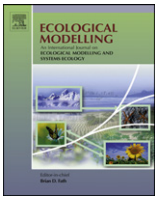
Ecological Modelling 222 (2011) 692–708

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



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

Thomas. J. Stewart[a,*], W. Gary Sprules[b,1]

[a] Ontario Ministry of Natural Resources, Lake Ontario Management Unit, RR # 4, Picton, Ontario, KOK 2T0, Canada
[b] University of Toronto, 25 Willcocks Street, Toronto, Ontario, M5S 3B2, Canada

ARTICLE INFO

Article history:
Received 1 April 2010
Received in revised form 8 October 2010
Accepted 28 October 2010
Available online 29 November 2010

Keywords:
Lake Ontario
Food web
Invasive species
Ecopath
Mass-balance
Carbon fluxes

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

---

[*] Corresponding author. Tel.: +1 613 476 1749; fax: +1 613 476 7131.
E-mail address: tom.stewart@ontario.ca (Thomas.J. Stewart).
[1] Tel.: +1 905 828 3987.

0304-3800/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2010.10.024

same period, whole-lake total epilimnetic plus metalimnetic zooplankton production declined by approximately half (Stewart et al., 2010). Cyclopoid copepod biomass and production declined disproportionately, consistent with increased predation pressure from alewives (*Alosa pseudoharengus*) and invasive predatory cladocerans. The zooplankton community was otherwise resilient to the disruption as species richness and diversity were unaffected (Stewart et al., 2010).

Alewives are the dominant offshore prey fish and their biomass and production declined by approximately half after the food web disruption (Stewart et al., in press), matching the observed decline in zooplankton production over the same period (Stewart et al., 2010). Reduced availability of zooplankton for alewife was suggested by extremely low stomach content weights at bathymetric depths <70 m following the disruptive changes of the 1990s and daily rations closer to shore were estimated to below levels required to maintain growth (Stewart et al., 2009, in press). During the mid-1990s, alewife distribution shifted farther offshore (O'Gorman et al., 2000). In 2004–2005, compared to pre-1990s, alewife shifted to a higher trophic position increasing their consumption rate of invasive predatory cladocerans and *Mysis diluviana*, hereinafter referred to as *Mysis*, and decreasing their consumption of zooplankton (Stewart et al., 2009, in press).

Shifts in alewife diets to a higher trophic level, might be expected to decrease the efficiency of transfer from primary consumers to alewife. However, this may be partially compensated for by increased growth efficiency due to a reduction in active metabolism or decreased handling time associated with feeding on larger particles (Kerr, 1971a,b; Sherwood et al., 2002a,b) and this was demonstrated experimentally for alewife feeding on *Mysis* (Crowder and Binkowski, 1983). Estimates of alewife consumptive demand in Lake Ontario (Stewart et al., in press) and Lake Michigan (Pothoven and Madenjian, 2008) following similar shifts to larger-particle diets, did not account for potential reductions in active metabolism, and may have overestimated consumptive demand by alewife (Stewart et al., in press). Changes in the trophic ecology of the various food web components described above altered the food web structure and pathways of energy and material flow. While many of the disruptive influences have been documented, there has never been a systemic analysis of potential changes to trophic structure and flows. Describing and understanding these changes at the food web-scale is important. Changes at one trophic level can lead to unanticipated indirect changes in other trophic components as has been documented for *Mysis* introductions to lakes (Koksvik et al., 2009). Also, how energy is transferred up or down the food web (*sensu* Hunter and Price, 1992) is influenced by food web structure and can impact fisheries (Pauly and Christensen, 1995) or identify potential opportunities or impediments to fisheries management activities such as stocking or species rehabilitation (Stewart et al., 1999).

