

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.

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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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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 $1.896 \times 10^{10} \text{ m}^2$, a volume of $1.64 \times 10^{12} \text{ m}^3$, 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 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-*

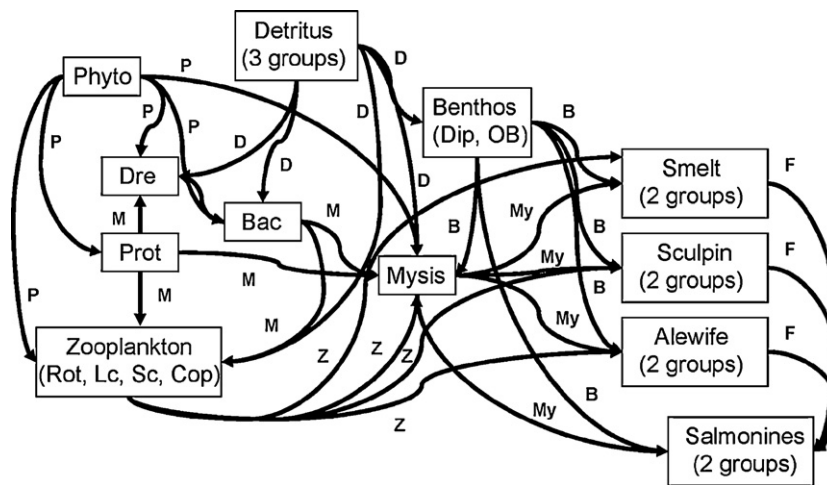


Fig. 1. Simplified Lake Ontario offshore food web. The arrows indicated major carbon flows (consumption) among groups with labels indicating categories of flows (P = from primary production, D from detrital groups, M = from microbial loop, Z = from zooplankton, B = from benthos, My = from Mysis, and F = from prey-fish; see Table 1 for species-group abbreviations).

gonus artedii) were not included as their populations are very small and restricted primarily to the outlet basin of eastern Lake Ontario (Hoyle et al., 2008). Given that large variance associated with estimating the biomass of major species-groups was accounted for during the mass-balance procedures, the exclusion of rare species, or composite representation of species of low abundance, was assumed to be of little consequence to the final mass-balance solutions.

2.3. The model

The specification and analysis of trophic structure was done using Ecopath (Christensen and Walters, 2004) in units of carbon (g C m^{-2}). Mass balance for each species-group on an annualized basis was described as

$$B_i \cdot \left(\frac{P}{B}\right)_i - \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot \text{DC}_{ji} - B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - \text{EE}_i) = 0$$

where B_i is the biomass of species-group (i), $(P/B)_i$ is the production to biomass ratio, $(Q/B)_j$ is the consumption to biomass ratio of predator (j), DC_{ji} is the fraction of prey (i) in the average diet of predator (j), and EE_i is the ecotrophic efficiency (proportion of a species-group production that is lost to predation), and n is the number of species-groups. A system of the above linear equations for each species-group is set-up and B and DC values are iteratively varied and the equations solved to estimate the EE value of each species-group, with the condition that each EE value must be less than 1. A second equation balances the flow within each group such that

$$Q_i = P_i + R_i + \text{GS}_i \cdot Q_i$$

where for the biomass of species-group (i), Q_i is consumption, P_i is production, R_i is respiration, and GS_i is the proportion of unassimilated food.

Two pathways for the flow of energy and matter were represented: the grazing chain (phytoplankton–zooplankton–fish) and the microbial loop (bacteria–protozoans). These pathways were linked via zooplankton consumption of bacteria and protozoans and direct consumption of phytoplankton by protozoans (Wetzel, 2001). In most cases, parameter estimates were derived from Lake Ontario studies specific to the two time periods. In some cases, it was necessary to use bioenergetic parameters and general diets derived from the literature.

2.4. Initial model inputs

To populate the model, the biomass (B ; g m^{-2}), fraction of prey in the diets (DC ; proportions), annualized production to biomass ratio (P/B ; yr^{-1}), consumption to biomass ratio (Q/B ; yr^{-1}), assimilation efficiency (proportion of consumption assimilated), and carbon content as a proportion of dry weight was estimated for each species-group during each time period. The details are documented elsewhere (Stewart et al., 2009, 2010, in press; Stewart, 2010) and are only briefly described here.

2.4.1. Dissolved, particulate, and detrital organic carbon

Three detritus groups were specified: sedimented detritus, particulate organic carbon (POC) and dissolved organic carbon (DOC). Estimates of sediment detritus were developed from data in Halfon et al. (1996) and estimates of allochthonous net import (import minus export) were from Kemp and Harper (1976) and dry weight and carbon conversions applied (Ahlgren, 1990; Verity et al., 1996). The concentration of POC and DOC were estimated approximately using graphical data presented in Johannsson et al. (1998). New detritus was allocated evenly to each of the three detritus groups.

2.4.2. Phytoplankton biomass and production

Lake Ontario seasonal (May to October) 1987–1991 mean photosynthetic production (PP; g C m^{-2} ; Millard et al., 1995) was applied to the earlier time period and corrected to annual PP based on Stadelmann et al. (1974). Estimates of phytoplankton biomass were determined for the same years from the data in Johannsson et al. (1998). Estimates of phytoplankton biomass include only larger phytoplankton (visible by up to 1500 \times magnification; Johannsson et al., 1998) but PP measurements included all sources of carbon uptake including picoplankton. Therefore, the estimated P/B ratio represents primary production scaled to the biomass of large microscopically visible phytoplankton. Biomasses were converted to carbon assuming a density of one and applying a conversion factor (Lee and Fuhrman, 1987).

Approximately 80% of the water flowing into Lake Ontario comes from Lake Erie (<http://www.epa.gov/glnpo/atlas>), so Lake Erie post-dreissenid PP:TP ratios (Depew et al., 2006) were applied to estimate PP of Lake Ontario during 2001–2005 from average seasonal TP for Lake Ontario determined during 2003 (Holeck et al., 2008; Stewart, 2010). It was assumed that the phytoplankton P/B estimated for the earlier time period applied.

2.4.3. Microorganism biomass and production

Microorganisms include heterotrophic bacteria, protozoans (nanoflagellates and ciliates), rotifers and dreissenid veligers. Fahnenstiel et al. (1998) determined the structure of the entire Lake Ontario planktonic food web (organisms in size from 0.2 μm to 2.5 mm) from 1993 to 1995 in units of carbon. Although the timing of their study does not overlap with this study time periods, they and others (Gates and Lewg, 1984) observed surprisingly consistent biomass proportions among aquatic food web components. Therefore, the relative proportionate biomass of microorganisms scaled to large microscopically visible phytoplankton (Fahnenstiel et al., 1998) was used to initially estimate the biomass of microorganisms. Rotifer biomass was estimated relative to total zooplankton biomass based on the median ratio of rotifer: total zooplankton reported for Lake Ontario studies (Sprules and Munawar, 1991; Makarewicz et al., 1995; Johannsson, 2003). It was assumed that the estimate of rotifer biomass represented only rotifers during 1987–1991 and rotifers and dreissenid veligers combined during 2001–2005 (Stewart, 2010). Specific growth and production rates from the literature were averaged to derive P/B values for bacteria (Pedros-Alio and Brock, 1982; Scavia et al., 1986; Cole et al., 1988; Straile, 1998; Bell et al., 1991), protozoans (Reynolds et al., 1984; Scavia et al., 1988; Taylor and Johannsson, 1991; Carrick et al., 1992; Straile, 1997) and rotifers (Makarewicz and Likens, 1979).

2.4.4. Zooplankton biomass and production

Whole-lake average annual zooplankton epilimnetic and metalimnetic production for both periods, and biomass and P/B ratios for 1987–1991 were from Stewart et al. (2010), corrected to account for hypolimnetic production (Kuns and Sprules, 2000; Stewart, 2010) and carbon conversion factors (Salonen et al., 1976) applied.

2.4.5. Feeding relationships among planktonic components

If it was not possible to reasonably estimate a diet proportion for planktonic species-groups, it was assumed that consumers were opportunistic and non-selective and initial diet components were estimated to be proportional to the initially estimated relative carbon production among their prey. It was assumed that bacteria metabolized both POC and DOC primarily released from phytoplankton (Wetzel, 2001). Nanoflagellates and ciliates were grouped but a low level of “cannibalism” (1.0%) was specified within this group to account for within group feeding interactions but otherwise it was assumed that their diet was comprised primarily of bacteria, picoplankton and algae (Wetzel, 2001; Sherr and Sherr, 2002). It was assumed that rotifers and veligers consumed algae, bacteria, and protozoans (Gilbert and Jack, 1993; Wallace and Snell, 2001). Copepods were assumed to be omnivores (Sprules, 1984) with 49.5% of their diet being algae and 49.5% being other heterotrophic plankton, not including invasive cladocerans or large cladocerans, but including a low level of cannibalism (1.0%). Large cladocerans were assumed to eat mostly algae (90%) with the rest of their diet composed of heterotrophic plankton other than predatory cladocerans (Sprules, 1984; Taylor and Johannsson, 1991; Dodson and Frey, 2001). It was assumed that small cladocerans ate algae, bacteria, protozoans and rotifers (Sprules, 1984; Dodson and Frey, 2001). Invasive predatory cladocerans were assumed to eat only copepods and small cladocerans (Schulz and Yurista, 1999; Warner et al., 2006).

