

Effects of an invasive bivalve on the zooplankton community of the Hudson River

MICHAEL L. PACE, STUART E. G. FINDLAY AND DAVID FISCHER

Institute of Ecosystem Studies, Box AB, Millbrook, New York, 12545, U.S.A.

SUMMARY

1. Previous studies documented that zebra mussels became abundant in the Hudson River during 1992 causing an 80–90% reduction in phytoplankton biomass. This study used intervention time series analysis of abundance, biomass and reproduction over the period 1987–95 to assess changes in zooplankton in response to the invasion.

2. Zebra mussels caused a size-dependent decline in zooplankton. Microzooplankton, including tintinnid ciliates, rotifers and copepod nauplii all declined in 1992 and were scarce thereafter. Mean abundances of post-naupliar copepods and of cladocerans were also lower following the invasion but these changes were not statistically significant ($P > 0.05$). Egg ratios and clutch sizes for the dominant cladoceran, *Bosmina freyi*, were not significantly related to zebra mussels, even though relatively low egg ratios were observed after the invasion.

3. The strong declines in microzooplankton were probably caused by direct zebra mussel predation. Estimated consumption rates by mussels were roughly equivalent to maximum microzooplankton growth rates.

4. The total biomass of zooplankton in the Hudson River declined by more than 70% following the invasion. Annual average zooplankton biomass was correlated with chlorophyll, but biomass per unit chlorophyll in the Hudson River was much lower than in lakes. The present study hypothesizes that this lower biomass reflects limitations by riverine flow and by predation during summer.

Introduction

The zebra mussel, *Dreissena polymorpha* Pallas, is currently spreading through the freshwaters of North America. After initial establishment in Lake St Clair and the Great Lakes (Hebert, Muncaster & Mackie, 1989), zebra mussels expanded their range into major river basins including the Mississippi, St Lawrence and Hudson drainages (Johnson & Carlton, 1996; Johnson & Padilla, 1996). Filter feeding by zebra mussels reduced phytoplankton biomass and increased water clarity in parts of the Great Lakes (Hebert *et al.*, 1991; Holland, 1993; Nicholls & Hopkins, 1993; Fahnenstiel *et al.*, 1995). Zebra mussels also compete for food and overgrow other bivalves (Ricciardi, Whoriskey & Rasmussen, 1995; Schloesser, Nalepa & Mackie, 1996), such that populations of many native bivalves are declining (Strayer & Smith, 1996).

These changes are clearly linked to the direct effects

of zebra mussels in removing phytoplankton or in attaching to and overgrowing other organisms. Many impacts on foodwebs, however, could result from indirect effects (MacIsaac, 1996); for example, will reductions of phytoplankton biomass reduce herbivorous zooplankton and zooplanktivorous fish? Will zebra mussels shift pathways of energy use to the benthos and promote bottom-feeding fish? The answers to these questions are uncertain. There are few long-term comprehensive studies of foodwebs in systems invaded by zebra mussels to provide data to evaluate their impacts on various populations and trophic groups. Further, compensatory responses at individual, population and community levels might ameliorate adverse effects of zebra mussels in many cases. Interactions among foodweb components are not sufficiently understood to allow sound predictions of the net effect of zebra mussels.

Examination of an analogous invasion by the Asiatic clam, *Pomatocorbula amurensis* (Schrenck), indicates that plankton and plankton-feeding fish can decline and remain at low levels. In this case, long-term data for San Francisco Bay show that grazing by *P. amurensis* caused large changes in phytoplankton (Alpine & Cloern, 1992), zooplankton (Kimmerer, Gartside & Orsi, 1994), and some fish (Moyle *et al.*, 1992). The three common copepod species declined by 50–90%, mostly because of direct feeding on copepod nauplii by *P. amurensis* (Kimmerer *et al.*, 1994).

Zebra mussels also feed on smaller zooplankton, such as rotifers and protozoans, but are less effective at consuming larger crustaceans (MacIsaac, Sprules & Leach, 1991; MacIsaac, Lonnee & Leach, 1995). In western Lake Erie, where zebra mussels have become abundant, rotifers and nauplii appear to have declined while changes in cladocerans and post-naupliar copepods have been transitory (MacIsaac *et al.*, 1995). The modest changes in larger zooplankton are surprising given that phytoplankton biomass declined during the same period (MacIsaac *et al.*, 1995). These changes agree, however, with a simulation model based on Great Lakes pelagic foodwebs which predicts strong negative effects of zebra mussels on large phytoplankton (hence lower chlorophyll concentrations) but only weak effects on small phytoplankton and herbivorous zooplankton (Padilla *et al.*, 1996). If the observations and models from the Great Lakes are general, a lack of change in the larger crustacean zooplankton may buffer changes in other trophic groups (zooplanktivorous fish) which depend heavily on crustacean prey.

The repeated invasion of aquatic ecosystems by zebra mussels provides large-scale experiments that have the potential to reveal key interactions and mechanisms of regulation in aquatic foodwebs. The present study considers the effects on zooplankton of a zebra mussel invasion of an ecosystem where a large and sustained reduction in phytoplankton occurred because of increased mussel grazing (Caraco *et al.*, 1997). Zebra mussels were first observed in the Hudson River estuary in 1991. By the end of 1992, the population had spread over the length of the tidal freshwater section (Strayer *et al.*, 1996). The mussel population increased rapidly and by September of 1992 there were 550 billion individuals river-wide with an average abundance in the tidal freshwater section of 4000 m⁻² (Strayer *et al.*, 1996). Post-invasion

density of the zebra mussel was sufficient to increase grazing pressure on phytoplankton more than ten times (Caraco *et al.*, 1997). Summer chlorophyll concentrations declined from an average of 30 µg L⁻¹ prior to the invasion to < 5 µg L⁻¹ following the establishment of the zebra mussel population.

Using data for years 1987–95, therefore including both pre- and post-invasion observations, the present study tests whether zooplankton declined in response to increases in zebra mussels and decreases in phytoplankton. Time series methods are applied to assess both the uncertainty and magnitude of changes in abundance and biomass. An analysis is made of whether changes in zooplankton occurred throughout the estuary or were restricted to areas of highest zebra mussel density. This study evaluates whether changes in zooplankton are related to a loss of phytoplankton food or increased direct predation from zebra mussels.

Materials and methods

The Hudson River estuary has a north–south orientation and extends from Battery Park at the southern tip of Manhattan Island in New York City to the Green Island Dam north of Troy, New York. Sampling focused on the freshwater and oligohaline sections of the estuary as described below (also see Findlay, Pace & Fischer, 1996 for additional detail on stations and long-term data).

Zooplankton sampling

The sampling, counting and biomass estimation methods used by this study for zooplankton in the Hudson River have previously been described (Pace, Findlay & Lints, 1992) and these are only briefly summarized here. From 1987 to 1995, zooplankton were sampled every 2 weeks during the ice-free season from April to early December at a station near Kingston, New York. This station is located at river km 152 as measured by the distance upstream from Battery Park. Macrozooplankton (postnaupliar copepods and cladocerans) were sampled by pumping 105 l of water through a 70- to 80-µm mesh net (except in 1987 when a 150-µm mesh net was used, see Pace *et al.*, 1992). For microzooplankton (nauplii, rotifers, tintinnids), 2-L samples were collected and passed through a 35-µm mesh net. For both macro- and microzooplankton, triplicate samples were collected

at each sampling time and preserved in a sucrose-formalin solution. In years 1992–95 the macrozooplankton were sampled every 3–7 days from the end of May to the middle of June, as part of a study to document the interactions between zooplankton abundance and larval fish (Limburg *et al.*, 1997). These data are included in the graphs illustrating zooplankton dynamics but are excluded from the time series analyses (described below), because these statistical methods require even time intervals between samples.