In this paper, the trophic structure of the offshore Lake Ontario food web is specified in terms of carbon for two major time periods when extensive observations were available (1987–1991 and 2001–2005), taking into account the postulated reduction in consumption demand of alewife associated with larger particle diets and distribution shifts (Stewart et al., in press). The magnitude of the initially estimated species-group biomass and diet compositions was stochastically varied using constrained optimization techniques (Kavanagh et al., 2004) to derive replicates of mass-balanced food web structures and carbon flows. The mass-balanced food web structures were used to (1) describe how species-group biomass, production, trophic levels, and ecotrophic efficiencies changed after the disruptive-influences on the food web, (2) evaluate changes in trophic transfer efficiency (TTE) from specific resource to consumers groupings, and (3) examine changes to the pathways of carbon flows to develop hypotheses describing trophic influences leading to the observed changes and possible indirect effects.

2. Methods

2.1. Study site

Lake Ontario (43.7°N, 77.9°W) is the eastern-most and smallest of the five Laurentian Great Lakes. It has a surface area of $1.896 \times 10^{10}\,\mathrm{m}^2$, a volume of $1.64 \times 10^{12}\,\mathrm{m}^3$, a mean depth of 86 m and a maximum depth of 244 m (Great Lakes Atlas, Environment Canada and U.S. Environmental Protection Agency, 1995). The major tributary to the lake is the Niagara River and the major outlet is the St. Lawrence River.

2.2. Food web structure

For each time period, the average biomass, production, diet, and consumption of all trophic groups comprising a simplified offshore Lake Ontario pelagic food web was determined (Fig. 1). It was assumed that the offshore food web was a balanced system such that cumulative consumption by predators could not exceed production of the prey and that any flows not represented in the model were minor. For example, on a whole-lake areal or volume basis, Lake Ontario embayments are very small relative to the much more extensive open water coastal areas and therefore, the higher production associated with embayments (Hall et al., 2003) was not accounted for. Variation in biomass with bathymetric depth was accounted for by determining weighted-means using the area of the lake for each depth-stratum as weights. This approach takes into account, for example, higher benthic biomass observed in nearshore shallow areas. The invasive predatory cladocerans were combined with other large cladocerans as their biomass and production were estimated to be too low (Stewart et al., 2010) to justify a separate species-group. Similarly, the production of calanoid copepods was small relative to cyclopoid copepods (Stewart et al., 2010) so their biomass was combined with the total copepod group. Round goby (*Neogobius melanostomus*) and three-spine stickleback (*Gasterosteus aculeatus*) were not included in the food web as they had very limited distribution and abundance in the offshore (Owens et al., 2003; Walsh et al., 2007).

Chinook salmon account for most of the consumptive demand on Lake Ontario offshore prey-fish (Jones et al., 1993; Rand and Stewart, 1998) and other salmonines (rainbow trout; *Oncorhynchus mykiss*, lake trout; *Salvelinus namaycush*, coho salmon; *Oncorhynchus kisutch* and Atlantic salmon; *Salmo trutta*) were represented as a composite (Fig. 1). Only Chinook salmon larger than 300 mm total length, which corresponds approximately to their size at their onset of piscivory, beginning at the end of their first growing season (Stewart, 1980; Keeley and Grant, 2001), were included. It was assumed most young-of-the-year (YOY) salmonines fed nearshore and on water surface accumulations of terrestrial organism and nearshore benthos (Johnson, 2008) and so the biomass and consumption of early YOY salmonines was not accounted for. Juvenile lake trout (<200 mm total length) fed offshore and consumed isopods, amphipods, and *Mysis* (Elrod and O'Gorman, 1991). However, the average annual biomass of age-1 lake trout during 1991 was estimated at less than $0.005\,\mathrm{g\,m}^{-2}$ (Rand and Stewart, 1998) and was considered too low to be included in the food web. Consumption of alewife by nearshore predators such as walleye (*Sander vitreus*) and double-breasted cormorants (*Phalacrocorax auritus*) was not represented in the food web as their consumption was estimated to be small relative to consumption by salmonines (Jones et al., 1993; Wesloh and Casselman, 1992). Lake whitefish (*Coregonus clupeaformis*) and lake herring (*Core-*