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Carbon-based balanced trophic structure and flows in the offshore Lake Ontario food web before (1987–1991) and after (2001–2005) invasion-induced ecosystem change

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ABSTRACT

Replicate mass-balanced solutions to Ecopath models describing carbon-based trophic structures and flows were developed for the Lake Ontario offshore food web before and after invasion-induced disruption. The food webs link two pathways of energy and matter flow: the grazing chain (phytoplankton–zooplankton-fish) and the microbial loop (bacteria–protozoans) and include 19 species-groups and three detrital groups. Mass-balance was achieved by using constrained optimization techniques to randomly vary initial estimates of biomass and diet composition. After the invasion, production declined for all trophic levels and species-groups except Chinook salmon. The trophic level (TL) increased for smelt, adult sculpin, adult alewife and Chinook salmon. Changes to ecotrophic efficiencies indicate a reduction in phytoplankton grazing, increased predation pressure on *Mysis*, adult smelt and alewife and decreased predation pressure on protozoans. Specific resource to consumer TTE changed; increasing for protozoans (8.0–11.5%), *Mysis* (0.6–1.0%), and Chinook salmon (1.0–2.3%) and other salmonines (0.4–0.5%) and decreasing for zooplankton (20.2–15.1%), prey-fish (9.7–8.8%), and benthos (1.7–0.6%). Direct trophic influences of recent invasive species were low. The synchrony of the decline in PP and species-group production indicates strong bottom-up influence. Mass balance required an increase of two to threefold in lower trophic level biomass and production, confirming a previously observed paradoxical deficit in lower trophic level production. Analysis of food web changes suggest hypotheses that may apply to other similar large pelagic systems including, (1) as pelagic primary productivity declines, overgrazing of zooplankton results in an increase in protozoan production and a loss of trophic transfer efficiency, (2) habitat and food web changes increased *Mysis* predation on *Diporeia* and contributed to their recent decline, and (3) production of Chinook salmon, the primary piscivore, was uncoupled from pelagic production processes. This study demonstrates the value of food web models to better understand the impact of invasive species and to develop novel hypotheses concerning trophic influences.

1. Introduction

During the 1990s, invasive species disrupted the Lake Ontario food web (Mills et al., 2003; O'Gorman et al., 2000; Stewart et al., 2009). The disruptive influences included the expansion of dreissenid mussels (*Dreissena* spp.) which was associated with increased water clarity and the population collapse of *Diporeia* (Lozano et al., 2001; Dermott, 2001; Watkins et al., 2007). Dreissenid mussels may be grazing phytoplankton and making it unavailable to support zooplankton production (Caraco et al., 1997, 2006; Madenjian, 1995). Also, selective feeding by dreissenid mussels has been implicated in a shift in the phytoplankton community to increased prevalence of blue-green algae and other large colonial forms of algae (Makarewicz et al., 1999; Nicholls et al., 2002; Bierman et al., 2005; Miller and Watzin, 2007; Naddafi et al., 2007) which may be less edible by zooplankton (Porter, 1973; Lehman and Sandgren, 1985). These changes may affect how efficiently primary production is transferred up the food web.

The invasive predatory cladoceran *Bythotrephes longimanus*, hereinafter referred to as *Bythotrephes*, was first observed in Lake Ontario during the early 1980s but their abundance has remained low and variable (Makarewicz and Jones, 1990; Johannsson et al., 1991; Holeck et al., 2008). Another invasive predatory cladoceran, *Cercopagis pengoi*, hereinafter referred to as *Cercopagis*, invaded and became abundant in 1998 (MacIsaac et al., 1999). Over the

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