Gross conversion efficiency (growth divided by consumption; P/Q) were used to estimate Q/B ratios for bacteria (Calow, 1977) and zooplankton (Straile, 1997), such that $Q/B = P/B$ divided by P/Q . Literature values were used for the fraction of ingested food unassimilated for zooplankton and protozoans (Franks et al., 1986) and for bacteria, protozoan, rotifers and veligers (Moran et al., 1988).

2.4.6. Mysis biomass, production, consumption and diet

Estimates of whole-lake *Mysis* production for Lake Ontario during 1990 (Johannsson, 1995) were applied to the 1987–1991 time period. *Mysis* P/B was estimated as the average annual values for Lakes Michigan and Huron (Sell, 1982) and this ratio was used to back calculate mean annual biomass from production. October indices of Lake Ontario *Mysis* biomass, indicated that the average *Mysis* biomass during 2001–2005 had declined to half the 1987–1991 biomass (Ora Johannsson, Department of Fisheries and Oceans, Burlington, personal communication), so *Mysis* biomass for the 2001–2005 period was estimated as half the 1987–1991 estimate. The *Mysis* P/B ratio was assumed to be the same for both time periods. *Mysis* Q/B was estimated by averaging Lake Ontario specific estimate of maximum daily ration and minimum maintenance ration determined from bioenergetic modelling (Stewart, 2010). The fraction of ingested food unassimilated was taken from (Rudstam, 1989) and dry weight to carbon conversion from Salonen et al. (1976).

Mysis are opportunistic and feed on diatoms, organic detritus, zooplankton, and amphipods (Parker, 1980; Pennak, 1978; Johannsson et al., 2001, 2003; Bailey et al., 2006). Among zooplankton prey, *Mysis* prefer cladocerans, but also consume calanoid and cyclopoid copepods (Bowers and Vanderploeg, 1982; Nero and Sprules, 1986a). *Mysis* diets were described as the average spring, summer and fall proportions of phytoplankton, zooplankton, and amphipods (assumed to be *Diporeia*) from (Johannsson et al., 2003). It was also assumed that 20% of the diet was detritus. The zooplankton proportion of the diet was allocated to cladocerans and copepods in proportion to the initial estimated carbon production of each group times the assumed prey selectivity values (1.0 for cladocerans; 0.45 for copepods) developed from data in Bowers and Vanderploeg (1982).

2.4.7. Benthic biomass, biomass, production, consumption and diet

Whole-lake benthic biomass for *Diporeia* spp., dreissenids (a composite of *Dreissena polymorpha* and *Dreissena bugensis*) and composite of all other benthos for the 1987–1991 time period based on depth strata specific data for 1990 in Dermott and Geminiuc (2003). To estimate biomass of benthic groups for 2001–2005 the relative changes in density derived from the data in Watkins et al. (2007) were applied. For *Diporeia* and dreissenids, relative changes in density from 1990 to 2003 were applied, and for other benthos relative changes in sphaeriids and oligochaetes from 1990 to 1999 (no data available for 2003) were applied.

Diporeia P/B was taken from Johannsson et al. (1985) and Q/B from Dermott and Corning (1988). For the other benthos the P/B ratio was determined as an average of the benthos community inhabiting offshore Lake Ontario (Johnson and Brinkhurst, 1971a). Oligochaetes P/B was determined from (Lindgaard, 1994) and applied to other benthos. It was assumed that the diets of *Diporeia* and other benthos in offshore Lake Ontario was 100% detritus (Johnson and Brinkhurst, 1971b) proportioned as 50% sedimented detritus and 50% particulate detritus. Literature values were assumed for the amount of ingested material unassimilated by *Diporeia* (Dermott, 1995) and to convert reported wet weights to carbon (Salonen et al., 1976; Wetzel et al., 2005) and applied to both *Diporeia* and other benthos.

The production and consumption of dreissenids was characterized differently for each time period. For the earlier time period it was assumed that dreissenids population was dominated by zebra mussel (*Dreissena polymorpha*; Watkins et al., 2007) and the average P/B for Lake Ontario dreissenids (Chase and Bailey, 1999) was applied. The Q/B was estimated from the reported P/Q from Hamburger et al. (1990) but was adjusted from the assumed assimilation efficiency of 50% to an updated observed assimila-

tion efficiency of 63% (Baldwin et al., 2002). For the 2001–2005 time period, it was assumed that the dreissenid population was dominated by quagga mussels (*Dreissena bugensis*; Watkins et al., 2007). The large mussel (>20 mm) P/B ratio determined by Chase and Bailey (1999) was applied, as it may be more typical of established populations of older slower growing dreissenids (Dermott et al., 2003). The same initial P/Q ratio as zebra mussels (Hamburger et al., 1990) was applied but Q/B was calculated by assuming a higher assimilation efficiency of natural seston determined for quagga mussels of 81% (Baldwin et al., 2002). Dreissenids filter approximately twice as much POC as they ingest releasing non-ingested material as pseudofeces (Juhel et al., 2006), so the Q/B was doubled and the assimilation efficiency halved to reflect the loss of POC and phytoplankton from the water column as deposited benthic detritus. This will overestimate the loss of phytoplankton from the water column due to mussel filtering because egested pseudofeces may contain living algae which could be resuspended (Roditi et al., 1997; Hecky et al., 2004). The diet of dreissenids was assumed to be a combination of POC, phytoplankton, bacteria, protozoans and rotifers (Ten Winkel and Davids, 1982; MacIsaac et al., 1991; Horgan and Mills, 1997). The initial POC diet proportion was estimated at 0.2 and all other diet proportions were assigned to remaining diet relative to the initial estimated production of carbon by each prey species-group. Values from the literature were used to convert wet weight estimates to carbon (Dermott and Geminiuc, 2003; Jurkiewicz-Karnkowska, 2005).

2.4.8. Alewife biomass, production, consumption and diet

Alewife populations were separated into two groups; larval fish combined with early YOY up to mid-September (E-YOY) and all other alewife age groups (OLDER). Estimates of biomass, production, P/B , and Q/B , and diets were developed for both groups for each time period using population-based bioenergetic models (Stewart, 2010; Stewart et al., in press) and converted to carbon using wet-weight to dry-weight conversions (Rand et al., 1994; Lantry and O'Gorman, 2007; Stewart, 2010) and assuming a carbon content for similar sized prey-fish (Penczak, 1985).

2.4.9. Other prey-fish biomass, production, consumption and diet

The biomass of smelt and slimy sculpins were estimated approximately using catches from standardized bottom-trawl indices of biomass (Owens et al., 2003) updated to 2005 (Maureen Walsh, United States Geological Survey, Oswego, New York, personal communication) as described in Stewart (2010). From populations studies of Lake Ontario smelt (Lantry and Stewart, 1993) and inland lake sculpin (Mousseau, 1983) the likely biomass of YOY relative to adults and their P/B ratios were estimated (Stewart, 2010). Smelt Q/B s were from Lantry and Stewart (1993) and the Q/B ratio determined for *Cottus gobio* (Meyer and Poepperi, 2004) was assumed to apply to for both adult and juvenile slimy sculpin. The fraction of ingested food unassimilated estimated for smelt (Hanson et al., 1997) was applied to both smelt and slimy sculpins.

Great Lakes smelt diets (Lantry, 1991; Lantry and Stewart, 1993) were used to describe adult and YOY smelt diets during 1987–1991 except that the zooplankton and fish components were proportioned into specific species-groups (Stewart, 2010). The diets of juvenile and adult sculpins for the 1987–1991 time period were taken from Owens et al. (2003), except that *Mysis* was excluded from juvenile diets (Mousseau, 1983) and reported diet item counts were converted to dry weights (Stewart, 2010). Diets for 2001–2005 were assumed to be unchanged for YOY smelt and new diet descriptions were developed for adult smelt, adult slimy sculpin and juvenile slimy sculpin based on stomach samples collected during 2004 and 2005 (Stewart, 2010).

2.4.10. Piscivore biomass, production, consumption and diet

The biomass of Chinook salmon age 1 and older during 1987–1991 was determined as the average of reported values for Lake Ontario during 1991 (Halfon and Schito, 1993; Rand and Stewart, 1998). The biomass of the other salmonines, was estimated as the ratio of their accumulated recreational fishery catch from 1985 to 1995 to the catch of Chinook salmon over the same period (Stewart et al., 2004). To estimate Chinook salmon and other salmonine biomass for 2001–2005 changes in the recreational angling catch rate from 1987–1991 to 2001–2005 (Ontario Ministry of Natural Resources, 2006) were assumed to track relative changes in biomass. Dry weights were determined based on Chinook salmon dorsal muscle samples collected during 2004–2005 (Stewart, 2010) and carbon conversions for rainbow trout (*Oncorhynchus mykiss*) were applied (Hendrixson et al., 2007). Estimates of P/B and Q/B ratios for Chinook salmon and other salmonine were developed from Rand and Stewart (1998) as described by Stewart (2010).

Diet descriptions for Chinook salmon and the composite of other salmonines for the 1987–1991 time period were based on reported diet proportion of salmonines collected during 1987–1988 (Rand and Stewart, 1998) and modified (Stewart, 2010) to include a small proportion of invertebrates observed during more intensive diet studies in Lake Michigan (Jude et al., 1987; Madenjian et al., 1998; Lantry, 2001). For the 2001–2005 period, composite diet descriptions for salmonines other than Chinook salmon were developed from diet proportion observed during 1998–1999 (Lantry, 2001) as described by Stewart (2010). Chinook salmon diets were described based on stomach samples collected during 2004–2005 (Stewart, 2010).

