

Predicting the effects of rainbow smelt on native fishes in small lakes: evidence from long-term research on two lakes

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Abstract: We assessed predictability of negative interactions between native fishes and exotic rainbow smelt (*Osmerus mordax*) through field experiments and long-term data analysis for two lakes in Wisconsin. Predictions were made based on thermal preferences, diet characteristics, and published accounts of interactions between smelt and yellow perch (*Perca flavescens*) and smelt and cisco (*Coregonus artedii*). Our results indicate predation is the most likely cause for the extirpation of cisco from Sparkling Lake in 1990. In Crystal Lake, native yellow perch experienced significant overlap in distribution and diet with smelt. The condition of adult perch was negatively correlated with smelt abundance indicating competition was occurring. Smelt feed on a wide size range of prey items making this species a threat to native fishes, especially when spatial overlap is high. Information on spatial and temporal overlap and diet enable useful predictions about the effect of smelt invasions on native fishes.

Résumé : Nous avons étudié la prévisibilité des interactions négatives entre des poissons indigènes et l'éperlan arc-en-ciel (*Osmerus mordax*) exotique en réalisant des expériences sur le terrain et des analyses des données à long terme relatives à deux lacs du Wisconsin. Les prévisions ont été réalisées à partir des préférences thermiques, des caractéristiques des régimes alimentaires et des données publiées sur les interactions entre l'éperlan et la perchaude (*Perca flavescens*) et entre l'éperlan et le corégone (*Coregonus artedii*). Nos résultats montrent que la prédation est la cause la plus probable de la disparition du corégone dans le lac Sparkling en 1990. Dans le lac Crystal, il y avait un chevauchement significatif de la répartition et du régime alimentaire de la perchaude indigène et de l'éperlan. L'état des perchaudes adultes était corrélé négativement avec l'abondance de l'éperlan, ce qui indique qu'il y avait compétition entre les deux espèces. L'éperlan se nourrit de proies de tailles très diverses et représente donc une menace pour les poissons indigènes dont le domaine vital chevauche celui de l'éperlan. Les données sur le chevauchement spatial et temporel et sur le régime alimentaire permettent de faire des prévisions utiles concernant l'effet des invasions d'éperlans sur les poissons indigènes.

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Introduction

Exotic fishes have lead to changes in native fish community structure in many aquatic ecosystems (Moyle 1986; Kaufman 1992; Lodge 1993). In recent years, many North American lakes have been invaded by exotic and native fishes that have expanded their range (Crossman 1991). Species invasions have played an especially important role in restructuring fish communities in the Laurentian Great Lakes (Wells and McLain 1972; Crowder 1980, 1986; Kitchell and Crowder 1986) as well as smaller inland lakes (Colby et al. 1987; Crossman 1991). A particular Great Lakes exotic, the rainbow smelt (*Osmerus mordax*), has been introduced or has invaded many smaller lakes in the upper Great Lakes region in Canada (Franzin et al. 1994) and the United States, and native fish species have suffered as a result (Evans and Loftus 1987; Colby et al. 1987; Evans and Waring 1987).

While the spread of smelt and other exotic fishes will

inevitably continue, predicting effects of exotic fishes on native fish communities is important to managing fisheries in affected water bodies and to preserving the integrity and stability of native species assemblages. Introductions of smelt have not been detrimental to native fish communities in all cases, but many examples show significant negative effects. Most recent studies citing the negative effects of rainbow smelt indicate predation as the most important mechanism. Smelt predation has been linked to reduced recruitment and the decline of native fishes, particularly coregonids (e.g., Crowder 1980; Loftus and Hulsman 1986; Evans and Loftus 1987). In all instances, spatial overlap between adult smelt and native fish larvae and the resulting predation ultimately led to declines in recruitment and population density. Negative impacts by smelt via competition also have been addressed (Anderson and Smith 1971; Crowder 1980, 1986), but the effects of competition resulting from the establishment of rainbow smelt and its importance in different environments, has not been adequately tested in the field (Evans and Loftus 1987).

Our intent here was to assess predictability of the effects of rainbow smelt on native fishes and to determine which predictors are most useful. We addressed interactions between invading smelt and the historically dominant, native cisco (*Coregonus artedii*) and yellow perch (*Perca flavescens*) in each of two lakes as smelt increased. We hypothesized that interactions will be governed by spatial overlap, similarity in

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feeding, and predation, with spatial overlap being an important component to interaction intensity.

We used long-term data supplemented with additional field studies describing the diet, growth, and distribution of the fish species to determine whether smelt had negative effects on native species in each of the lakes and by what mechanisms.

