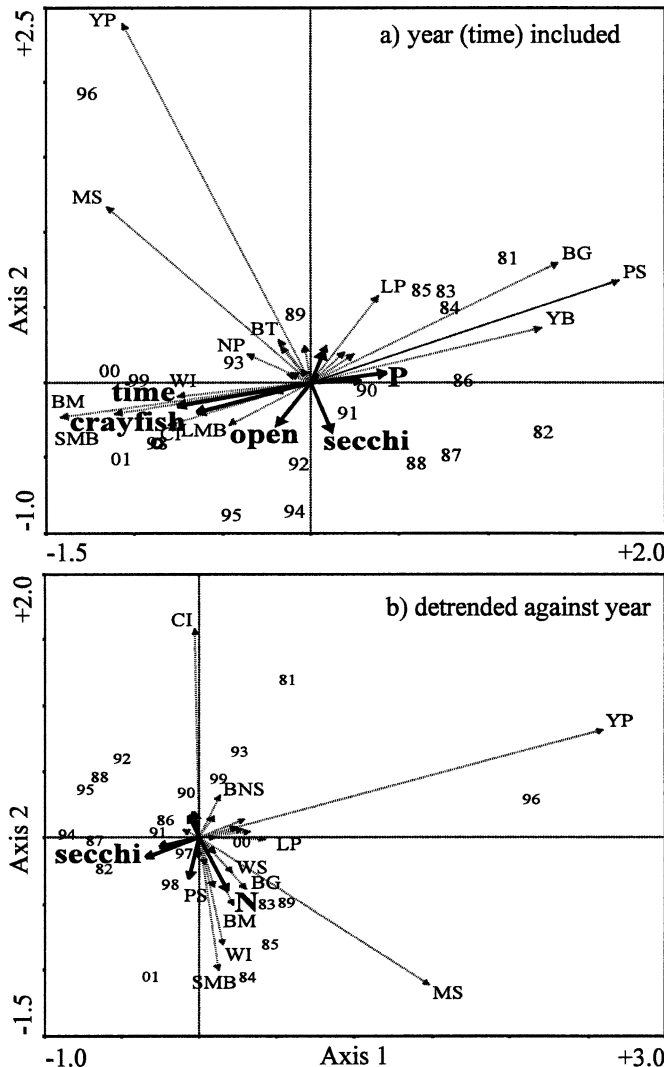


Fig. 2. Big Muskellunge Lake RDA in three element plots (triplot) showing the ordination of the fish community by years with respect to influences of environmental gradients (bold line and type); species gradients are also shown. (a) Ordination with year (synonymous with time on figure) included in the environmental matrix as an explanatory variable; axis 1 eigenvalue = 0.4, axis 2 eigenvalue = 0.16, Monte Carlo distribution $p = 0.0001$. (b) Ordination with year excluded from the environmental matrix and included in the partial RDA as a detrending covariable; axis 1 eigenvalue = 0.18, axis 2 eigenvalue = 0.1, Monte Carlo distribution $p = 0.0001$. Longer lines indicate that an environmental variable has a stronger gradient and more influence on the fish community in years that lie along that gradient. The further from the origin a year is along a gradient the stronger the influence of the gradient on the fish community in that year. For clarity, only vectors longer than 0.43 ($p < 0.05$) are labeled on the graph. For species codes, see Table 3.

cyprinid generalists compensating for declines in benthivorous fishes that occurred in response to the increases in crayfish. Negative pairwise variance ratios suggest that increases in bluntnose minnow and mimic shiner compensated for declines in bluegill, pumpkinseed, and rock bass, whereas increases in smallmouth bass compensated for declines in white sucker, bluegill, and pumpkinseed.

