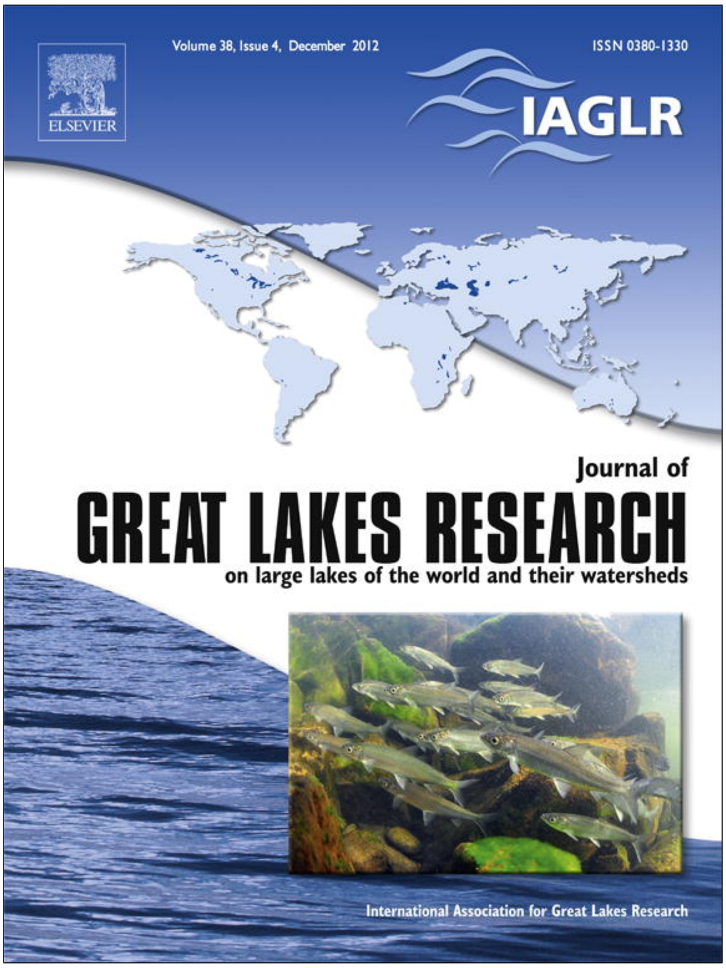
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Towards the development of an ecosystem model for the Hamilton Harbour, Ontario, Canada

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ABSTRACT

Our main objective is to undertake a synthesis of the Hamilton Harbour ecosystem and to elucidate the relative importance of the underlying trophic relationships using the mass-balance modeling software Ecopath with Ecosim (EwE). We present a conceptual model comprising all the essential food web components of the system, which was parameterized using both local and literature-based information. Among the trophic relationships considered by the Hamilton Harbour ecosystem model, our analysis highlights the central role of round goby demonstrating a wide range of effects on a number of functional groups at both higher and lower trophic levels. Several ecosystem attributes (e.g., primary production/biomass, biomass/total throughput, system omnivory index, amount of recycled throughput, and Finn's cycling index) provide evidence that the Hamilton Harbour is an immature and fairly simple system with linear food chain structure, although the internal redundancy and the system overhead estimates indicate that the Harbour possesses substantial reserves to overcome external perturbations. The aggregation of the ecosystem into discrete trophic levels suggests that most of the trophic flows are concentrated within the first two trophic levels, while flows were practically insignificant at the higher trophic levels of the food web. The fairly low ecotrophic efficiency values for both carnivorous and herbivorous cladocerans are indicative of low zooplanktivory levels in the system. Finally, our study identifies knowledge gaps and critical next steps to rigorously assess the credibility of the model and to consolidate its use for predictive purposes.

Introduction

Hamilton Harbour, also known as Burlington Bay, is a large embayment located at the western tip of Lake Ontario (Fig. 1). For decades, waste discharges from industrial and municipal activities had converted this scenic port into one of the most polluted sites in the Laurentian Great Lakes (Barica, 1989; Mayer and Johnson, 1994; Wolfe et al., 2000). As early as the 1850s, the Harbour was considered an unsuitable source of drinking water due to concerns about raw sewage contamination from the surrounding urban area. Toxic wastes from the steel and iron industry contaminated the system with heavy metals and coal tar that contained polyaromatic hydrocarbons and polychlorinated biphenyls (Poulton, 1987). By the 1940s, local beaches were closed to swimming and soon thereafter the Harbour water quality deteriorated to its lowest level, resulting in limited public access to the shoreline. The water quality problems were primarily manifested as excessive algal blooms, low water transparency, predominance of toxic cyanobacteria, and low hypolimnetic oxygen concentrations during the late summer (Gudimov et al., 2010, 2011; Hiriart-Baer et al., 2009; Leslie and Timmins, 1992; Ramin et al., 2011). Further, the elimination of the vegetated littoral zone and the disappearance of essential wetlands and fish nursery habitats, due to infilling for industrial activities as well as for railway or highway construction along the south and east shores of the Harbour, posed major threats to the integrity of the native fish community (Burley, 2007; Holmes and Whillans, 1984; Minns et al., 1994).

