EXOTIC INVERTEBRATES, FOOD-WEB DISRUPTION, AND LOST FISH PRODUCTION: UNDERSTANDING IMPACTS OF DREISSENID AND CLADOCERAN INVADERS ON LOWER-LAKES FISH COMMUNITIES AND FORECASTING INVASION IMPACTS ON UPPER-LAKES FISH COMMUNITIES

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INTRODUCTION

Early in the 20th century, Great Lakes fish communities were profoundly disrupted by a wave of vertebrate invaders: the sea lamprey, alewife, and rainbow smelt (Eshenroder and Burnham-Curtis 1999). These disruptions were largely focused at the upper end of food webs, and, hence, traditional fishery models could be adapted to quantify the associated impacts. During the last 15 years, the lower Great Lakes especially have suffered a second wave of invasions featuring invertebrates: two species of dreissenids–zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. bugensis*)–and two predatory cladocerans–*Bythotrephes cederstroemi* and *Cercopagis pengoi* (MacIsaac 1999; MacIsaac et al. 1999). These four invertebrates, the focus of this paper, are expected to disrupt, or have already disrupted, Great Lakes fish communities in ways quite different from the earlier wave of vertebrate (fish) invaders. Invertebrate disruptions start at lower trophic levels and percolate up through the food web with potentially serious consequences for fisheries (Dermott et al. 1999; Ryan et al. 1999; Johannsson et al. 2000; Vanderploeg et al., submitted).

An ecosystemic approach to both field studies and modeling is needed to deal with the second wave of invertebrate invaders. Such an approach can be advanced through a research program with two broad thrusts: 1) document the consequences of ongoing invasions through an integrated series of process studies and empirical comparisons focused on severely affected smaller lakes (e.g., Oneida Lake, Hart Lake, the Finger Lakes), the lower Great Lakes (where impacts are advanced), and the upper Great Lakes (where impacts are less advanced) and 2) develop ecosystem-level management models to assess the continuing impacts of these invasions on the food webs of the lower Great Lakes and to forecast the eventual extent of colonizations and their impacts on the food webs of the upper Great Lakes.

A special focus on invertebrate invaders is warranted for several reasons:

1) invertebrates, unlike fish, are not routinely sampled by existing user groups; hence early detection of the arrival and accurate mapping of the dispersal of an invertebrate invader will require dedicated sampling (Johnson and Padilla 1996);

2) the two dreissenids, especially, sit near the base of Great Lakes food webs and can influence a variety of trophic levels in different ways; the specific details of their impacts vary locally within and across lakes; clarifying the causal links that definitively demonstrate impacts requires a focused and specialized set of sampling programs that look comprehensively at the ecosystems affected; such sampling programs cannot be attached to existing commercial activities, such as fishing;

3) impact assessment has previously relied on traditional fishery methodologies; for instance, sea lamprey impacts have been successfully examined by augmenting the natural mortality term in fishery models (Walters et al. 1980; Youngs 1980; Sitar et al. 1999), and shifts in the composition of the forage-fish community have been examined successfully using individual-based bioenergetics models (Jones et al. 1993); assessment of invertebrate invasions requires application of ecosystem-level models that capture the essential nature of an invader's impact on the flow of energy to fish, while retaining a sufficiently simple structure to be manageable and intelligible; meeting these requirements likely will require development of new models that include strategic simplifications of the complexities involved in dealing with the broad range of temporal and spatial scales operative in a typical Great Lakes food web;

4) misinterpreting the nature of invertebrate impacts can result in a situation where their true effects are attributed to other causes, creating a demand for potentially costly and ineffective management actions;

5) insertion of an invader into an existing food web can significantly affect contaminant burdens of fish (Rasmussen et al. 1990; Cabana et al. 1994), potentially affecting consumption advisories.

