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The effects of an exotic fish invasion on the prey communities of two lakes

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Summary

1. We examined changes in prey (zooplankton) communities resulting from the invasion of an exotic predator, the rainbow smelt (*Osmerus mordax* Mitchill), using long-term data sets from two lakes in Wisconsin, USA.

2. Food webs in the two lakes differed originally both in the dominant native planktivorous fish species and in relative biomasses of major zooplankton groups.

3. Zooplankton communities in each lake changed dramatically, coinciding with the exotic predator invasion. The communities in the two lakes became more similar to each other, with cyclopoid copepods becoming dominant.

4. Time-series analyses demonstrated that the long-term responses of the two lake prey communities were driven primarily by direct predation effects of planktivorous fish. Indirect effects acting through competitive interactions among zooplankton were present but were comparatively small in the long term.

5. Results suggest that zooplankton populations were subject to both predator and resource limitation but that the composition (relative species abundance) of the zooplankton community was dictated in the long term by predation.

Key-words: exotic invasions, multivariate autoregressive models, non-metric multidimensional scaling, rainbow smelt, zooplankton community structure.

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Introduction

The invasion of communities by exotic species has alarmed both ecologists and managers as the number of invasions increases world wide (Mooney & Hobbs 2000). Many studies have focused on competitive displacement of native populations by exotic species (Hrabik, Magnuson & McLain 1998; Byers & Goldwasser 2001). Fewer studies have examined the food web disruption caused by exotics across trophic levels in unmanipulated systems. Replacement of a native predator by an exotic may lead to changes in prey community structure that result directly from predation, indirectly via food web interactions between prey, or both. In this study we take advantage of a rare long-term time-series documenting predator and prey dynamics over two decades. Our goal is to determine the effect of the invasion of an exotic planktivorous fish (predator) on the zooplankton (prey) community structure in two lakes. We also ask how these changes are manifested, either directly through top-down effects of predation, or indirectly through interactions between prey population groups.

Introducing a new predator to a food web most probably changes overall predation rates. Shifts in prey biomass following this change can reveal mechanisms of limitation and control (*sensu* Osenberg & Mittelbach 1996) at work in the community. Limitation represents the extent to which a population's per capita growth rate is influenced by the action of a particular factor like predation or resource competition. With a change in predation rates (either more or less), population 'limitation', measured as short-term change in biomass, will be affected. Longer-term prey biomass changes with altered predation rates measure the degree to which predation 'controls' the prey. Controlling factors affect populations by setting the long-term average biomass. In our study of a predator invasion, we will examine responses of the prey community both in terms of short-term (limitation) and long-term (controlling) factors.

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Rainbow smelt (*Osmerus mordax*) invaded Crystal and Sparkling Lakes in northern Wisconsin, USA, in the 1980s, as documented by routine sampling of the North Temperate Lakes Long-term Ecological Research (NTL-LTER) programme. Hrabik *et al.* (1998) demonstrated differences between lakes in the native planktivorous fish communities that occurred before invasion, and differences in the mechanisms by which smelt displaced the native species. Because of these differences, we expected that changes in the zooplankton communities accompanying smelt invasion would also differ between lakes.

Crystal Lake had a native planktivore community dominated by yellow perch (*Perca flavescens* Mitchill). Rainbow smelt were first detected in 1985 and replaced yellow perch as dominant planktivores by 1994. There was a large overlap in diets of these fish species (Hrabik *et al.* 1998) with 61–88% of native perch and 72–76% of smelt feeding on zooplankton during the invasion. Calanoid copepods were most selected by both fish species. Detailed studies show that exploitative competition with smelt led to perch extirpation (Hrabik *et al.* 1998).

Smelt were detected earlier (1982) in Sparkling Lake. Here, the native planktivore, cisco (*Coregonus artedii* LeSueur), was replaced by smelt much more quickly (by 1987) than in Crystal Lake. In contrast to smelt, which is a diet generalist, cisco feed almost exclusively on macrozooplankton in the pelagic zones of lakes (Johnson & Kitchell 1996). Cisco did not recruit successfully after the first detection of smelt (Hrabik *et al.* 1998). Less diet overlap occurred between the native cisco and the exotic smelt, with 72% of cisco but only 15–21% of smelt consuming zooplankton. The rest of the smelt diets were unidentifiable small fish, most probably made up in large part by young-of-year cisco. There was no evidence of a decline in the body condition of cisco as smelt invaded Sparkling Lake, implicating predation by smelt as the cause of cisco decline rather than competition with smelt as occurred in Crystal Lake (Hrabik *et al.* 1998).

We predicted that predation was the most important factor determining short-term (biweekly) and long-term (annual) changes in the zooplankton communities following smelt invasion in these lakes. The magnitudes of the responses in the zooplankton communities, however, should depend on the similarity of feeding habits between native and exotic planktivorous species. For Crystal Lake, we expected relatively little change in the zooplankton community, because smelt replaced a planktivore with similar diet through competitive exclusion. In contrast, in Sparkling Lake the replacement of the zooplankton specialist, cisco, by the diet generalist, smelt, should lead to larger changes in relative predation rates on prey species, and hence larger changes in long-term relative abundance. With changes in predation rates, we also expected competitive interactions between zooplankton species to be more important. The suppression of some zooplankton populations by smelt predation should result in com-

pensatory increases in less preferred prey released from limitation by competition in the short term.

We also ask the more general question of whether the invasion of two dissimilar communities by the same predator will make the communities more similar. There is a great deal of evidence that vertebrate planktivores can structure zooplankton communities (e.g. Hrbáček *et al.* 1961; Brooks & Dodson 1965; Mills & Schiavone 1982). We have an opportunity here to examine whether prior differences in zooplankton community structure are reduced by the introduction of a shared novel predator in natural ecosystems.

