Ecological Forecasting of Impacts of Ponto-Caspian Species in the Great Lakes: Describing, Understanding, and Predicting a System in Transition

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Abstract

This paper summarizes results relevant to ecological forecasting from a study that described, explained, and predicted Great Lakes ecosystem impacts of six Ponto-Caspian (the region including the Caspian, Black, and Azov Seas) endemic species of mussels, crustaceans, and fishes that recently invaded the Great Lakes via ballast water (Vanderploeg et al. *2002). These are the zebra mussel (*Dreissena polymorpha*), the quagga mussel (*D. bugensis*), the predatory cladoceran (*Cercopagis pengoi*), the benthic amphipod (*Echinogammarus ischnus*), the round goby (*Neogobius melanostomus*), and the tubenose goby (*Proterorhinus marmoratus*).*

The ecology and possible mechanisms of ecosystem impact were reviewed for each species using information from a variety of studies and sites, including the Great Lakes. This information was combined with experiments and monitoring on the Great Lakes to describe ecosystem change, the underlying invader species mechanisms of impact, and predict future changes.

Introduction

Several Ponto-Caspian endemics have recently invaded the Great Lakes: the zebra mussel (*Dreissena polymorpha*), the quagga mussel (*D. bugensis*); the predatory cladoceran (*Cercopagis pengoi*), the benthic amphipod (*Echinogammarus ischnus*); the round goby (*Neogobius melanostomus*), and the tubenose goby (*Proterorhinus marmoratus*). All these euryhaline species arrived in ballast water.

The Great Lakes have undergone and continue to undergo profound ecological changes in response to these invaders. There are also changes from oligotrophication, piscivorous fish stocking, and other exotic species, some of which are in concert with effects of the Ponto-Caspian species. So it is difficult to separate impacts from these invaders from other anthropogenic changes and makes it challenging to forecast the impacts of these species on water quality and fisheries of the Great Lakes.

It is important to document changes in the system since invasion and attribute them to the invaders. But it is also necessary to relate – ideally quantitatively – the changes through a set of plausible underlying mechanisms to these recent invaders to define relative contributions of all factors. This is an overview of results from a large synthesis relevant to ecological forecasting of spread and ecosystem impacts of Ponto-Caspian species in the Great Lakes and other water bodies (Vanderploeg *et al.* 2002).

Case Study

The study began with a synthesis of the ecology of each Ponto-Caspian invader and the mechanisms they use to spread and affect ecosystems. This was derived from studies in the laboratory, in the Great Lakes, and in other systems.

To generate as holistic as possible case studies of invader-induced change, the underlying causes, and predictions for the future, information from the ecological synthesis was applied to areas in the Great Lakes where the ecosystem has been monitored. This exercise was extremely important not only for impact description but also for revealing mechanisms and interactions not suspected from prior knowledge of each

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invader alone or from current understanding of aquatic ecosystem processes.

The areas of study included shallow bays and basins – Saginaw bay (inner bay mean depth = 5.1 m), western Lake Erie (mean depth = 5.7 m), Lake St. Clair (mean depth = 3.0 m) Long Point Bay on Lake Erie (inner bay mean depth = 2 m) – as well as deep basins of Lakes Erie, Ontario and Michigan (Figure 1). Long Point Bay was of particular interest in that it is one of the most important staging areas for waterfowl in North America.