2.5. Balancing the food webs

The models were balanced using the Ecopath (version 5.0) auto-balance routine (Kavanagh et al., 2004). The procedure randomly selects the initial values of biomass (B) and DC (the fraction of each prey in the average diet of predator) for each-species group from a pre-defined range of values specified by confidence interval widths (CIW). The B and DC values were assumed to have a uniform distribution. After the initial values are selected, a second perturbation step randomly varies species-group estimates of B and prey DC values until a solution with an EE < 1 for all species groups is obtained. The cost function decision logic provided with the software that simultaneously minimizes the maximum EE values and the sum of all EE values > 1 was chosen for the second perturbation step (Kavanagh et al., 2004; Link et al., 2006) to optimize the search.

The CIW of species-group B and DC estimates were specified to reflect measures or judgments of the relative magnitude of variation in the quantities among food web components. A CIW for primary production of 50% was assumed approximating the estimated 95% CIW of mean annual primary production estimates (Millard et al., 1999). A CIW of the B and DC values associated with lower heterotrophs (microorganism, zooplankton, *Mysis*, and benthos, including dreissenids) of 80% was applied as the biomass of these groups is highly variable and their diets were only generally known. For alewife and salmonids the CIW of B values was assumed to be 50% approximating the estimated 95% CIW for mean estimated annual alewife biomass (Stewart et al., in press). For prey-fish other than alewife, a CIW of 50% for B values and 80% for DC values were assumed, as the biomass and diets of these fish were less studied than alewife. For alewife and salmonids DC values, a CIW of 30% was assumed as their diets were well described (Lantry, 2001; Stewart et al., 2009).

For each run of the autobalance routine a unique set of initial B and DC values for all species groups were selected at random within a range of 50% of the confidence interval (CI). Start-

ing with these initial values, new random values were selected from within a range of 100% of the CI to attempt to achieve a balance. This was repeated up to 10,000 times or until a mass-balance solution was obtained. If a mass-balance solution was not obtained after 10,000 attempts the process was repeated. The randomization routine would often result in diet proportions that summed to less than one. In those cases, diet proportions were adjusted to sum to one, and the food web was rebalanced using the same criteria. It was required that EE values for all species-groups were less than or equal to 0.98 and the ratio of total respiration to assimilation was less than 1.0 (Christensen et al., 2004). It was determined that 25 replicate mass-balance solutions, each based on up to 10,000 iterations, adequately reflected variation in simulated balanced food web structures (Stewart, 2010).

Using this approach it was initially possible to balance the 1987–1991 food web but no mass-balance solutions could be determined for the 2001–2005 food web. Therefore, we attempted to obtain a mass-balance solution for the 2001–2005 food web using a postulated reduction in alewife Q/B associated with the shifts in behaviour, distribution and diet observed after the food web disruption (Stewart et al., in press). It was postulated that Lake Ontario alewife consumptive demand was reduced during this time period due to lower activity cost of feeding on larger particles and the exploitation of spatial variation in temperature and diet (Stewart et al., in press). Based on this study and other laboratory (Kerr, 1971a,b) and field (Rennie et al., 2005) studies of fish activity costs it was determined that reducing the Q/B ratio of adult alewife by 40% was a reasonable estimate of the potential reduction in the Q/B of alewife (Stewart, 2010). After implementing this change it was still not possible to derive mass balance solutions for the 2001–2005 time period using the original uncertainty criteria, and so the random perturbations from initial B and DC values was increased from 100% of the CIW to 160%, and mass-balance solutions were achieved. Also, for these solutions, the ratio of production to respiration for juvenile sculpins persisted at approximately 1.2 suggesting a problem with the assumed bioenergetic ratios for this minor species-group, which was tolerated.

2.6. Evaluating changes to food web structures

It was assumed that the mean and variance of the estimated model parameters derived from a set of 25 independent mass-balance solutions represented a repeatable and robust characterization of food web structure. This assumption was supported by an observed asymptotic relationship between the number replicates and the coefficient of variation and the mean biomass across species-groups (Stewart, 2010). The distributions of all estimated biomass (B), diet fractions (DC), trophic transfer efficiencies (TTE) and ecotrophic efficiencies (EE) values determined for the mass-balanced solutions did not deviate significantly from normality (Kolmogorov–Smirnov test; $\alpha = 0.05$) except for estimated DC values of the consumption of very rare diet items (<0.01% of total predator consumption). Therefore, changes in food web structure between time periods were compared using 95% confidence intervals and specific differences were evaluated using simple t -tests ($\alpha = 0.05$). Changes to specific resource to consumer trophic transfer efficiency (TTE) were evaluated for the transfer of primary production (PP) to bacteria, protozoans, zooplankton, *Mysis*, and benthos production, the transfer of invertebrate production (zooplankton, *Mysis*, and benthos excluding dreissenids) to all prey-fish, and the transfer of older alewife production and all-prey-fish production to the production of Chinook salmon, other salmonines, and all salmonines combined.

3. Results

The initial estimates of species-group biomass, production, Q/B and P/B ratios (Tables 1 and 2) and diet (Tables 3 and 4) reflect the changes documented in source publications and as modified in Section 2 above for each time period. After the ecosystem changes associated with invasions the initial descriptions, prior to mass-balance attempts, suggest that biomass and production of all species groups declined, except for dreissenids and Chinook salmon which increased. The biomass and production of copepods, *Diporeia*, and other salmonines declined proportionally more than other species-groups. The proportion of *Mysis* increased in the diets of older smelt, adult sculpin and older alewife and the proportion of

Table 1

Initial parameter values for the 1987–1991 Lake Ontario offshore food web (Unass.=proportion of unassimilated food, Plk=Phytoplankton, Bac=Heterotrophic bacteria, Prot=Nanoflagellates and ciliates, Rot=Rotifers and veligers, Lc=Large cladocerans, Sc=Small cladocerans, Cop=Copepods, Dre=Dreissenid mussels, Dip=*Diporeia*, Ob=Other benthos, Mys=*Mysis*, SmO=smelt age 1 and older, SmY=Smelt YOY, Ascl=Adult sculpin, Jscl=juvenile sculpin, AIO=Late YOY and older alewife, AIEY=Early YOY alewife, Ch=Chinook salmon, OS=Other salmonines, DOC=Dissolved organic carbon, POC=Particulate organic carbon, and Det Imp=Imported detritus).

Species-group	Production ($\text{g C m}^{-2} \text{ yr}^{-1}$)	Biomass (g C m^{-2})	P/B	Q/B	Unass.
Plk	207.24	0.71	290.96	–	–
Bac	105.70	0.50	212.43	382.37	0.38
Prot	26.10	0.19	139.19	556.78	0.38
Rot	4.23	0.10	43.50	174.00	0.38
Lc	4.20	0.14	29.68	119.47	0.30
Sc	5.48	0.20	27.92	111.68	0.30
Cop	15.91	0.74	21.40	85.60	0.30
Dre	0.0004	0.0003	1.39	16.84	0.74
Dip	2.02	1.00	2.02	91.47	0.60
Ob	1.40	0.74	1.90	19.00	0.60
Mys	1.23	0.43	2.82	26.72	0.15
SmO	0.19	0.19	1.00	6.88	0.16
SmY	0.05	0.02	2.42	12.61	0.16
Ascl	0.05	0.25	0.22	5.22	0.16
Jscl	0.15	0.06	2.40	5.22	0.16
AIO	4.50	3.09	1.46	12.43	0.16
AIEY	3.49	0.62	5.59	19.66	0.16
Ch	0.04	0.03	1.40	6.36	0.21
OS	0.03	0.03	1.00	5.56	0.21
DOC		410.86	–	–	–
POC		37.19	–	–	–
Sed		13.51			
Det Imp		2.48			

Table 2

Initial parameter values for the 2001–2005 Lake Ontario offshore food web (see Table 1 for species-group abbreviations).

Species-group	Production (g C m ⁻² yr ⁻¹)	Biomass (g C m ⁻²)	P/B	Q/B	Unass.
Plk	167.61	0.58	290.96	–	–
Bac	85.48	0.40	212.43	382.37	0.38
Prot	21.11	0.15	139.19	556.78	0.38
Rot	1.62	0.04	43.50	174.00	0.38
Lc	2.43	0.08	29.68	119.47	0.30
Sc	2.92	0.10	27.92	111.68	0.30
Cop	4.85	0.23	21.40	85.60	0.30
Dre	0.16	0.18	0.87	8.20	0.38
Dip	0.21	0.10	2.02	91.47	0.60
Ob	0.47	0.25	1.90	19.00	0.60
Mys	0.61	0.22	2.82	26.72	0.15
SmO	0.03	0.03	1.00	6.88	0.16
SmY	0.01	0.004	2.42	12.61	0.16
Ascl	0.03	0.13	0.22	5.22	0.16
JscI	0.08	0.03	2.40	5.22	0.16
AIO	1.51	1.61	0.93	5.69	0.16
AIEY	1.39	0.24	5.88	19.16	0.16
Ch	0.05	0.04	1.40	6.36	0.21
OS	0.01	0.01	1.00	5.56	0.21
DOC		410.86	–	–	–
POC		18.60	–	–	–
Sed		13.51			
Det Imp		2.48			

Table 3

Initial diet proportions (%) for each species-group during 1987–1991 (see Table 1 for species-group abbreviations).

