Predicting Bioaccumulation in Dynamic Food Webs: Ontogeny, Seasonality and Invasional Successions

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Abstract

The structure of aquatic food webs has changed dramatically at the global scale. Overfishing, persistent chemical contamination, and the rapid spread of non-indigenous species have caused the loss of the "big fish"—traditional predator species that once formed the basis of the fishing industry. This decline in pelagic diversity, coupled with the effect of invasive species like the zebra mussel, has led to the benthification of many aquatic systems, particularly in the Great Lakes. Often, the interactions between chemical contaminants and invasive species in these dynamically altered, benthified food webs have unexpected consequences. Yet, management and restoration strategies for such systems are based on the contaminant transfer patterns observed in pelagic food webs. In pelagic systems, contaminant levels increase with increasing trophic level, such that the largest predator fish are the most contaminated – a trend that often conforms to the persistent, yet overly simplified, notion of a "food chain." We have developed a modeling strategy that combines a seasonal, stage-structure food web model with a fugacity-based Mackay type bioaccumulation model to predict contaminant fate in food webs under "trophic flux" via seasonal diet changes, ontogeny, or invasional succession. We show how changes in species' diets lead to complex trophic dynamics, even in seemingly simple food webs, often creating contaminant feedback loops that change bioaccumulation patterns in unexpected ways, with profound implications for ecosystem management strategies and for the minimization of human health risks from fish consumption.

Introduction

Calumet Harbor is located on the southern shore of Lake Michigan, and is part of the Grand Calumet Area of Concern (AOC), one of the 42 most deteriorated areas in the Great Lakes [1]. Like many Great Lakes ecosystems, it has undergone substantial benthification due to the proliferation of two non-indigenous species: the round goby (*Neogobius melanostomus*) and the zebra mussel (*Dreissena polymorpha*). They have dominated, by biomass, a food web of relatively low species diversity, which in addition to the goby and zebra mussel include only benthic invertebrates (primarily amphipods), crayfish, and smallmouth bass (*Micropterous dolomieu*), a native epibenthic species and the harbor's sole predator fish. More recently, the quagga mussel *(Dreissena bugensis)*, another species native to the Ponto-Caspian region, has replaced the zebra mussel in most offshore and many nearshore areas of Lake Michigan with surprising speed. This succession has caused concern due to the quagga mussel's ability to colonize soft substrates and survive at deeper depths, allowing it to spread much farther into Lake

Michigan than the zebra mussel, which requires hard substrates and shallow waters, and is thus limited to nearshore rocky habitats.

Calumet Harbor Model Prior to Quagga Invasion

In our previous study of Calumet Harbor, we combined stable isotope and stomach content analyses with literature dietary and bioenergetic data to formulate a seasonal, stage-structured description of the Calumet Harbor food web both prior to and post the quagga mussel succession. This food web model was coupled to a standard fugacity-based bioaccumulation model to predict contaminant fate. We sought to understand, using our integrative modeling strategy, how much ecological detail was necessary to describe a highly altered ecosystem. In a food web with few species would a simple description suffice, or would greater ecological resolution be needed to accurately predict chemical transfer?

Based on our analysis, we constructed a detailed description of the Calumet Harbor ecosystem (Fig. 1a), which integrated three significant components: (i) ontogenetic diet shifts in the goby and bass; (ii) seasonally available fish eggs in the goby diet; and (iii) the consumption of detritus by benthic invertebrates and crayfish.

