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Simulation of rapid ecological change in Lake Ontario

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ABSTRACT

Lower trophic level processes are integral to proper functioning of large aquatic ecosystems and have been disturbed in Lake Ontario by various stressors including exotic species. The invasion of benthic habitats by dreissenid mussels has led to systemic changes and native faunal declines. Size-dependent physiological rates, spatial differences and connectivity, competition, and differential population dynamics among invertebrate groups contributed to the change and system complexity. We developed a spatially explicit, individual-based mechanistic model of the benthic ecosystem in Lake Ontario, with coupling to the pelagic system, to examine ecosystem dynamics and effects of dreissenid mussel invasion and native fauna losses. Benthic organisms were represented by functional groups; filter-feeders (i.e., dreissenid mussels), surface deposit-feeders (e.g., native amphipod *Diporeia* spp.), and deposit-feeders (e.g., oligochaetes and other burrowers). The model was stable, represented ecological structure and function effectively, and reproduced observed effects of the mussel invasion. Two hypotheses for causes of *Diporeia* loss, competition or disease-like mortality, were tested. Simple competition for food did not explain observed declines in native surface deposit-feeders during the filter-feeder invasion. However, the elevated mortality scenario supports a disease-like cause for loss of the native amphipod, with population changes in various lake areas and altered benthic biomass transfers. Stabilization of mussel populations and possible recovery of the native, surface-deposit feeding amphipod were predicted. Although further research is required on forcing functions, model parameters, and natural conditions, the model provides a valuable tool to help managers understand the benthic system and plan for response to future disruptions.

Introduction

Lake Ontario is a large, complex ecosystem that has suffered physical, chemical, and biological disturbances for over a century (Schelske and Hodell, 1991; Mills et al., 2003). Arguably, the most disruptive events have been associated with the invasion of exotic aquatic organisms, particularly dreissenid mussels (*Dreissena* spp.) (Mills et al., 1994; Karatayev et al., 2015). This invasion caused region-wide systemic changes in ecological function and processes, and large-scale declines in native fauna, most notably the benthic amphipod *Diporeia* spp. (hereafter *Diporeia*) (Lozano et al., 2001; Watkins et al., 2007). *Diporeia* was a key species in the lake's ecology and food web, contributing greatly to support of multimillion dollar fisheries (Dermott, 2001; Rothlisberger et al., 2010; Minns, 2014).

The decline in *Diporeia* and benthic infauna was closely associated with the invasion and proliferation of dreissenid mussels and is well documented by a number of observations (Dermott, 2001; Lozano et al., 2001; Watkins et al., 2007), but the exact mechanisms of change that lead to native fauna losses have not been identified. Before the mussel invasion, deep-water benthic fauna consisted primarily of *Diporeia*, with lesser abundances of oligochaetes, chironomids, and sphaeriid clams (Nalepa and Thomas, 1976). *Diporeia* is a surface deposit-feeder restricted to feeding within the surface layer of the benthos (Sly and Christie, 1992), while oligochaetes, chironomids, and sphaeriid clams are deposit-feeders burrowing throughout the sediment column. These macrobenthic organisms rely on the steady rain of organic matter to the bottom, which includes epilimnetic diatoms and other phytoplankton, as well as non-living organic matter (Dermott and Corning, 1988; Thomann et al., 1992).

The dreissenid mussel invasion introduced a novel functional group of filter-feeders, causing dramatic changes to the Lake Ontario ecosystem and affecting both benthic and pelagic systems (Lozano et al., 2001). Their establishment and activity have so greatly changed the Lake Ontario system that a new term for this ecological shift, "benthification", was coined by Mills et al. (2003). The invasion involved two species of exotic mussels (zebra mussels, *Dreissena polymorpha* and quagga mussels, *Dreissena rostriformis bugensis*) and occurred over the course of a decade, starting in shallow nearshore areas and expanding to the profundal basin (Hecky et al., 2004; Watkins et al., 2007). By 2008, quagga mussels accounted for 98% of offshore benthic macroinvertebrate community biomass' and *Diporeia* was nearly extirpated

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from most areas of the lake (Birkett et al., 2015). While most predictions are dire for *Diporeia*, there is also recent evidence of decline in mussels and modest recovery of *Diporeia* in some areas (Dittman pers. comm.). An array of successful invaders has colonized Lake Ontario and more are likely (Mills et al., 1994; Snyder et al., 2014). For example, after the mussels arrived, the benthic system was further disrupted by invasion of round goby (*Neogobius melanostomus*), a predator on the mussels (Walsh et al., 2007).

Several plausible hypotheses have been presented to explain the decline in *Diporeia* populations (Nalepa et al., 2009) and two have been identified as most likely, 1) competition with mussels for food and 2) mortality caused by a disease-like factor associated (or at least coincident) with mussel invasion (Watkins et al., 2007, 2012). However, it is difficult to sample all of the pertinent components of a complex food web to document cause and effect, and no single hypothesis provides a clear explanation. It is important to better understand invader success, native species response (often declines), and the mechanisms of change (Strayer et al., 1999). Such insight would help managers prepare for likely changes associated with new ecosystem disruptions.