Predator-group	Prey-group																					
	Plk	Bac	Prot	Rot	Lc	Sc	Cop	Dre	Dip	Ob	Mys	SmO	SmY	Ascl	JscI	AIO	AIEY	Ch	OS	DOC	POC	Sed
Bac																				91.7	8.3	
Prot	65.56	33.44	1.00																			
Rot	61.13	31.18	7.70																			
Lc	90.00	6.71	1.66	0.27		0.35	1.01															
Sc	60.37	30.79	7.60	1.23																		
Cop	49.50	36.97	9.13	1.48		1.92	1.00															
Dre	48.30	24.63	6.08	0.99																		
Dip																					20.00	
Ob																					25.00	75.00
Mys	16.00				15.29	19.94	26.06		2.70												25.00	75.00
SmO					10.80	0.54	15.66		23.00	1.00	48.00		0.01		0.04		0.94					20.00
SmY					3.84	15.47	50.39		7.94	3.17	17.46		0.02		0.07		1.64					
Ascl									33.04	1.86	65.10											
JscI									94.66	5.34												
AIO					25.39	3.54	61.31		0.32	6.05	3.39											
AIEY				4.50		51.50	44.00															
Ch												21.33				78.67						
OS									0.40	0.40	0.40	12.76		0.26		85.78						

Table 4

Initial diet proportions (%) for each species-group during 2001–2005 (see Table 1 for species-group abbreviations).

Predator-group	Prey-group																					
	Plk	Bac	Prot	Rot	Lc	Sc	Cop	Dre	Dip	Ob	Mys	SmO	SmY	Ascl	JscI	AIO	AIEY	Ch	OS	DOC	POC	Sed
Bac																				91.70	8.30	
Prot	65.56	33.44	1.00																			
Rot	61.13	31.18	7.70																			
Lc	90.00	7.37	1.82	0.14		0.25	0.42															
Sc	60.77	30.99	7.65	0.59																		
Cop	49.50	38.08	9.40	0.72		1.30	1.00															
Dre	48.61	24.79	6.12	0.47																		
Dip																					20.00	
Ob																					25.00	75.00
Mys	16.00				19.76	23.79	17.75		2.70												25.00	75.00
SmO					0.38	0.02	0.49		0.00	1.42	97.68											20.00
SmY					3.84	15.47	50.39		7.94	3.17	17.46		0.02		0.07		1.64					
Ascl					0.79				9.82	7.99	81.40											
JscI									55.16	44.84												
AIO					14.73	7.35	54.82		0.04	0.73	22.32											
AIEY				4.50		51.50	44.00															
Ch												4.41				95.59						
OS									1.20	1.20	1.20	5.01		0.38		91.01						

Diporeia declined. In the diets of adult and juvenile sculpin the proportion of other benthos increased. In the diets of Chinook salmon and other salmonines the proportion of older alewife increased.

The initial parameterizations of the food webs were not balanced. During 1987–1991, there was an apparent deficit in the production of *Mysis* (EE = 2.4), all zooplankton groups (EE = 2.0–2.8), other benthos (EE = 1.6) and DOC (EE = 1.3). During 2001–2005, there was an apparent deficit in the production of *Mysis* (EE = 4.6), small cladocerans (EE = 1.6), and copepods (EE = 1.7).

The \log_{10} original unbalanced and final balanced food web production values were plotted against the trophic level for each species-group (Fig. 2). On this scale, spanning six orders of magnitude in production, the changes required to achieve mass-balance solutions were modest. The structural difference between the food webs representing each time period also appear modest at this scale, with the exception of an increase in the production of dreissenid mussel production of two orders of magnitude (Fig. 2). However, at a finer-scale a number of important changes are evident.

Major changes in the biomass required to balance the 1987–1991 food web were, a greater than twofold increase in the biomass and production of zooplankton, a somewhat less than twofold increase in the biomass and production of phytoplankton, *Diporeia*, other benthos, and *Mysis*, with little change necessary in the biomass and production of prey and predator fish (Table 5). Changes required to balance the 2001–2005 model were similar except that the biomass and production of *Diporeia* need to be more than double and *Mysis* biomass and production needed to be increased by threefold. Changes to the initial diet proportions of the species-groups required to balance the food web were small and final diet proportions (Tables 6 and 7) are very similar to initial diet proportions (Tables 3 and 4). For 1987–1991, the mean change in diet proportions across all species-groups was 0.00 ± 0.14 (SD) and 95% of the deviations were within the range of -0.32 to 0.34 . For 2001–2005, the mean change in diet proportions across all species groups was 0.00 ± 0.12 (SD) and 95% of the deviations were within the range of -0.30 to 0.31 .

Changes in estimated mass-balanced species-group biomass, production, TL and EE values between time periods are shown in Table 8. Primary production and bacteria production exhibited declines of similar magnitude, but the production of protozoans declined to a lesser degree. Production and biomass of large and small cladocerans declined by less than half, but copepod and

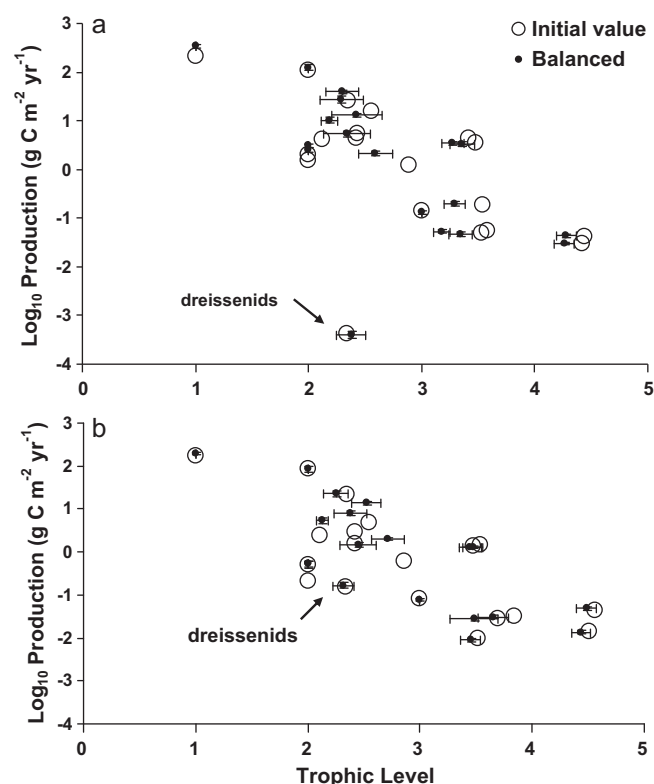


Fig. 2. Mean and 95% confidence interval of production and trophic level for each species-group for the original unbalanced and mass-balance solutions for the 1987–1991 (a) and 2001–2005 (b) time periods.

rotifer production and biomass declined proportionately more. For the benthic community, the increase in the biomass and production of dreissenid mussels was associated with large declines in the biomass and production of both *Diporeia* and other benthos. The mass-balanced solutions indicated that *Mysis* biomass and production declined only slightly. The prey-fish community changed with large reductions in the biomass and production of rainbow smelt and more modest declines in sculpin. The biomass of older alewife declined by about 40% and the production declined by about 60%. The biomass and production of early YOY alewife both declined by

Table 5

Mean and 95% confidence intervals ($N=25$) of the changes in biomass required to balance the 1987–1991 and 2001–2005 food webs (see Table 1 for species-group abbreviations).

Species-group	1987–1991		2001–2005	
	Multiplier to balance	95% CI	Multiplier to balance	95% CI
Plk	1.7	1.5, 1.7	1.2	1.0, 1.2
Bac	1.2	1.0, 1.3	1.0	0.8, 1.1
Prot	1.0	0.8, 1.1	1.1	0.9, 1.2
Rot	1.2	1.0, 1.4	0.9	0.8, 1.0
Lc	2.5	2.1, 2.8	2.3	1.9, 2.6
Sc	2.4	2.1, 2.5	2.8	2.4, 3.1
Cop	2.5	2.2, 2.7	2.9	2.6, 3.1
Dre	1.0	0.8, 1.1	1.1	0.8, 1.2
Dip	1.5	1.3, 1.6	2.5	2.0, 2.9
Ob	1.7	1.5, 1.8	1.1	0.8, 1.2
Mys	1.8	1.5, 1.9	3.3	3.0, 3.5
SmO	1.0	0.9, 1.1	1.0	0.8, 1.0
SmY	1.0	0.8, 1.0	0.9	0.8, 1.0
Ascl	1.0	0.8, 1.0	1.0	0.8, 1.0
JscI	0.9	0.8, 0.9	1.0	0.9, 1.0
AlO	0.8	0.7, 0.8	0.9	0.8, 0.9
AlEY	1.0	0.8, 1.0	0.9	0.8, 1.0
Ch	1.1	0.9, 1.1	1.1	0.9, 1.1
OS	1.0	0.9, 1.0	1.0	0.8, 1.0

Table 6
Mean diet proportions (%) for each species-group for the 1987–1991 food webs. Means were determined from the replicated ($N = 25$) mass-balance solutions (see Table 1 for species-group abbreviations).