We determine first whether smelt invasion changed the zooplankton community composition of Crystal and Sparkling Lakes, and increased their similarity. We then conduct a more detailed analysis of the change in prey community composition to ask whether the change in composition through time coincides with the increase in the exotic predator. For both of these, we are concerned with controlling factors (long-term effects). We use time-series analyses to explore the direct effects of changes in planktivore community on different groups of zooplankton, and ask whether these direct effects of predation were augmented by indirect effects acting through competition between prey groups. The analyses take advantage of short-term (2-week) fluctuations in zooplankton abundances to quantify responses of prey groups to predation and competition. After quantifying these responses, we use the time-series model to assess the relative importance of predation vs. competition in explaining the long-term change in the zooplankton community composition from before to after smelt domination of the planktivorous fish community.

Materials and methods

Crystal and Sparkling Lakes are oligotrophic lakes in Vilas County, WI, USA (46°N, 89·7°W) and are part of the North Temperate Lakes Long-term Ecological Research (NTL-LTER) project (http://lter.limnology.wisc.edu). Crystal Lake is 37 ha with a maximum depth of 20·5 m. There are no piscivores and no substantial recreational fishery in Crystal Lake. Sparkling Lake is 64 ha with a maximum depth of 20 m. Piscivorous walleye are stocked occasionally in Sparkling Lake and has a small recreational fishery.

Data were obtained from the NTL-LTER database for 1981–99 for Crystal Lake and for 1981–93 for Sparkling Lake. Zooplankton data for Sparkling Lake after 1993 were too sparse for inclusion. There were six dates of measured zooplankton densities per year taken biweekly from June to September. Zooplankton samples were taken at the deepest point in each lake at 1-m depth intervals using a 45-L Schindler-Patalas trap with 53 μm mesh. Samples were preserved in formalin, and samples from different depths were integrated volumetrically before two replicate 1 mL subsamples were counted and macrozooplankton were identified to species. Zooplankton densities were converted into

dry biomass using average lengths and length–weight regressions (McCauley 1984).

Macrozooplankton were grouped into four major classes for analysis: *Daphnia* spp. (D), non-daphnid cladocerans (CL), calanoid copepods (CAL) and cyclopoid copepods (CYC). The non-daphnid cladocerans were *Bosmina longirostris* and *Diaphanosoma birgei*, and low densities of *Chydorus sphaericus*. The calanoid and cyclopoid copepod groups were each dominated by a single species, *Leptodiaptomus minutus* and *Diacyclops thomasi*, respectively. Zeroes in the data set were converted to half the minimum biomass for that taxon before aggregation into major categories.

Chlorophyll samples were taken at the deepest part of the lake at 1-m depth intervals using a peristaltic pump. In the laboratory, chlorophyll was extracted in methanol and measured spectrophotometrically. Average values across all depths were used as a covariate in the time-series analysis.

Gillnets were used to obtain catch per unit effort (CPUE) data on pelagic fish species annually. These data were converted to proportion of smelt in gillnet catches. Because we are interested in the consequences of a shift in planktivore community composition to smelt, we use the proportion of smelt, rather than separate abundances of each planktivorous species. Using raw CPUE would not summarize the change in planktivore community composition in a single variable. Furthermore, CPUE data give the composition of fish communities with greater certainty than absolute abundances of fish species, which have considerable measurement error.

PRE- AND POST-INVASION COMMUNITIES

For both lakes, we computed the difference between the zooplankton communities based on species-level biomasses 1 year prior to invasion and 5 years after invasion using a geodesic metric of community dissimilarity (Pielou 1984). This measure is the shortest on-the-surface distance (*S*) between points *A* and *B* on a sphere upon which the compositions of two communities are mapped. It is also called the cosine separation between communities *A* and *B*. The geodesic dissimilarity index is calculated as:

$$g(A,B) = \arccos S_{AB}. \qquad \text{(eqn 1)}$$

The geodesic measure (*g*) can range from a minimum dissimilarity of 0 (identical communities) to a maximum of $\pi/2$ (1·576) for maximum dissimilarity. This metric was calculated for the observed zooplankton community compositions and for 10 000 bootstrapped matrices of the genus-level relative biomass data matrix for each lake before and after smelt invasion. In all, there were four years in the genus × time–lake matrix (two lakes, each with 2 years represented). The biomass data were shuffled by rows and columns in the matrix, and the dissimilarity between lakes before and after

invasion were calculated. The observed *g* from the data was compared to the distribution of bootstrapped values to test for significance of the observed value.

TEMPORAL CHANGE IN COMMUNITY COMPOSITION

To assess the change in zooplankton communities in the two lakes over time, nonmetric multidimensional scaling (NMS) was implemented using PC-ORD (McCune & Mefford 1999). NMS is appropriate for most ecological data because it has no assumptions about the structure of the data (e.g. normality). It is especially useful for comparing community changes over time in different systems because the distance between values in ordination space represent actual dissimilarities between samples (McCune & Mefford 1999). The input matrix consisted of each of the six data points per summer for each of the four taxonomic groups (*Daphnia*, non-daphnid cladocerans, calanoid and cyclopoid copepods). Both lakes were analysed together to allow for comparisons between as well as within lakes. Biomass data were log-transformed prior to analysis, and Euclidean distances were used to calculate the distance matrix. Representation of the data using three axes was most appropriate according to the scree plot (stress values). The centroids of the six points in multivariate space were calculated for the three axes. We then calculated Euclidian distances between the presmelt invasion year and each subsequent year in each lake. Plots of these values enabled visualization of the change in community dissimilarity over time. Also, Euclidian distances between lakes were calculated for each year following invasion to assess dissimilarity between the communities in the two lakes as smelt invasion progressed.