Recognition of the broader repercussions of pollution to ecosystem functioning led to the designation of the Hamilton Harbour as one of 17 Canadian Areas of Concern (AOC) by the International Joint Commission (IJC) (International Joint Commission, 1988). Notably, several of the Beneficial Use Impairments (BUIs) and delisting objectives referred directly to fish, such as restrictions on fish and wildlife consumption, tainting of fish and wildlife flavour, degradation of fish and wildlife populations, fish tumours or other deformities, and loss of fish and wildlife habitat. Hamilton Harbour and its watershed previously supported more than 106 fish species and the local fish community historically contained a mixture of coldwater, coolwater, and warmwater species (Holmes, 1988). The system was considered an important habitat for lake trout (*Salvelinus namaycush*), Atlantic salmon (*Salmo salar*), lake herring (*Coregonus artedii*), and lake whitefish (*Coregonus clupeaformis*),

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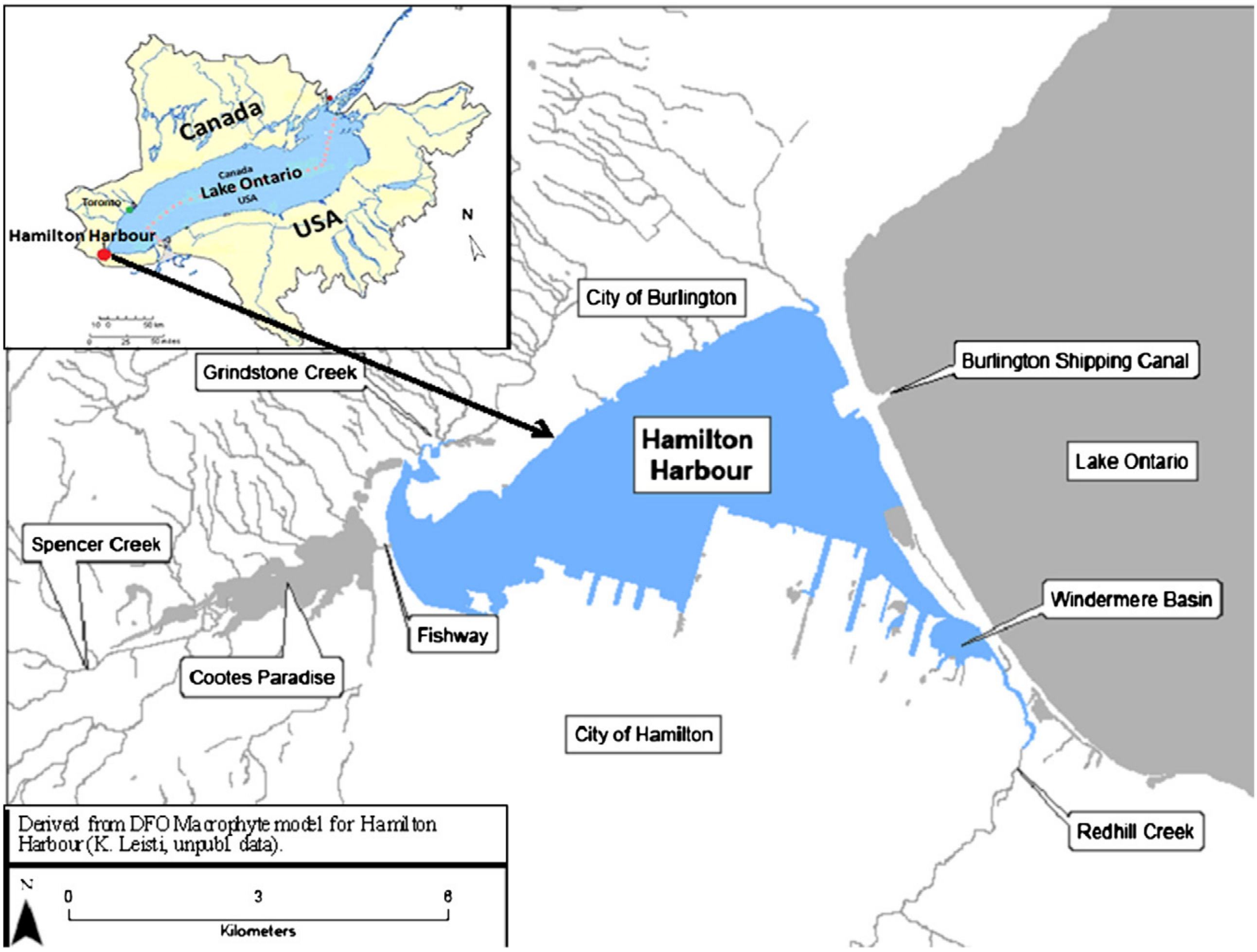