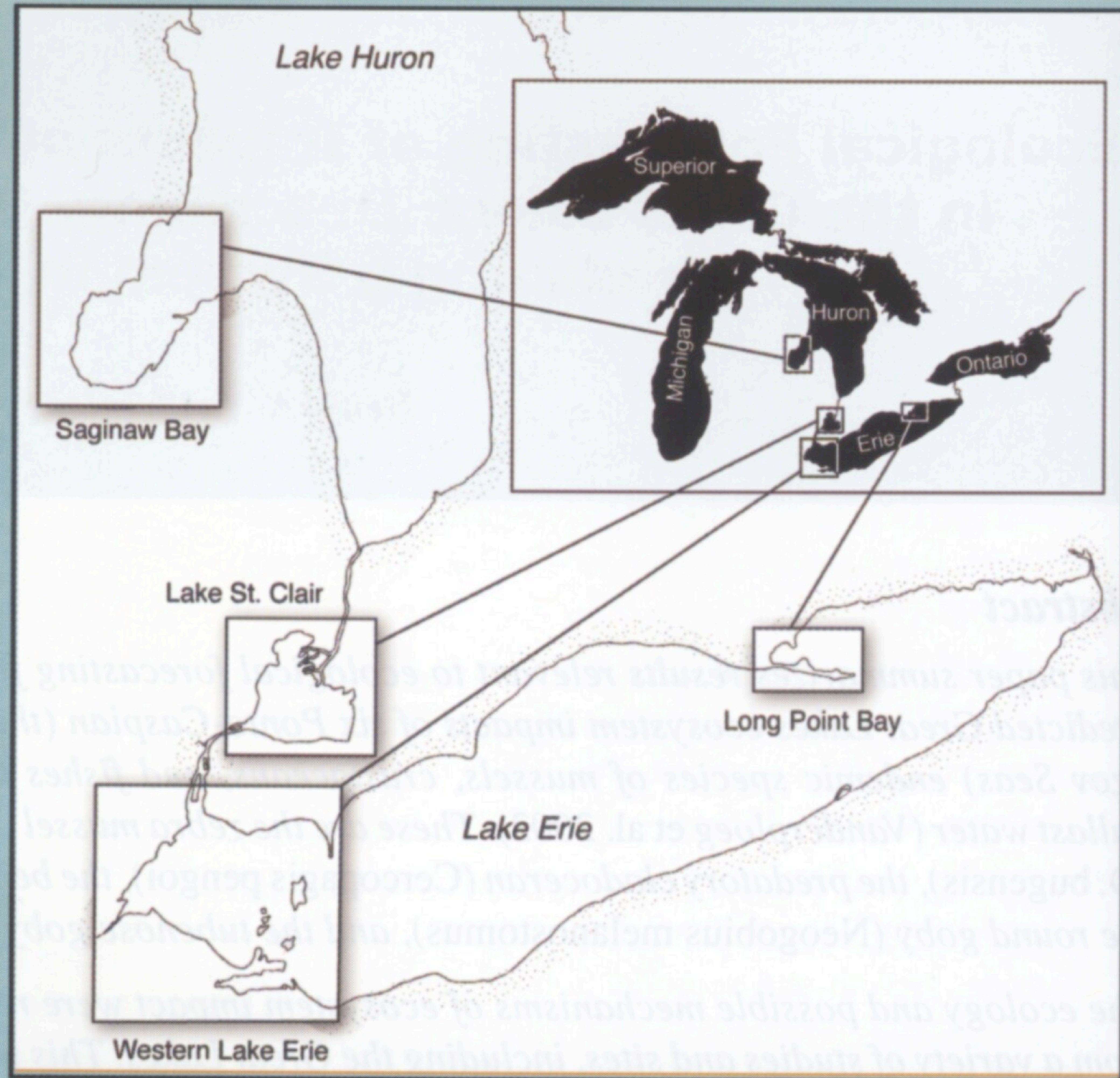

Figure 1. Case study sites, where monitoring and experimental work permitted description and mechanisms of invader impact.

Lessons Learned

The zebra and quagga mussels are changing ecosystem function through ecosystem engineering (increased water clarity and reef building), fouling native mussels, high particle filtration rate with selective rejection of colonial cyanobacteria in pseudofeces, and alteration of nutrient ratios. They also facilitate the rapid spread of their Ponto-Caspian associates, the benthic amphipod and the round goby, which feed on zebra mussels.

High concentrations of zebra mussels and quagga mussels in shallow regions of the Great Lakes (<30 m) continue to dominate energy flow and nutrient cycling by their high filtration rate and nutrient excretion. Dreissenids are able to clear the water in spring in bays and shallow basins of the Great Lakes, but not in summer because of reduced filtering and selective rejection of unpalatable algae in pseudofeces. This same selective rejection mechanism may be increasing the probability of toxic blooms of the colonial cyanobacterium *Microcystis* on Saginaw Bay and western Lake Erie.

Dreissena, round gobies, and *Echinogammarus* form an 'invasional meltdown' assemblage in the Great Lakes that is becoming an important part of the food web in many areas of the Great Lakes. That is, rather than restricting invasion by other species, zebra mussels facilitated invasion of the Great Lakes by their Ponto-Caspian associates. *Dreissena* provides substrate (shell) and food (pseudofeces and feces) to *Echinogammarus*. Round gobies and other fishes feed on *Echinogammarus*. Round gobies are efficient predators of *Dreissena*, and are eaten by a variety of game fishes. Tubenose gobies, which are too small to feed on *Dreissena*, are not expected to cause significant impacts.