TIME-SERIES ANALYSIS

To quantify the direct effects of changes in the planktivore community on zooplankton dynamics and the indirect effects of interactions between zooplankton, we used first-order multivariate (or vector) autoregressive models, MAR(1) (Reinsel 1997; Ives, Carpenter & Dennis 1999; Ives *et al.* 2002). MAR(1) models are conceptually similar to using multiple regression in which the dependent variable is the population abundance of a taxon in one sample and the independent variables include the abundances of all taxa in the preceding sample plus any external variables (e.g. proportion smelt and chlorophyll). Due to the serial structure of the data, however, multiple regression is not statistically appropriate, whereas MAR(1) models explicitly account for the serial autocorrelation of time series. If the level of an external variable affects changes in the abundance of a taxon between samples, this will appear as a non-zero autoregression coefficient for the external variable in the MAR(1) model. Similarly, if changes in the abundance of one taxon depend on the abundance of a second taxon, this appears as a non-zero

autoregression coefficient for the interaction between the second and the first taxon.

Autoregression coefficients are not the same as 'interaction coefficients' as commonly defined in the literature (e.g. Paine 1980; Abrams 2001). The autoregression coefficients depend on the correlated response of one variable to others in the time series in hand, and therefore they depend on the patterns of change in the data (Ives *et al.* 1999). Thus, if a given external variable does not change, then it cannot be responsible for the observed changes in abundance of taxa in the data set, and the corresponding autoregression coefficients will be zero. This can occur despite the fact that the external variable has a strong effect on taxa in the community. For example, in our data set resource abundance (chlorophyll) potentially has a large impact on the zooplankton community, because zooplankton must eat something. None the less, if resource abundance does not change in the time series, then the importance of resources for zooplankton remains silent in the MAR(1) model. Only if changes in resources were responsible for changes in the zooplankton abundance would a nonzero autoregression coefficient appear. The same argument applies to interactions among zooplankton taxa. Even though the autoregression coefficients are not the same as interaction coefficients, they are none the less useful to identify interactions that potentially underlying observed changes in the zooplankton communities. The MAR(1) model for n taxonomic groups and m external variables is:

$$x_i(t+1) = (a_i + \alpha_i z) + \sum_{j=1}^{n}(b_{ij} + \beta_{ij}z)x_j(t) + \sum_{k=1}^{m}(c_{ik} + \chi_{ik}z)u_k(t) + \varepsilon_i(t),$$ (eqn 2)

where $x_i(t)$ is the observed log biomass of species i in sample t, $u_k(t)$ is the value of an external variable (e.g. proportion of smelt) in sample t, a_i is a constant, b_{ij} is the autoregression coefficient for the relationship between the log biomass of species j in sample t and the log biomass of species i in sample $t + 1$, c_{ik} represents the effect of $u_k(t)$ on the biomass of species i, and $\varepsilon_i(t)$ is unexplained variability. The variates $x_i(t)$ in the model were *Daphnia*, non-daphnid cladocerans, calanoid copepods and cyclopoid copepods. The external variables $u_k(t)$ were proportion smelt in the planktivore community, chlorophyll and temperature. To apply the model simultaneously to both lakes, we included a categorical variable z that equals 0 for Crystal Lake and 1 for Sparkling Lake. Therefore, the autoregression coefficient for the relationship between the log biomass of species j in sample t and the log biomass of species i in sample $t + 1$ is b_{ij} in Crystal Lake and $b_{ij} + \beta_{ij}$ in Sparkling Lake. Differences between lakes in the effect of changes in the proportion smelt will be captured in the term χ_{ij}, since the effect of proportion smelt is c_{ij} in Crystal and $c_{ij} + \chi_{ij}$ in Sparkling Lake.

The MAR(1) model was fitted to the data using conditional least-squares (Ives *et al.* 1999; Ives *et al.* 2002).

Because the last sample in 1 year was separated by winter from the first sample in the following year, we excluded this interval from the analyses. Equation 1 can be thought of as a suite of models depending on which coefficients (b_{ij}, c_{ik}, β_{ij}, and χ_{ij}) are set to zero. The best-fitting model from this suite of models was chosen by applying the Akaike information criterion (AIC). The AIC is a measure of model fit that includes a penalty factor for the number of parameters (Burnham & Anderson 1998). We identified the best-fitting AIC model using an exhaustive search of models either including or excluding (setting to zero) each of the coefficients. The model was constrained to allow only negative interactions between zooplankton. Three positive interactions were excluded as a result. The unconstrained model gave a positive value for the coefficient for the effect of cladocerans on cyclopoid copepods, and weak positive values for the effects of cladocerans on calanoids and for cyclopoids on cladocerans. We report the results only from the constrained the model, however, because positive interactions between zooplankton are unlikely (Ives *et al.* 1999). Analyses of the unconstrained model give the same general conclusions as those of the constrained model.

To test whether the time-series data could be fitted without accounting for interactions between species, bootstrapped log-likelihood ratio tests were performed to compare the best AIC model to the null model that included no zooplankton interaction coefficients (i.e. b_{ij} and $\beta_{ij} = 0$) but retained the other coefficients of the best AIC model. The null model was first fitted to the data and the resulting residuals obtained. The parameterized null model (called null-1 MAR) was then used to simulate 10 000 bootstrapped replicate data sets. For the simulations, the log biomasses of each taxon at the beginning of a year was set to the observed value in the data set, and the parameterized null model was iterated for the remaining five samples of the year by selecting randomly (with replacement) from the residuals from all years obtained by fitting the null model to the data. The residuals for a given sample for each of the four taxonomic groups were selected together as a unit, thereby retaining the covariance structure of residuals among groups observed in the data. For each replicate data set, the null and best AIC models were parameterized and the log-likelihood ratio calculated. The resulting bootstrap distribution of log-likelihood ratios will approximate the true distribution of log-likelihood ratios under the assumption that the null model is correct (Efron & Tibshirani 1993). Therefore, we compared the log-likelihood ratio calculated for the true data to the bootstrap distribution of log-likelihood ratios to obtain statistical confidence in the difference between null and best AIC models.

For completeness, we also compared the best model (null-1 MAR) with an alternative null model (called null-2 MAR). In this case, the entire previous methodology was used except that after the zooplankton coefficients were set to zero, the model was not refitted to

the data. Instead, the same parameters were used for other interactions generated by the original best AIC model. Null-2 MAR asks about the structure of the best model and what happens when zooplankton interactions are removed. This contrasts with the previous analysis because null-2 MAR asks whether species interactions are necessary at all for long-term predictions. The results from both analyses have similar conclusions. Because we were more interested in comparing between the 'truth' that involves species interactions with a 'truth' that does not, we present the results from the original null-1 MAR analysis here.