SCIENCE IN SUPPORT OF FORECASTING INVASION IMPACTS

Successful invasions are defined here as those that end with the invader widespread and abundant in the new environment. A successful invasion has four stages (Levin 1989; Morton 1997): arrival (invader enters the new ecosystem oftentimes in numbers too small to be easily detectable), establishment (small, self-sustaining populations develop), expansion (populations increase substantially in both abundance and geographic distribution), and accommodation. During the expansion phase, existing food webs are disrupted. In the accommodation phase, the food web reorganizes and takes on a new form that includes the presence of the invader. The transition from expansion to accommodation may involve several phases of crash and recovery (Morton 1997). Accommodation typically involves the emergence of predators/pathogens acting to constrain the invader (Lodge 1993).

Simberloff (1989) discusses the difficulties inherent in forecasting successful invasions: any species could be a potential invader, every invasion is a unique event shaped by the character of the invading species, and general and reliable guidelines for identifying likely invaders are lacking. More recently, Ricciardi and Rassmussen (1998) have argued against such pessimism, but they still recognize that forecasting remains a difficult problem. There is agreement on the minimal analysis required for an invasion in progress: an assessment of the abiotic and biotic environments that the invading species inhabits in its native range and an identification and mapping of analogous environments in the invaded system (Simberloff 1989).

Given this background, we identify the broad elements of an invertebrate-invader research program based on the following:

1) prevention of arrival is the most effective management action, but a perfect enforcement system is unrealizable (Ricciaridi and Rasmussen 1998; Ricciaridi and MacIsaac 2000);

2) once an invader has arrived, the probability for success or failure can be determined on a species-specific basis and depends on the compatibility between the receiving environment and the life-history characteristics and environmental tolerances of the invader; success or failure also depends on the number of individuals that arrive together and the frequency with which such groups reach the receiving environment (Simberloff 1989); other important factors include: the availability of vacant niches and the extent that stresses (e.g., contaminants and management practices) suffered by the host ecosystem limit resistance to invasion;

3) once an invader has established itself, eradication is essentially impossible (Leach et al. 1999).

Given this background, goals for science include:

1) improving and extending risk assessments of potential invaders (e.g., Ricciardi and Rasmussen 1998);

2) improving the efficiency of prevention/detection/mitigation programs;

3) developing tools for forecasting the rate, extent, and ultimate food-web impacts of invasions in progress.

We propose a research program that deals with the most tractable aspect of the final goal: developing tools to forecast the impacts of the two dreissenids and two predatory cladocerans (hereafter the focal invaders) on fish production. The Board of Technical Experts is building a partnership among various agencies to support this program and intends to provide scientific oversight for the associated research. The Board's concept is ambitious and will require new field and laboratory data for documenting and understanding the food-web disruptions and reorganizations that occur during the expansion and accommodation phases of the four focal invasions. It will also require development of new models that can be used to predict the impacts of these and other functionally similar invertebrate invasions on food webs. In the first part of this paper we provide a concept, approach, and agenda for the proposed research. In the second part, we present a call for proposals that identifies priority research elements.

INVERTEBRATE INVASIONS IN THE GREAT LAKES

Research Focus

The character of the receiving environment is critical for determining whether an invader will be successful. Receiving environments in the Great Lakes can be categorized in different ways. We will build our research proposal around the following scheme:

1) characteristic habitats: offshore versus near-shore
2) characteristic food webs: pelagic versus benthic

The nature and strength of the linkages between benthic and pelagic food webs vary systematically between offshore and near-shore habitats. The links that connect offshore webs with near-shore webs are strongly influenced by basin morphometry, lake physics, climate, and nutrient loading. The life history and diet of an invader will determine which food web(s) it will disrupt and how that disruption is expressed. Thus, information on the basic biology of invaders can be used to sort individual species into functional groups that reflect commonality in the type of food web that they are likely to disrupt and in the nature of the disruption. Since the invasion process is inherently species-specific, forecasting range expansions and food-web impacts requires comparative analysis of invasions that exemplify particular functional groups. The two dreissenid and two predatory-cladoceran invasions currently in progress in the Great Lakes and in inland lakes in the basin should make excellent case studies for this type of comparative analysis:

1) the dreissenid invasions represent intrusions into near-shore and offshore benthic food webs whereas the two cladoceran invasions (*Bythotrephes* and *Cercopagis*) represent intrusions into near-shore and offshore pelagic food webs; these invasions are impacting the four distinct food webs that support fish production in the Great Lakes;
2) these four invasions roughly pair as functional replicates: two invasions of attached, benthic filter feeders and two invasions of mobile, pelagic predators;
3) all four invasions are in progress and are successful in that high abundances and broad distributions have been achieved in at least several of the Great Lakes;
4) all four invasions are well advanced in at least one of the lower lakes;
5) all four invasions are changing existing Great Lakes food webs in ways that will significantly impact the productivity of existing fish communities (Appendix).