In some shallow systems, certain sport fishes and waterfowl have benefited from habitat and food web changes caused by the zebra mussel (Figure 2). Zebra mussels are a food source for diving ducks. After the zebra mussel invasion of Long Point Bay, waterfowl use days increased from 0.04 to 3.5 million. Game fishes such as smallmouth bass and muskellunge have additional feeding and spawning habitat created by the macrophytes that grew because of the increased light resulting from suspended particle removal by zebra mussel filtration. Improved habitat and predation on round gobies have resulted in increased populations of these game fishes. In Lake St. Clair, a particularly important area for sport fishing, abundance of smallmouth bass and muskellunge increased 3-fold.

On the other hand, there are negative consequences to the new food web. Populations of walleyes, which prefer low light, have decreased by 50 to 75 percent in Lake St. Clair and the reproductive success of diving ducks may be affected by contaminants associated with zebra mussels. Thus, there is concern that Long Point

Bay may be a magnet for contamination of continental populations of certain diving ducks. And the zebra mussel → round goby → game fish food chain may increase contaminant loads in game fishes.

Zebra mussels, through their fouling native unionid mussel shells, have removed them from most areas except for refuge areas in marshes and wave-exposed shallow areas. Surprisingly, despite dominance of shallow benthic communities by dreissenids, non-dreissenid benthic invertebrates other than mussels remained at pre-invasion levels. The provision of substrate by mussel shells and increased primary production of benthic plants enhanced by increased water clarity (Figure 2) may have compensated for the expected loss of the phytoplankton food base removed by mussel filtering. Microzooplankton have strongly declined in shallow areas as a result of dreissenid filtering, but crustacean zooplankton have not been greatly affected in areas examined, and growth of fish dependent on them has not decreased.

The quagga mussel, a close relative of the zebra mussel that can colonize soft substrates, has invaded many deep areas of the Great Lakes (>30 m) and is extending the impacts of *Dreissena* to this region since it too is a voracious filter feeder. *Diporeia*, an amphipod that has historically dominated the benthos in deep water (>30 m), is now in decline in many of the Great Lakes (Michigan, Huron, Ontario, Erie); this decline may harm many fishes that prey on it. It is hypothesized that dreissenids are intercepting algae before they can reach *Diporeia* at the sediment surface.