Macrozooplankton were counted with a stereomicroscope at 25× magnification and microzooplankton were counted with an inverted microscope at 100× magnification. Tintinnids were not consistently counted during 1987 and so data for this year were excluded. To estimate biomass, mean weights determined from measurements made in an earlier study were used (Pace *et al.*, 1992). These weights were 1.21, 0.737, 0.363 and 0.0324 µg dry weight (DW) per individual for post-naupliar copepods, cladocerans, nauplii and rotifers, respectively. Using a single mean weight for each group introduces uncertainty to the estimate of biomass, but species and size-composition within the post-naupliar copepods, cladocerans and nauplii were low. Rotifers were more diverse, but nevertheless, all of the most abundant groups had individual weights within a factor of two of the mean estimate used. For tintinnid ciliates a weight of 0.0197 µg DW per individual was used, derived from volume estimates of *Tintinnopsis lacustris* Entz [= *Codonella cratera* (Leidy)] made by Pace (1982) and using a weight to volume conversion factor of 0.279 pg DW µm⁻³ (Gates, Rogerson & Berger, 1982).

The eggs of ovigerous copepods and cladocerans were counted. Copepod egg counts, however, were unreliable because of detachment during sampling and preservation. The egg ratio (eggs per female) and clutch size of cladocerans were calculated as indices of reproduction. The egg ratio is directly related to the birth rate as a function of temperature and food (Edmondson, 1972; Urabe, 1991).

In addition to the temporal sampling series at the Kingston station, transects were conducted longitudinally along the north–south axis of the Hudson River estuary (see maps in Pace *et al.*, 1992 and Findlay *et al.*, 1996 for further details). Six stations were sampled at river km 65, 79, 122, 152 (Kingston), 193 and 228. For much of the year all of these stations are tidal

freshwater. During summer, the salinity front (1 ppt) extends above the two most seaward stations (river km 65 and 79) and in the driest summers reaches the station at river km 122 (near Poughkeepsie, New York). Transects were conducted monthly or every other month from April–October or November over the years 1988–95. Consistently macrozooplankton but not microzooplankton were sampled on these transects.

Statistical analysis

To test whether zooplankton declined in concert with the establishment of the zebra mussel population, data were fit to an intervention time series model. Intervention analysis accounts for autocorrelation in time series and assesses whether a non-random change occurred associated with an event such as the zebra mussel invasion (Wei, 1990). Analysis of whether the zebra mussel actually caused a change is dependent on ecological interpretations that are consistent with the observed response (see Carpenter, 1993). The following model was used:

$$X(t) = \mu + 1/\phi(B) + a(t) + \alpha M(t) \quad (1)$$

where $X(t)$ represents zooplankton indexed at time interval t , μ is the mean of the series, and $a(t)$ a series of uncorrelated residuals. B is the backshift operator which expresses the effects on X of prior values of X (e.g. $BX_t = X_{t-1}$). $\phi(B)$ is the autoregressive operator represented as a polynomial in the backshift operator. For nearly all the models fit to the zooplankton time series, $\phi(B)$ was a polynomial for observations one time unit (2 weeks) and 1 year (seventeen samples per year) in the past ($1 - \phi_1 B_1 - \phi_{17} B_{17}$). $M(t)$ represents a manipulation series of dummy values which were either zero before the zebra mussel population was established or one after establishment. Time of the intervention was set as the point where zebra mussel populations were measured in 1992 (= 1 September) and found to be at high densities (Strayer *et al.*, 1996). The parameter α expresses the magnitude of the change in $X(t)$ following the manipulation. The magnitude and the direction of α is the statistic of interest. The standard error of the estimate, as well as the probability that α is significantly different from zero, is tested by comparison with the standard t -distribution. Models were fit with the ARIMA

procedure in SAS using the maximum likelihood method (SAS Institute, 1993).

All time series of abundances and biomass were log-transformed for analysis. Prior to log transformation, measurements of zero densities were set at the theoretical limit of detection— 0.5 L^{-1} for microzooplankton and 0.01 L^{-1} for macrozooplankton. Missing values were estimated by linear interpolation.

Sampling at the transect stations was not conducted at even time intervals so that time series analysis of this data was not possible. Instead, means from each station were compared before and after the invasion using a *t*-test. Serial correlation in the transect time series was either non-existent or not severe, probably because the time interval between sampling was long (monthly or every other month). Consequently, the assumption of independence in the observations (required for a *t*-test) was reasonable for these data.

Results

Zooplankton community composition

The zooplankton community of the Hudson is simple. There are two dominant cyclopoid copepods, *Diacyclops bicuspidatus thomasi* Forbes and *Halicyclops* sp. The routine counts did not distinguish between these species. Calanoids also occur but tend to be less abundant in the freshwater section relative to cyclopoids and more abundant in the oligohaline seaward stations. The principal calanoid is the estuarine copepod, *Eurytemora affinis* (Poppe). Harpacticoid copepods are also found in plankton samples at abundances typically $< 1 \text{ L}^{-1}$. Cladocerans are almost exclusively *Bosmina* (subgenus *Sinobosmina*) *freyi* De Melo & Hebert (*B. longirostris* O.F. Mueller using older nomenclature, see De Melo & Hebert, 1994). Species of *Daphnia*, *Diaphanosoma* and *Chydorus* are present, as is the predatory cladoceran *Leptodora kinditi* (Focke). The latter species was not, however, adequately sampled with the methods used in the present study. The rotifer community is dominated by *Polyarthra* spp., *Keratella cochlearis* Gosse, and *Trichocerca* spp. Species of the genera *Asplanchna*, *Ascomorpha*, *Brachionus*, *Collotheca*, *Filinia*, *Kellicottia*, *Notholca*, *Pleosoma* and *Synchaeta* were also commonly observed. Sampling and counting methods in the present study were not sufficient for quantitative estimates of ciliates, except for the freshwater

tintinnid, *Tintinnopsis lacustris*, which was retained on the 35- μm mesh net and easily counted along with the other microzooplankton.

The individual species are aggregated below into groups for the analysis of time series. The post-naupliar copepods are essentially the two cyclopoid species. Nauplii are an aggregate of all species. Cladoceran dynamics are equivalent to the dynamics of *B. freyi*. Rotifers represent a suite of species but *Polyarthra* and *Keratella* were almost always dominant. Tintinnids are one species.

Did zooplankton decline?

Beginning in mid-1992, and continuing through 1995, all microzooplankton groups declined dramatically (Fig. 1). Microzooplankton were most abundant during the summer but after the invasion these seasonal increases were virtually absent except for nauplii. Tintinnids were variably abundant among years but in some pre-zebra mussel years reached densities of several thousand per litre. Following the invasion, tintinnids never exceeded 250 L^{-1} (Fig. 1a). Similarly prior to the invasion, rotifers typically increased in summer to densities $> 1000 \text{ L}^{-1}$ but did not exceed 200 L^{-1} after the mussel population became established in late 1992 (Fig. 1b). Nauplii were also less abundant following the mussel invasion (Fig. 1c), although the change was less dramatic relative to tintinnids and rotifers.