Detailed descriptions of both the expansion and accommodation phases for at least one pair of these invertebrates can be developed in a relatively cost-effective manner for at least some parts of the lower Great Lakes. These data will provide an empirical basis for developing predictive models designed to forecast future food-web impacts for these species and for other potential invaders with similar functional attributes.

In effect, each of these invasion pairs can be treated as two similar experimental probes of the types of food webs common in the Great Lakes. Studying the consequences of these probes will yield new knowledge specific to the particular invasions examined. It will also provide new knowledge about the resilience and stability of these food webs. This knowledge will be very useful in forecasting the susceptibility and likely responses of these food webs to functionally similar types of invaders that may appear in the future (Johnson and Padilla 1996).

Research Approach

Invasion studies in the Great Lakes suffer from two serious methodological difficulties that make clear attribution of invasion impacts difficult:

1) many of the readily-available biological time series from the Great Lakes are short and/or intermittent making it difficult to construct clean before/after comparisons;

2) all of the lakes have been subject to multiple concurrent stresses (e.g., reductions in nutrient loading, changes in contaminant loading, changes in fishing pressure, regional climate change) operating over the same time frame as the invasions; hence, even when there is strong evidence for food-web changes, definitive attribution of these changes to a particular invasion is difficult.

Two approaches can be used to mitigate these difficulties, and they should play a major role in this research program:

1) reconstruction of the past: historical time series can be refined and extended by focused and comprehensive searches of existing data archives and by the application of new technologies to historical materials such as tissue archives and sediment cores; ideally, such techniques could generate temporally staggered before-/after-invasion time series for local habitats within the Great Lakes–this approach would permit identification of the most common responses to a particular invasion, as well as the range of possible responses;

2) field study of model systems: better understanding of invader impacts in the Great Lakes may be achieved by coupling studies of impacts on smaller lake systems (so-called model systems) with confirmatory experimental or observational studies on the Great Lakes; such model systems should meet specific criteria, for example:

- an invasion of interest is the only significant change experienced by the system;
- the system is small enough to permit direct observation of processes and events that are logistically impossible to study intensively on large systems like the Great Lakes.

Research Agenda

The program will be focused around the following lines of research:

1) describing the invasion process: mobilize existing databases and use new technology to generate new data bases that

- provide fine-scale maps documenting historical changes in, and the current status of, the spatial distribution and abundance of dreissenids, *Bythotrephes*, and *Cercopagis*

- permit statistical assessment of those habitat factors (e.g., lake levels, substrates, large scale physics) most closely associated with variations in invader density at large spatial scales

2) understanding the invasion process: conduct comparative laboratory and field studies on the focal invaders aimed at assessing how
- differences in physical habitats (e.g., bottom complexity, thermal structure) shape the relative strengths of specific food-web interactions
- overall food-web efficiency is impacted and the implications of those impacts
- food-web impacts are modified as the invasion moves from an expansion to an accommodation phase and how that transition is mediated by the existing complex of potential predators (e.g., see Johannsson et al. 1999)
- invaders modify the links connecting benthic and pelagic food webs in near-shore habitats and in offshore habitats
- invaders modify the links that connect near-shore benthic/pelagic food webs with offshore benthic/pelagic food webs
- the above are modified by the differences in morphometry, productivity, and climate that exist across the Great Lakes,
- the above will allow assessment of the relative influence of other factors (i.e., other exotics, reduced nutrient loadings, resource management, climatic change) in causing food web changes