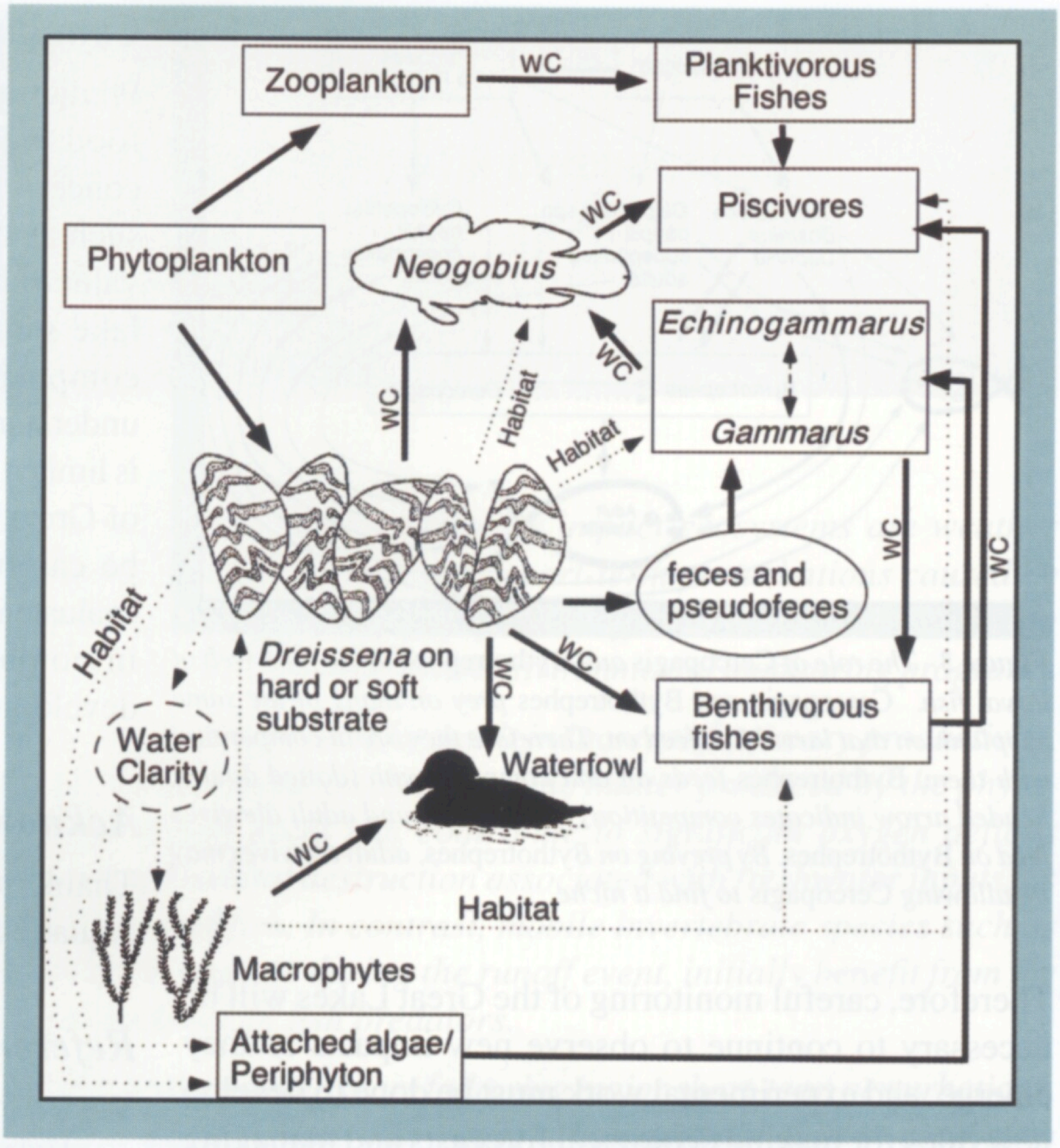

*Figure 2. Food-web and ecosystem-engineering mechanisms of impact of the Ponto-Caspian benthic assemblage (*Dreissena, Neogobius, *and* Echinogammarus*) in bays (e.g. Saginaw Bay, Long Point Bay), interconnecting waterways (Lake St. Clair) and nearshore or shallow (Lake Erie) areas of the Great Lakes. Solid arrows indicate food-web connections. The dashed double-headed arrow indicates potential competitive interactions between the native amphipod,* Gammarus, *and the non-indigenous amphipod* Echinogammarus, *and the dotted arrows indicate the influence of ecosystem engineering through the mechanisms of habitat provision of mussel shells (autogenic engineering) and water clarity (allogenic ecosystem engineering). WC (for water clarity) is placed next to solid arrows for predation by vertebrate (visual) predators (fishes and waterfowl) to indicate possible increases in predation rate associated with increased water clarity that results from zebra mussel filtering. Because their filtering activities increase the water clarity, zebra mussels promote growth of benthic plants, providing habitat for fishes. The shells of the mussels provide habitat for a variety of invertebrates. The zebra mussel → round goby → piscivore food chain and increased macrophytes (cover and spawning habitat of fishes) have resulted in increased production of certain fish species in shallow areas.*

Cercopagis pengoi, a predatory cercopagid cladoceran with large tail spine, is protected from predation by small fishes because of its tail spine, and will compete with small fishes for cladocerans and other zooplankton (Figure 3). It is now found in abundance in summer in both nearshore and offshore waters of Lake Ontario and inshore waters of Lake Michigan. Distribution and impact of Cercopagis in Lake Michigan may be controlled somewhat by predation by *Bythotrephes*, another larger cercopagid that invaded the Great Lakes from northern Eurasia in 1985.

Next Steps

The Great Lakes ecosystems have been radically modified, are in a state of transition, and impacts will continue to evolve. For example, over 90 percent of the secondary production, grazing, and nutrient excretion in many areas of the Great Lakes is associated with zebra and quagga mussels. Thus, old rules of ecological forecasting and management no longer apply.

