

HYDROLOGY AND GRAZING JOINTLY CONTROL A LARGE-RIVER FOOD WEB

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Abstract. Inputs of fresh water and grazing both can control aquatic food webs, but little is known about the relative strengths of and interactions between these controls. We use long-term data on the food web of the freshwater Hudson River estuary to investigate the importance of, and interactions between, inputs of fresh water and grazing by the invasive zebra mussel (*Dreissena polymorpha*). Both freshwater inputs and zebra mussel grazing have strong, pervasive effects on the Hudson River food web. High flow tended to reduce population size in most parts of the food web. High grazing also reduced populations in the planktonic food web, but increased populations in the littoral food web, probably as a result of increases in water clarity. The influences of flow and zebra mussel grazing were roughly equal (i.e., within a factor of 2) for many variables over the period of our study. Zebra mussel grazing made phytoplankton less sensitive to freshwater inputs, but water clarity and the littoral food web more sensitive to freshwater inputs, showing that interactions between these two controlling factors can be strong and varied.

Key words: alien species; anthropogenic change; bivalve; *Dreissena polymorpha*; estuary; food webs; freshwater flow; herbivory; invasive species; long-term study; regime shift; zebra mussel.

INTRODUCTION

Many ecosystem properties are controlled by multiple processes, but the relative importance of, and interactions among, controls may be difficult to quantify, and there are still few examples for which the influence of multiple controls is well understood. Because many ecosystems are now influenced by several human impacts, it is increasingly important to understand how multiple factors control ecosystems (e.g., Cloern 2001). Long-term studies may be a valuable tool for investigating this subject, if the record is long enough to include a wide range in the independent variables. Here, we use long-term records of the Hudson River ecosystem to assess the relative importance and interactions of two controlling factors, inputs of fresh water and grazing by an invasive species.

Inputs of fresh water (“flow”) and grazing are important in many rivers, estuaries, lakes, and coastal waters. Flow determines the magnitude of advective losses, water residence time, degree of stratification, and inputs or dilution of nutrients and other materials, which may in turn set water clarity, leading to strong and pervasive effects on many parts of aquatic ecosystems (e.g., Gillanders and Kingsford 2002, Kimmerer 2002a, b). Grazing, whether by pelagic grazers like crustacean zooplankton or benthic grazers such as bivalves, can have strong effects on phytoplankton and other edible particles as well (e.g., Dame 1996,

Carpenter et al. 2001). Grazing effects also ramify throughout aquatic ecosystems, affecting water clarity, nutrient concentrations, and populations of consumers, rooted plants, and microbes (e.g., Vanderploeg et al. 2002). Because both flow and grazing are strongly affected by widespread human activities such as water withdrawals, river regulation, land-use change, climate change, harvesting, and species introductions, managing human impacts on aquatic ecosystems requires us to understand the joint effects of changing flow and grazing. Nevertheless, studies that estimate the simultaneous effects of flow and grazing are rare (e.g., Jassby et al. 2002, Kimmerer 2002a). Here, we will show that both variables determine the character of the Hudson River ecosystem, and that their interactions may be strong and varied.

METHODS AND MATERIALS

Our study area is the freshwater tidal part of the Hudson River in eastern New York (Fig. 1), extending from RKM 100–248 (river kilometers upriver of The Battery in New York City). This section of the Hudson averages 8 m deep and 0.9 km wide. About 15% of the study area is shallow (<3 m deep at mean low tide) and supports extensive beds of submersed vegetation (Nieder et al. 2004). Tidally driven currents run in both directions throughout the study area, reaching peak velocities of 40–80 cm/s, ~10× as great as typical net downriver currents (Geyer and Chant 2006), and prevent stratification. The water is moderately hard (pH = 7.6, Ca concentration = 27 mg/L) and nutrient rich (NO₃-N concentration = 0.5 mg/L; PO₄-P concentration = 11 µg/L [Caraco et al. 1997]).

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TABLE 1. Summary of statistical models.