Predator-group	Prey-group																					
	Plk	Bac	Prot	Rot	Lc	Sc	Cop	Dre	Dip	Ob	Mys	SmO	SmY	Ascl	JscI	AIO	AIEY	Ch	OS	DOC	POC	Det
Bac																				63.6	36.4	
Prot	71.4	26.8	1.8																			
Rot	68.2	24.3	7.5																			
Lc	83.1	11.0	3.3	0.6		0.6	1.5															
Sc	60.5	30.7	7.6	1.2																		
Cop	72.1	20.4	5.6	0.9		0.5	0.4															
Dre	45.4	28.9	5.8	0.9																		18.9
Dip																					29.1	70.9
Ob																					36.5	63.5
Mys	23.7				6.6	13.1	23.2		3.1													30.3
SmO					14.8	0.6	21.3		29.6	1.4	30.9		0.0		0.1		1.2					
SmY					3.8	15.3	53.6		7.5	2.9	15.4		0.0		0.1		1.4					
Ascl									66.8	3.8	29.4											
JscI									90.2	9.8												
AIO					20.9	3.6	67.7		0.3	4.8	2.7											
AIEY				4.7		43.5	51.8															
Ch												21.5				78.5						
OS									0.5	0.4	0.4	14.8		0.3		83.7						

about 60%. Chinook salmon biomass stayed the same while production increased slightly. The biomass and production of other salmonines declined. The trophic level of copepods, all the prey-fish (except juvenile sculpin), Chinook salmon, and other salmonines increased. EE values declined for primary production, protozoans and other benthos and increased for *Mysis*, adult smelt and older alewife, but were otherwise unchanged.

There was no significant change in the TTE of PP to bacteria (Fig. 3a). TTE of primary production to protozoans (8.0–11.5%; Fig. 3a) and to *Mysis* (0.6–1.0%; Fig. 3a) increased, but declined for zooplankton (20.2–15.1%; Fig. 3b) and benthos (1.7–0.6%; Fig. 3b). TTE from all invertebrates to all prey-fish decline (9.7–8.8%) but was unchanged for older alewife (4.6–4.2%; Fig. 3b). TTE increased for all prey-fish to Chinook salmon (1.0–2.3%) and to other salmonines (0.4–0.5%; Fig. 3b).

The predominant carbon flows were from phytoplankton to zooplankton and from detritus to bacteria and benthos (Fig. 4). The magnitude of these major carbon flows decreased for phytoplankton to zooplankton and detritus to benthos and increased for detritus to bacteria during 2001–2005 (Fig. 4). The reduction in biomass of phytoplankton, zooplankton, benthos, and alewife are also evident (Fig. 4). Examination of changes in lesser flows

is summarized as the mean proportion of the total consumption of a species-group (Tables 1-A and 2-A, Appendix 1, Supplementary Data to be accessed via web) but flows for selected species-groups were plotted (Fig. 5). Before the invasion-induced disruption, the dominant flows of primary production were to copepods, but after the disruption the dominant flows changed to protozoans (P flows Figs. 1 and 5). The flows of large cladocerans were predominantly to *Mysis* and alewife but after the disruption, flows to older alewife declined and flows to *Mysis* increased (Z flow Fig. 1; Fig. 5a). The flows of small cladocerans were predominantly to *Mysis* and E-YOY alewife, but after the disruption flows to E-YOY alewife declined and flows to *Mysis* increased (Z flow Fig. 1; Fig. 5b). Flows of copepods were primarily to alewife of both age groups but flows to *Mysis* increased after the disruption (Z flow Fig. 1; Fig. 5c). Flows of copepods to large cladocerans, which included the invasive predatory cladocerans, were very small (Fig. 5d). Flows of *Mysis* were primarily to older alewife in both time periods but the predominance of the flows to alewife increased after the disruption (My flows Fig. 1; Fig. 5e). Flows of *Diporeia* to species-groups were highly variable but were dominated by *Mysis* and sculpins (B flows Fig. 1; Fig. 5f). Despite the rare estimated occurrence of *Diporeia* in *Mysis* diets (3.2% in 1987–1991; Table 5 and 1.2% 2001–2005;

Table 7
Mean diet proportions (%) for each species-group for the 2001–2005 food webs. Means were determined from the replicated ($N = 25$) mass-balance solutions (see Table 1 for species-group abbreviations).

Predator-group	Prey-group																					
	Plk	Bac	Prot	Rot	Lc	Sc	Cop	Dre	Dip	Ob	Mys	SmC	SmY	Ascl	JscI	AIO	AlEY	Ch	OS	DOC	POC	Det
Bac																				51.6	48.4	
Prot	75.3	23.0	1.7																			
Rot	57.3	34.9	7.7																			
Lc	88.2	8.7	2.2	0.2		0.2	0.5															
Sc	64.3	28.5	6.7	0.5																		
Cop	51.4	36.9	9.1	0.6		0.9	1.0															
Dre	50.0	23.1	6.5	0.4																		
Dip																					20.0	
Ob																					15.7	84.3
Mys	21.5																				26.6	73.4
SmO					15.9	17.2	18.9		1.2													25.3
SmY					1.4	0.2	2.3		0.0	6.7	89.4		0.0		0.0		0.0					
Ascl					3.6	17.5	59.1		8.2	2.4	8.0		0.0		0.0		1.2					
JscI									17.5	16.0	66.3											
AIO									44.3	55.7												
AlEY					15.9	6.1	63.7		0.0	0.7	13.5											
Ch				5.3		43.7	51.1															
OS												5.6					94.4					
									1.3	1.5	1.2	6.1		0.5		89.5						

Table 8

Mean and 95% confidence interval of species group biomass (B ; g C m^{-2}), production (P ; $\text{g C m}^{-2} \text{ yr}^{-1}$), trophic level (TL), and ecotrophic efficiencies (EE) for each time period. Means and confidence intervals were determined from the replicated ($N=25$) mass-balance solutions (see Table 1 for species-group abbreviations).

Species-group	1987–1991		2001–2005		1987–1991		2001–2005		1987–1991		2001–2005		1987–1991		2001–2005	
	B	95% CI	B	95% CI	P	95% CI	P	95% CI	TL	95% CI	TL	95% CI	EE	95% CI	EE	95% CI
Plk	1.18	1.10, 1.25	0.68	0.63, 0.71	343.22	321.2, 365.2	196.41	183.9, 208.9	1.0		1.0		0.83	0.77, 0.87	0.75	0.69, 0.80
Bac	0.58	0.50, 0.65	0.40	0.34, 0.45	123.13	106.2, 139.9	84.38	72.9, 95.8	2.0		2.0		0.71	0.64, 0.78	0.69	0.61, 0.75
Prot	0.20	0.16, 0.22	0.16	0.13, 0.18	27.52	23.58, 31.44	22.75	19.3, 26.1	2.3	2.1, 2.3	2.2	2.1, 2.3	0.64	0.55, 0.72	0.49	0.39, 0.57
Rot	0.12	0.10, 0.14	0.03	0.03, 0.03	5.33	4.55, 6.11	1.49	1.30, 1.67	2.3	2.2, 2.4	2.4	2.3, 2.5	0.55	0.47, 0.63	0.54	0.46, 0.62
Lc	0.35	0.29, 0.39	0.19	0.15, 0.21	10.34	8.84, 11.8	5.50	4.67, 6.32	2.2	2.1, 2.2	2.1	2.1, 2.1	0.78	0.70, 0.84	0.76	0.69, 0.83
Sc	0.47	0.43, 0.50	0.29	0.25, 0.33	13.10	12.06, 14.13	8.18	7.07, 9.29	2.4	2.3, 2.5	2.4	2.3, 2.4	0.77	0.70, 0.83	0.77	0.70, 0.83
Cop	1.85	1.67, 2.01	0.65	0.59, 0.70	39.64	35.9, 43.3	14.01	12.78, 15.23	2.3	2.2, 2.3	2.5	2.4, 2.5	0.84	0.78, 0.89	0.85	0.79, 0.89
Dre	<0.001	0.00, 0.00	0.19	0.16, 0.22	<0.001	0.00, 0.00	0.17	0.14, 0.19	2.4	2.3, 2.4	2.3	2.2, 2.3	0.00	0.00, 0.00	0.00	0.00, 0.00
Dip	1.53	1.38, 1.68	0.26	0.21, 0.30	3.10	2.79, 3.39	0.53	0.43, 0.61	2.0		2.0		0.74	0.68, 0.79	0.72	0.64, 0.80
Ob	1.26	1.12, 1.39	0.26	0.21, 0.30	2.55	2.27, 2.81	0.52	0.42, 0.61	2.0		2.0		0.62	0.54, 0.69	0.54	0.45, 0.63
Mys	0.76	0.68, 0.83	0.71	0.65, 0.76	2.14	1.92, 2.36	1.99	1.83, 2.14	2.6	2.5, 2.6	2.7	2.6, 2.7	0.78	0.72, 0.83	0.85	0.80, 0.90
SmO	0.20	0.17, 0.21	0.03	0.02, 0.03	0.20	0.17, 0.21	0.03	0.02, 0.03	3.3	3.2, 3.3	3.7	3.5, 3.7	0.37	0.32, 0.42	0.57	0.51, 0.63
SmY	0.02	0.01, 0.02	0.00	0.00, 0.00	0.05	0.04, 0.05	0.01	0.01, 0.01	3.3	3.2, 3.3	3.5	3.4, 3.4	0.00	0.00, 0.00	0.00	0.00, 0.00
Ascl	0.24	0.22, 0.26	0.13	0.11, 0.13	0.05	0.04, 0.05	0.03	0.02, 0.03	3.2	3.1, 3.2	3.5	3.3, 3.5	0.01	0.01, 0.01	0.01	0.01, 0.01
JscI	0.06	0.05, 0.05	0.03	0.03, 0.03	0.13	0.12, 0.14	0.08	0.07, 0.08	3.0		3.0		0.01	0.01, 0.01	0.00	0.00, 0.00
AlO	2.37	2.17, 2.56	1.43	1.32, 1.52	3.46	3.17, 3.75	1.33	1.23, 1.42	3.3	3.2, 3.3	3.5	3.4, 3.5	0.09	0.08, 0.09	0.21	0.19, 0.23
AlEY	0.61	0.54, 0.67	0.22	0.20, 0.24	3.40	3.03, 3.76	1.30	1.18, 1.41	3.4	3.3, 3.4	3.4	3.3, 3.4	0.01	0.01, 0.01	0.00	0.00, 0.00
Ch	0.03	0.02, 0.03	0.03	0.03, 0.03	0.04	0.04, 0.04	0.05	0.04, 0.05	4.3	4.2, 4.3	4.5	4.4, 4.5	0.00	0.00, 0.00	0.00	0.00, 0.00
OS	0.03	0.02, 0.03	0.01	0.01, 0.01	0.03	0.02, 0.03	0.01	0.01, 0.01	4.3	4.2, 4.3	4.4	4.3, 4.4	0.00	0.00, 0.00	0.00	0.00, 0.00