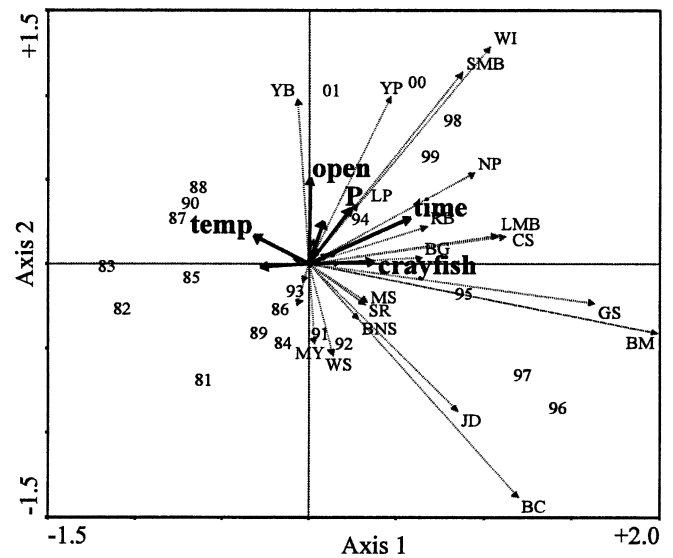


Fig. 3. Allequash Lake RDA triplot. Labels for species and environmental variables with vectors < 0.43 have been omitted from the graph for clarity. Ordination with year (synonymous with time on figure) included in the environmental matrix as an explanatory variable only; axis 1 eigenvalue = 0.27, axis 2 eigenvalue = 0.09, Monte Carlo distribution $p = 0.006$ (shown). Ordination with year excluded from the environmental matrix and included in the partial RDA as a detrending covariable was not significant; axis 1 eigenvalue = 0.15, axis 2 eigenvalue = 0.07, Monte Carlo distribution $p = 0.16$. For species codes, see Table 3. Environmental gradients are in bold arrows and type.

Increases in *O. rusticus* and *O. propinquus* between 1981 and 2001 would have represented large increases in the biomass of organisms obtaining energy from the benthic invertebrates in Trout, Big Muskellunge, and Sparkling Lakes. When grouped into the same feeding guild, declines in white sucker, log perch, mottled sculpin, bluegill, and pumpkinseed, alongside dramatic increases in crayfish, could be viewed as maintenance of the benthic invertivore guild at a supportable biomass. Compensatory dynamics have been documented by other researchers in guilds and communities of organisms under extrinsic stress (Tilman 1996; Klug et al. 2000; Ernest and Brown 2001). Compensatory dynamics in fishes is not well documented as an explicit phenomenon (but see Vinebrooke et al. 2003), but population expansion and retraction related to changes in niche space, often as a result of competition through invasion, are replete in the fish literature and hint at species compensation. For example, *Coregonus* spp. in the Laurentian Great Lakes declined in the presence of invasive/exotic rainbow smelt and alewife (Madenjian et al. 2002; Dobiesz et al. 2005), especially when smelt and alewife experienced reduced predation from piscivores. Whole-lake manipulations that increased predation pressure on invaders resulted in apparent drops in exotic planktivores and expansion of *Coregonus* spp. populations (Dobiesz et al. 2005; Krueger and Hrabik 2005). The estimation of biomass and consumption of the benthic invertivore guild and crayfish over time is beyond the scope of this paper. However, we do propose this as an intriguing topic for future research.

Table 4. Variance ratios calculated from pairwise comparison of a subset of benthic insectivorous fish species in Trout, Big Muskellunge, and Sparkling Lakes. Fish species chosen were present in all three lakes and were the 10 highest ranked benthic insectivorous species from Table 3. See Web Appendix 1, http://www.aslo.org/lo/toc/vol_51/issue_6/2808al.pdf, for specific names and Table 3 for species codes to common names. Variance ratios followed by an asterisk were significant at $0.05 > p > 0.95$ on the basis of within-species, among-year Monte Carlo simulations of fish abundance ($n = 999$). Values significantly < 1.0 indicated that a species pair responded inversely to a common stimulus or each other, possibly resulting in species compensation.

Species code	BM	BG	WS	MS	PS	MTS	SMB	CS	RB	YP
Trout Lake										
BG	0.93									
WS	0.99	1.18								
MS	1.15	0.97*	0.99							
PS	0.98	0.97	0.76	0.99*						
MTS	0.99	1.13*	1.31*	1.00	0.98					
SMB	0.95	0.92	0.72*	0.99	1.28	0.97				
CS	0.95	0.99	0.96	0.99	0.69*	0.98	0.86			
RB	0.93	1.24	1.04	0.98*	1.06	1.02	0.91	1.64*		
YP	0.99	0.96	1.01	0.93	1.00	1.00	1.05	0.98	0.98	
Big Muskellunge Lake										
BG	0.51*									
WS	1.11	1.09								
MS	1.11	0.96	1.02							
PS	0.49*	1.70*	1.10	0.94						
MTS	1.02	0.99	0.99	1.00	0.99					
SMB	1.65*	0.71*	1.03	1.19*	0.58*	1.01				
CS	0.99	0.98	0.97	1.00	0.98	0.95	1.00			
RB	0.91	1.22	1.02	1.08*	1.05	0.99	1.01	1.01		
YP	1.00	1.00	1.00	1.06	1.00	1.00	1.00	1.00	1.00	1.00
Sparkling Lake										
BG	1.01									
WS	0.93	1.11								
MS	1.20*	1.00	1.01							
PS	0.99	0.96	0.68*	1.00						
MTS	1.01	1.22	1.00	1.00	0.97					
SMB	1.48*	1.01	0.86*	1.08	1.07*	1.00				
CS	0.97	1.07	0.86	1.00	1.43*	0.95	1.03			
RB	1.41*	0.99	0.83*	1.02	1.11*	1.01	1.63*	1.02		
YP	0.83	1.00	1.00	0.94	0.98	1.00	0.63*	0.99	0.80	