Materials and methods

Study sites

Crystal and Sparkling lakes are small oligotrophic lakes located in Vilas County, Wisconsin, that are studied by the North Temperate Lakes – Long-term Ecological Research project (NTL–LTER) (see Magnuson et al. 1984, 1994). Sparkling Lake is a 68-ha seepage lake with a maximum depth of 20 m and approximately 50% of its area deeper than 7 m in depth. Secchi depth during the ice-free season averages approximately 6 m. Its littoral zone is narrow, with emergent and submergent vegetation, abundant coarse woody debris, and rocky boulder habitat. Portions of the hypolimnion become anoxic in late summer, but fish kills as a result of anoxia have never been noted, and significant portions of the hypolimnion remained oxygenated during the entire study period. Crystal is a 46-ha precipitation-dominated lake with a maximum depth of 20.5 m and over 50% of its area greater than 7 m. The Secchi depth during the ice-free season averages approximately 9 m. The hypolimnion of Crystal Lake rarely exhibits anoxic conditions. The littoral zone is sandy, with little coarse woody debris and few macrophytes. Crystal Lake contains few piscivorous fish and supports no substantial recreational fishery.

Long-term data collection

The NTL–LTER conducts a yearly fish survey during which relative abundance, length, and mass data are collected on fish communities using six different sampling gears (see Magnuson et al. 1994). We used yearly NTL–LTER survey data from 1981 to 1994 to obtain estimates of relative abundance, age structure, as well as measures of relative condition for fish present in Crystal and Sparkling lakes.

Trends in relative condition of smelt and perch in Crystal Lake and smelt and cisco in Sparkling Lake were assessed using a linear weight versus total length relationship for each species. The linear model was applied to log-transformed body mass and total length data pooled according to species and lake from NTL–LTER fish surveys that took place from 1981 to 1994. Fish <75 mm were excluded from the analysis because of error associated with measuring their mass in the field. The mean residual for each species in each year represented the relative condition of fish >75 mm of each species in each respective year.

Field studies

Diet, distribution, growth, and (or) relative condition of each native fish species and smelt were monitored in each lake. Fish were collected using vertical gillnets ranging from 19- to 89-mm bar mesh set in the deep basin of each lake. The overlap in vertical distribution of Crystal Lake perch and smelt and Sparkling Lake cisco and smelt across a thermal strata was determined by applying Schoener's (1970) proportional overlap to distribution data for both species collected by the LTER program during August of 1981–1993. Thermal overlap was calculated using the epilimnion, metalimnion, and hypolimnion as resource strata. We considered the epilimnion the area above the depth at which the temperature decreased 1°C or more within a metre, the metalimnion included the area where temperature decreased more than 0.99°C·m⁻¹, and the hypolimnion was considered the area below the metalimnion. Thermal overlap in Crystal Lake during the thermally stratified period of 1994 was also estimated to assess seasonal patterns of overlap in a year of high smelt abundance.

In Sparkling Lake, fish diet samples were collected from fish caught in gillnets set for 1–5 h. The digestive tract of each fish was removed and individually preserved in 10% buffered formalin and

later examined. In Crystal Lake, diet samples were collected using shorter duration gillnet sets (30–90 min), and the fish were immediately placed on ice to curtail digestion. Diet selectivity was estimated for perch and smelt in Crystal Lake only. Prey abundance and distributions were estimated using a 2-m long, 45-L Schindler–Patalas trap. Feeding preferences of perch and smelt were determined using Chesson's alpha (see Chesson 1978) and presented graphically using Vanderploeg and Scavia's (1979) relativized E^* . Diet overlap between smelt and perch in Crystal Lake was assessed using Hurlbert's (1978) index of niche overlap on diet and zooplankton data collected during 1992 and 1994.

Stomachs of fish collected in 1994 were weighed before being emptied so that the mass of food in them could be estimated. The mass of the empty stomach was calculated based on a linear relationship between empty stomach mass and body mass for both perch and smelt. These relationships were obtained by weighing the stomachs of fish starved for 48 h in the laboratory and calculating linear relationships between stomach mass and fish mass. For smelt, empty stomach mass was equal to $0.017(\text{fish mass}) + 0.034$ ($r^2 = 0.966$). For perch, empty stomach mass was equal to $0.012(\text{fish mass}) + 0.010$ ($r^2 = 0.953$). The generalized gastric evacuation model presented in He and Wursbaugh (1993) was then applied using the estimated food masses and temperature data obtained from field samples. This allowed correction for food left over from feeding bouts prior to the sampling period in which each fish was collected.

Age and growth of fishes were determined using scale analysis. For cisco, scales were collected during yearly LTER surveys from 1981 to 1989. Fish lengths at each scale annulus were back calculated using the linear regression method described by Bagenal and Tesch (1978), and 55 mm as the size at which cisco become completely scaled (Hogman 1970). For perch, a von Bertalanffy growth curve (Ricker 1958) was calculated using scale data to allow ages to be estimated for each fish caught in each year throughout the long-term record.