Fig. 1. A map of Hamilton Harbour (43°N, 79°W) located in western tip of Lake Ontario, Canada. The study area is highlighted with a light blue colour.

and was also characterized by a thriving nearshore fish community that included populations of northern pike (*Esox lucius*), muskellunge (*Esox masquinongy*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieui*), yellow perch (*Perca flavescens*), and white sucker (*Catostomus commersonii*) (Whillans, 1979). Fish species diversity has been substantially reduced due to the altered state of the Harbour, and the current fish community is mainly dominated by benthivores such as brown bullhead (*Ameiurus nebulosus*), common carp (*Cyprinus carpio*), and white perch (*Morone americana*), and planktivores such as alewife (*Alosa pseudoharengus*) and gizzard shad (*Dorosoma cepedianum*). These species tolerate low dissolved oxygen conditions and high suspended solid concentrations, while their feeding and spawning activities uproot vegetation and stir up bottom sediments (Scheffer and van Nes, 2004). The predominance of pollution-tolerant species has consequently kept many desirable fish species at low levels, such as northern pike, largemouth bass, and walleye (*Sander vitreus*), while the role of the dominant piscivore in the system has been assumed by the (more adaptable in polluted habitats) channel catfish (*Ictalurus punctatus*) (Bowlby et al., 2009). Aside from the impaired diversity and abundance of fish and wildlife communities, tumours/lesions and other deformities have been reported on several fish species (Baumann, 1992; Baumann et al., 1996; Smith et al., 1989), stemming from exposure to carcinogenic and teratogenic chemicals (Marvin et al., 2000; Mayer and Johnson, 1994). Further, concerns for an edible fishery and consumption limitations arose from the elevated contaminant levels in Hamilton Harbour (Hamilton Harbour Remedial Action Plan, 1992).

In the mid-1980s, the Hamilton Harbour Remedial Action Plan was formulated through a variety of government, private sector, and community participants with the mandate of restoring and protecting environmental quality and beneficial uses (Hall et al., 2006). The first phase of the Hamilton Harbour RAP process focused on the identification of the environmental problems along with the determination of the underlying causes (Stage 1); the second phase involved public participation to establish community and stakeholder goals and to reach consensus on recommended actions, implementation plans and monitoring strategies (Stage 2); and the current (third) stage aims at implementing actions and monitoring progress (Stage 3), with its completion scheduled for 2015 (Hall et al., 2006). In early stages, local stakeholders selected the warm water fishery as a priority use for the Harbour (Hamilton Harbour Remedial Action Plan, 1992). Acknowledging that the aforementioned structural shifts in the fish community of Hamilton Harbour reflect the transition from a moderately enriched (mesotrophic) environment to a nutrient enriched (eutrophic) ecosystem, a multiple remedial action plan (restoration of destroyed or preservation of existing habitats, control of undesirable and introduction of desired species) was outlined, aiming to restore the piscivorous populations and to ultimately bring the warmwater fish community as close as possible to the historical norms. In particular, apart from their importance in the local fishery, northern pike and largemouth bass have been identified as focal species, because of their sensitivity to known (and thus potentially mitigable) stresses on the Harbour ecosystem, i.e., decline in the submerged vegetation required as spawning habitat.