Time series models confirmed the strong declines in microzooplankton. All *t*-values for the intervention term, α , were significant ($> \pm 1.96$) and magnitudes were large (Table 1). The meaning of these models can be assessed with an example. Assuming rotifer abundances of 1000 L^{-1} at 2 weeks and 1 year prior to time *t* (see eqn 1), predicted rotifer abundances at *t* would be 303 L^{-1} and 42 L^{-1} in the absence and presence of zebra mussels, respectively. Note that rotifer abundances decrease for both scenarios because abundances of 1000 L^{-1} are considerably above the mean. The key point is the difference in the predicted abundances before and after the invasion.

Changes in the abundance of the two principal macrozooplankton groups were harder to discern (Fig. 2). Cladocerans were extremely variable due to the dynamics of the dominant species *B. freyi*, which increased each year from abundances less than 0.1 L^{-1} to a brief maximum in early June often > 100

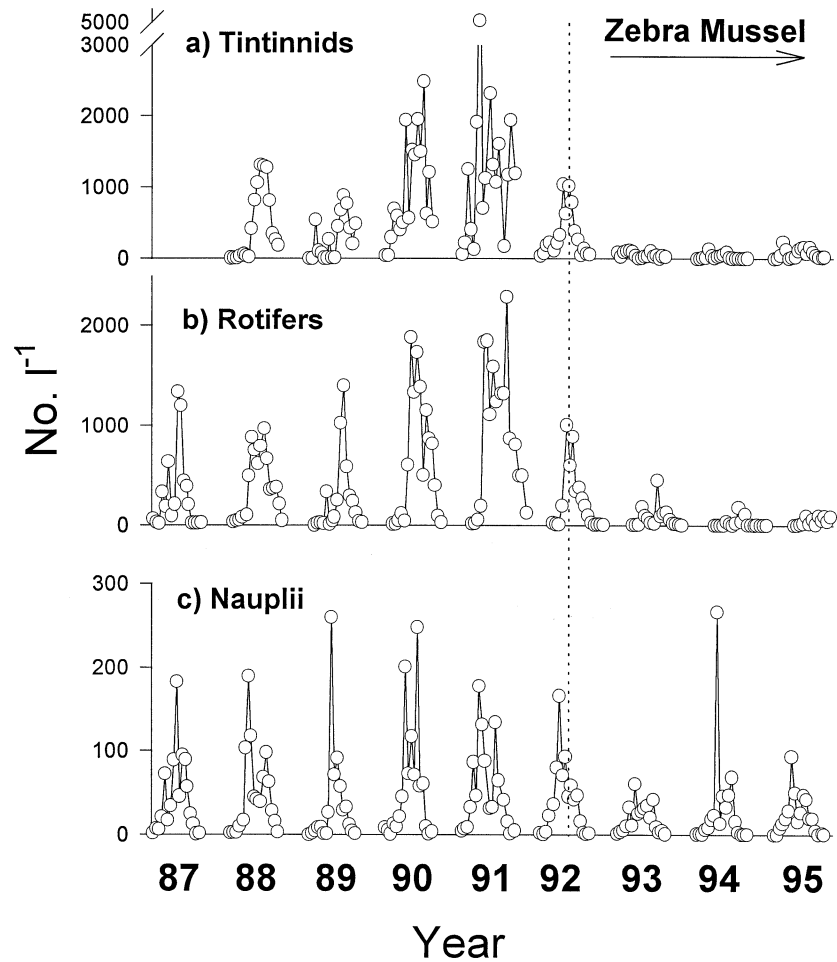


Fig. 1 Abundance of microzooplankton, including (a) tintinnids, (b) rotifers, and (c) copepod nauplii at the Kingston station, 1987–95. The dashed line in this and succeeding figures indicates the point where the zebra mussel population became strongly established, based on population estimates conducted in September 1992.

Table 1 Parameters for intervention models fit to time series following eqn 1. For each parameter the estimated standard error and *t*-value are shown. All data were log-transformed. $n = 155$ for all cases except tintinnids where $n = 138$. *t*-values $> \pm 1.96$ indicate the estimated parameter value is significantly different from 0 at $P = 0.05$. Last row is cladoceran egg ratio

Group	$\mu \pm SE$	<i>t</i>	$\phi_1 \pm SE$	<i>t</i>	$\phi_{17} \pm SE$	<i>t</i>	$\alpha \pm SE$	<i>t</i>
Tintinnids	2.30 ± 0.26	9.00	0.508 ± 0.069	7.37	0.252 ± 0.070	3.58	-0.804 ± 0.302	-2.66
Rotifers	2.18 ± 0.21	10.29	0.589 ± 0.063	9.30	0.238 ± 0.065	3.66	-0.854 ± 0.239	-3.58
Nauplii*	1.22 ± 0.12	9.85	0.448 ± 0.067	6.71	0.286 ± 0.075	3.80	-0.393 ± 0.181	-2.17
Cladocerans	0.17 ± 0.27	0.62	0.325 ± 0.063	5.16	0.495 ± 0.07	7.42	-0.420 ± 0.245	-1.71
Copepods	0.23 ± 0.21	1.08	0.427 ± 0.066	6.47	0.433 ± 0.072	6.05	-0.044 ± 0.182	-0.24
Biomass	1.44 ± 0.29	4.97	0.500 ± 0.06	47.79	0.439 ± 0.067	6.54	-0.481 ± 0.153	-3.14
Clad. ER*	0.24 ± 0.02	11.21	0.188 ± 0.079	2.39	-0.226 ± 0.093	2.44	0.022 ± 0.035	0.62

*For nauplii an additional term ϕ_8 was included in the model to account for a strong seasonal signal in this time series ($\phi_8 = -0.186 \pm 0.065$, $t = -2.87$). For egg ratio the second term is ϕ_6 and not ϕ_{17} as denoted in the column heading.

individuals L^{-1} . Following this maximum the population declined rapidly and then recovered with a second but less pronounced increase in September–October. The June maximum was observed in each of the 3 years following the invasion, although densities never reached 100 individuals L^{-1} , as observed in some

previous years (Fig. 2a). Because samples were taken every 3–7 days during the *Bosmina* bloom period in 1992–95, the lower peaks are probably not due to undersampling. Prior to the invasion, *Bosmina* also increased to densities of $> 10 L^{-1}$ in September–October. The autumn increase did not occur at

all in 1992 when zebra mussels were reaching their maximum densities. The autumn increase occurred in 1993 and 1994 but maximum densities were less than 10 L^{-1} . In 1995, however, the autumn increase was similar in magnitude to the pre-zebra mussel years (Fig. 2a). Overall, cladoceran densities appeared lower after the zebra mussel invasion, although seasonal dynamics followed patterns observed prior to the invasion.

Copepods were least affected by the invasion. Abundances and dynamics in 1993–95 generally resembled pre-invasion years. Copepods were scarce in 1992, the year of highest zebra mussel densities. The late season increase to densities $> 10 \text{ L}^{-1}$, characteristic of 1988–91 did not develop in 1992 or 1993.

Both macrozooplankton groups declined (negative intervention term) but the magnitude of the zebra mussel effect was clearly different for the two major groups. The intervention term for copepods was small and not significant. For cladocerans the estimate of α was less than twice its standard error (Table 1), the normal criterion for retaining a term in time series models (Wei, 1990). Nevertheless, the magnitude of α was large. Thus, there is a strong possibility that cladocerans declined but because of high variability in the time series, the effect of zebra mussels was difficult to differentiate clearly. Type II error (wrongly

accepting the hypothesis of no change) is a concern in this case.