Variable	No. years	Range of variation (maximum/minimum)	R^2 of full model	P
Phytoplankton biomass	18	11	0.89	<0.0001
POC (including phytoplankton C)†	18	2.6	0.75	0.0002
Rotifers	18	141	0.73	0.0003
K_d ‡	18	2.0	0.70	0.0006
Deepwater zoobenthos	11	3.4	0.70	0.03
Nauplii	18	23	0.69	0.0008
Cladocerans	18	25	0.56	0.008
Tintinnids	18	75	0.56	0.008
Suspended sediments	18	2.3	0.54	0.01
Littoral zoobenthos	11	5.0	0.47	0.19
DOC§	18	2.3	0.42	0.05
Littoral fish	31	32	0.27	0.03
Open-water fish	31	32	0.23	0.07
Bacterial density	18	3.7	0.20	0.35
Copepods	18	4.1	0.19	0.37
Bacterial production	18	5.7	0.16	0.48
Heterotrophic flagellates	12	2.7	0.08	0.87

† Particulate organic carbon.

‡ Extinction coefficient.

§ Dissolved organic carbon.

Our methods are described in previous papers (Findlay et al. 1996, 1998, Pace et al. 1998, Strayer and Smith 2001, Strayer et al. 2004, Caraco et al. 2006). Briefly, we took samples for pelagic variables every one to two weeks during the ice-free season at RKM 144–149. Data analyzed here are means from 1 May to 30 September of each year. Data for zoobenthos are means of samples taken from eight stations throughout the estuary in September, and exclude zebra mussels. We omit benthic data from 1999 because a hurricane interrupted our sampling campaign. “Deepwater” zoobenthos came from unvegetated sites at water depths >5 m; “littoral” zoobenthos came from vegetated sites at water depths ~1 m at low tide. Data for fish are river-wide standing crops averaged over weeks 32–40 of each year, estimated from beach-seine samples. We created two composite variables for fish: “littoral fish” and “pelagic fish” are the sums of all common littoral zone (except for threespine stickleback) and open-water fish, respectively, as defined by Strayer et al. (2004). To allow comparisons across variables, we normalized all dependent variables by dividing them by their pre-zebra mussel invasion means.

We ran multiple regression models to predict each dependent variable from freshwater flow, zebra mussel grazing, and the interaction between flow and grazing. Inspection of residuals showed that they were well behaved, except in the case of rotifer and tintinnid data, which were heteroscedastic. Log-transforming these variables corrected the heteroscedasticity, but produced models that were qualitatively similar to those based on untransformed data. To allow comparisons across variables, we present results from models based on untransformed data, but also show some results from the models based on log-transformed rotifer and tintinnid densities. We used the annual mean of freshwater flow from 1 May to 30 September (2005

data available online).² We treated zebra mussel grazing as a binary variable (this provided better model fits than treating zebra mussel grazing as a continuous variable); 1974–1992 were preinvasion years and 1993–2004 were

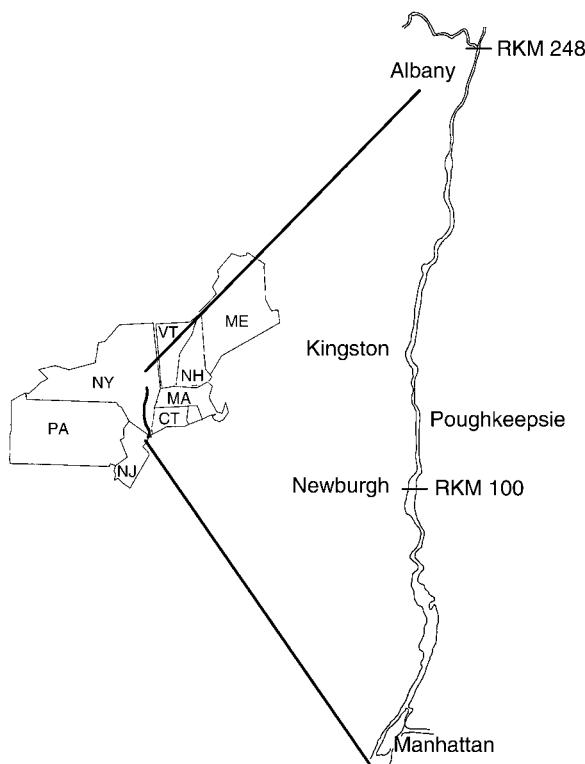


FIG. 1. The Hudson River estuary in eastern New York, USA. RKM = river kilometer (i.e., kilometers upriver from The Battery in Manhattan).