The foundation of the remedial measures reflected an ecosystem-type approach that considers the complex interplay among physical factors, chemical variables and biotic components pertinent to the Harbour's beneficial uses (Hiriart-Baer et al., 2009). Specifically, the warm water fishery was related to a critical total phosphorus (*TP*) level following a "causal model" that dissected the eutrophication problem in the Harbour into a sequence of causal links, i.e., fish need aquatic plants for shelter and reproduction, aquatic plants need light to grow, light will only penetrate the water column if chlorophyll *a* levels are sufficiently low, low chlorophyll *a* levels are achieved through sufficiently low *TP* concentrations (Charlton, 2001; Dermott et al., 2007). Based on empirical relationships between water clarity and the maximum depth of colonization of submerged plants (Canfield et al., 1985; Chambers and Kalff, 1985), it was estimated that the Secchi disc transparency of 3.0 m was expected to provide approximately 170 ha for plant colonization, which was then associated with a targeted level of exogenous phosphorus loading (142 kg day^{-1}) and critical values of total phosphorus ($TP<17$ μg L^{-1}) and chlorophyll *a* (5–10 μg L^{-1}) concentrations (Charlton, 2001). Responding to HHRAP's (1992) propositions, significant nutrient loading reductions were achieved and substantial efforts have been made to improve the fish habitat around the edge of the Harbour (Hiriart-Baer et al., 2009). Yet, the actual impact of these restoration efforts to the local fish community as well as to the Harbour ecosystem as a whole remains to be assessed. One important question that needs to be addressed is the examination of the current status of the fish community and the likelihood of meeting the delisting objectives of the system as an AOC. In the same context, equally important unknowns are the ecosystem attributes that better reflect the integrity of its functioning and the realistic delineation of what should be perceived as "success" of the contemporary restoration efforts.

In this study, our main objective is to undertake a synthesis of the Hamilton Harbour ecosystem and to elucidate the relative importance of the underlying trophic relationships using the mass-balance modeling software Ecopath with Ecosim (EwE) (Christensen et al., 2005). Our first step was to design a conceptual model comprising all the essential biotic components that effectively depict the food web dynamics of the Harbour. The second step was to compile all the existing information from the system (or the literature) to parameterize the model and to subsequently examine the impact of the assumptions made about different input parameters (i.e., species-specific biomass, consumption and production rates) to critical model outputs. Our study presents the results of a network analysis (flow indices, cycles and pathways) and examines the different attributes (e.g., primary production/biomass, biomass/total throughput, system omnivory index) of the system in its current state. Finally, we pinpoint knowledge gaps and critical next steps to rigorously assess the credibility of the model and to consolidate its use for predictive purposes.

Methods

Study site

Hamilton Harbour is a cone-shaped small body of water with an area of 20.97 km^2 and maximum depth of 24 m (Fig. 1). Only one-eighth of the total Harbour area is shallower than 5 m, while approximately half of the total area of the system is more than 15 m deep. The Harbour is connected with Lake Ontario through a 9.5 m deep shipping canal (Burlington Canal) and with Cootes Paradise (a shallow marsh-pond system at its western end) through the Fishway, the Great Lakes' first two-way channel and carp barrier located at the mouth of the Desjardins Canal. It drains a watershed of 494 km^2 that includes three major tributaries: the Red Hill, Spencer and Grindstone Creek. Hamilton Harbour is the main water body that serves the cities of Hamilton and Burlington, which represent a population of approximately 500,000. Around 46% of the Harbour's 45 km shoreline is occupied by industrial uses; 10% by residential, and the remaining 44% by private, institutional or public open space. Treated and combined sewage discharges from the two cities contribute most of the inflows (>75%) into the Harbour. Besides the tributaries and municipal sewage treatment facilities, the remaining inflows stem from steel manufacturing facilities as well as urban and rural runoff from the surrounding watershed. Wastes from the steel industry and associated coking facilities contaminated the sediments with heavy metals such as copper, cadmium, and zinc; iron-manganese oxides; polyaromatic hydrocarbons and polychlorinated biphenyls (Fox et al., 1996; Mayer and Manning, 1990). Hamilton Harbour also experiences hypoxia every year during the stratification summer period, but undersaturation can also occur in winter when ice cover is extensive (Hiriart-Baer et al., 2009). The severity and duration of hypoxia is modulated by natural factors, such as the thickness of the hypolimnion and the hydraulic exchanges with Lake Ontario as well as anthropogenic nutrient inputs that enhance chemical (nitrification) and biological processes (organic matter decomposition) (Barica, 1989; Hiriart-Baer et al., 2009).