Crayfish compete with littoral fishes for benthic invertebrates (Momot 1995; Dorn and Mittelbach 1999) and might suppress recruitment of fish predators by consuming fish eggs (Dorn and Wojdak 2004).

Climate measures formed significant, though not dominant, gradients of change in our analysis. Initially when the LTER study began in 1980, lakes in northern Wisconsin were considered less susceptible to invaders and human disturbance than lakes in southern Wisconsin (Magnuson et al. 1984). However, during the study period, climatic variation included three El Niño events, a drought, and the after effects of the Mt. Pinatubo eruption (Rusak et al. 1999; Magnuson et al. 2006b), which resulted in aberrantly warm and cold summers and longer ice-free periods. Interestingly, although climate variables were statistically significant for all lakes, no one climate variable was significant in all lakes. Of the four lakes that contained invading species, number of ice-free days was statistically significant in three lakes. Additionally, Secchi depth was a minor gradient in two lakes and O₂ stress temperature in one lake. All climate variables were less important than the abundance of invasive species except in Allequash Lake,

with no invasive species, in which the number of ice-free days was second in importance after year. These results suggest that the presence of invasive species masked the effects of climate on fish community composition, in part because the invasive species exhibited strong temporal trends in abundance and therefore were highly correlated with year. Thus, in most cases, regional and internal actors on fish community dynamics were visible only if year (i.e., lag-one serial autocorrelations) remained in the ordination.

Climate conditions, starting with the 1988 drought, might have had their greatest effect on fish community composition by facilitating the expansion of these invasive populations by complementing characteristics of invading species, including fecundity (Hrabik et al. 1998 and references therein) and thermal preference (Layne et al. 1987). At the same time, dominant native species might have been affected negatively by the climate variation observed. Strong shifts in the fish species composition of ecosystems in the North Pacific and in upwelling zones off the Peruvian coast were attributed to regime shifts, sudden and persistent changes in the physical and biological marine ecosystem concurrent with changes in large-scale

atmospheric conditions (Gitay et al. 2001; Polovina 2005). During the later 1990s in our lakes, warm springs led to early ice melt and earlier stratification. These conditions tend to produce a relatively shallow, warmer epilimnion and a colder, better oxygenated hypolimnion in clear water lakes (Destasio et al. 1996; King et al. 1999b). Adult rainbow smelt prefer colder water temperatures (King et al. 1999a); trends in oxygen stress temperature indicated that more cold water fish habitat was available in the late 1990s, which corresponds to a time of increased smelt abundance in Sparkling Lake. At the same time, crayfish production would have benefited from warmer epilimnetic temperatures and longer growing seasons (Payette and McGaw 2003); in Sparkling and Big Muskellunge Lakes, crayfish abundance and growing season length were closely related environmental gradients. *O. rusticus* were present in Sparkling Lake circa 1970, well before the start of the LTER program (Capelli 1982), and *O. propinquus* likely became established in Big Muskellunge Lake between 1930 and the 1970s (Horns and Magnuson 1981; Capelli 1982), but our evidence indicates that neither became ultra-abundant until the 1990s.

Our study primarily considers extrinsic factors in shaping the fish communities of relatively small glacial outwash lakes. Previous studies have considered intrinsic factors in shaping temperate fish communities, including density dependence, prey production, predation, and regional gradients (e.g., lake size and pH), as being important (Matthews 1998; Arnott et al. 2006). However, in many cases, these results are ultimately responses to extrinsic drivers like climate, invasive species, and anthropogenic eutrophication. Species invasions are obviously not a new occurrence of the last 20–30 yr, but changing conditions related to region-scale environmental drivers, like climatic change and the expansion of human settlement, have increased the frequency of invasions as well as the probability that introductions will be successful (Gitay et al. 2001). The NTL-LTER fish data document both the dominance of invaders and climate in affecting lake biology. The dominance of invasive species and climatic variables in this analysis are an example of how these variables overwhelm, or at least mask, community change associated with other factors such as nutrient fluctuations in the five LTER lakes in northern Wisconsin. We suggest that other lake areas could be experiencing similar dynamics that will be revealed by long-term study.

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