² (<http://waterdata.usgs.gov/nwis/sw>)

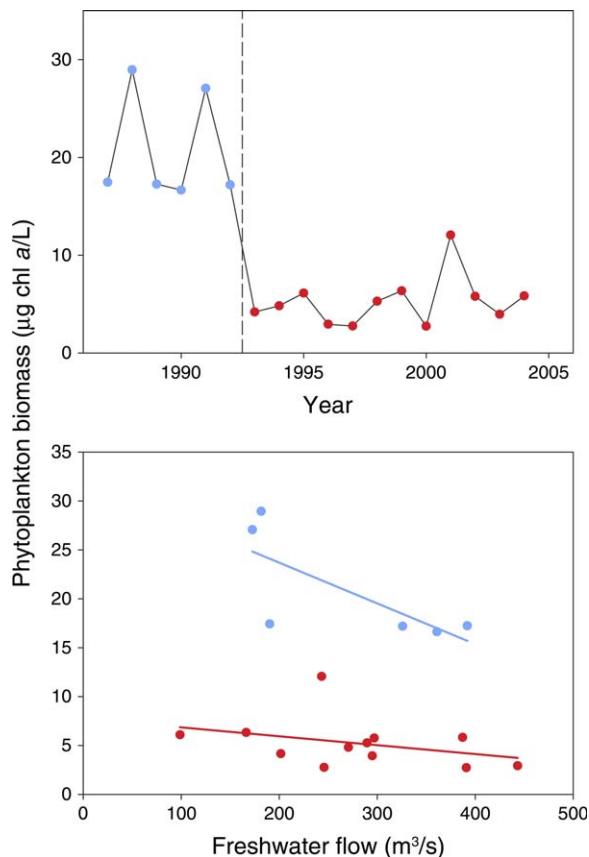


FIG. 2. Interannual variation in phytoplankton biomass in the Hudson River. The upper panel shows the time series, with the zebra mussel invasion shown by the vertical dashed line; data points before the invasion are shown in blue, and those after in red. The lower panel shows interannual variability in relation to the effects of grazing (the difference between the blue circles before the zebra mussel invasion and the red circles after the zebra mussel invasion), flow (the slopes of the regression lines), and the interaction between flow and grazing (the difference in slopes of the two regression lines).

postinvasion years. The interaction term is simply the product of freshwater flow and zebra mussel grazing.

To compare the strength of effects of flow and grazing, we calculated the “scope” of variation due to each variable (see Appendix) as

$$S_Q = \text{range}[(Q_{\text{obs}} - \bar{Q})(m_Q + m_{\text{int}}Z_{\text{obs}})]$$

$$S_Z = \text{range}[(Z_{\text{obs}} - \bar{Z})(m_Z + m_{\text{int}}Q_{\text{obs}})]$$

where S is scope, Q_{obs} and \bar{Q} are observed and mean freshwater discharge, Z_{obs} and \bar{Z} are observed and mean zebra mussel grazing, and m_Q , m_Z , and m_{int} are the partial regression slopes for flow, zebra mussels, and their interaction, respectively. Scope provides an estimate of how much the variation in each independent variable has affected each dependent variable over the period of study (calculated for 1987–2004), and allows direct comparisons of the effects of flow and grazing.

RESULTS

The Hudson ecosystem was highly variable from year to year, with annual mean values for different variables ranging by twofold to >100-fold over the period of study (Table 1). Much of this interannual variation is correlated with freshwater flow, grazing, and their interaction (Fig. 2), although the success of flow–grazing models in accounting for interannual variation and the relative importance of flow and grazing differ widely across variables (Table 1, Fig. 3).

Phytoplankton, cladocerans, and particulate organic carbon (POC) declined at high flow (Fig. 3). No variables increased with flow, although many were insensitive to flow. All plankton except for bacteria, heterotrophic flagellates, and adult copepods declined with zebra mussel grazing, as did POC, the extinction coefficient K_d (showing that zebra mussel grazing was associated with clearer water), and deepwater zoobenthos. Littoral fish and zoobenthos, in contrast, tended to rise with zebra mussel grazing ($P = 0.18$ and 0.12 , respectively).