Overall, the magnitude of zooplankton decline was size dependent (Fig. 3). Zebra mussels had the strongest effect on groups with average body sizes $< 0.1 \mu\text{g DW}$. Decline was also substantial in groups with body sizes in the $0.1\text{--}1.0 \mu\text{g}$ range, while decline was minimal for animals with body sizes $> 1 \mu\text{g}$. This conclusion, however, is limited by the small number of size classes considered in the present study and the large gap between size groups less than and greater than $0.1 \mu\text{g}$ (Fig. 3).

Total zooplankton biomass also declined after the invasion of the zebra mussel (Fig. 4). This change was large (over 70%) and significant based on the intervention model (Table 1); for example, assuming a biomass of $100 \mu\text{g DW L}^{-1}$ at 2 weeks and 1 year before time t , predicted zooplankton biomass at t would have been 75 and $25 \mu\text{g DW L}^{-1}$ prior to and following the invasion of the zebra mussel, respectively. The changes in zooplankton biomass reflect the large contribution of the three microzooplankton groups to total biomass; for example during 1991, microzooplankton were 79–99% of the zooplankton biomass, except on one date when *Bosmina* exceeded 300 L^{-1} . After the zebra mussel invasion, microzooplankton were still frequently 50% or more of the biomass, despite their lower abundance.

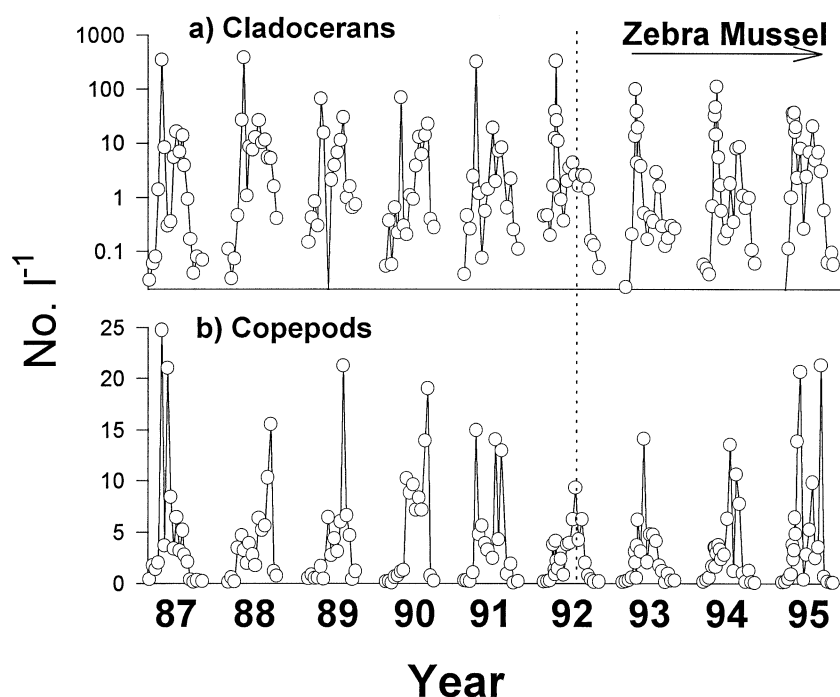


Fig. 2 Abundance of macrozooplankton, including (a) cladocerans (note log scale), and (b) post-naupliar copepods at the Kingston station, 1987–95.

The importance of microzooplankton in the Hudson reflects the general dominance of the community by animals (including the crustaceans) of small size.

Longitudinal patterns of zooplankton in relation to zebra mussels

Zebra mussels are not uniformly abundant in the Hudson River. Strayer *et al.* (1996) documented highest

biomass (> 10 g DW m⁻²) in the section of the estuary from river km 150–213, which includes the Kingston time series station. Upstream of this section (river km > 213), mussel biomass decreased by a factor of ten. Downstream of this section (river km < 150), mussel biomass decreased by a factor of 100. The mid-estuary section (km 150–213) of highest mussel biomass was also the region where phytoplankton biomass and productivity were greatest prior to the invasion (Caraco *et al.*, 1997). After the invasion, phytoplankton were strongly reduced throughout the estuary above river km 100 (Caraco *et al.*, 1997).

Given this distribution of mussels and phytoplankton, a decline in zooplankton was expected at the longitudinal sampling stations located upstream of river km 100 and little change downstream of that point. Four of the stations (1–4) were located above river km 100 (see Methods). Two of these stations (2 and 3) were located in the region of highest mussel density and greatest phytoplankton decline.

Spatial patterns in macrozooplankton abundance were consistent with observations at the time series station. There was little evidence of change in the copepods (Fig. 5a). Lower means were observed after the invasion at station 2 but not at station 3. None of the means were significantly different (*t*-test, all *P* > 0.3). Cladoceran abundances were lower at all stations after the invasion, especially at stations 2 and 3 (Fig. 5b). Cladocerans were also highly variable, however, so that none of the declines were significant (*t*-tests, *P* > 0.2 except station 3, *P* = 0.09). The patterns of change generally matched expectations of the study but, again, macrozooplankton decline was either slight (copepods) or marked but difficult to detect because of sampling variability (cladocerans).

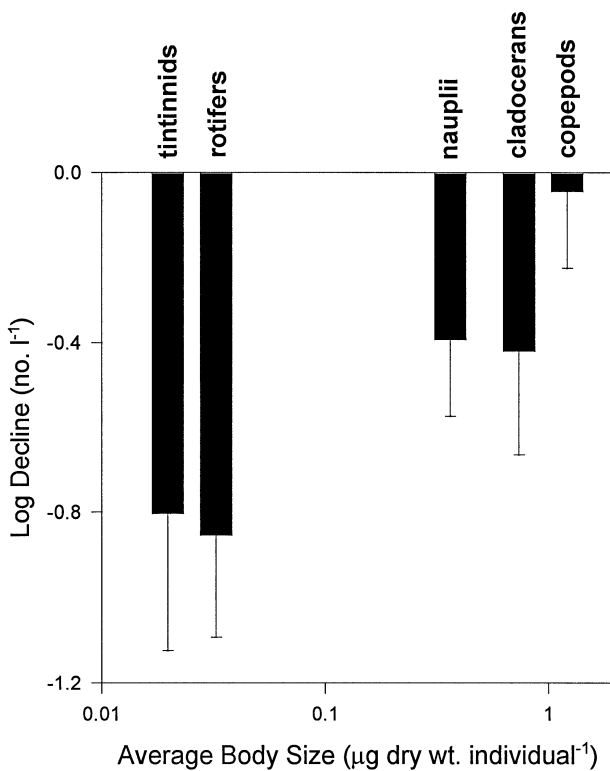


Fig. 3 Average body size of the five major zooplankton groups (tintinnids, rotifers, nauplii, cladocerans, post-naupliar copepods) and the magnitude of the decline as measured by the intervention term (α). Error bars are one standard error of α .