The MAR(1) model assesses changes in the abundances of taxa between the six samples per year. We are also interested, however, in the long-term change in the zooplankton community caused by smelt invasion from beginning to end of our data sets to provide a measure of controlling factors. We used the MAR(1) model to predict the long-term changes in zooplankton community. The auto-regressive model (eqn 2) can be written in matrix form as:

$$X_z(t + 1) = A_z + B_z X(t) + C_z U(t) + E_z(t), \qquad \text{(eqn 3)}$$

where $X_z(t)$, $U_z(t)$, and $E_z(t)$ are the vectors of log taxon biomass, external variables, and unexplained variability, respectively, in lake z ($z = 0$ for Crystal Lake, 1 for Sparkling Lake), A_0 and A_1 are vectors of constants a_i and $a_i + \alpha_i$ for Crystal and Sparkling Lakes, and B_0, B_1, C_0, and C_1 are matrices containing coefficients b_{ij}, $b_{ij} + \beta_{ij}$, c_{ij}, and $c_{ij} + \chi_{ij}$, respectively. For this MAR(1) model, the n-dimensional mean of the stationary distribution is

$$\bar{X}_z = (I - B_z)^{-1}(A_z + C_z \bar{U}) \qquad \text{(eqn 4)}$$

where $\bar{X}_z$ and $\bar{U}_z$ are the mean log biomass and mean value of the external variables, respectively, in lake z, and I is the identity matrix (Ives 1995). Therefore, eqn 4 can be used to predict the mean log biomass of zooplankton before and after smelt invasion using the MAR(1) model and the values of $\bar{U}_z$ observed in the data. To compare these predictions with the observed changes in zooplankton biomasses, and to test the ability of the model to make long-term predictions, we also computed the mean log biomass of the taxonomic groups before smelt invasion (Sparkling Lake 1981–82; Crystal Lake 1981–84) and at the end of the time-series (Crystal Lake 1997–99; Sparkling Lake 1991–93).

The reason for calculating the predicted mean zooplankton biomasses before and after smelt invasion using the MAR(1) model was to determine whether interactions among zooplankton could be important as a controlling mechanism of the long-term response of the zooplankton community to smelt invasion. Even though zooplankton interactions might be important as limiting factors that explain changes in zooplankton biomass between successive samples within a year, they need not be important in explaining the long-term changes in mean biomass. To assess statistically the

importance of zooplankton interactions for long-term changes in response to smelt invasion, we computed the difference in predicted log zooplankton biomasses between the beginning and end of the time-series for the best AIC model and the null model assuming the coefficients for zooplankton interactions are zero. To obtain statistical confidence, we used a bootstrap procedure similar to that used to test the statistical significance of the coefficients for species interactions. We generated 1000 bootstrap replication data sets by simulating the parameterized best AIC model (rather than the null model), and for each replication data set, we estimated parameters for the best AIC model. For each parameterization, we used eqn 4 to compute the predicted change in mean log biomass for each zooplankton taxon. This procedure gives the approximate distribution for the predicted change in mean log biomass under the assumption of the best AIC model. From this approximate distribution we obtained approximate 95% confidence bounds for the predicted mean change in log biomass for each zooplankton taxon.

Results

The proportion of the pelagic planktivore community consisting of smelt increased more rapidly but fluctuated more in Sparkling Lake than in Crystal Lake (Fig. 1a). The large decline in the proportion of smelt in Sparkling Lake in 1988 was due to a very large increase in yellow perch that year. In all other years yellow perch abundances were very low in Sparkling Lake. The most noticeable trend in the zooplankton was a large increase over time in the relative biomass in the cyclopoid copepod group (Fig. 1b).

PRE- AND POST-INVASION COMMUNITIES

The relative biomass of zooplankton groups showed larger changes in Sparkling Lake than in Crystal Lake for summer means taken 1 year before and 5 years after smelt invasion (Fig. 2). In Crystal Lake, the largest changes were increases in cyclopoid copepods and declines in calanoid copepods. In Sparkling Lake, similarly, cyclopoid relative biomass increased to a very large degree at the expense of all other groups, especially of *Daphnia* and nondaphnid cladocerans. The geodesic dissimilarity indices showed a significant decrease ($P < 0.001$) in dissimilarity between the zooplankton communities of the two lakes following smelt invasion. One year prior to invasion the two lake communities differed with $g = 1.35$ and 5 years after the invasion, the community dissimilarity index was reduced to $g = 0.18$ (where maximum similarity is represented by $g = 0$).

TEMPORAL CHANGE IN COMMUNITY COMPOSITION

The distances between the zooplankton community centroids (annual means) from the NMS are shown in