Both flow and grazing were important in determining interannual variation in several variables (Fig. 4), causing substantial variation in cladocerans, littoral zoobenthos, POC, and K_d . Other variables (tintinnids, rotifers, nauplii, phytoplankton, and deepwater benthos) were affected more than twice as much by variation in grazing as by variation in flow. Only littoral fish populations were controlled chiefly by flow and not by grazing. We could not detect strong main effects of either flow or grazing on microbial variables (density and production of bacteria, heterotrophic flagellates), adult copepods, DOC, suspended sediments, or pelagic fish.

Although our estimates for the interaction between flow and grazing were relatively imprecise (Fig. 3), we could discern two different kinds of interaction between flow and grazing. For phytoplankton ($P = 0.07$) and POC ($P = 0.02$), the negative effects of flow became less severe after the zebra mussel invasion (Figs. 2, 3). In contrast, the effects of flow on K_d ($P = 0.006$), suspended sediments ($P = 0.11$), and littoral animal populations ($P = 0.11$ and 0.16 for benthos and fish, respectively) tended to become more pronounced after the zebra mussel invasion. These variables, which had been relatively insensitive to flow before the invasion, became very sensitive to flow after zebra mussels arrived (Figs. 3, 5).

DISCUSSION

Freshwater flow, zebra mussel grazing, and their interactions all are important in setting the character of the Hudson River ecosystem. Flow and grazing were roughly equally important, in terms of the amount of variation in most dependent variables that they have caused over the period of our study (Fig. 4). Heterotrophic flagellates, bacteria, and bacterial production were largely insensitive to flow and grazing, suggesting

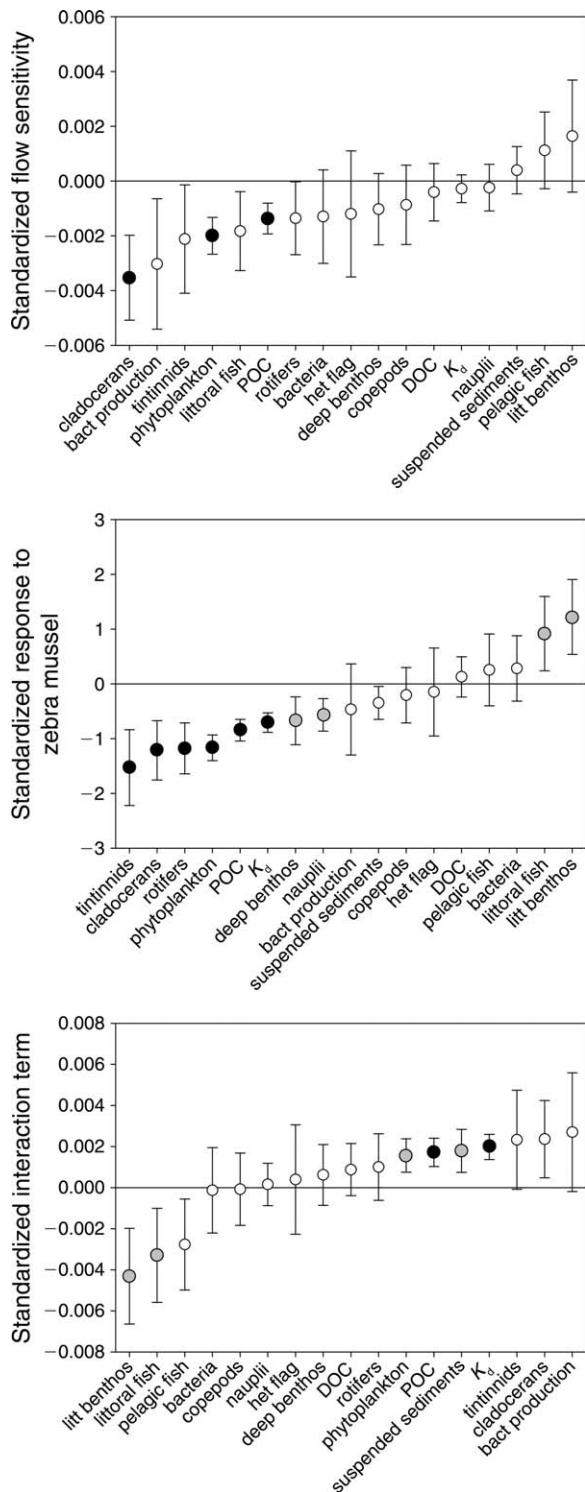


FIG. 3. Effects of freshwater flow, zebra mussel grazing, and the interaction between flow and grazing on various parts of the Hudson River ecosystem. Data are partial regression coefficients (slopes, mean \pm SE) for the dependent variables, each of which is standardized to its preinvasion mean. That is, a slope of -0.002 against flow means that the variable declined by 0.2% of its pre-zebra mussel invasion mean for every $1 \text{ m}^3/\text{s}$ increase in freshwater flow. Solid black circles are significantly

regulated by other factors at the annual scale considered here.