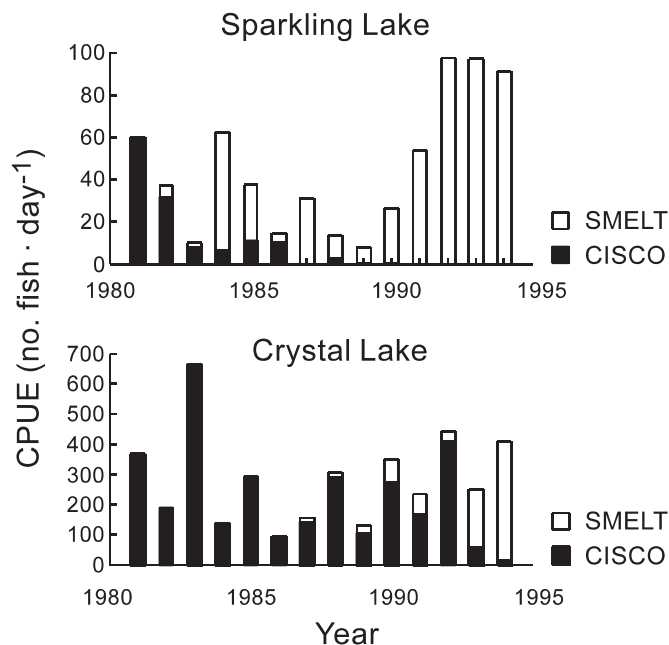
Results

Changes in native fish communities

Historically, cisco dominated the pelagic fish community in Sparkling Lake (Hile 1936). Smelt replaced cisco as the dominant fish species by 1985 (Fig. 1). Cisco declined to low abundance during 1987, 1988, and 1989 and were not detected in yearly LTER fish surveys after 1990. The age distribution of cisco shows that most fish caught after 1982 were born in 1981 and 1982 (Table 1). After the smelt invasion, the absence of young-of-the-year (YOY) and 1+ fish gillnet catches between 1985 and 1990 reveals the dramatic decline in young cisco survival (Table 1). Larval cisco were present during the spring of 1987, moderately abundant in May 1988, and present in June 1988, indicating that adult cisco were producing offspring during the population decline (McLain 1991). The young cisco were not, however, surviving their first year of life.

The fish community in Crystal Lake was historically dominated by yellow perch. Smelt were detected by the yearly NTL–LTER fish survey in 1985 and reached high abundances in 1993 and 1994 replacing perch as the dominant fish species (Fig. 1). Perch were abundant during the 1980s and early 1990s, suggesting that any interaction occurring between the two species did not have an immediate effect on the density of perch. In contrast to Sparkling Lake cisco, Crystal Lake perch did have successful reproduction and recruitment after adult smelt were numerous (Table 1). Perch abundance, however,

Fig. 1. Gillnet catch per unit effort (CPUE) standardized for a 24-h set for smelt and cisco in Sparkling Lake. CPUE was summed over all gears for perch and smelt in Crystal Lake from 1981 to 1994. Abundance for Crystal Lake was presented as total CPUE because of smelt and perch being frequently caught in more than one gear. In Sparkling Lake, smelt and cisco are caught predominantly in gillnets.



has recently declined with 1994 showing the lowest abundance level recorded (Fig. 1).

Diet characteristics

Diet samples from 1985 to 1989 show that adult smelt and cisco in Sparkling Lake ate zooplankton, aquatic stages of insects, and small fish (Table 2). While zooplankton were the most prevalent diet item in adult smelt and cisco stomachs, each species consumed small fish and a relatively high proportion of the smelt caught often contained small fish (Table 2).

In Crystal Lake, diets of smelt and perch most consistently contained zooplankton. In 1992, both species also ate fish and insect larvae, and a fairly high proportion of smelt contained fish in their diet relative to perch. In 1994, however, zooplankton and insect larvae and pupae were the most prevalent diet items found.

In Crystal Lake, we conducted detailed field sampling on fish diet characteristics, feeding selectivity, and feeding chronology. The feeding rate of perch and smelt was highest during the day for both species in 1994 (Fig. 2). The maximum smelt feeding rates in Crystal as well as Sparkling Lake occurred during midmorning (Fig. 2). Crystal Lake smelt also fed in the evening, with feeding decreasing thereafter until reaching the lowest level just before dawn (Fig. 2). Perch feeding in Crystal Lake was maximum during the early afternoon with secondary periods of feeding activity at dawn and dusk. Feeding rates were lowest during the midafternoon and predawn periods (Fig. 2).

Diet selectivity of Crystal Lake smelt and perch collected in 1994 indicates that both species select small and large

Table 1. Age frequency of Sparkling Lake cisco and Crystal Lake perch caught in August in each year.