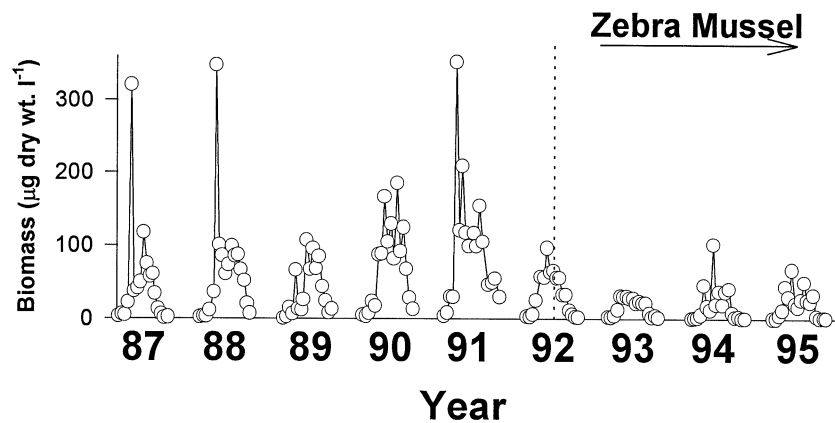


Fig. 4 Biomass of zooplankton at the Kingston station, 1987–95.

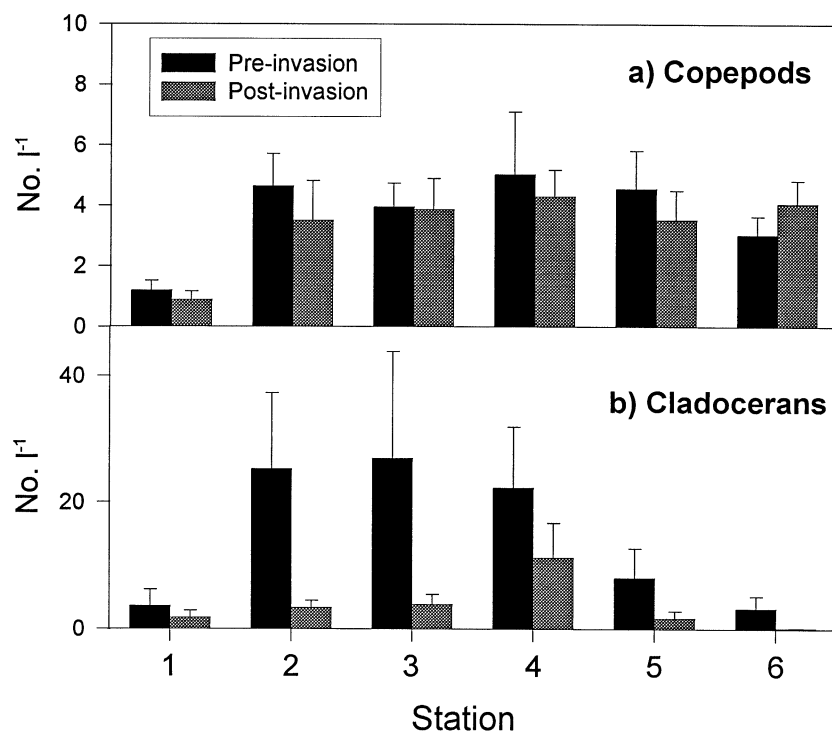


Fig. 5 Annual means and standard errors before (1988–91) and after (1993–95) the zebra mussel invasion for (a) copepods and (b) cladocerans. Stations are located on the north–south axis of the Hudson River (see text). Station 1 is the most northerly, upstream station. Station 6 is the most southerly, downstream station. Note that stations 2 and 3 are the regions of highest zebra mussel biomass.

Predation on zooplankton by zebra mussels

Specific predation (day^{-1}) by zebra mussels on zooplankton was estimated from average mussel density (Strayer *et al.*, 1996), published clearance rates, and the average depth of the Hudson River (8 m). The water column of the Hudson River is well mixed, with no temperature stratification, so the entire zooplankton community was available to zebra mussels. MacIsaac *et al.* (1992) measured zebra mussel clearance rates in the range of 20–100 mL per mussel h^{-1} and 1–2 mL per mussel h^{-1} on rotifers and macrozooplankton (*Bosmina* and cyclopoids), respectively. These ranges, using large zebra mussels (> 20 mm), agree well with measurement from other studies (Shevtsova *et al.*, 1986; MacIsaac *et al.*, 1995).

Estimated zebra mussel predation was compared with the maximum rates of zooplankton increase based on laboratory studies and on observations in the Hudson River (Table 2). Maximum growth rates of rotifers fall within the range of estimated predation rates. Predation alone, even at the lower mussel densities observed in 1995, appeared sufficient to suppress rotifers and other microzooplankton of similar size. Predation on macrozooplankton was two orders of magnitude lower than maximum growth rates (Table 2). Although zooplankton growth is

Table 2 Maximum growth rates of zooplankton and estimated predation rates due to zebra mussels

(a) Growth (day^{-1})			
Species or group	r_{max} (day^{-1})	Lab/Field	Source
<i>Keratella cochlearis</i>	0.28	Lab	Stemberger & Gilbert (1985)
<i>Polyarthra vulgaris</i>	0.39	Lab	Stemberger & Gilbert (1985)
Rotifers	0.09–0.17	Field	Hudson River (87–91)
<i>Bosmina longirostris</i>	0.27	Lab	Goulden <i>et al.</i> (1982)
<i>B. freyi</i>	0.30–0.41	Field	Hudson River (87–91)
Copepods	0.024–0.17	Field	Hudson River (87–91)
(b) Predation (day^{-1})			
Year	Zebra mussels ($n \text{ m}^{-2}$)	Predation on microzooplankton	Predation on macrozooplankton
1992	3900	0.240–1.180	$12.0\text{--}24.0 \times 10^{-3}$
1993	2600	0.150–0.770	$7.7\text{--}15.0 \times 10^{-3}$
1994	1400	0.080–0.410	$4.1\text{--}8.1 \times 10^{-3}$
1995	610	0.037–0.180	$1.8\text{--}3.7 \times 10^{-3}$

frequently below maximum rates, zebra mussel predation was probably not a significant loss term for copepods and cladocerans in the Hudson River.

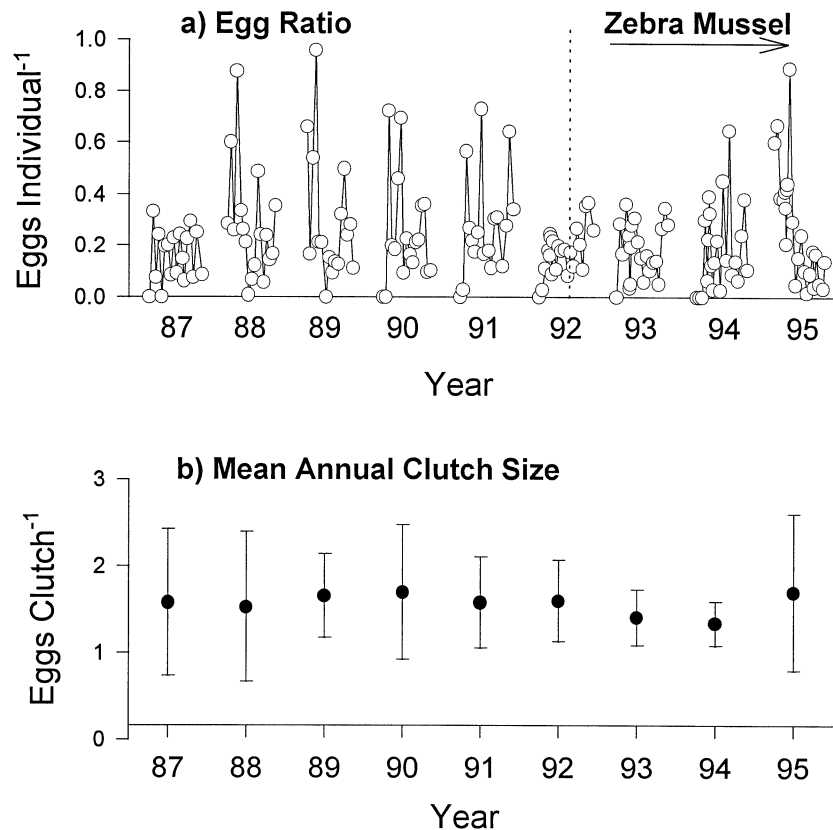


Fig. 6 Reproductive indices of *Bosmina freyi* at the Kingston station, 1987–95, based on (a) egg ratios and (b) mean annual clutch size.