Crystal Lake   Sparkling Lake
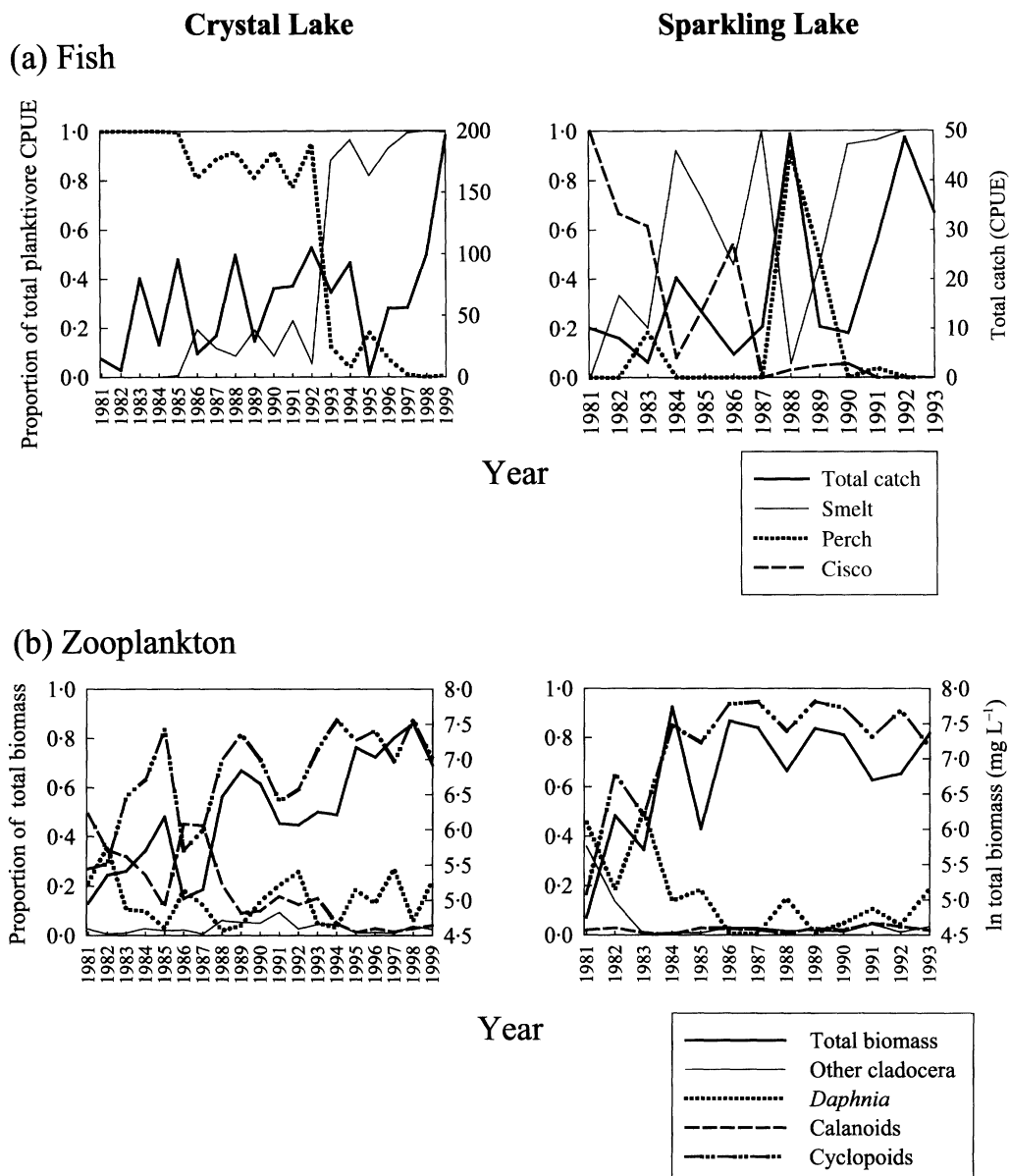
(a) Fish

(b) Zooplankton

Fig. 1. Time-series of (a) fish species catches and (b) mean annual zooplankton taxon biomass for Crystal and Sparkling lakes.

Fig. 3. Comparison of the zooplankton communities in each lake over time to the community in the year immediately preceding smelt invasion (Fig. 3a) shows clear increases in dissimilarity. In Crystal Lake, community dissimilarity from initial conditions began tracking the proportion of smelt only once the proportion smelt increased beyond 0·8. In Sparkling Lake, coherence between the community dissimilarity and the proportion smelt trajectories was observed from the first year of smelt detection. Also, the change over time was greater initially, and over the entire time-series in Sparkling Lake than in Crystal (Fig. 3a). In the comparison between lakes for each year following smelt invasion (Fig. 3b), the results of the NMS corroborate the decline in geodesic dissimilarity between the two lakes over time (Fig. 2), with lakes being especially similar 5, 11 and 12 years after smelt invasion.

TIME-SERIES ANALYSIS

We used the MAR(1) model to identify evidence for both direct and indirect effects of changes in planktivore species on changes in log biomasses of the four zooplankton taxa. The time series to which the MAR(1) model was fitted is shown in Fig. 4, along with the one-step-ahead predictions from the best AIC model. The coefficients of the model are given in Table 1 for the covariates and in Table 2 for the biotic interactions.