High freshwater flow tended to reduce populations throughout the Hudson's food web, and did not have clearly positive effects on any part of the food web (Fig. 3). In contrast, high freshwater flows often are associated with high biological productivity in estuaries (e.g., Gillanders and Kingsford 2002, Kimmerer 2002a). High freshwater flows may enhance nutrient loading, increase stratification in saline waters, or produce inhospitable conditions for an important consumer (e.g., Livingston et al. 1997), all of which may increase productivity. Because the freshwater Hudson estuary is not nutrient-limited (Cole and Caraco 2006), does not stratify, and always has suitable chemistry for zebra mussels, high freshwater flow does not have these stimulating effects on the food web.

Grazing generally had strong, negative effects on plankton in the Hudson, but strengthened the littoral food web (Fig. 3). The zebra mussel invasion substantially increased populations of littoral zoobenthos and fish (see also Strayer et al. 2004), and Caraco et al. (2000) estimated that increased water clarity associated with the zebra mussel invasion caused a 38% increase in primary production of submersed macrophytes. Many studies have shown that the pelagic food web in other aquatic ecosystems is sensitive to increases or decreases from pelagic or benthic grazers (Dame 1996, Carpenter et al. 2001, Jassby et al. 2002, Kimmerer 2002a). In many ecosystems, grazing-related losses of phytoplankton lead to increases in macrophyte biomass and littoral zone productivity (Sheffer 1999, Vanderploeg et al. 2002, Zhu et al. 2006). This connection is however absent or weak in aquatic ecosystems too deep to support much littoral growth or where water clarity is low because of high loads or resuspension of particles (e.g., San Francisco Bay).

We saw two kinds of interactions between flow and grazing. First, there was a positive interaction between flow and grazing for phytoplankton, suggesting a simple multiplicative interaction between these variables (i.e., a unit increase in flow caused the same fractional decrease in phytoplankton biomass before and after the zebra mussel invasion). Because grazing greatly decreased mean phytoplankton biomass, both the slope of the flow-phytoplankton regression and interannual variation in phytoplankton biomass flattened after the zebra mussel invasion (Fig. 2).

←
different from zero at $P < 0.05$, solid gray circles are marginally significant ($0.05 < P < 0.2$), and open circles are not significant ($P > 0.2$). Models of log-transformed rotifer and tintinnid densities detected zebra mussel effects at $P=0.15$ and $P=0.009$, respectively, and no other significant effects. Abbreviations are: bact, bacterial; litt, littoral; POC, particulate organic carbon; het flag, heterotrophic flagellates; DOC, dissolved organic carbon; K_d , extinction coefficient.