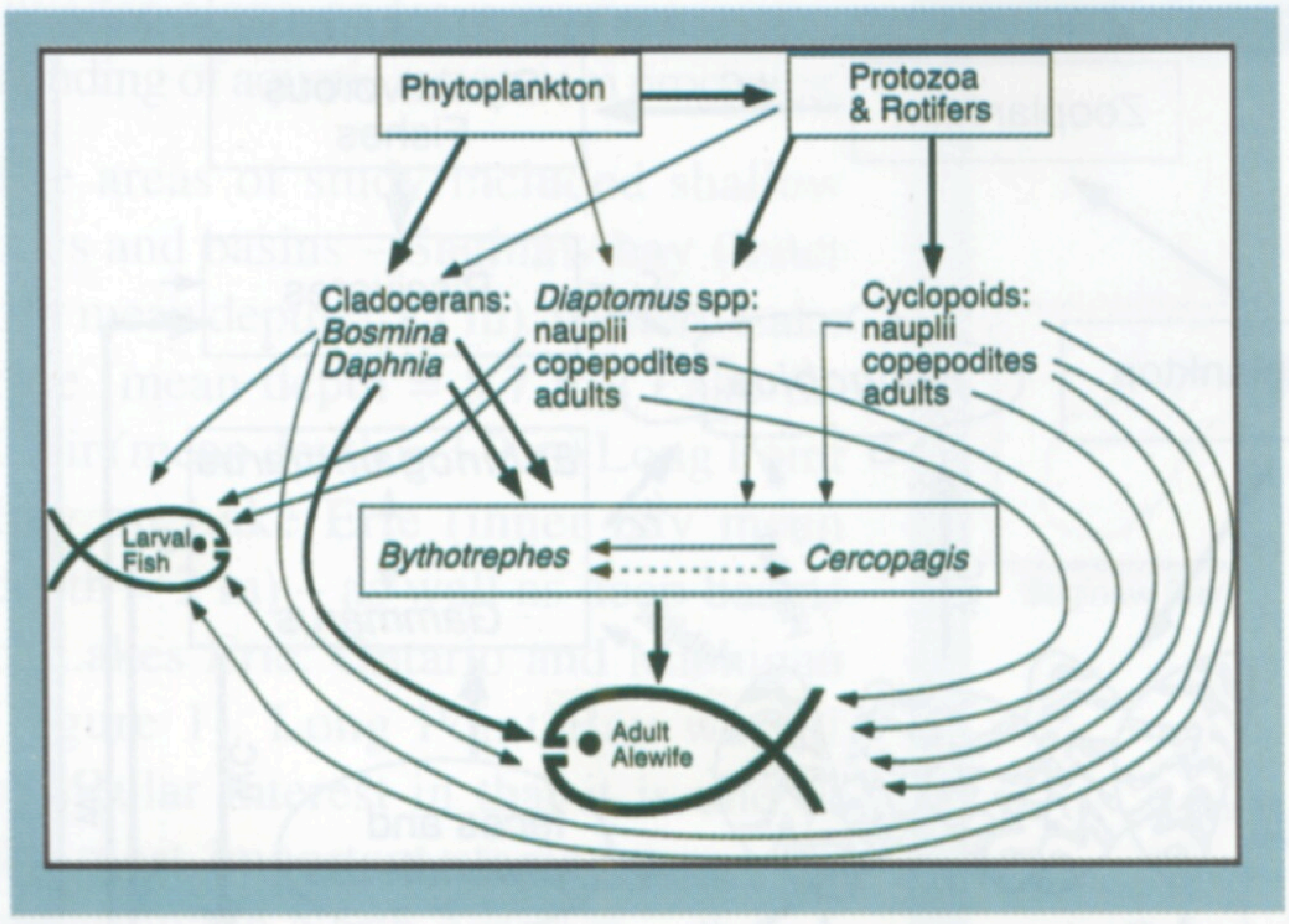

***Figure 3**. The role of* Cercopagis *and* Bythotrephes *in the food web of larval fish.* Cercopagis *and* Bythotrephes *prey on many of the same zooplankton that larval fish feed on. Therefore they are in competition with them.* Bythotrephes *feeds on and competes with (dotted double headed arrow indicates competition)* Cercopagis, *and adult alewives feed on* Bythotrephes. *By preying on* Bythotrephes, *adult alewives may be allowing* Cercopagis *to find a niche.*

Therefore, careful monitoring of the Great Lakes will be necessary to continue to observe new impacts as they emerge, and experimental work must be done to develop new rules for making ecological forecasts and managing these systems

Conclusion

Predictions of impact require intimate knowledge of food web structure and function in the area of concern. Extrapolations of impacts from other sites, such as those in Eastern Europe, often have limited value for the Great Lakes because of differences in lake morphometry, nutrient loading, and species composition, particularly fishes. The ability to understand present impacts and predict future impacts is limited by insufficient monitoring and understanding of Great Lakes food webs. The Great Lakes need to be carefully monitored to observe changes and to evaluate impacts of these changes. Experimental work in conjunction monitoring will be necessary to develop ecological forecasting tools and models.

Acknowledgements

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References

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