		Year									
		1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
Age	0+	79	2								
	1+	31	53	1	2						
	>1+	7	3	14	10	22	20		6	1	1

		Year									
		1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
Age	0+		24	68	93			25	4	66	
	1+	74	3	47	666	132	7		3	19	1
	>1+	523	177	251	56	118	574	363	820	129	47

crustacean zooplankton, during the day (Fig. 3). At night, perch selected small zooplankton, but *Daphnia* were largely not eaten during low light. The high electivity for bosminids as well as cyclopoid copepods may be an artifact of low consumption of prey resources by perch at night, with both prey items making up a large proportion of the diet of perch relative to that found in the environment. The absence of *Daphnia* in perch diets at night suggests that a decrease in the effectiveness of perch visual feeding at low light levels reduced the amount of larger zooplankton consumed by this species. Smelt exhibited high preference for *Daphnia* under the same low light conditions and appear at least somewhat capable of feeding selectively at night (Fig. 3). The small amounts of food eaten by both species at night relative to that consumed during the day, however, suggests that food resources present during the day are the most important for both species (Figs. 2 and 3).

Prey preferences for both fish species in 1992 were strikingly different from those in 1994, but each species preferred similar prey to each other in each year. Perch and smelt both preferred *Daphnia* over all other zooplankton in 1992 with *Daphnia* and cyclopoid copepods being the most numerically common zooplankton prey (Fig. 3). In 1994, perch and smelt preferred cyclopoid copepods, *Daphnia* and bosminids, which were the most common zooplankton found in their diets. Bosminids and cyclopoids were eaten by both perch and smelt in 1992 but were preferred less than in 1994. Differences in prey selectivity between perch and smelt on *Leptodora* in 1994 and bosminids in 1992 were apparent but of little consequence, as each of the two prey items made up less than 2% of the diet on any sampling date in each year.

Overlap in prey resource use (*L*) (see Hurlbert 1978) by perch and smelt in 1992 ranged from less than one in early June to >600 times more likely than if the two species had fed at random in late June (Fig. 4a). In 1994, diet overlap was approximately eight times greater than expected had both species selected prey at random during late summer and early fall (Fig. 4b). Diet overlap was maximal during the peak of the growing season in 1994 when sampling extended from late May to November.

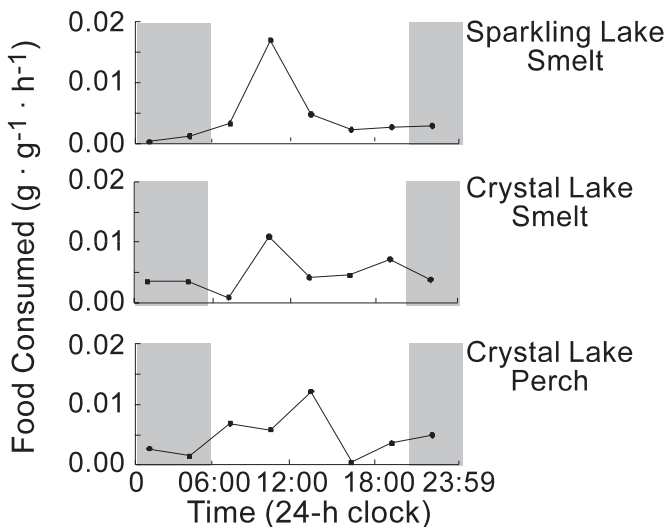
Length distributions of *Daphnia* and *Diacyclops*, the most common zooplankton in the diets of both species in 1994 were significantly different than the length distributions of both *Daphnia* and *Diacyclops* observed in the environment

Table 2. Diet composition of cisco and smelt in Sparkling Lake and perch and smelt in Crystal Lake.

Lake	Species	Date	Zooplankton	Insects	Fish	N
Sparkling	Cisco	May–June 1986	0.72	0.17	0.06	18
	Smelt	August 1985	0.21	0.53	0.26	19
		May–June 1986	0.15	0.74	0.08	39
		August 1988	0.56	0.67	0.44	9
Crystal	Perch	May–July 1992	0.88	0.30	0.04	87
	Smelt	May–July 1992	0.76	0.37	0.42	38
	Perch	May–July 1994	0.61	0.38	<0.01	89
	Smelt	May–July 1994	0.72	0.34	<0.01	135

Note: Values are the proportion of the total fish collected that contained each diet item.

Fig. 2. The average mass of food in smelt and perch stomachs corrected for stomach evacuation rates estimated for fish collected over the 24-h cycle in Crystal Lake and Sparkling Lake in 1994. Shaded areas indicate low light levels. Equations taken from He and Wurtsbaugh (1993) were used to correct for stomach evacuation rates.