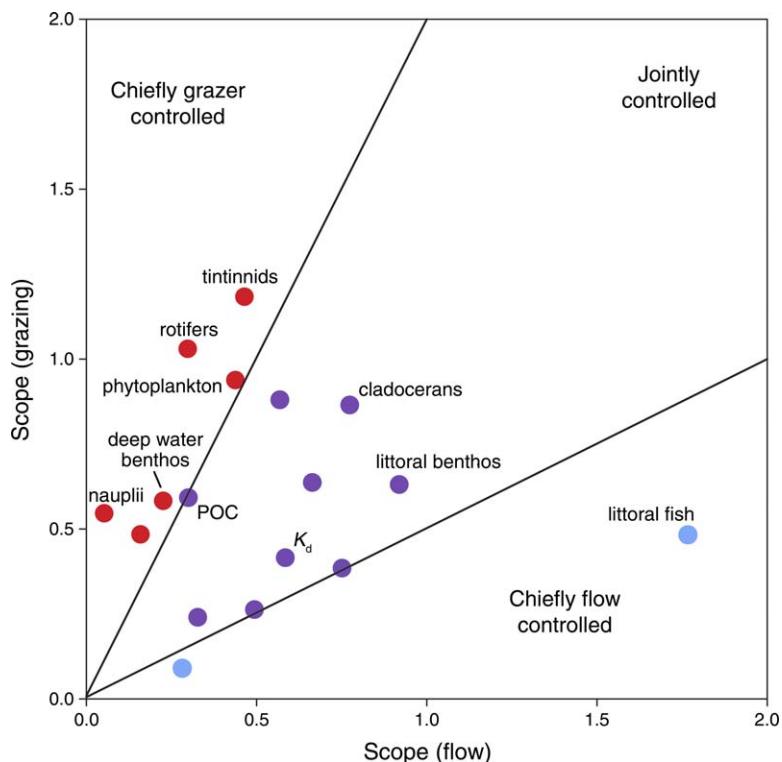


FIG. 4. Comparison of the range of effects of freshwater flow and zebra mussel grazing over the period 1987–2004. See *Materials and methods* for details of how scope was calculated. Unlabeled points are variables for which neither the partial regression coefficient for flow nor for grazing was significant at $P < 0.2$, and include suspended sediments, DOC, bacterial density, bacterial production, copepods, heterotrophic flagellates, and open-water fish. Diagonal lines are the 2:1 and 1:2 lines, and arbitrarily divide a zone of joint control by flow and grazing (purple circles) from zones of predominant control by grazers (red circles) or flow (blue circles).

More remarkably, we saw evidence that the arrival of zebra mussels caused a regime shift in the littoral food web: a change in the way that water clarity (the extinction coefficient, K_d) and littoral animals responded to freshwater flow (Fig. 5). Before the zebra mussel invasion, neither K_d nor littoral animal populations was sensitive to freshwater flow (although our statistical power to detect such effects is limited), but after the zebra mussel invasion, they became distinctly sensitive to flow. After the zebra mussel invasion, wet years were associated with poor water clarity and low populations of littoral animals, while dry years had the opposite effect. This increased sensitivity to flow caused large fluctuations between dry and wet years in water clarity and the littoral food web after the zebra mussel invasion. Production of submersed plants in the Hudson is thought to be light-limited (Harley and Findlay 1994), so the increased sensitivity of the littoral food web to flow presumably is a result of increased sensitivity of water clarity (K_d) to flow after the zebra mussel invasion. Factors controlling K_d and, in particular, suspended sediments in the Hudson are not well understood, but the decrease in sensitivity of phytoplankton to flow (Fig. 2) probably made K_d more sensitive to flow after the zebra mussel invasion. That is,

before the zebra mussel invasion, a strong negative relationship between phytoplankton and flow helped to offset a positive relationship between suspended sediments and flow, reducing variability in K_d . This compensatory mechanism weakened after high grazing rates reduced phytoplankton biomass (cf. Caraco et al. 1997) and thereby the ability of variation in phytoplankton biomass to offset variation in suspended sediments. Thus, an invasive species changed the fundamental relationships between ecosystem properties and controls (flow and littoral production). Other invasive species also have been shown to cause regime shifts in ecosystems (e.g., invasive plants and flammability [Brooks et al. 2004]), which can greatly complicate attempts to understand and manage ecosystems.

To what extent can we generalize about the effects of flow and grazing on aquatic ecosystems? The effects of grazing appear to be consistent across systems, with two caveats. First, inedible phytoplankton appear in response to intense grazing in some but not all ecosystems (Vanderploeg et al. 2001, 2002, Raikow et al. 2004). Second, the strength of the positive relationship between grazing and littoral production depends on system morphology. The effects of freshwater flow might seem to be more difficult to generalize because of the