3) forecasting invasion impacts: mobilize new knowledge to extend (or reconstruct) existing management models, or develop new models capable of
- accounting for the known food-web impacts of the focal invaders
- forecasting future food-web impacts of the focal invaders at both local and lake-wide levels for each of the Great Lakes
- forecasting future food-web impacts of other potential invaders

CALL FOR PROPOSALS: RESEARCH ON UNDERSTANDING IMPACTS OF INVERTEBRATE INVADERS ON GREAT LAKES FOOD WEBS AND CONSEQUENCES FOR FISH PRODUCTION

Hypothesis-driven research proposals are needed for developing a capability to forecast the impacts of invertebrate invasions on Great Lakes food webs and their consequences for fish production. The research should focus on four recent, most-successful invaders: zebra mussels, quagga mussels, *Bythotrephes*, and *Cercopagis*. The ultimate products of the research should advance development of forecasting tools for these four focal invaders. This research will require the collection of field and laboratory data relevant to documenting and understanding the food web disruptions and reorganizations that occur during the expansion and accommodation phases of these invasions. New models are needed for predicting the food-web impacts of these invertebrate invasions at spatial scales that permit the assessment of the heterogeneity of impacts both within and among the Great Lakes.

This research program will be supported by a partnership of funding agencies. Some of the partners have narrow geographic mandates, but the issues identified here are most effectively studied at broad spatial scales (e.g., the whole-lake level, the Great Lakes basin level). Proponents should consider submitting collaborative proposals to several partners to support work across jurisdictions. The science advisor, Great Lakes Fishery Commission, will advise proponents on the solicitation process.

Suggestions Regarding Scope and Content of Proposals

Proponents are encouraged to develop proposals that include:

1) detailed reconstructions of the four focal invasions: refine and extend historical time series via focused and comprehensive searches of existing data archives and by the application of new technologies to historical materials such as tissue archives and sediment cores; these techniques will generate temporally staggered, before-/after-invasion time series for multiple local habitats within the Great Lakes and enable identification of the most common response to a particular invasion, as well as the range of possible responses;

2) comparative and multidisciplinary studies of small lakes (model systems) and the Great Lakes: the chosen model systems must contribute to the overall objectives of the research program by being small enough to permit direct observation of processes and events that are logistically difficult to study in the Great Lakes and by providing a clear before/after picture of the food-web impacts of an invasion; this approach is most effective as part of an integrated program that includes confirmatory experimental or observational studies on Great Lakes environments;

3) development of new methodologies: Table 1 provides examples of the kinds of technological approaches that appear to be relevant to the objectives of the program; proposals should thoroughly explain the relevance of such approaches to the overall objectives of the program.

Table 1. New technologies with potential for addressing the objectives identified in this proposal.

Focus	Technique	Measurement
System productivity	Crustacean molting enzyme[1]	Secondary productivity
	Continuous sensor for C-fixation[2]	Primary productivity
	Chlorophyll extinction coefficients[2]	
Inshore-offshore links	Stable isotopes[3]	Tracers for flow of materials
	Lipids/essential fatty acids[4]	
	Contaminants[5]	
Short-time horizons	Otolith/scale microchemistry[6]	Short-term changes in energy flow, habitat use, environmental conditions (e.g., temperature)
	Stable isotopes[3]	
Mapping	Multi-spectral sidescan sonar[7]	Benthic and pelagic habitats and spatial distributions of organisms
	Multi-beam sonar[8]	
	LIDAR (light detection and ranging) laser technology[9]	
	Advanced acoustics and software[10]	
	Optical sensors[11]	
	Chemical probes[12]	

[1]J. C. Roff, pers. com., Dept. Zool., U. Guelph; [2]G. Sprules, pers. comm., Dept. Zool., U. Toronto; [3]Peterson and Fry (1987), Kling et al. (1992), Cabana and Rasmussen (1994), Keough et al. (1996); [4]Arts et al. (2001); [5]Russell et al. (1999); [6]Campana and Thorrold (2001); [7]Phaneuf (1997), Smith and Greenhawk (1998) Piazzi et al. (2000); [8]Ryan and Flood (1996), Mayer et al. (1998), Gerlotto et al. (1999); [9]Churnside and McGillivary (1991), Churnside et al. (1997); [10]Mason et al. (1995), Murphy et al. (1995), Phaneuf (1997), Yin et al. (1998), Haltuch et al. (2000); [11]Sprules et al. (1998); [12] Piunno et al. 1995, Watterson et al. 2000.