(Kolmogorov–Smirnov paired distribution test; $\alpha < 0.05$) (Fig. 5). The length distributions of *Diacyclops* and *Daphnia* found in the stomachs of smelt and perch did not statistically differ (Kolmogorov–Smirnov paired distribution test, $\alpha > 0.50$), indicating that perch and smelt selected similar sized individuals of each prey type (Fig. 5).

Thermal distribution

We caught YOY cisco in the epilimnion of Sparkling Lake during May and early June of 1988, but our sampling of adult fish during May from 1986 through 1988 yielded no adult smelt <4 m in depth (McLain 1991). Over 80% of our smelt catch occurred in depths of 10 m or greater (McLain 1991). In 1981, a year when substantial number of young of year and adult cisco were caught in vertical gillnets during the NTL–LTER fish sampling, YOY cisco were located in the cold-water areas along with the adult (median temperature for YOY cisco $7.9 \pm 1.9^\circ\text{C}$; mean $\pm$ SD) moved from the epilimnion to hypolimnetic areas of Sparkling Lake between early June and August. Thermal resource use by smelt and cisco in Sparkling Lake indicated thermal overlap between smelt and

cisco averaged approximately 55% over the 8 years the two species co-occurred and was over 50% during August in every year but 1982 (Fig. 6a).

Thermal resource overlap by smelt and perch in Crystal Lake ranged from 30 to 70% during August from 1986 to 1993 (Fig. 6b). The years of 1990 and 1993 had the highest overlap (Fig. 6b), with values over 60%. The overlap between perch and smelt also increased in relation to the historical average after 1989 and remained near 50% after 1990. The seasonal overlap during 1994, a year with extremely high adult smelt abundance, showed greater than 60% overlap in May, July, and August (Fig. 6c) suggesting that increases in smelt abundance may have led to increases spatial overlap.

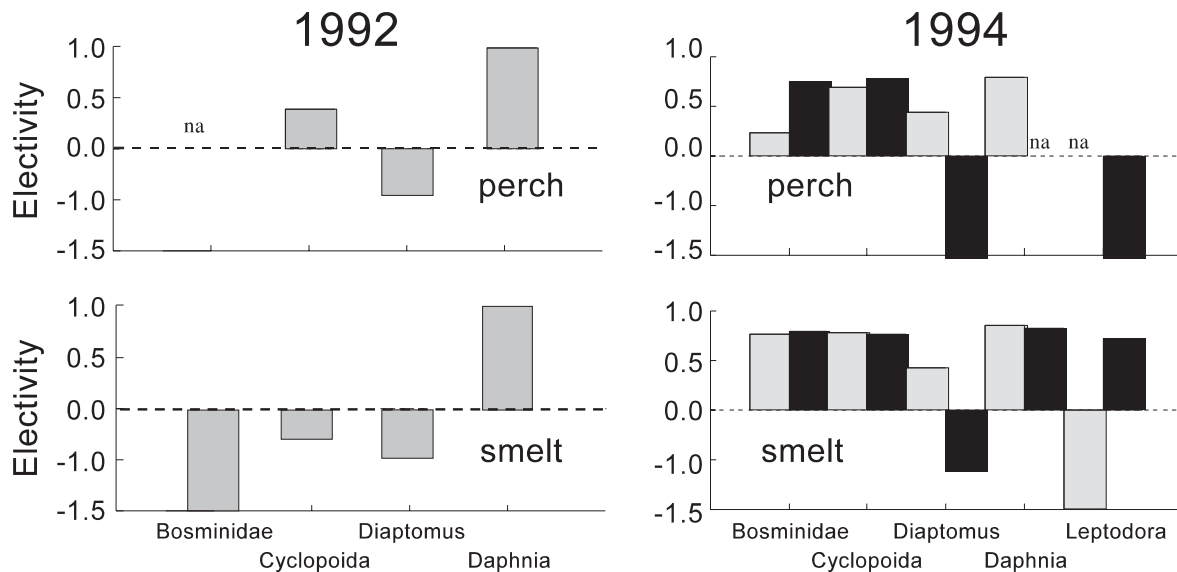
Relative condition of perch in Crystal Lake declined significantly and progressively as smelt increased in abundance ($r = 0.741$, $p < 0.05$ for perch relative condition vs. the natural log of smelt catch per unit effort). The relative condition of perch and smelt was correlated ($r = 0.824$, $p < 0.05$) indicating that both species responded similarly to environmental changes that occurred in the lake throughout the record. These results indicate that the average individual of both species realized a decrease in feeding success with the increase in smelt abundance and responded similarly to changes in their environment (Fig. 7).

In Sparkling Lake, increases in smelt abundance had no negative effect on the relative condition of cisco or smelt (Fig. 7). In 1986, cisco relative condition was significantly below the historical mean. With this exception, cisco condition in years prior to, as well as after, 1986 was either not significantly different or was higher than the historical average (Fig. 7). The results of scale analysis on cisco hatched before and after the smelt invasion indicates that the average length of cisco at the first annulus was not significantly different before and after the smelt invasion (t test, $t = 1.125$, $p = 0.225$, $df = 118$). The relative condition of Sparkling Lake smelt was variable and showed no significant pattern (Fig. 7).