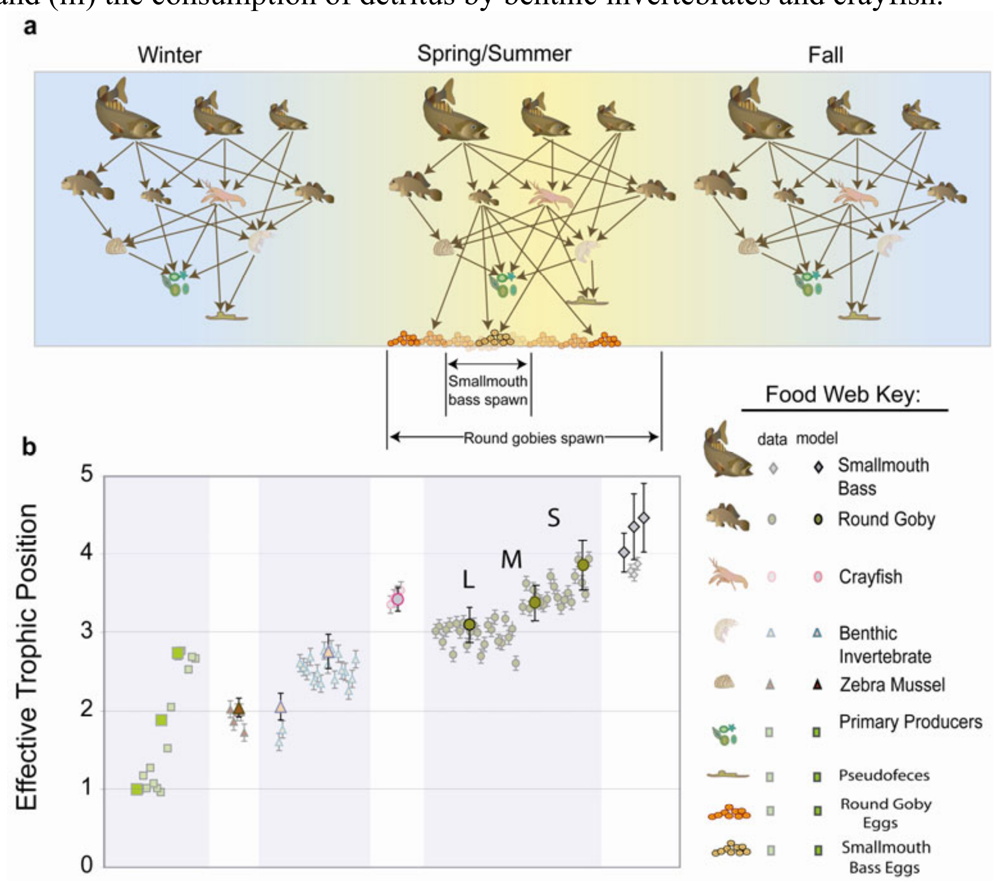

Figure 1: Seasonal, stage-structured food web model of the Calumet Harbor ecosystem prior to quagga mussel invasion. Zebra mussel feces and pseudofeces are included in the diets of deposit feeders (benthic invertebrates and crayfish). The diet of the small goby changes with season, as bass and goby eggs become available for consumption during the spring and summer. Bass populations are also stage structured.

It is visually apparent that our model captures all features of the empirical trophic profile data, which depict effective trophic levels of the species in Calumet Harbor as measured by stable nitrogen isotopes. Note that, within the round goby population, the *smallest* size class actually has the highest effective trophic position, due to consumption of detritivorous benthic invertebrates and fish eggs, whereas the *largest* size class, which consumes only zebra mussels, is at the lowest trophic position.

Our coupled model (now including PCB accumulation) predicts that young gobies, which feed on both detritivorous benthic invertebrates and fish eggs, have the highest total PCB concentration (C_{PCB}), as they are exposed to both of Calumet Harbor's detritus-based "contaminant feedback loops" (Fig. 2). Their high contaminant load is due in greatest part to fish egg consumption, even though it constitutes only 16% of their diet over the year. Medium gobies, which feed on zebra mussels in addition to benthic invertebrates, have a lower C_{PCB}, whereas large gobies, which feed exclusively on zebra mussels, in fact have the lowest C_{PCB}. Our model predictions contradict typical "food-chain-based" bioaccumulation assumptions of increasing contaminant concentration with organism age or size.