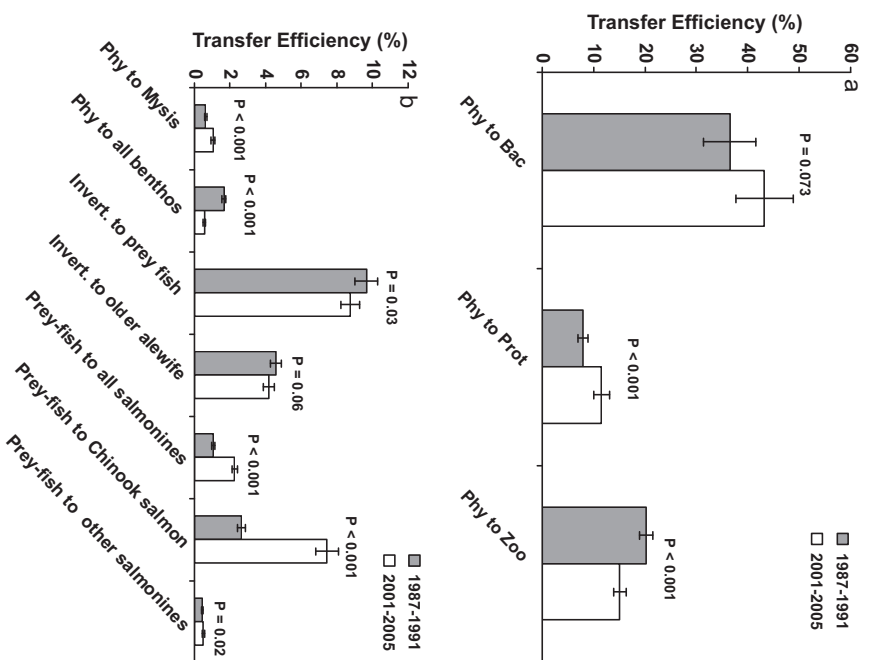


Fig. 3. Mean and 95% confidence interval of selected lower trophic level resource to consumer TTE (see Table 1 for species-group abbreviations, invert. = zooplankton, Mysis, Diporeia, and other benthos, prey-fish = all adult smelt and sculpin, and older alewife). The P -value from a t -test comparing the means is shown above the bar.

Table 6), the flows of *Diporeia* to *Mysis* were substantial. After the disruption, the flows of *Diporeia* to juvenile sculpin declined, flows to smelt dropped to negligible levels, and increased for *Mysis*.

4. Discussion

The replicated mass-balanced solutions represent robust estimates of the food web structures and flows during each of the two-time periods. The changes to species-groups biomass required to balance the models were similar between the two periods suggesting a common source of estimation bias or an incomplete model. However, there was good agreement among the relative magnitudes of the average species-group biomass of replicate final mass-balance solutions for 1987–1991 and earlier preliminary 1991 Lake Ontario mass balance studies (Halfon and Schito, 1993; Halfon et al., 1996; Stewart, 2010). Based on this consistency and robustness among models the results can be used to better understand and generalize the complex changes in the structure and function of the Lake Ontario food web associated with invasion-induced disruption.

4.1. Primary production

Dreissenid mussel grazing has been implicated in declines of chl-*a* in the Hudson River (Caraco et al., 2006). In western Lake Erie, grazing by dreissenid mussels was estimated to remove 26% of the primary production (Madenjian, 1995). The observed PP decline in offshore Lake Ontario cannot be attributed to dreissenid mussel grazing as dreissenids accounted for less than 1.0% of total phy-

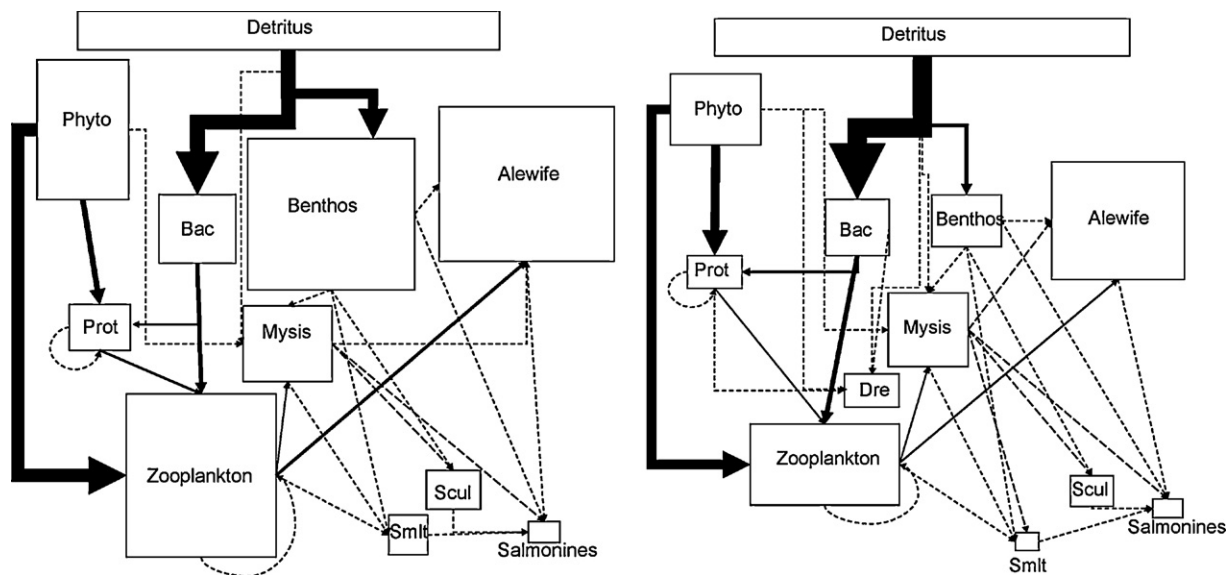


Fig. 4. Carbon flows ($\text{g C m}^{-2} \text{ yr}^{-1}$) and biomass (g C m^{-2}) of aggregated species-groups during 1987–1991 (left) and 2001–2005 (right). Areas of the boxes are proportional to the biomass (except for the detritus box which is only a schematic representation). The width of arrows is proportional to the percent contribution of the sum of all flows among aggregated species-groups. Dashed lines represent flows which contributed less than 1% of the total carbon flow (Phyto = phytoplankton, Zooplankton = all crustaceans and rotifers, Smilt = all smelt, Scol = all sculpin, Salmonines = all salmonines, Alewife = all alewife, Benthos = Diporeia and “other” benthos, Dre = dreissenids, Bac = heterotrophic bacteria, Prot = protozoans).

toplankton grazing during 2001–2005 and overall grazing rates, as measured by a reduced EE of phytoplankton, declined. In offshore Lake Ontario, dreissenid mussel densities may be too low relative to the extent of total water column primary production, to greatly influence phytoplankton grazing pathways. In Lake Ontario, the extent of the littoral zone is small with only 13% of the total lake area at a bathymetric depth of <20 m where dreissenids could spatially overlap with the euphotic zone. However, dreissenids could still be limiting the transfer of nutrients to the offshore by changing the way nutrients are cycled in the nearshore (Hecky et al., 2004) and this effect would not be detected at the scale of this study. This study demonstrates that the direct trophic impact of dreissenids on ecosystems is site-specific and is likely higher in shallower systems or only in the littoral zone of deeper lakes where the euphotic zone is closer to the lake bed. Declines in primary productivity may have been associated with reductions in nutrient loads (Millard et al., 1996), nearshore shunting of nutrients to the benthos and loss to along shore currents (Hecky et al., 2004). However, approximately 80% of the water flowing into Lake Ontario comes from Lake Erie (<http://www.epa.gov/glnpo/atlas>), and declines in Lake Ontario nutrients and chl-a (Holeck et al., 2008) linked to declining primary production, are undoubtedly strongly related to changes in nutrient and phytoplankton dynamics Lake Erie.