Examples Of Relevant Work

1) Describing the Invasion Process

Questions: What habitat factors shape the current spatial distributions of zebra and quagga mussels in Lakes Ontario and Erie? Can the history of dreissenid dispersal be reconstructed for Lakes Ontario and Erie? Can present knowledge predict the quantitative distribution of dreissenids in the Lower Great Lakes? Can this model be extended to the upper Great Lakes? What habitat factors determine seasonal distribution patterns of *Bythotrephes* and *Cercopagis* in Lakes Ontario and Erie?

Potential Approaches: Describe the lake-wide spatial heterogeneity of any of the four focal invertebrates at a scale of approximately 1 km, and assess associations between relative abundance and the major limnological features (habitat) of the lake (e.g., bathymetry, current patterns, distinct water masses, upwelling zones) with the view of developing empirical relationships that could be used to forecast the likely colonization zones for the same invader in lakes Huron, Michigan and/or Superior.

2) Understanding the Invasion Process and Impacts on Fish Communities

A. Dreissenids

Question: How have fishes altered their diet and behaviour to accommodate increased flow and accumulation of energy and material in benthic food webs invaded by dreissenids? Can benthic and pelagic production be quantified separately to more precisely assess offshore versus near-shore versus whole-lake impacts?

Potential Approaches: Use food-web tracers (e.g., stable isotopes, contaminants, essential fatty acids) to compare and contrast the role of benthic food sources in local food webs that include dreissenids with food webs that do not include dreissenids. Undertake historical reconstructions of changes in benthic food sources when benthic food webs are invaded by dreissenids. Use novel techniques to make accurate estimates of primary and secondary production (e.g., crustacean-molting-enzyme concentrations, continuous sensor for C-fixation).

Question: Does a dreissenid invasion alter offshore food webs and offshore benthic-pelagic couplings such that fish production becomes more dependent on pelagic food sources? To what extent can near-shore and offshore fishes accommodate the decline/loss of *Diporeia* by switching to *Mysis*? How does the alteration of food-webs impact contaminant and energy transfer? How will sport and commercial fisheries be impacted by a complete loss of *Diporeia*?

Potential Approaches: Use food-web tracers to compare and contrast the relative role of pelagic food sources (e.g., *Mysis*) with benthic food sources (e.g., *Diporeia*) in regions of Lake Michigan (or other affected lakes) with and without large offshore colonies of dreissenids. Undertake historical reconstructions to describe changes in the availability of pelagic/benthic food sources when food webs are invaded by dreissenids.

Question: Do near-shore changes in benthic species composition and in benthic and pelagic secondary production associated with establishment of zebra mussel beds have negative or positive impacts on fish condition and growth particularly for young-of-the-year? Are such impacts, if they occur, species-specific and what are the underlying mechanisms?

Potential Approaches: Use food-web tracers and advanced otolith methodologies to assess fish growth in the presence/absence of dense zebra mussel beds.

Question: Do near-shore dreissenid colonies reduce the offshore transport of nutrients and algae? To what extent is offshore fish production dependent on near-shore primary production? To what degree do zebra mussel beds impact food webs and fish communities at more-distant locales where zebra mussel beds are less common?
Potential Approaches: Use innovative techniques such as food-web tracers and quantification of circulation processes to track the transport of materials from near-shore to offshore food webs.

Question: Is the spread of the round goby linked to the spread of dreissenids? Is the joint colonization of the lower lakes by dreissenids and gobies a major factor in the expansion of smallmouth bass populations?
Potential Approaches: Compare and contrast bass populations in the presence/absence of both dreissenids and gobies with a view to identifying systemic differences and causative mechanisms.