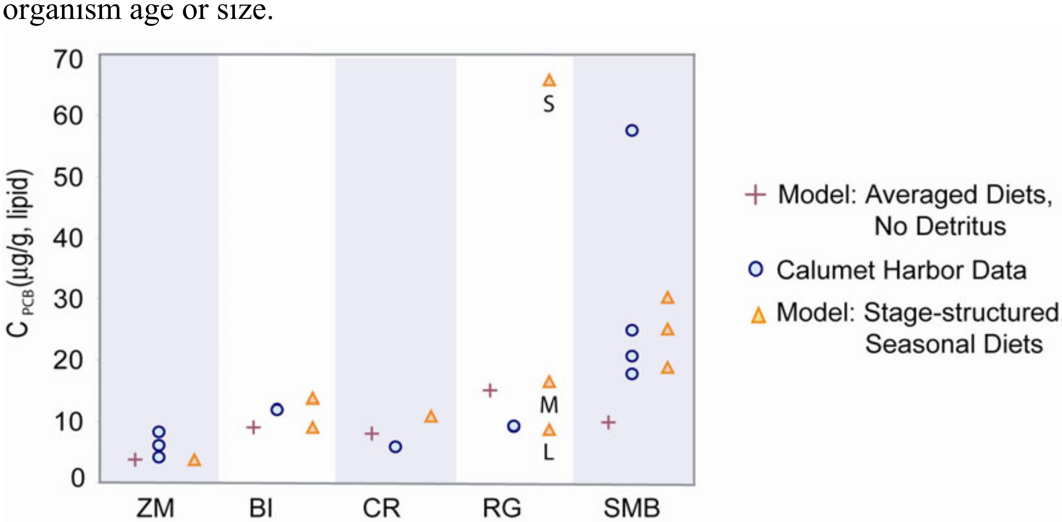

Figure 2: Bioaccumulation of total PCBs in the Calumet Harbor food web. The effect of using an "averaged diet" approach to food web construction becomes clear in gobies and bass. The average model (merging goby size classes, no eggs) over-predicts goby C_{PCB}, while our seasonal, stage-structured model prediction for C_{PCB} in large gobies is very close to measured values. Note that the gobies sampled were 80-100 mm, and therefore were in medium-to-large size classes. Our model predicts that goby C_{PCB} *decreases* with size, as small gobies consume benthic invertebrates and, seasonally, fish eggs. In addition, goby C_{PCB} is equivalent to or exceeds C_{PCB} in bass, and bass derive their high concentrations by consuming smaller, more highly contaminated gobies, a feature the averaged model fails to capture. These predictions may explain results of recent studies of benthic-dominated food webs [2, 3].

Calumet Harbor Model Post Quagga Mussel Invasion

We returned to Calumet Harbor to collect round goby samples in 2005, approximately seven years after the original sampling date. We sought to validate the results of the original model, but at the time of this more recent sampling trip, the zebra mussels in Calumet Harbor had been almost completely replaced by quagga mussels, another invasive dreissenid species, making such validation impossible. We therefore applied our original model to the new food web to see if we could explain the effects of this recent invasional succession on contaminant bioaccumulation in the harbor's round gobies.

Total C_{PCB} in medium and large round gobies collected in August 2005 were, on average, three times lower than those predicted for medium/large gobies by the pre-quagga mussel model and measured for the medium gobies in 1999 (Figure 3). We surmise that this large drop in C_{PCB}, which did not coincide with any dredging activity in the sampling area or with natural weathering of the PCBs (K_{ow} remained high and weathering of such highly chlorinated PCBs could not occur in such a short time), might be due to the quagga mussel population increase. Though in many respects the two dreissenid species are quite similar, quagga mussels can colonize sandy substrates at deeper depths, whereas zebra mussels require hard surfaces on which to attach, and are limited to shallow waters.

In Calumet Harbor, periphyton communities (the complex matrix of algae and heterotrophic bacteria attached to submerged surfaces in aquatic environments) are concentrated on stable rocky substrates. These communities have been shown to substantially bioaccumulate contaminants [4-7]. We therefore expect that zebra mussels, which are more closely associated with rocky substrates and therefore with the periphyton community, will be more contaminated, while quagga mussels subsisting on periphyton-free sandy substrates will provide a "cleaner" food source for the round goby.

The gobies sampled in 2005 range in size from 63 to 150 mm, corresponding to the medium and large size classes. We find that the range of PCB values observed in these fish is consistent with our predictions for medium and large gobies given a quagga mussel succession of approximately 80% (Fig. 3b), a value that matches well with current observations of quagga populations in the area [8, 9].