4.2. Bottom-up or top-down control?

So what does this study suggest are the predominate forces structuring the offshore Lake Ontario food web; resource availability (bottom-up) or predation (top-down)? For Lake Ontario, the persistent linear relationship between \log_{10} species-group production and trophic level, and the general synchrony in the decline in PP and species-group production suggest that bottom-up forces strongly regulated the potential biomass that can be supported at any TL. Lower nutrients, means lower PP, and lower zooplankton, prey-fish and predator fish production. However, this view is too simplistic, as the results also suggest that individual species-groups can respond differently and in significant ways. For example, *Diporeia*, other benthos, copepods, and other salmonines declined proportionately more than the decline in PP. *Mysis* declined pro-

portionately less than declines in PP, and Chinook salmon biomass and production increased.

For top-down effects to be a strong structuring influence, predators must be able to significantly reduce their prey beyond their compensatory ability (Fretwell, 1977; Strong, 1992). In the food web model, this relative potential strength of top-down influence is indicated by high EE values. Phytoplankton EE values were very high, suggesting strong top-down influence, but phytoplankton EE values declined during 2001–2005. Rotifers, bacteria, and protozoans, and other benthos had lower EE values suggesting less top-down influence. During 2001–2005 the EE values of these groups either declined further or did not change. *Mysis* had high EE values, and the mean EE value during 2001–2005 was the highest observed for any species-group, suggesting strong top down influence. However, this view is too simple, because the mass-balance solutions also suggest that *Mysis* may have been able to increase their production relative to PP, despite this intense predation. Prey-fish species-groups all had very low EE values suggesting very limited top-down control of prey-fish populations, but this statement also needs to be qualified. Rand and Stewart (1998) estimated EE values for yearling and adult alewife (comparable to our older alewife group) during 1991 of 0.11 very similar to this study estimate of 0.09 during 1987–1991. However, they also estimated a specific EE values for alewife age two and older which exceeded one, suggesting salmonid predation may be a major controlling influence on this alewife age-group. Additionally, predator–prey models of Lake Ontario at about the same time (Jones et al., 1993) determined that predation rates on alewife were generally sustainable, but would be quickly exceed if alewife were to experience natural, but episodic, high over-winter mortality. Also, EE values more than doubled for alewife and increased substantially for smelt during 2001–2005, suggesting that the top-down influence of salmonids on prey-fish populations increased.

4.3. Trophic influence of invasive predatory cladocerans

The trophic influence of the invasive predatory cladocerans may be low in Lake Ontario. Other studies have suggested that the disproportionate decline in copepods in Lake Ontario were due to increased predation from invasive predatory cladocerans (Warner

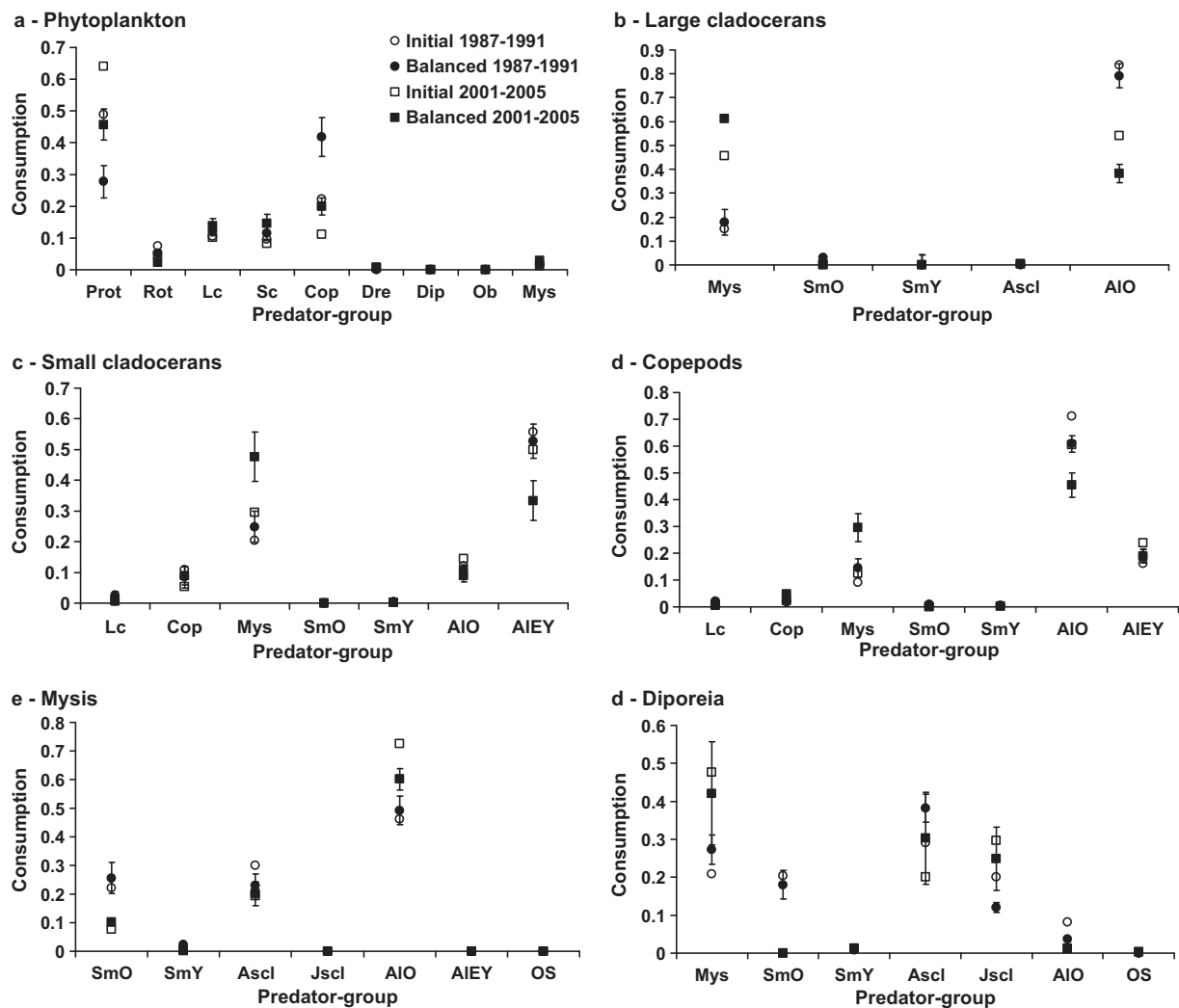


Fig. 5. Mean and 95% confidence interval of the total predation loss ($\text{g C m}^{-2} \text{yr}^{-1}$) of (a) Phytoplankton, (b) Large cladocerans, (c) Small cladocerans, (d) Copepods, (e) Mysis, and (f) Diporeia attributed to each predator-group during both time periods 2001–2005 for the un-balanced (initial) and replicated ($N = 25$) mass-balanced food web solutions (see Table 1 species-groups for predator-group abbreviations). Only the predator-groups that consumed the prey-group are shown.

et al., 2006). However, recent studies suggest alewife predation was also a major influence (Stewart et al., 2009, in press). Direct estimates of consumption of copepods by *Bythotrephes* and *Cercopagis* were not determined in the food web models as these species were combined with the large cladoceran species-group. During 2001–2005, invasive predatory cladocerans accounted for approximately 15% of the total combined large cladoceran production (Stewart et al., 2010). Assuming their consumption was proportional to their production, that their diet was 50% copepods and 50% small cladocerans and applying these assumptions to the replicate mass balance solutions they could account for 14.5 ± 5.1 (SD) and 29.9 ± 13.1 (SD) of the total consumption of these groups, respectively. Alewives and Mysis are the principal consumers of copepods and small cladocerans and have much more potential to affect their abundance and distribution. However, other studies suggest that invasive predatory cladocerans may have had indirect effects on zooplankton depth distribution, growth and behaviour (Pangle and Peacor, 2006; Pangle et al., 2007).

4.4. Increasing importance of the microbial loop

The dominant grazers in Lake Ontario, prior to the disruptive changes of the 1990s, were copepods. The mass-balance solutions suggest copepod biomass and production declined proportionately

more after the disruption, consistent with field studies (Stewart et al., 2010). However, the mass balance solutions additionally estimate that the food web response to the change was that protozoans became the dominant grazer of phytoplankton. This is consistent with numerous studies linking changes in the metazooplankton community structure with transfer of dominant flows of primary production to the microbial loop. For example, experimental nutrient additions had modest impacts on metazooplankton, but protozoans were determined to be the dominant grazers of bacteria and phytoplankton (Kankaala et al., 1996). Increases in herbivorous or omnivorous zooplankton suppress biomass and growth of bacteria and protozoans (Pace et al., 1990; Carrick et al., 1991; Burns and Schallenberg, 2001; Zollner et al., 2003). In reverse, experimental removal of *Daphnia* spp. increased the biomass of protozoans and bacteria (Langenheder and Jurgens, 2001). In Lake Ontario, copepod grazing declined from approximately 35 to 50% to about 20% of total grazing, while protozoan grazing increased from 25–30% to 45–50%. This may account for the decline in the TTE of zooplankton and prey-fish due to the respiratory losses from the extra step required to transfer PP through protozoans to zooplankton rather than by the more efficient direct grazing of PP by zooplankton.

The importance of the carbon flows from PP to protozoan to zooplankton was recognized as an important, but often neglected pathway in Lake Michigan food webs models (Carrick et al.,

1991). The results of this study confirm the importance of this link and its potential influence on efficiency of carbon transfer to higher trophic levels. Furthermore, the results suggest that overgrazing of zooplankton during periods of declining productivity could be the mechanism enhancing protozoan production. Zooplankton populations respond quickly to changes in primary productivity with population turn-over rates measured in days. However, production of their predators responds more slowly due to the fact that their populations are comprised of many cohorts accumulated over years. This may lead to overgrazing during periods of declining productivity because of the carry-over effect of multi-age predator populations produced during times of higher productivity feeding on zooplankton produced during periods of lower productivity. It is hypothesized that this may be a general response in pelagic systems, including other Great Lakes, experiencing relatively rapid oligotrophication and warrants further investigation.