Question: How do the morphometric, climatic, and productivity differences among the Great Lakes determine the relative dominance and linkages between offshore and near-shore food webs? Are habitat alterations associated with dreissenids more important in shallow, productive lakes and embayments than in deeper, less-productive lakes?
Potential Approaches: Compare and contrast the extent and rate of dreissenid colonization among local environments that vary systematically across climatic and productivity gradients in the Great Lakes and in model systems.

B. Exotic Cladocerans

Question: How will the spread of long-spined predatory cladocerans affect the mortality and growth of larval and older planktivorous fish? Can long-spined cladocerans out-compete and thereby limit the food of larval fishes? Which fish are most at risk?
Potential Approaches: Use food-web tracers within a Great Lake to link heterogeneities in the spatial distributions of *Bythotrephes* with heterogeneities in planktivorous fish distributions.

3) Forecasting Invasion Impacts

Question: Where are the yet-to-be colonized areas in the Great Lakes for each of the focal invaders?
Potential Approaches: Conduct integrated laboratory and field studies to identify a standard set of limiting habitat requirements (e.g., thermal tolerances, effects of temperature on consumption/respiration rates, substrate preferences, and diurnal and seasonal migratory patterns and associated cues) for the focal invertebrates, but particularly for *Cercopagis*, which is not well studied. Map areas in the Great Lakes where these requirements for future colonization are met.

Question: How will variation in the spatial distribution of a focal invader affect fishery sustainability during the expansion phase of the invasion?

Potential Approaches: Extend existing ecosystem models, e.g., LEEM (Locci and Koonce 1999) and ECOSIM (Walters et al. 1999, 2000), to assess how fishery sustainability responds to variation in the spatial distribution of a focal invader during the expansion phase of an invasion.

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APPENDIX

Selected examples of impacts associated with invasions of dreissenids and exotic cladocerans in North America with special reference to the Great Lakes. References with asterisks are from abstracts of recent conference papers.

Species	Lake	Observed Effect	Possible Impacts on Food Webs
Bythotrephes & *Cercopagis*	All lakes	Protective spine on both species renders them unpalatable to very small fish (Barnhisel 1991; Barnhisel and Harvey 1995).	Zooplankton production consumed by these invaders will not be available to young-of-year fish potentially imposing a bottleneck on recruitment.
	All lakes	*Bythotrephes* is consumed by larger life stages of some Great Lakes fish (e.g., alewife, Bur and Klarer 1991; Barnhisel and Harvey 1995; Coulas et al. 1998); in Lake Ontario, *Bythotrephes* is rarely seen due to alewife predation (Johannson et al. 1991).	Passage of zooplankton production to fish through predatory zooplankton (such as *Bythotrephes* or *Cercopagis*) will cause a significant change in trophic efficiency. A new link in the food web between herbivorous zooplankton and fish will lead to losses of fish production which may be offset by the potential savings in search costs for fish because of the large body size and aggregating behavior characteristic of these predatory zooplankters (Mills et al. 1992; Johannsson et al. 1999; W.G. Sprules, Dept. Zoology, U. Toronto, pers. comm.)
	Lake Michigan (e.g., Burkhardt and Lehman 1994; Yurista and Schulz 1995) and other North American sites (Yan and Pawson 1997; Wahlstrom and Westman 1999)	*Bythotrephes* consumption rates exceed midsummer recruitment rates for small cladocerans.	A significant fraction of annual herbivorous zooplankton production may pass through *Bythotrephes* with possible trophic transfer consequences as outlined above. Intense predation on herbivorous zooplankton by *Bythotrephes* could significantly reduce herbivorous grazing pressure leading to increases in chlorophyll concentrations and reductions in water clarity (Hutchinson et al. 1995)
	Lake Michigan (Lehman 1991; Makarewicz 1995)	Large declines in cladoceran diversity occurred when *Bythotrephes* appeared.	The production of herbivorous zooplankton passing through exotic cladocerans in some of the Great Lakes in some years is of sufficient magnitude to alter both the species composition of the native zooplankton communities and the flow of energy to fish.
	Lake Erie (Johannsson et al. 1999; Johannsson unpubl. data)	*Bythotrephes* biomass was inversely related to biomass of its principle zooplankton prey; *Bythotrephes* consumed up to 60% of zooplankton production in the west-central basin of Lake Erie in 1993.	
	Lake Michigan (Branstrator 1995); Lake Erie (Johannsson et al. 1999)	*Bythotrephes* appeared to suppress *Leptodora* (an important native predatory cladoceran) in both lakes through competition and predation.	
	Lake Ontario (Benoit and Johannsson 2000*; Warner et al. 2000*)	Abundance of *Bosmina*, calanoids, and cyclopoids declined with the appearance of *Cercopagis* in 1998/1999. Seasonal depression of small copepods (nauplii, small copepodids) observed when *Cercopagis* abundant.	
dreissenids	Lake Ontario (Bay of Quinte) (Bailey et al. 1999) and all other invaded systems	Increase in water clarity associated with dreissenid invasion.	Shunting of primary production and nutrients from the water column to the benthos; shunting may lead to reduced production of zooplankton and planktivorous fish.