Discussion

Predicting the effects of smelt on native fishes in regions where smelt are spreading is of interest to ecologists, lake managers, and the public. Smelt often negatively influence native fishes when introduced in freshwater lakes. Evans and Loftus (1987) provided 26 case studies where smelt were introduced into lakes with non-coevolved species; 18 cases had negative impacts on a native species. Prediction of negative impacts may be possible if information is available on native species in lakes likely to be invaded. Prior information on native fish

Fig. 3. Prey electivities for the most common zooplankton prey in perch and smelt stomachs from Crystal Lake in 1992 and 1994. Electivities for 1994 were calculated for day and night across 2-m depth intervals for both fish and prey. Solid bars represent estimates for fish and zooplankton collected at night; shaded bars represent estimates for fish and zooplankton collected during the day. Electivities for 1992 were calculated from fish collected during the day, dusk, and night and zooplankton abundance from day samples. Values represent weighted means using fish from all sampling dates.



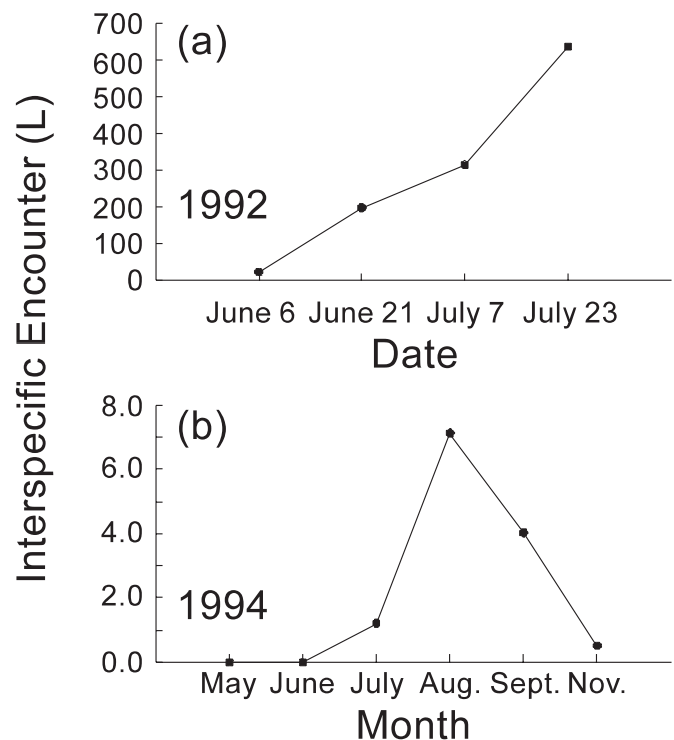
species in the lakes or watersheds of concern, however, are often absent or limited. Obtaining data on the characteristics of fish populations is costly and labor intensive. Thus, prediction of smelt effects based on specific, attainable parameters would be beneficial to assessing potential lake management strategies.

In both Crystal Lake and Sparkling Lake, smelt and native species used similar thermally defined areas. In Sparkling Lake, smelt and cisco preferred cold-water areas and exhibited substantial overlap in thermal distribution (Fig. 6). Overlapping distributions of cisco and smelt did not reduce feeding success of cisco, but predation on young cisco forced to occupy cold water by life-history traits has apparently led to recruitment failure. Thermal overlap in this case may have placed young cisco in close proximity to predatory adult smelt during the summer months and indirectly led to the extirpation of cisco from the lake by 1990; only 8 years after smelt were detected.

In contrast, thermal overlap between perch and smelt in Crystal Lake resulted in reduced feeding success for perch because of similarity in prey resource use relative to smelt. Increases in smelt abundance led to a progressive decline in the relative condition of perch showing the negative effects of competition with smelt. Unlike young cisco, however, juvenile perch in Crystal Lake are distributed in shallow areas of the epilimnion and in the littoral zone (T. Hrabik, unpublished data). Furthermore, recruitment of Crystal Lake perch is known to have occurred in recent years. McCauley and Read (1973) showed that juvenile perch preferred temperatures warmer than adult perch, with a final preferendum near 23°C. Thus, juvenile perch may avoid extended periods of predation from adult smelt because of a much warmer thermal preference.