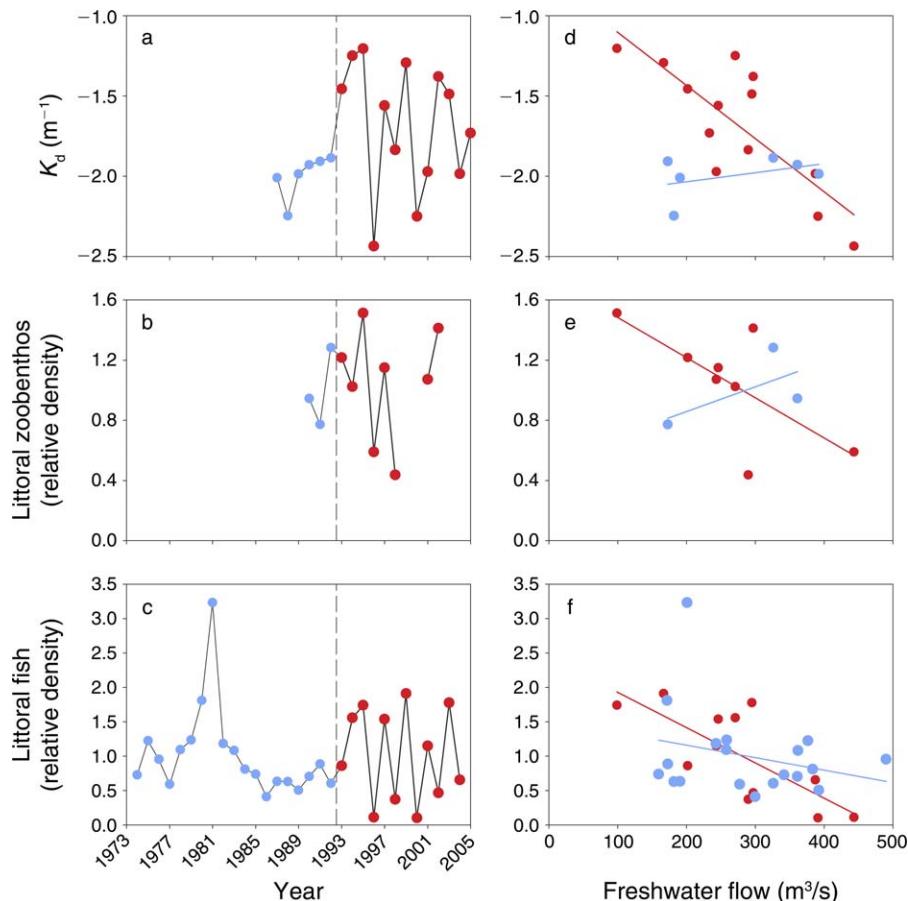


FIG. 5. Changes in the response of the littoral food web following the zebra mussel invasion (vertical dashed line in left-hand panels). Panels (a)–(c) show the time courses for the extinction coefficient K_d (with less negative values indicating clearer water), littoral zoobenthos, and littoral fish recruitment; panels (d)–(f) show relationships between these same variables and freshwater flow before (blue circles) and after (red circles) the zebra mussel invasion. Correlations with flow strengthened after the zebra mussel invasion for all these variables: K_d , $r^2 = 0.18$ and $P = 0.4$ (pre) vs. $r^2 = 0.63$, $P = 0.001$ (post); zoobenthos, $r^2 = 0.40$, $P = 0.56$ (pre) vs. $r^2 = 0.48$, $P = 0.057$ (post); fish, $r^2 = 0.07$, $P = 0.27$ (pre) vs. $r^2 = 0.55$, $P = 0.006$ (post).

multiple roles of flow (increasing nutrient inputs, strengthening stratification, increasing turbidity, increasing advection). Nevertheless, if we specify the properties of an ecosystem (Are phytoplankton nutrient limited? Is salinity high enough to allow stratification? Is turbidity controlled by freshwater inputs? Is residence time short enough that advective losses are important?), it may be possible to predict the effects of freshwater flow across a wide range of aquatic ecosystems. The interaction between flow and grazing may be the most difficult to generalize. The particular interaction that we saw depends on water clarity being controlled jointly by edible and inedible particles, which respond in different ways to flow; grazers being able to reduce concentrations of edible particles; and there being large areas suitable for littoral production.

Thus, interactions between controlling factors may be important, varied, and difficult to predict a priori. These difficulties may be especially severe if the controlling factors are both disparate and uncorrelated, as were flow

and grazing in the Hudson. If ecologists are to satisfactorily understand and manage human impacts on ecosystems, we will need to acknowledge the widespread existence of multiple interacting controls, and develop empirical data and models to effectively describe and predict their joint effects.

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APPENDIX

Notes on the calculation of scope (*Ecological Archives* E089-002-A1).