A number of mass-balance models have improved our understanding of Great Lakes food web structure and function (Stewart and Sprules, 2011; Langseth et al., 2012, for example). However, there remains a critical need for improved predictive models of Lake Ontario ecosystem dynamics (Fussell et al., 2016; Stewart et al., 2016). Mechanistic models help us represent the state of knowledge of ecosystem function. Their implementation helps us to simulate ecosystem dynamics, testing theoretical constructs and hypotheses about mechanisms of change (Kremer and Nixon, 1978; Grant, 1986). In complex systems, simulation modeling often offers the only feasible means of examining mechanisms and estimating frequent changes in spatially distinct areas of large aquatic systems (Thomann et al., 1992; Stewart and Sprules, 2011). To test our understanding of the filter-feeder (FF) (i.e., dreissenid mussels) invasion and hypotheses about the associated declines in surface deposit-feeders (SDF) (e.g., *Diporeia*) and benthic infaunal deposit-feeders (DF), we developed a mechanistic simulation model of carbon flow through the benthic system of Lake Ontario.

We hypothesize that the spatial pattern of dreissenid mussel invasion of Lake Ontario and native benthic fauna responses are the result of competition for common food resources, size-dependent physiological rates, spatial patterns of immigration and emigration, and mortality. Our objectives were to: 1) develop an effective mechanistic simulation model of carbon flow through the benthos of Lake Ontario, 2) apply that model to simulate pre- and post-invasion of filter-feeders in Lake Ontario and the response of native benthic fauna, and 3) identify the mechanisms of change and test two hypotheses of *Diporeia* decline due to disease or competition for food. We focus on FF and SDF because their changes are documented best. This is an experimental simulation approach with controlled forcing functions and simplified benthic dynamics (Grant, 1986), intended to test the feasibility of the various scenarios and efficacy of our model benthic system to represent mechanisms of change in the Lake Ontario benthic ecosystem.

Methods

Efforts modeling the Great Lakes and invasion dynamics using the Ecopath and Ecosim mass-balance methods have provided valuable information about the Lake Ontario ecosystem, but rely on ecological ratios (e.g., Production: Respiration) and have had variable success in fitting model predictions to observed data (Stewart and Sprules, 2011; Langseth et al., 2012). In order to examine potential cause and effect relationships, we chose to develop a mechanistic model, which uses generalizations from many other studies to conceptually represent carbon flow through a benthic system that is sustained by a pelagic system, with emphasis on macrofauna. Empirical data were only used to develop forcing functions and to guide parameter estimation. The model is implemented as a simulation that can address many questions about benthic structure and rates of change, including mechanisms of change in macrofauna during invasion of a new guild (e.g., filter-feeders). In this study, the model was parameterized to best represent Lake Ontario.

General modeling approach

The model includes simulation of precipitation of organic matter to the benthos, physical mixing of sediment due to bioturbation, respiration of microbes and meiofauna, and macrofauna physiology and population dynamics (Fig. 1). Our main focus was on macrofauna populations, their dynamics, and dispersion throughout Lake Ontario. These represent a major conduit of mass and energy flow from the benthos to fish and are important for lake management. The macrofauna are represented as functional groups, characterized by feeding and reproductive methods, and their abundance, biomass, and size structure are computed by the model. Input (i.e., food) to each individual of each functional group is either suspended or sedimentary organic matter, and physiological processing of food is temperature and allometrically regulated. Environmental temperature and food availability is modeled as annually repeating functions with values generated on a daily time step. All individuals of a functional group within a given area will compete for the common food resources; interspecies competition may also occur where a common resource is being exploited by more than one group. Spawned macrofauna larvae drift with the circulation for various lengths of time, specific to each functional group, before settling to the benthos. Macrofauna mortality was simulated as proportions removed from populations and represented transfer to predators and all other forms of death (e.g., decomposers). Microbial metabolism was a sink of sedimentary organic matter, modeled as a function of temperature. Mortality rates, food availabilities, and model parameters may be manipulated for experimental purposes.

We chose to develop a deterministic model, because ecological values and rates of processes are often poorly known for Lake Ontario and variability is rarely known. We follow the methods of McKenna (1987) and represent macrofauna as generalized functional feeding groups. Because so many of the model parameters are poorly known, we also follow the approach of Kremer and Nixon (1978) and use a Standard Run (i.e., baseline simulation, Grant, 1986) as the benchmark with which to compare model system changes due to experimental manipulations. In this application of the model, the Standard Run represents pre-mussel invasion conditions in Lake Ontario. Even modern data on the benthic communities are sparse for this large aquatic system, but pre-mussel data and particularly much older data are very rare (Hiltunen, 1969; Nalepa and Thomas, 1976; Barton and Anholt, 1997). Thus, our mechanistic approach provides an estimation of pre-mussel conditions and only qualitative evaluation can judge the reasonableness of the model representation of historic benthic dynamics.

Standard Run – Setting initial conditions

Specific values of the physiological coefficients, initial physical conditions, and forcing functions must be used for each simulation, despite the wide and often unknown variability in many of these variables. The Standard Run serves to explain basic behavior of the model and provides a scale with which to compare experimental simulations (Kremer and Nixon, 1978; McKenna, 1987). Annual cycles of water temperatures, suspended organic matter production and settling rates, and zooplankton consumption of larvae drive the system. The simulation time step was one day; and the biomass, abundance, and mean body size of each cohort of individuals of each benthic functional group are tracked within each spatial area of the lake, as well as rates of change and larval development. Only spot measurements of benthic community abundances are available from selected areas of the lake during the ice-free period (Hiltunen, 1969; Nalepa and Thomas, 1976; Barton and Anholt, 1997; Dittman and Walsh, 2007; Dermott, 2001; Lozano et al.,