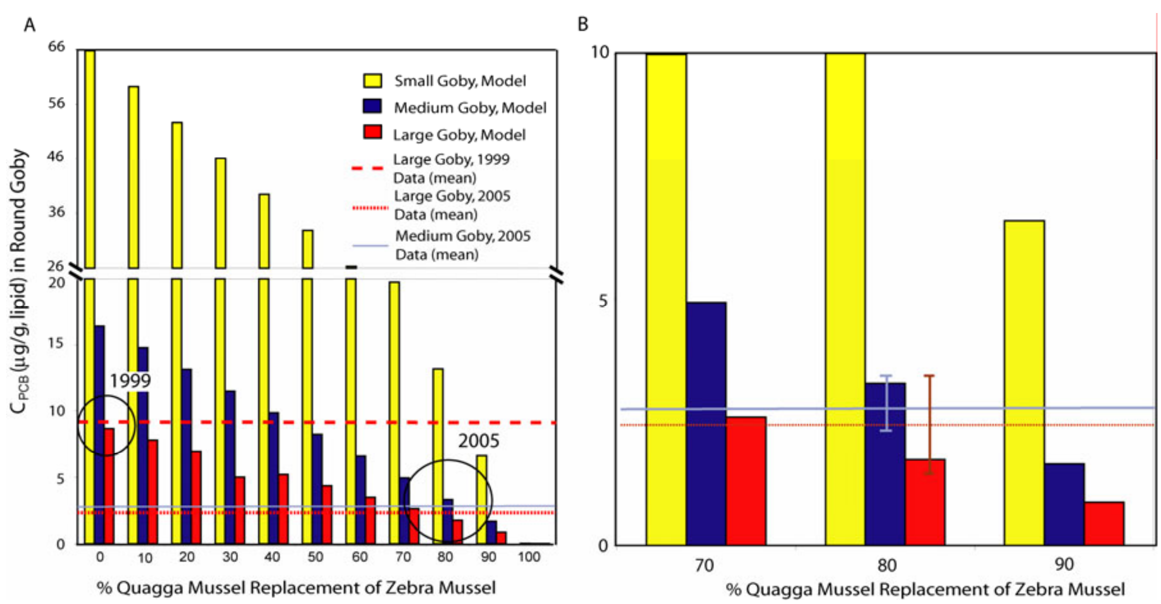

Figure 3: Effect of Quagga mussel succession. (**A**) C_{PCB} in Calumet Harbor's large (yellow column), medium (blue column) and small (red column) round gobies decreases due to

replacement of zebra mussels by less contaminated quagga mussels. Small goby C_{PCB} decreases more rapidly than in medium or large gobies, illustrating the "feedback" effect of contaminant cycling through consumption of both fish eggs and detritivorous amphipods. Measured C_{PCB} in large gobies in 1999 (red dashed line) corresponds to 0%. (**B**) Range of C_{PCB} in medium (blue solid line is mean; bar shows range) and large (red dotted line is mean; bar shows range) 2005 gobies correspond to a simulated quagga replacement of about 80%. This is in good agreement with recent observations in the area [8].

Dynamic Calumet PCB Model: Preliminary Results

Finally, we present some preliminary results of the next step in our modeling strategy—rather than using the simple fugacity-based model used in the previous two analyses, we extend this model to take a more dynamic look at contaminant bioaccumulation in Calumet Harbor. Our preliminary results illustrate the utility of our modeling strategy in testing food web scenarios to better understand contaminant fate in food webs that shift with species age, season, and species composition (e.g., new invasions).