Did zooplankton reproduction decline after the invasion?

Zooplankton reproduction is sensitive to both food quantity and quality. The large reductions in phytoplankton observed after mid-1992 (Caraco *et al.*, 1997) suggest that reproduction could have declined if phytoplankton were limiting. The egg ratio and clutch size of *B. freyi* were used to assess this possibility.

Egg ratios were highly variable seasonally and among years (Fig. 6a). Ratios increased and often were highest during the spring period of maximum abundance. Relatively low egg ratios were observed in the years 1992, 1993 and 1994 (Fig. 6). Zebra mussel densities were highest and chlorophyll concentrations lowest during these years (Caraco *et al.*, 1997). However, low egg ratios were also observed in 1987, many years prior to the mussel invasion, and high egg ratios were observed in 1995 (Fig. 6a). There was no significant impact of the zebra mussel invasion on the egg ratio time series based on intervention analysis (Table 1).

Clutch size is also an index of reproduction that is sensitive to food (Pace, Porter & Feig, 1984) and is less influenced by age structure than the egg ratio, where, for example, high juvenile abundance might depress the egg ratio of an otherwise fecund population. Analysis was not performed for time series of clutch sizes, because some samples had only a few reproductive individuals, so that clutch size estimates for specific dates were highly uncertain. Instead, mean annual clutch size was calculated by averaging clutch size for all sampling times where reproductive individuals were present. Clutch sizes were similar for all years ranging from 1.3 to 1.7 eggs per reproductive individual (Fig. 6b). Lowest mean clutch sizes were observed in the first two full years (1993 and 1994) following the zebra mussel invasion but variability in these years was well within the range observed over the entire period and mean clutch size in 1995 was as high as any other year. Thus, losses of food did not lead to a clear, long-term drop in reproduction of *B. freyi* in the Hudson River as measured either by the egg ratio or clutch size.

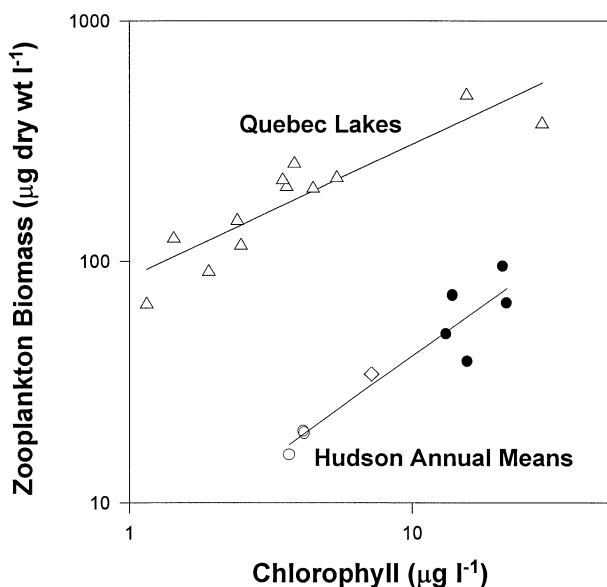


Fig. 7 Relationship between annual mean concentration of chlorophyll *a* and zooplankton biomass in the Hudson River and for a set of twelve Quebec lakes studied by Pace (1986). Δ are Quebec lakes. Symbols for the Hudson reflect pre-zebra mussel years (\bullet , 1987–91), transition year (\diamond , 1992), and post-zebra mussel years (\circ , 1993–95).

Discussion

The main result of this analysis is that zebra mussels caused a strong size-dependent decline in zooplankton, severely depleting the microzooplankton. The magnitude and timing of the change were best related to the invasion and establishment of the zebra mussel population. The timing of the decline was consistent with a similar decline observed for phytoplankton, also attributed to zebra mussels (Caraco *et al.*, 1997). Other factors such as river flow and temperature were unrelated to the changes in zooplankton; for example, the initial years following the invasion (1993 and 1994) were relatively low and high flow years, respectively (see Caraco *et al.*, 1997), and 1995 was a year of very low freshwater flow (United States Geological Survey, unpublished data). Zooplankton biomass in the Hudson River is negatively correlated with flow (Pace *et al.*, 1992) so, in the absence of zebra mussels, zooplankton biomass should have been relatively high in 1993 and 1995 but was not (Fig. 7).

A probable cause of the reductions in tintinnids, rotifers and nauplii was direct predation by the zebra mussel. The loss of phytoplankton food cannot be ruled out as a contributing cause of the microzooplankton decline, because the present study has no

measures of reproductive rates, which would have dropped after the invasion if food was limiting. Further, a decline in nauplii could also have resulted from lower egg production by adult copepods. Nevertheless, mussel predation alone appears sufficient to account for the decline of all three groups of microzooplankton.

Decline in macrozooplankton was less clear. Zebra mussels had little overall effect on copepods, although the average abundance of copepods was lower after the invasion. Cladocerans may well have declined, but the intervention term of the time series analysis was not significant at the 0.05 level. The analysis of the cladoceran time series indicates that, even with long-term data, important changes may be very difficult to detect in highly variable populations.

Zebra mussels have two possible impacts on macrozooplankton. (i) They could consume some smaller copepods and cladocerans, but these projected predation rates were modest relative to expected growth rates (Table 2). (ii) Mussels are also competitors for phytoplankton. Loss of phytoplankton food did not result in a decline in the dominant cyclopoids. These copepods are omnivorous but, given the loss of both microzooplankton prey and phytoplankton, it is somewhat surprising that these species were not affected. In addition, nauplii were also reduced so fewer juvenile copepods were present to recruit to the larger copepodite stages. These observations suggest that the abundance of post-naupliar copepods is independent of nauplii abundance in the Hudson River. There may have been more subtle effects on copepod demography, but the present study did not include the stage-specific or species-specific analyses required to examine this possibility.

In addition to phytoplankton, crustacean zooplankton can use bacteria, protozoans and detritus as food. Bacteria have not declined since the invasion (S. Findlay, M. L. Pace & D. Fischer, unpublished data). Cyclopoid copepods are not efficient at feeding on particles as small as bacteria but do consume protozoa (Sanders & Wickham, 1993). *Bosmina* does feed on bacteria and, in the Hudson River, these potentially account for a significant portion of this animal's carbon requirement (Vaqué *et al.*, 1992). The Hudson River is a heterotrophic ecosystem with substantial degradation of allochthonous carbon (Howarth, Schneider & Swaney, 1996; Raymond, Caraco & Cole, 1997) and very high rates of bacterial production (Findlay *et al.*,

1991). Resources derived from these heterotrophic pathways may buffer crustacean zooplankton against the loss of phytoplankton.