The direct effect of the proportion of smelt on changes in log biomass of the zooplankton taxa differed between lakes (Table 1). In Crystal Lake all taxa were positively affected by the increase in proportion smelt except calanoid copepods, for which there was a slightly negative autoregression coefficient. In contrast, in Sparkling Lake the proportion smelt had large positive autoregression coefficients for all prey taxa.
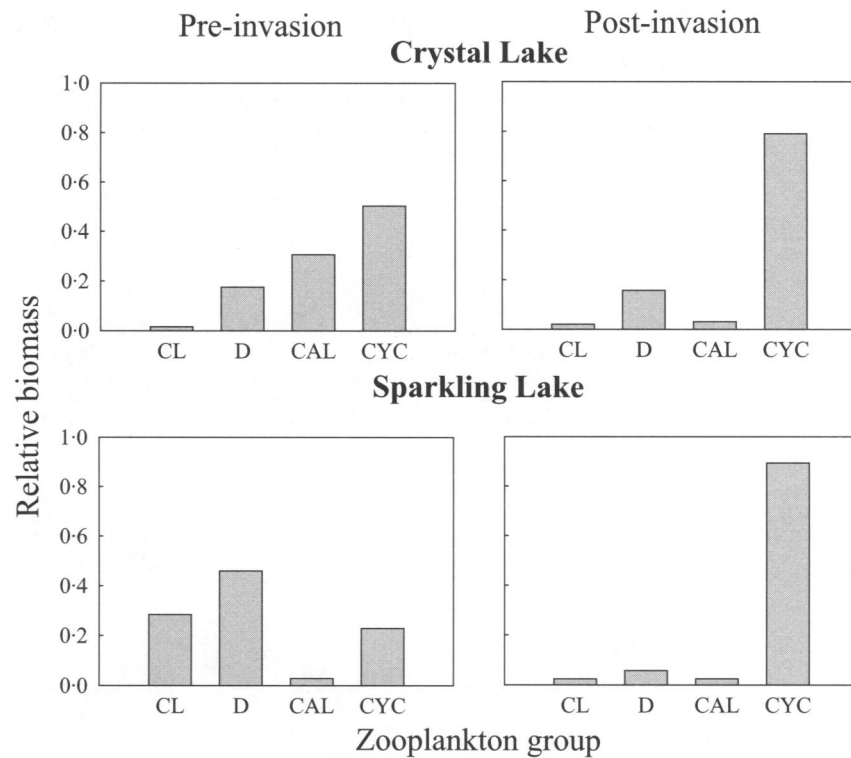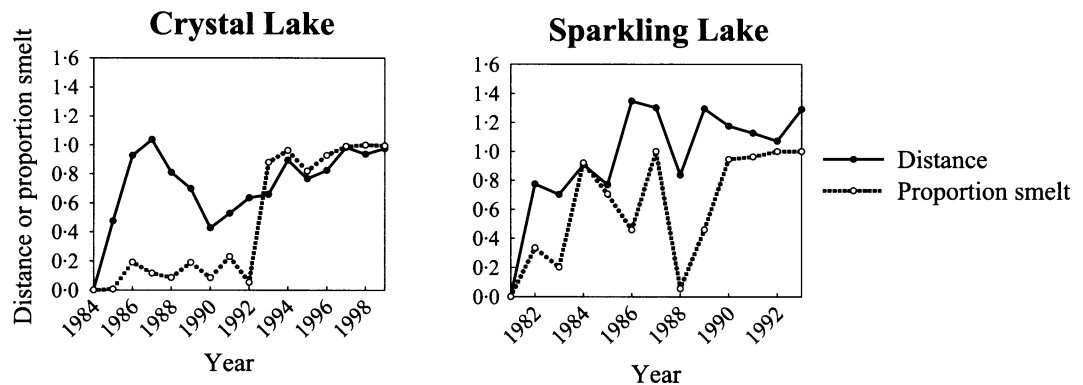
Fig. 2. Means over time of the relative biomasses of the four major zooplankton taxa 1 year prior to and 5 years following the invasion by smelt for Crystal and Sparkling lakes.

(a) Comparison to pre-smelt condition

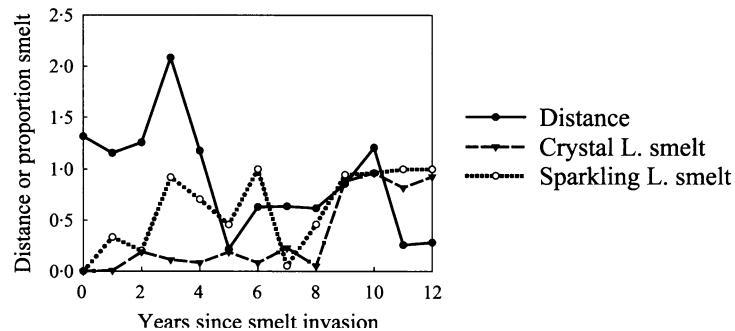### (b) Between-Lake comparison

Fig. 3. Change in the Euclidian distance between annual centroids from the three-dimensional non-metric multidimensional scaling (NMS) fit. Distances were calculated for (a) each year from the last presmelt year (presmelt years were 1981 for Crystal Lake 1984 for Sparkling Lake) and for (b) the distance between communities in the two lakes in each year following smelt invasion. For reference purposes, the proportion of smelt in each lake is also shown.
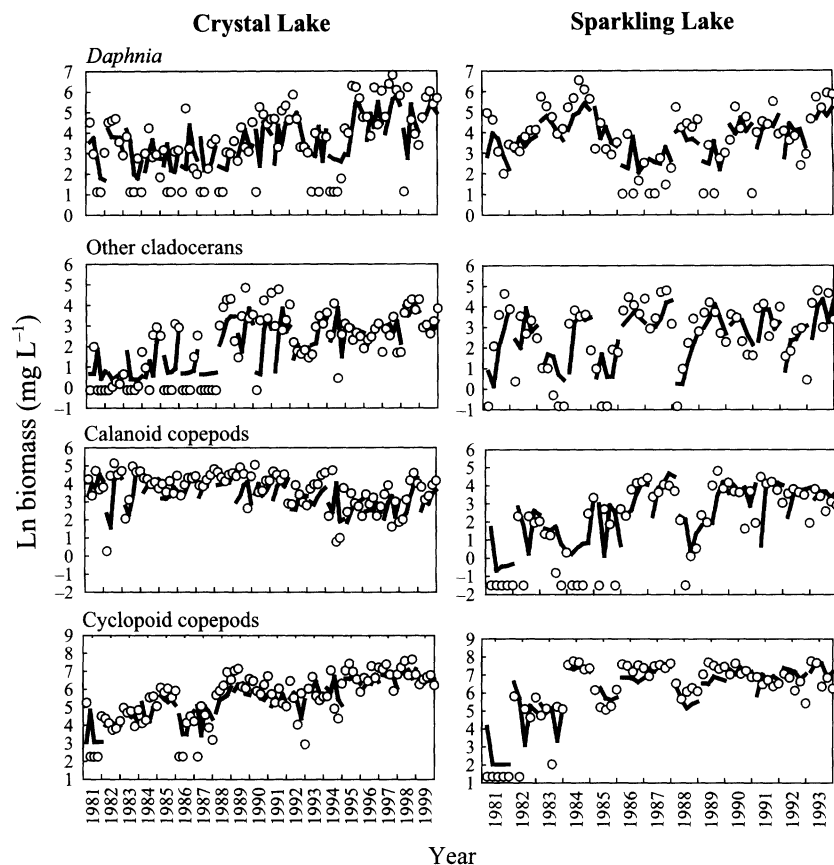
Fig. 4. Within-season time-series plots of $\log_e$ biomass (mg L^{-1}) of the four major zooplankton taxa in Crystal and Sparkling Lakes. Circles represent the observed data and the lines are the one-step-ahead predictions from the MAR(1) model.