	Lake Ontario (south shore bays) (Hall et al. 2000*); Lake Erie (Millard et al. 1999; Nicholls et al. 1999)	De-coupling of linkage between phosphorus and chlorophyll after dreissenid invasion.	
	Georgian Bay (Severn Sound) (Coulas et al. 2000*); Lake Erie (Holland 1993; Munawar et al. 1999, 2000*)	Diatom decline associated with dreissenid invasion.	
	Lake Erie & Lake Huron (Fahnenstiel et al. 1995; Nicholls and Hopkins 1993)	Decline in phytoplankton abundance associated with dreissenid invasion.	
	Lake Huron (Saginaw Bay) (Nalepa and Fahnenstiel 1995)	Shift in primary production from the water column to benthos associated with dreissenid invasion.	
	Lake Erie (Lam et al. 2000*)	Increase in loss of phosphorus from water column associated with dreissenid invasion.	
	Lake Erie (eastern basin) and other sites (Dermott and Munawar 1993; Dermott and Kerec 1997; Dermott 2000*); Lake Ontario (east and south) (Owens et al. 2000a, 2000b*); southern Lake Michigan (Nalepa et al. 2000*)	Decline of *Diporeia* in the offshore benthos associated with dreissenid invasion.	If *Diporeia* is not replaced, productivity of the cold-water fish community (e.g., lake whitefish) will decline significantly as production is redirected from the offshore fish community to the inshore benthic fish community.
	Lake Ontario (Hoyle 2000*)	Decline in abundance and condition of whitefish associated with dreissenid invasion.	Whitefish population decline related to dreissenid-induced disappearance of *Diporeia*, formerly the primary diet item for whitefish.
	Lake Erie (Johannsson et al. 2000; Parker et al. 2000*)	Zooplankton production tracked decline in primary production due to dreissenid filtering, and therefore overall pelagic secondary production declined. In the shallow regions of Long Point Bay, zooplankton production was 15% of the potential set by total phosphorus. Declines in smelt growth and abundance were associated with reductions in both zooplankton abundance and divesity.	Dreissenid-induced reduction in primary production followed by declines in production of both zooplankton and planktivorous fish.
	Lake Ontario (Perkins and Johannsson 2000*)	No decline in growth and abundance of *Mysis* associated with dreissenid invasion.	Mysids may be available to only a portion of the fish community affected by declines in *Diporeia* and may not be able to fill the void created by these declines. Those fish dependent on *Diporeia* may decline substantially (Kitchell et al. 2000).

	Lake Erie (Stewart 1998; Johannsson et al. 2000)	Dreissenid shell masses increase benthic habitat complexity and biomass of macrobenthos in shallow waters. Dreissenid production greater than 80% of total benthic production	Transfer of production from pelagic to benthic food web.
	Lake St. Clair (MacLennan et al. in press)	Increase in water clarity and biomass of emergents change availability of preferred habitat of fish: abundance of smallmouth bass and muskellunge increases, walleye abundance declines.	Prey community shifts in response to functional differences and biomass of piscivores.