The residual phytoplankton in the Hudson River may also be sufficient to sustain crustacean zooplankton at, or near, their long-term densities. This possibility is supported by a simulation model of Green Bay in Lake Michigan (Padilla *et al.*, 1996). In that model zebra mussel grazing resulted in a dramatic reduction of large phytoplankton but only modest reduction in small phytoplankton and crustacean zooplankton. Zooplankton were supported by increased productivity of small phytoplankton released from nutrient competition with large phytoplankton (Padilla *et al.*, 1996). Nutrient competition among phytoplankton is much less important in the turbid Hudson River because of light limitation (Cole, Caraco & Peierls, 1992). There is, however, evidence that specific phytoplankton growth rates increased after the invasion of the zebra mussel due to increases in summer transparency and shifts to more rapidly growing species (Caraco *et al.*, 1997).

Figure 7 illustrates the annual mean of total zooplankton biomass (includes macro- and micro-zooplankton) and chlorophyll at the time series station for 1987–95 compared with data from Quebec lakes collected using similar methods by Pace (1986). In the Hudson River, average biomass ranged from 39 to 96 $\mu\text{g DW L}^{-1}$ prior to the invasion, was 34 $\mu\text{g DW L}^{-1}$ in 1992, and was 16–20 $\mu\text{g DW L}^{-1}$ for 1993–95. Lower zooplankton biomass in the Hudson River was well related to chlorophyll concentrations based on these annual means (regression: $r^2 = 0.89$). The decline, however, probably reflects the similar effect of zebra mussel grazing on phytoplankton and microzooplankton rather than a loss of food for zooplankton, as argued above. Zooplankton biomass in the Hudson River is roughly tenfold lower than that in lakes at similar chlorophyll concentrations. While net primary production in the Hudson River is low (Cole *et al.*, 1992), resources derived from allochthonous carbon and heterotrophic bacterial production are potentially abundant (Vaqué *et al.*, 1992). The lower zooplankton biomass relative to lakes is therefore surprising. This paper has previously implied that water residence limits population development (Pace *et al.*, 1992), and this view is supported by a strong positive relationship between water residence time and zooplankton biomass for thirty-one rivers studied by Basu & Pick

(1996). This explanation, however, is not complete in the case of the Hudson River because water residence times during summer (months) are much longer than zooplankton generation times (days to weeks).

These observations suggest that predation by invertebrates and vertebrates may be an additional important limitation for Hudson zooplankton. First, the predatory cladoceran, *Leptodora kindtii*, increases to a density of 0.1–1.0 L^{-1} after the *Bosmina* population maximum in early June and may exert significant predation pressure on macrozooplankton (M.L. Pace & K.E. Limburg, unpublished data). Second, the Hudson has many resident and anadromous fish with zooplanktivorous life stages. These stages are most abundant in both the freshwater and oligohaline sections of the river during summer (Gladden *et al.*, 1988; Limburg, 1996). Finally, the zooplankton community is dominated by small-bodied species, a trait characterizing intense size-selective predation from fish (Brooks & Dodson, 1965). This hypothesis of significant top-down control of zooplankton requires further evaluation but, if correct, would help to explain why zebra mussels have had a limited impact on the macrozooplankton.

If the main pathway of interaction between zebra mussels and zooplankton is direct consumption, which is highly size dependent, systems dominated by small zooplankton should suffer larger declines when invaded. Typically small zooplankton dominate systems when predation from planktivorous fish is intense (Brooks & Dodson, 1965). Planktivorous fish strongly select the largest zooplankton, while zebra mussels have their greatest impact on small zooplankton. So zebra mussels and fish are complementary predators.

A key concern about the zebra mussel invasion is that mussel grazing may alter the foodweb supporting desired fish species. In particular, many fishes depend on zooplankton during their early life stages and this is especially true for the anadromous species that use the Hudson River as a nursery (Limburg, 1996; Limburg *et al.*, 1997). Despite the substantial reductions of phytoplankton and microzooplankton, however, the availability and use of zooplankton by fish in the Hudson River may not have changed as a consequence of the invasion. The present study documented high selectivity of larval white perch, *Morone americana* (Waldbaum), and striped bass, *M. saxatilis* (Gmelin), for copepods and cladocerans during 1994 (Limburg *et al.*, 1997). These species depend almost entirely

on macrozooplankton, and the gut contents of fish observed in this study are similar to those found in pre-zebra mussel years (Hjorth, 1988; R. Schmidt, unpublished data). If dependence on, and high selectivity for, the largest macrozooplankton (copepods) is characteristic of other Hudson River fish species, then the decline of zooplankton biomass may be of little consequence to fish populations. This is an example of how specific trophic interactions can buffer species from substantial alterations of productivity and energy flow in foodwebs.

The zebra mussel invasion in the Hudson River represents a phytoplankton-removal 'experiment' at an ecosystem scale. Perhaps the most surprising result of this analysis is the persistence of crustacean zooplankton, especially copepods, at or near levels observed prior to the experiment. We would not have predicted this result but, before the invasion, would rather have argued for a stronger dependence of zooplankton on phytoplankton. The lack of dependence illustrates the value of studying large-scale perturbations to ecosystems. The results suggest an interesting hypothesis about top-down regulation of estuarine and riverine zooplankton communities, indicate that the loss of phytoplankton may not cascade up the foodweb to fish, and support the idea that zooplankton in systems like the Hudson River use a variety of energy sources, not just phytoplankton production.

Acknowledgments

This work was supported by grants from the Hudson River and National Science Foundations. We thank our collaborators on the Hudson River zebra mussel project, N. Caraco, J. Cole and D. Strayer, for sharing data, discussion and comments on this manuscript. The paper benefited from the reviews and editorial suggestions of A. Hildrew, H. MacIsaac and W. DeMott.