Table 1. Model coefficients for the covariates (c_{ik}) in the best-fitting MAR(1) model. Significance of coefficients was determined by bootstrapping, and *$P < 0.05$

Zooplankton group	Lake	Smelt in Crystal	Smelt in Sparkling	Chlorophyll	Temperature
Daphnia	0·24*	0·24*	0·24*		
Other cladocera		0·21*	0·21*		
Calanoid copepods		−0·07*	0·49*		0·23*
Cyclopoid copepods		0·30*	0·62*		

Table 2. Model coefficients for the variates (b_{ij}) in (a) Crystal Lake and (b) Sparkling Lake in the best-fitting MAR(1) models. The table should be read as the group heading the column having the specified effect on the group indicated in the row where the coefficient appears. Significance of coefficients was determined by bootstrapping, and *$P < 0.05$

	Daphnia	Other cladocera	Calanoid copepods	Cyclopoid copepods
(a) Crystal Lake				
Daphnia			−0·19*	
Other cladocera				
Calanoid copepods				
Cyclopoid copepods				
(b) Sparkling Lake				
Daphnia			−0·19*	
Other cladocera				
Calanoid copepods	−0·41*			
Cyclopoid copepods	−0·12*			

The zooplankton interactions from the best AIC model show a negative coefficient for the effect of calanoid copepods on *Daphnia* in Crystal Lake, and additional effects of *Daphnia* on calanoid copepods and *Daphnia* on cyclopoid copepods in Sparkling Lake (Table 2). The identification of a greater number of autoregression coefficients in Sparkling Lake could be due to greater overall variability in the log biomasses of taxa in the data set, since the ability of MAR(1) models to detect interactions depends on the variance in the data. The bootstrapped log-likelihood ratio test rejected the null model with no non-zero autoregression coefficients for zooplankton interactions in favour of the best AIC model; all 10 000 bootstrapped log-likelihood ratios calculated under the null hypothesis were less than the log-likelihood ratio calculated from the data ($P << 0.001$).

Using the best AIC MAR(1) model to predict changes in the zooplankton community before and after smelt invasion (circles in Fig. 5) gave reasonable values in comparison to the change in observed mean log biomasses calculated from the raw data (bars in Fig. 5); all observed values were well within the 95% prediction intervals obtained by bootstrapping the best AIC model. Predictions based on the null MAR(1) including no coefficients for interactions between zooplankton taxa (x in Fig. 5) are close to those from the best AIC model and lie with the 95% prediction intervals.

Discussion

By examining the time series simultaneously from two lakes, we showed that the effect of invasion by an exotic predator on prey communities depended upon the identity and feeding habits of the native predator species that were displaced. Invasion by the exotic predator into both communities had large effects, causing the two initially dissimilar prey communities to converge to a similar structure. Interactions between prey taxa, as measured by autoregression coefficients, were important in explaining the short-term dynamics of the prey community (between samples within a summer), but were relatively unimportant in explaining the long-term change in prey communities over years. Rather, these were driven by direct effects of changes in predation patterns.

SHORT-TERM PATTERNS (LIMITATION FACTORS)

The effect of invading rainbow smelt depended on which native species of planktivore were already present in the lakes. The three main planktivore species involved in the food webs of Crystal and Sparkling Lakes, cisco, yellow perch and rainbow smelt, are known to have different feeding and behavioural habits (Johnson & Kitchell 1996). Thus, the differences in response of the zooplankton communities to changes in the planktivore communities revealed in our MAR(1) analysis are not surprising. In all but one case, the proportion of smelt in the planktivore communities had positive autoregression coefficients for zooplankton prey. This implies that smelt was a weaker predator on most zooplankton taxa than perch, and especially
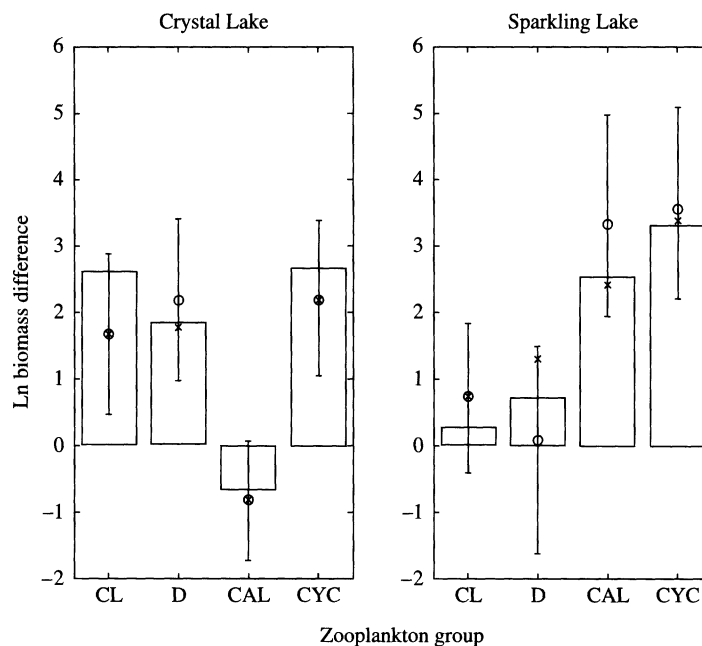

Fig. 5. The observed (bars) and MAR(1) model predictions (circles with error bars and xs) for changes in means of each zooplankton taxon between the years preceding and including initial smelt invasion (Sparkling 1981–82; Crystal Lake 1981–84) and the final 3 years of the time-series (Crystal Lake 1997–99; Sparkling Lake 1992–94). The circles represent the prediction of the best AIC MAR(1) model for the change in mean log biomass of the different taxa, with error bars giving the 95% the bootstrapped confidence intervals. The xs are the predictions from the null MAR(1) model excluding coefficients for the effects of interactions between taxa.

than cisco. The exception is the negative coefficient for the effect of proportion smelt on calanoid copepods in Crystal Lake, which suggests that smelt had a greater feeding impact on this taxon than did perch. Overall, the MAR(1) analysis demonstrates direct changes in predation rates on the different zooplankton taxa caused by smelt invasion.