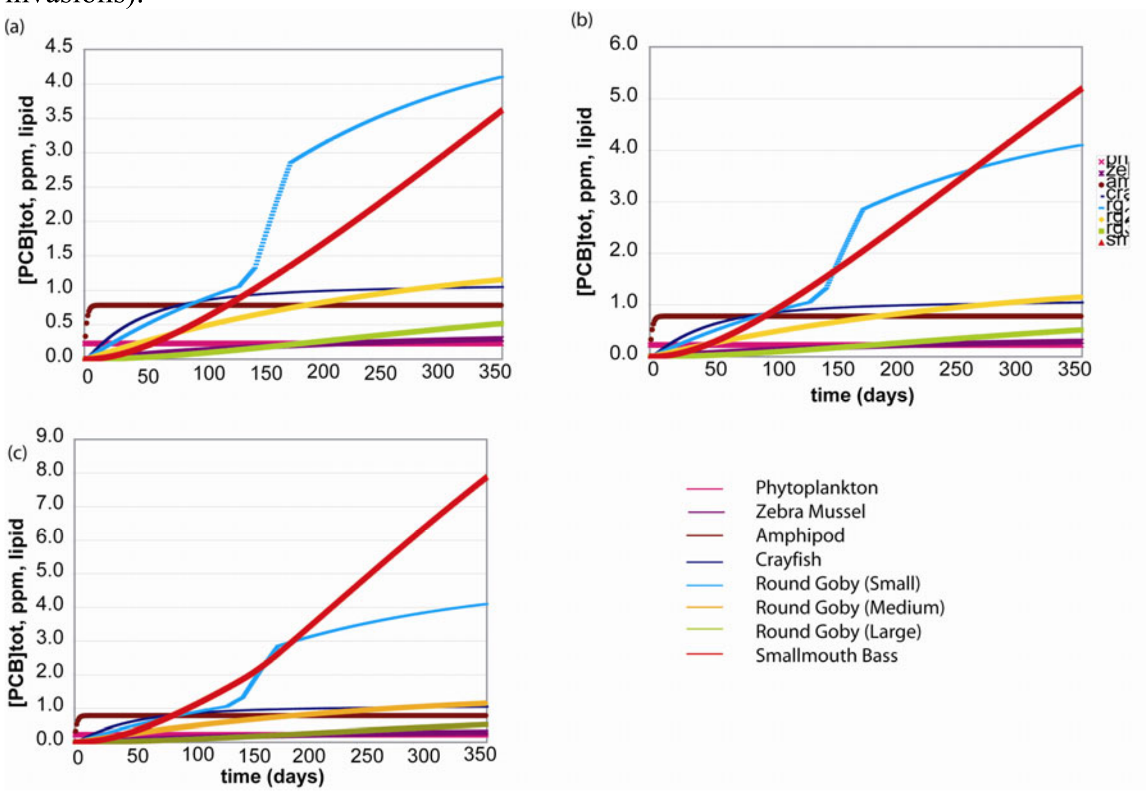

Figure 4: Effect of goby stage structure on smallmouth bass PCB concentration. **(a)** Bass consume only the largest class of round gobies. **(b)** Bass consume large and medium gobies. **(c)** Bass consume all three goby size classes. High concentrations of PCBs in bass are due to consumption of the smallest, most contaminated round gobies which have elevated PCB concentrations in the summer, after spawning season makes egg consumption possible.

Conclusion

Our results illustrate the inadequacy of current approaches to ecosystem monitoring and human health protection in these ever-shifting ecosystems. If we are to account for the interaction between changing food web structure and contaminant accumulation, the advice given to the public regarding safe fish consumption, for example, and the sampling practices used to monitor a wide range of native and invasive species, must also change. Current fish consumption advisories suggest opting for smaller, younger fish to minimize health risk, a practice that, for the round goby, would do just the opposite. Smaller size classes must be included in monitoring strategies, and invasive species and small forage fish must be considered as potential entry points for contaminants to the human food web, particularly for those subsistence fishers who are often constrained to consume what is most likely to be caught in a given environment (in Calumet Harbor, this would invariably be the round goby—a species that is routinely eaten in the Black Sea, its native range).

Our results also point to the challenges in properly defining what should be accomplished by ecosystem restoration. Despite our best efforts, non-indigenous species continue to spread—and thrive—in most navigable waters. Successful invasive species have altered the environment to such an extent that native or pristine systems are unlikely to be reestablished. In many cases, this ecological restructuring has paved the way for the next invader. Yet these non-indigenous species can have both positive and negative effects on ecosystem quality, as evidenced by the contrasting contribution of zebra and quagga mussels to Calumet Harbor's PCB contamination patterns. The goal of restoration, then, must be to determine the set of actions necessary to both establish diverse, self-sustaining ecosystems and protect human health, in such a way as to restore the full range of an ecosystem's goods and services, albeit in an altered form and with a new set of species.

Indeed, as emphasized in the 91st Dahlem Workshop on sustainable development, there is a need for science to shift from a "knowledge-centered" endeavor to one that is "learning-centered"—a recognition of the dynamic nature of ecosystems and our limited knowledge of their properties [10]. Food web bioaccumulation models that can simulate shifts in contaminant pathways and predict potential contaminant "feedback loops" are potentially critical guidance tools to formulate more protective and effective policy strategies.

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