Without question, the most accurate assessment of interaction intensity will come from actual measurements of smelt

Fig. 4. Hurlbert's (1978) measure of diet overlap (L) calculated for perch and smelt in Crystal Lake biweekly for the early to midsummer period of 1992 (a) and monthly for the ice-free season of 1994 (b).



and native fish resource use in each system invaded by smelt. However, managers are often faced with implementing management strategies based on little or no information. There are very few studies that document thermal occupancy of smelt in

Fig. 5. Length–frequency distributions of *Diacyclops* and *Daphnia* in the environment and those found in smelt and perch stomachs in Crystal Lake in 1994. Distributions with an asterisk are significantly different from the length distribution found in the environment. Differences in distributions were tested using a Kolmogorov–Smirnov paired distribution test with $\alpha = 0.05$.

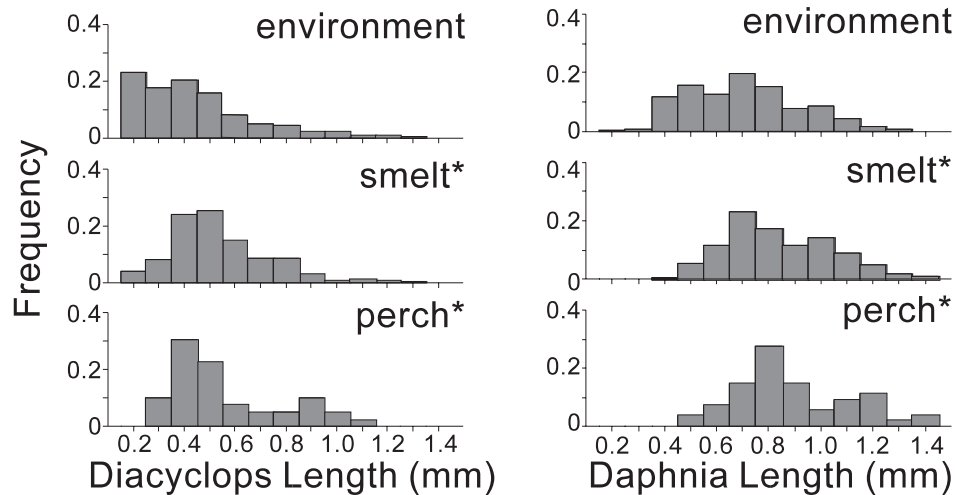
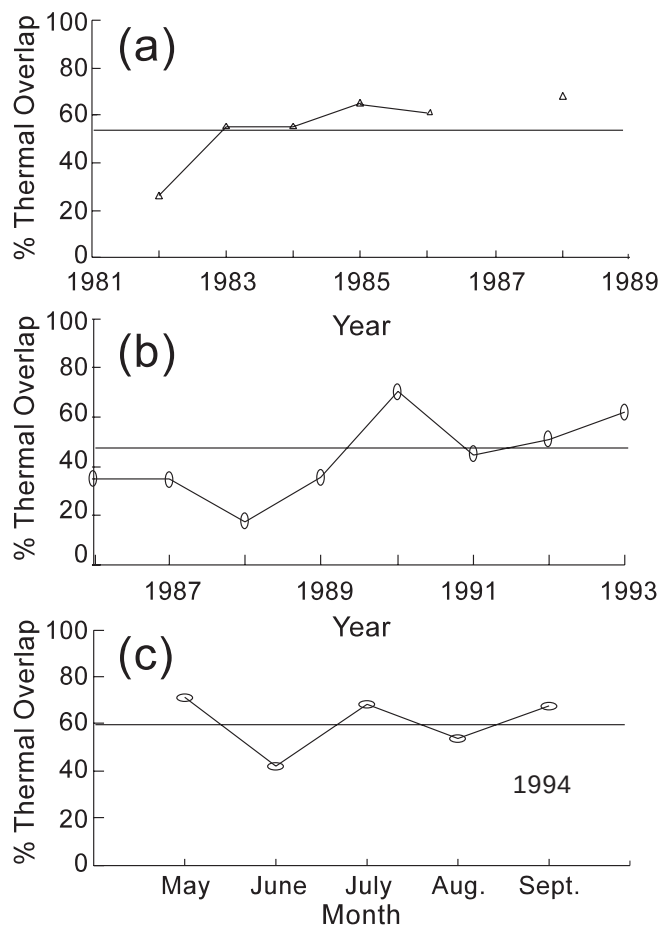


Fig. 6. Thermal niche overlap calculated using the epilimnion, metalimnion, and hypolimnion thermal strata as resource states for historical data collected on Crystal Lake from 1985 through 1993 (a) and Sparkling Lake from 1982 through 1989 (b). Thermal niche overlap for perch and smelt in Crystal Lake in 1994 over the thermally stratified portion of the ice-free season (c). The horizontal line in all panels shows the historical mean.