The autoregression coefficients reveal the pathways through the food webs of the two lakes which explain the observed changes in taxa abundances during smelt invasion. In Sparkling Lake, smelt caused a decline of cisco through direct predation (Hrabik *et al.* 1998). Therefore, smelt acted as an intraguild predator (Polis & Holt 1992). The positive effects of proportion smelt on zooplankton indicate that the direct effect of smelt on zooplankton via predation was smaller than the indirect effect caused by the predation of smelt on cisco and the consequent reduction in cisco predation on zooplankton. The strong effect of intraguild predation implies that smelt acted primarily as a temporary fourth trophic level of piscivores and induced a trophic cascade (Oksanen *et al.* 1981; Carpenter, Kitchell & Hodgson 1985), in which cisco (at the third trophic level) were reduced and zooplankton (at the second trophic level) were increased. Differences in the responses of zooplankton to reductions in cisco predation in turn revealed competitive interactions between zooplankton taxa, as those taxa released from predation (especially *Daphnia*) exerted greater competitive effects other taxa. The key role of the large-bodied *Daphnia* as both a superior competitor and vulnerable prey has been shown repeatedly (Leibold 1989; Mazumder 1994; Cottingham & Schindler 2000).

The food-web pathways explaining the response of the zooplankton community to smelt invasion in Crystal Lake were different. Here, smelt displaced perch via resource competition (Hrabik *et al.* 1998), not as an intraguild predator. The impact of smelt invasion on predation on calanoid and cyclopoid copepods was less than that found for Sparkling Lake, indicating that smelt and perch did not have greatly differing predation rates on these two taxa. Only one negative autoregression coefficient between zooplankton was revealed (calanoid copepods on *Daphnia*). Absence of the two additional interactions identified in Sparkling Lake (for effects of *Daphnia* on calanoid and cyclopoid copepods) is explained by the similar predation of smelt and perch on zooplankton; changes in zooplankton abundances were not sufficient to reveal possible competitive interactions.

LONG-TERM PATTERNS (CONTROLLING FACTORS)

The most striking result of exotic predator invasion was the convergence in structure of the previously dissimilar prey communities in the two lakes. This illustrates the role of planktivory in structuring zooplankton communities (e.g. Hrbáček *et al.* 1961; Brooks & Dodson 1965; Mills & Schiavone 1982) and

the magnitude of the effect that a single planktivore species can have. Both zooplankton communities after smelt invasion were dominated by cyclopoid copepods (mainly *Diacyclops thomasi*), the taxon which the MAR(1) model identified as experiencing the greatest release from predation following smelt invasion. The rate at which zooplankton communities changed following smelt invasion paralleled the rate at which smelt replaced the native planktivores (Fig. 3a), especially once smelt had become established in Crystal Lake. The faster displacement of the native planktivore in Sparkling Lake was associated with faster change in the zooplankton community and establishment of cyclopoid domination. All these patterns suggest strong top-down effects of planktivorous fish on the zooplankton communities.

Similar convergence patterns induced by invasive species across landscapes have been observed in other systems. These can arise because of the actual movement of species themselves, as has occurred with fish across the United States (Rahel 2000). The movement of species has led to a homogenization of fish community composition at the continent-wide scale. Landscape-level patterns can also arise because of effects of exotics on the native species in communities, as was observed in our study and by Gotelli & Arnett (2000), who observed a decline in the competitive hierarchies of native ant communities with invasion of the red imported fire ant. Evidence is mounting that competitive interactions between species can be altered by the introduction of invasive species (Mack *et al.* 2000).

Composition of the zooplankton communities shifted in a directional way towards dominance by cyclopoid copepods in both lakes. Such a shift with smelt invasion is expected for a number of reasons. Smelt have a wide temperature tolerance and demonstrate diel vertical migration, moving into the epilimnion of lakes at night (Evans & Loftus 1987). This, combined with observations that smelt can deplete large-bodied *Daphnia* populations (Reif & Tappa 1966; Galbraith 1967), suggests that taxa of vertically migrating, larger-bodied species like *Daphnia* and calanoid copepods may be especially vulnerable to smelt predation, thereby releasing cyclopoids. Increases in the cyclopoid *D. thomasi* were also noted in Castle Lake, California, with the release of strong planktivory (Elser *et al.* 1995). Furthermore, cyclopoid copepods may have a competitive advantage over other zooplankton because they have an omnivorous feeding habit that allows them to derive energy from micrograzers as well as from phytoplankton (Adrian & Frost 1993; Hansen & Hairston. 1998).

Our analyses address whether convergence between the zooplankton communities in the two lakes was the result solely of changes in direct predation caused by smelt invasion or whether they also involved indirect effects caused by interactions between zooplankton taxa. In the MAR(1) model, the AIC model with negative autoregression coefficients for the interactions between

zooplankton taxa fitted the data much better ($P < 0.001$) than a null model without these coefficients. In contrast, using the MAR(1) model to predict the change in zooplankton communities before and after smelt invasion revealed little effect of interactions between zooplankton taxa. This suggests that, for long-term predictions or questions of controlling factors, zooplankton interactions are much less important than the direct effects of changes in planktivory caused by smelt invasion.

Crystal and Sparkling Lakes give an example in which an invading predator caused the convergence of two prey communities. Together, they show that species invasion may lead to homogenization of community structure (Mack *et al.* 2000), not only through spread of invaders themselves, but also through the direct and indirect impacts of the invaders on other species in the community. Examination of the communities in these lakes also shows that not all planktivore species are ecologically equivalent. Bigger shifts in prey communities may be expected when life histories and behaviour of exotic and native predator species are more disparate.

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