4.5. Changing ecological role of *Mysis*

The results suggest an important and changing ecological role for *Mysis*. Following introductions to North America and Scandinavia, it was realized that the predatory role of *Mysis* was an important structuring force, often resulting in unexpected food web consequences (Lasenby et al., 1986; Nero and Sprules, 1986b; Koksvik et al., 2009). In Lake Ontario, *Mysis* rivaled alewife as a consumer of all zooplankton groups and were also significant consumers of *Diporeia*. This was evident in initial determinations of food web structure and only strengthened through the mass-balance procedures. Additionally, the mass-balance solutions suggest an increasing top-down influence of this predator. The best available data suggested that *Mysis* biomass declined by 50% between the two time periods, but the mass-balance solutions required that *Mysis* production be largely maintained. This was required to account for independently observed increased consumption of *Mysis*, by all prey-fish species, including an estimated sixfold increase in the relative consumption of *Mysis* by alewife (Stewart et al., in press).

Diporeia declines in Lakes Huron, Erie, and Ontario have been linked to dreissenid invasions, either through food limitations or associated toxins or pathogens (Dermott and Kerec, 1977; Dermott et al., 2005; Nalepa et al., 2009; McNickle et al., 2006; Watkins et al., 2007). However, despite considerable research effort, it has been difficult to find evidence of the direct causal mechanism (Nalepa et al., 2009), other than a modest increase in mortality of *Diporeia* exposed directly to dreissenid pseudofeces in the laboratory (Dermott et al., 2005). In Lake Ontario, *Diporeia* populations in waters >90 m bathymetric depth declined before dreissenids expanded to these depths (Watkins et al., 2007). The decline of *Diporeia* in deeper water, prior to colonization by dreissenids mussels in both Lake Michigan and Lake Ontario has been attributed to remote effects, possibly associated with transport of an unknown agents in the biodeposits of nearshore dreissenids to offshore waters (Watkins et al., 2007; Nalepa et al., 2009). However, it is difficult to imagine that byproducts from dreissenid pseudofeces could precipitate large scale ecological responses in distant populations of *Diporeia* in a well mixed system. Parsimony dictates the consideration of other causative agent, perhaps coincident with the mussel invasions, but without a direct link. Did *Mysis* have a role in the decline of *Diporeia*?

Mysis and *Diporeia* are coevolved marine relics occupying similar habitats (Juday and Birge, 1927) and would be expected to have strong interactions (Parker, 1980). This study confirmed that, in Lake Ontario, *Mysis* are trophically linked to all major pathways of energy and material flow. *Mysis* are significant predators on *Diporeia*, and with the decline in other *Diporeia* predators (smelt and

sculpin) became increasingly dominant. *Mysis* predation rapidly eliminated juvenile amphipods (*Gammarus tigrinus*) in microcosm experiments (Bailey et al., 2006). In microcosms with wild assemblages of benthos, *Mysis* actively fed on *Diporeia* and eliminated them (Parker, 1980). Both *Diporeia* and *Mysis* feed on sedimented and particulate detritus, but alternative food resource for the omnivorous *Mysis* may confer a competitive advantage, perhaps strengthened by lake-wide or local declines in the availability of detrital resources. *Mysis* perform extensive diel migrations from the benthic habitat where they reside during the day to the lower metalimnion where they feed on zooplankton and algae (Beeton and Bowers, 1982). These migrations are governed by temperature and light (Beeton and Bowers, 1982; Boscarino et al., 2009). When water clarity is low and the water depth high, *Mysis* may remain suspended in the water column (Rudstam, 2009). When water clarity increases, *Mysis* may more often reside on the bottom and stay on the bottom for a longer time period. It is hypothesized that the combination of a shift in *Mysis* habitat, sustained *Mysis* production, and perhaps declines in alternative *Mysis* food supplies, may have increased predation pressure on *Diporeia* and contributed to their recent decline.

4.6. Is Chinook salmon production uncoupled from pelagic production?

The increase in Chinook salmon biomass and production, despite significant declines in most other species-groups was unexpected. Estimates were linked to changes in the angling fishery so it could simply reflect changes in catch rates, unrelated to changes in abundance. However, Lake Ontario angler-catch rates were correlated with independent fishway counts of the abundance of returning adult rainbow trout (1978–2005; $r^2 = 0.43$, $p = 0.002$; Ontario Ministry of Natural Resources, 2006) suggesting angler catch rates track abundance. Also, despite documented declines in lower trophic level production and biomass (Holeck et al., 2008; Stewart et al., 2010, in press), trout and salmon fisheries are being sustained with near record high catch rates (New York State Department of Environmental Conservation, 2010). Production of Chinook salmon may vary independent of pelagic production. Early production of Chinook is dependent on tributary conditions for wild fish and intensive stocking of hatchery juveniles (Stewart et al., 1999) and young lake-resident Chinook salmon do not rely on pelagic food resources but rather feed on surface accumulations of terrestrial insects and nearshore benthos (Johnson, 2008). Additional nearshore resources for juvenile Chinook salmon could also include recently expanding populations of round gobies. Lake trout caught in nearshore waters (12–35 m bathymetric depth) in eastern Lake Ontario were observed to be consuming round gobies, although alewife still dominated their diet (Dietrich et al., 2006). Chinook salmon are oriented closer to shore and in warmer temperatures than lake trout (Stewart and Bowlby, 2009) and young Chinook salmon may have greater access to round goby. Early life-history influences on Chinook salmon and the modelling results are consistent with the hypotheses that Chinook salmon production is uncoupled from pelagic production processes.

4.7. The paradox of supply and demand

Mass-balance solutions required two to threefold increases in lower trophic level production. This confirms the results of an earlier independent determination that predation on both *Mysis* and zooplankton in Lake Ontario exceeded their production by 1.2–2.0 times (Rand et al., 1995). The same was not true in Lake Michigan with lower levels of planktivore production (Rand et al., 1995). This persistent paradox is similar to the long standing

“Allen’s paradox” observed in stream ecosystems (Allen, 1951; Hynes, 1970; Waters, 1988; Allan, 1995). Propagation of systemic error and natural variability leads to very high variation in estimates of secondary production (Huryn, 1996; Blukacz et al., 2005; Raborn et al., 2007; Stewart et al., in press) which when combined with high ecotrophic efficiencies will continue to result in apparent imbalances in prey supply and predator demand. Accounting for unmeasured food sources helped resolve this paradox in one stream (Huryn, 1996). However, the persistent Lake Ontario imbalance may point to systemic bias in the estimation of productivity and consumption. Using observed spatial heterogeneity in food and temperature it was shown that zooplankton could substantially increase their energy intake compared to uniform distributions of food and temperature (Blukacz et al., 2010). Presumably, *Mysis* could also exploit temperature or prey patchiness in a similar manner reducing their food requirements. In this study, increased growth efficiency associated with alewife exploitation of spatial variation in temperature and increased prey particle size was accounted for, but these effects may have been underestimated and exploiting prey patchiness may have further increased efficiency. Alternatively, alewife biomass and production may have been overestimated. Alewife production in Lake Ontario was high relative to other Great Lakes and was based on surveys only in the southern regions of Lake Ontario (Stewart et al., in press). Lower alewife densities in northern regions would reduce estimates of whole-lake alewife production and further alleviate the apparent imbalances.

4.8. Limitations of the study

There are several limitations to this study which could have influenced estimates of food web structure and flow. Limited data were available to describe diets of lower trophic levels (protozoans, zooplankton species-groups, *Mysis*), but the initial and final representations are consistent with current understanding of feeding relationships. Although estimates of *B* and *DC* are more variable than the bioenergetic ratios of *P/B* and *Q/B* (Stewart et al., in press), and the most sensitive parameters influencing mass balance (Christensen et al., 2004), it would be insightful to compare outcomes from applying alternative mass-balance procedures such as inverse modelling (Vezina and Pace, 1994) or simultaneous variation of diet, biomass, and energetic parameters (Pinkerton et al., 2008). The potential influence of nearshore processes on nutrient supply (Hecky et al., 2004) was likely captured by estimating PP in the offshore, but other unaccounted for nearshore linkages could be important. The best example, example, as discussed above, is the importance of nearshore littoral processes on the early life-history of Chinook salmon. It would also be beneficial to validate the dynamics of the protozoan–bacteria–zooplankton pathways suggested by the mass-balance solutions, perhaps with in situ mesocosm experiments. The use of multi-year annual “snap-shots” of the food web relegates annual and seasonal variation to error and could be misleading, as carbon flow dynamics are known to vary seasonally (Straile, 1998).

While it is tempting to use the results of this study to compare the structure and function of the Lake Ontario food web to other food webs to gain more general insights, this must be done with extreme caution. Methodologies, food web structures, and assumptions vary tremendously and will influence the outcomes (Pauly and Christensen, 1993). However, it would be revealing to develop comparative food web descriptions with common approaches across the continuum of anthropogenic disturbance typical of the Great Lakes. In particular, as demonstrated by this study, such comparisons may change perceptions of the importance of key trophic linkages and lead to better understanding and management of the Great Lakes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.10.024.

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