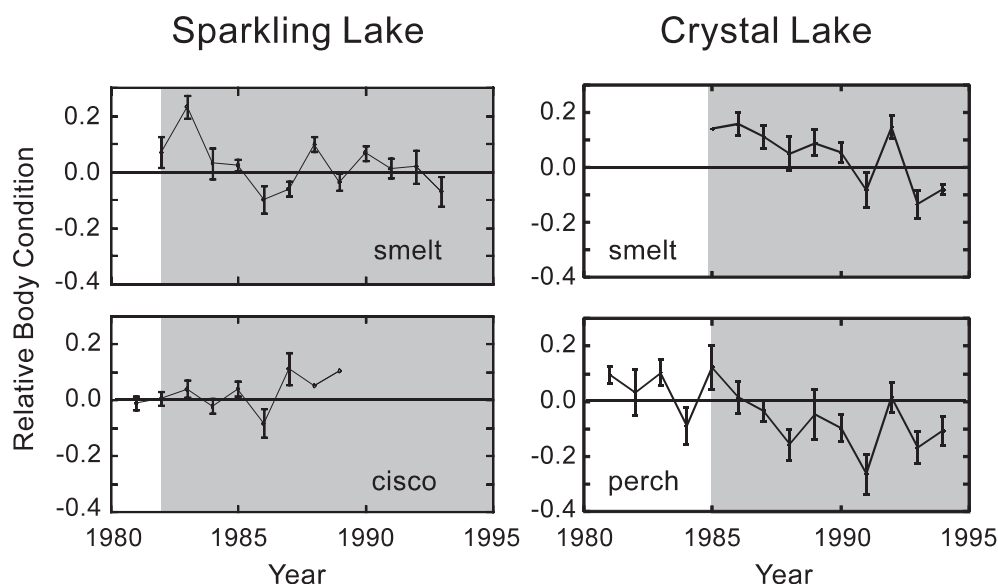
small lakes. Our estimates of smelt thermal preference in both Crystal and Sparkling lake are similar to those found in other lakes (see Wismer and Christie 1987). Based upon our findings and published thermal preferendum (see Wismer and Christie 1987), smelt are found consistently between 8 and 16°C, with 12–13°C being the most common temperature preferendum. Given the apparent consistency in smelt thermal preference, smelt thermal distribution could be estimated and compared with thermal distributions of native fish in waterbodies expected to be invaded by smelt prior to an invasion taking place. This type of prior assessment would allow management action to be taken previous to any potential negative effects taking place.

Published thermal preferences for adult perch, however, show that yellow perch exhibit variability in thermal preferendum, and preferences may be dependent upon the population and season with final preferendum ranging from 7 to 30°C and most commonly occurring between 19 and 22°C (Wismer and Christie 1987). During our study, thermal occupation by yellow perch in Crystal Lake during summer averaged approximately 16°C, which is below the temperature perch most commonly prefer. Thus, predicting interactions between species with wide thermal tolerances should not be considered without collecting information on specific populations of concern.

Predation effects by smelt include recruitment reductions, population declines, and potentially the extirpation of the native species. Spatial overlap between smelt and native fish, with a body diameter smaller than the gape of adult smelt, will likely result in predation effects by smelt on the native fish. Negative effects of predation would likely manifest in reductions in recruitment, native species population declines and possibly the extirpation of the native species.

Interspecific competition occurs when common limiting resources are utilized by more than one species with the extent of overlap in resource use potentially dictating the strength of competition (Larkin 1956). While overlap in spatial distribution indicates that competition is possible, competition may also occur if there is no overlap in distribution but other

Fig. 7. Relative condition of smelt and cisco in Sparkling Lake and smelt and perch in Crystal Lake from 1981 to 1994. Shaded areas indicate dates after smelt were detected. Error bars are 95% confidence intervals.



resources are being shared. For example, if two fish species feed on zooplankton that perform diel vertical migration in the water column, each species may utilize the same food resource during different periods of the day. Thus, while no spatial overlap may occur between smelt and native species, utilization of the same food resource may cause a reduction in the success of the native species resulting from consumption by smelt. If two species overlap in distribution and have similar prey preferences, however, competition is more likely because of the high potential for common use of spatial as well as food resources. Detailed diet information is needed to accurately predict exploitation competition. Potential effects of competition would include a shift in resource use after an invasion, a reduction in the fitness of the native as a result of resource use, and reductions in the population level of the native species.

Our study shows that smelt had strong negative effects on native fishes both NTL–LTER study lakes that have been invaded. The mechanisms of interactions in each case were unique, but spatial overlap is common to each case. Plasticity in the habitat choices of fishes is common making comparisons between generalized thermal preferences, and diet characteristics of smelt and native species are uncertain predictors of species interactions at best. Prior information on native fish spatial distribution and prey resource use along with information on invading smelt is essential to accurately predicting competitive interactions and predation effects. Finally, any purposeful introduction of smelt into freshwater lakes should be done with great caution; the ability of smelt to effectively consume a wide range of prey makes introducing this species an uncertain proposition at best.

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