References

- Alpine A.E. & Cloern J.E. (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography*, **37**, 946–955.
- Basu B.K. & Pick F.R. (1996) Factors regulating phytoplankton and zooplankton biomass in temperate rivers. *Limnology and Oceanography*, **41**, 1572–1577.
- Brooks J.L. & Dodson S.I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28–35.
- Caraco N.F., Cole J.J., Raymond P.A., Strayer D.L., Pace M.L., Findlay S.E.G. & Fischer D.T. (1997) Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. *Ecology*, **78**, 588–602.
- Carpenter S.R. (1993) Statistical analysis of the ecosystem experiments. *The Trophic Cascade in Lakes* (eds S. R. Carpenter and J. F. Kitchell), pp. 26–42. Cambridge University Press, Cambridge.
- Cole J.J., Caraco N.F. & Peierls B. (1992) Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? *Limnology and Oceanography*, **37**, 1608–1617.
- De Melo R. & Hebert P.D.N. (1994) A taxonomic reevaluation of North American Bosminidae. *Canadian Journal of Zoology*, **72**, 1808–1825.
- Edmondson W.T. (1972) Instantaneous birth rates of zooplankton. *Limnology and Oceanography*, **17**, 792–795.
- Fahnenstiel G.L., Lang T., Bridgeman G.A., McCormick M.J. & Nalepa T.F. (1995) Phytoplankton productivity in Saginaw Bay, Lake Huron: effects of zebra mussel (*Dreissena polymorpha*) colonization. *Journal of Great Lakes Research*, **21**, 465–475.
- Findlay S.E.G., Pace M.L., Lints D., Cole J.J., Caraco N.F. & Peierls B. (1991) Weak coupling of bacterial and algal production in a heterotrophic ecosystem, the Hudson Estuary. *Limnology and Oceanography*, **36**, 268–278.
- Findlay S., Pace M. & Fischer D. (1996) Spatial and temporal variability in the lower food web of the tidal freshwater Hudson River. *Estuaries*, **19**, 866–873.
- Gates M.A., Rogerson A. & Berger J. (1982) Dry to wet weight biomass conversion constant for *Tetrahymina ellioti* (Ciliophora, Protozoa). *Oecologia*, **55**, 145–148.
- Gladden J.B., Cantelmo F.R., Croom J.M. & Shabot R. (1988) Evaluation of the Hudson River ecosystem in relation to the dynamics of fish populations. *American Fisheries Society Monograph*, **4**, 37–52.
- Goulden C.E., Henry L. & Tessier A.T. (1982) Body size, energy reserves, and competitive ability in three species of Cladocera. *Ecology*, **63**, 1780–1789.
- Hebert P.D.N., Muncaster B.W. & Mackie G.L. (1989) Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1381–1388.
- Hebert P.D.N., Wilson C.C., Murdoch M.H. & Lazar R. (1991) Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. *Canadian Journal of Zoology*, **69**, 405–409.
- Hjorth D.A. (1988) Feeding selection of larval striped

- bass and white perch in the Peekskill region of the Hudson River. *Fisheries Research in the Hudson River* (ed. C. L. Smith), pp. 134–147. State University of New York Press, Albany, NY.
- Holland R.E. (1993) Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, western Lake Erie since the establishment of the zebra mussel. *Journal of Great Lakes Research*, **19**, 617–624.
- Howarth R.W., Schneider R. & Swaney D. (1996) Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. *Estuaries*, **19**, 848–865.
- Johnson L.E. & Carlton J.T. (1996) Post-establishment spread in large-scale invasions: dispersal mechanisms of the zebra mussel *Dreissena polymorpha*. *Ecology*, **77**, 1686–1690.
- Johnson L.E. & Padilla D.K. (1996) Geographic spread of exotic species—ecological lessons and opportunities from the invasion of the zebra mussel *Dreissena polymorpha*. *Biological Conservation*, **78**, 23–33.
- Kimmerer W.J., Gartside E. & Orsi J.J. (1994) Predation by an introduced clam as the likely cause of substantial declines in zooplankton of the San Francisco Bay. *Marine Ecology Progress Series*, **113**, 81–93.
- Limburg K.E. (1996) Modeling the ecological constraints on growth and movement of juvenile American shad (*Alosa sapidissima*) in the Hudson River Estuary. *Estuaries*, **19**, 794–813.
- Limburg K.E., Pace M.L., Fischer D. & Arend K.K. (1997) Consumption, selectivity, and utilization of zooplankton by larval *Morone* spp. in a seasonally pulsed estuary. *Transactions of the American Fisheries Society*, **126**, 607–621.
- MacIsaac H.J. (1996) Potential biotic and abiotic impacts of zebra mussels on the inland waters of North America. *American Zoologist*, **36**, 287–299.
- MacIsaac H.J., Sprules W.G. & Leach J.H. (1991) Ingestion of small bodied zooplankton by zebra mussels (*Dreissena polymorpha*): Can cannibalism on larvae influence population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 2051–2060.
- MacIsaac H.J., Sprules W.G., Johannsson O.E. & Leach J.J. (1992) Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Oecologia*, **92**, 30–39.
- MacIsaac H.J., Lonnee C.J. & Leach J.H. (1995) Suppression of microzooplankton by zebra mussels: importance of mussel size. *Freshwater Biology*, **34**, 379–387.
- Moyle P.B., Herbold B., Stevens D.E. & Miller L.W. (1992) Life history and status of delta smelt in the Sacramento-San-Joaquin Estuary, California. *Transactions of the American Fisheries Society*, **121**, 67–77.
- Nicholls K.H. & Hopkins G.J. (1993) Recent changes in Lake Erie (north shore) phytoplankton: cumulative effects of phosphorus loading reductions and the zebra mussel introduction. *Journal of Great Lakes Research*, **19**, 637–647.
- Pace M.L. (1982) Planktonic ciliates: their distribution, abundance, and relationship to microbial resources in a monomictic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 1106–1116.
- Pace M.L. (1986) An empirical analysis of zooplankton community structure. *Limnology and Oceanography*, **31**, 45–55.
- Pace M.L., Porter K. & Feig Y. (1984) Life history variation within a parthenogenetic population of *Daphnia parvula* (Crustacea: Cladocera). *Oecologia*, **63**, 43–51.
- Pace M.L., Findlay S.E.G. & Lints D. (1992) Zooplankton in advective environments: The Hudson River community and a comparative analysis. *Canadian Journal of Fisheries and Aquatic Science*, **49**, 1060–1069.
- Padilla D.K., Adolph S.C., Cottingham K.L. & Schneider D.W. (1996) Predicting the consequences of dreissenid mussels on a pelagic food web. *Ecological Modeling*, **85**, 129–144.
- Raymond P.A., Caraco N.F. & Cole J.J. (1997) CO₂ concentration and atmospheric flux in the Hudson River. *Estuaries*, **20**, 381–390.
- Ricciardi A., Whoriskey F.G. & Rasmussen J.B. (1995) Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1449–1461.
- Sanders R.W. & Wickham S.A. (1993) Planktonic protozoa and metazoa: predation, food quality and population control. *Marine Microbial Food Webs*, **7**, 197–223.
- SAS Institute (1993) *SAS/ETS user's guide*. SAS Institute Inc, Cary, North Carolina.
- Schloesser S.W., Nalepa T.F. & Mackie G.L. (1996) Infestation of unionid bivalves (Unionidae) in North America. *American Zoologist*, **36**, 300–310.
- Shevtsova L.V., Zhdanova G.A., Movchan V.A. & Primak A.B. (1986) Experimental interrelationship between *Dreissena* and planktonic invertebrates. *Hydrobiological Journal*, **22**, 36–39.
- Stemberger R.S. & Gilbert J.J. (1985) Body size, food concentration, and population growth in planktonic rotifers. *Ecology*, **66**, 1151–1159.
- Strayer D.L. & Smith L.C. (1996) Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of the zebra mussel invasion of the Hudson River. *Freshwater Biology*, **36**, 771–778.
- Strayer D.L., Powell J., Ambrose P., Smith L.C., Pace M.L. & Fischer D.T. (1996) Arrival, spread, and early dynamics of the zebra mussel (*Dreissena polymorpha*) population in the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1143–1149.

Urabe J. (1991) Effect of food concentration on growth, reproduction, and survivorship of *Bosmina longirostris* (Cladoceran): an experimental study. *Freshwater Biology*, **25**, 1–25.

Vaqué D., Pace M.L., Findlay S.E.G. & Lints D. (1992) Fate of bacterial production in a heterotrophic ecosystem:

Grazing by protists and metazoans in the Hudson Estuary. *Marine Ecology Progress Series*, **89**, 155–163.

Wei W.W.S. (1990) *Time Series Analysis*. Addison-Wesley, New York.

(Manuscript accepted 11 August 1997)