Ecosystem model

Ecopath with Ecosim (EwE) is a free suite of ecosystem modeling tools, available at http://www.ecopath.org/, consisting of three main components: Ecopath, which provides a static, mass-balanced snapshot of the system (Christensen and Pauly, 1992; Polovina, 1984); Ecosim, representing a time dynamic module for policy analysis (Walters et al., 1997); and Ecospace, a spatial and temporal dynamic module aiming to delineate impacted sites (Pauly et al., 2000; Walters et al., 2000). Ecopath with Ecosim (EwE) has been extensively used to examine ecosystem attributes, to evaluate ecosystem effects of fishing pressure, to analyze the impact of habitat restoration and the integrity of protected areas, and to predict fate and transport of contaminants (Ecotracer) (Christensen and Booth, 2006). The Ecopath model is founded upon a system of linear equations that express mass-balance over a given time period as follows:

$$B_i{}^*(P_i/B_i){}^*EE_i = Y_i + \sum_{j=1}^{n} B_j{}^*(Q/B)_j{}^*DC_{ji} \qquad (1)$$

where B_i is the biomass of the group *i* during the study period, $i=1, \ldots, n$ functional groups, $(P/B)_i$ is the production/biomass of group *i* (equal to total mortality under the equilibrium assumption), EE_i is the ecotrophic efficiency (fraction of production consumed within the system or exported from it, including harvesting), Y_i is the fishing yield of the group *i* ($Y_i=F_iB_i$ where F_i is the fishing mortality rate), B_j is the biomass of the consumer *j*, $(Q/B)_j$ is the consumption/biomass of *j*, and DC_{ji} is the fraction of *i* in the diet of *j*. Eq. (1) expresses the steady-state model for each ecosystem component that guides the trophic flow analysis.

We used a wide range of criteria to delineate a total of 26 functional groups (Table 1). The detritus compartment was divided into two groups (pelagic detritus and sedimented detritus) to better reflect the role of particulate organic matter in the system. Generic phytoplankton, epiphytes, autotrophic picoplankton, and macrophytes were the four groups of primary producers considered in the model. Recognizing differences in behavioural/dietary patterns, the zooplankton community of the model explicitly considers the following functional groups: carnivorous and herbivorous cladocerans, calanoid and cyclopoid copepods, and micro-zooplankton. Benthic invertebrates were classified into oligochaetes and chironomids, miscellaneous benthos, gastropods and bivalves, and dreissenids. The fish assemblage of the model was primarily designed to depict the interplay between the current eutrophic fish community and the "desired" one that is expected to emerge, if the RAP restoration efforts are successful. Despite their low biomass levels, northern pike and largemouth bass were represented as independent groups to evaluate their current ecological state. Ontogenetic

Table 1
Functional groups and diet sources of the Hamilton Harbour ecosystem model. Diet assumptions are based on footnoted references. The complete information of the corresponding papers is provided in the on-line Supplementary Information section.

No.	Group name	Description
1	Cormorants[1]	*Phalacrocorax auritus*
2	Adult northern pike[2]	*Esox lucius* (fish ≥ 150 mm)
3	YOY northern pike[3]	*Esox lucius* (fish < 150 mm)
4	Adult largemouth bass[4]	*Micropterus salmoides* (fish ≥ 45 mm)
5	YOY largemouth bass[5]	*Micropterus salmoides* (fish < 45 mm)
6	Toxic tolerant fish[6]	*Ictalurus punctatus* and *Ameiurus nebulosus*
7	Desired forage fish[7]	*Perca flavescens* and *Morone chrysops*
8	Centrarchids[8]	*Lepomis macrochirus, Lepomis gibbosus* and *Ambloplites rupestris*
9	Other forage fish[9]	*Alosa pseudoharengus, Morone Americana, Dorosoma cepedianum* and *Catostomus commersonii*
10	Round goby[10]	*Neogobius melanostomus*
11	Small pelagic fish[11]	*Notropis atherinoides, Notropis hudsonius* and *Notemigonus crysoleucas*
12	Common carp[12]	*Cyprinus carpio*
13	Oligochaetes and chironomids[13]	Oligochaeta and Chironomidae (Diptera)
14	Miscellaneous benthos[14]	Hydrachnids, Amphipods and Isopods
15	Gastropods and bivalves[15]	Sphaeriids., *Pisidium sp.*, and *Physella sp.*
16	Dreissenids[16]	*Dreissena polymorpha, Dreissena bugensis*
17	Cladocerans carnivorous*	*Leptodora kindtii* and *Cercopagis pengoi*
18	Calanoid and cyclopoid copepods*	Calanoid, copepodids, calanoid nauplii, *Leptodiaptomus siciloides*, cyclopoid nauplii, cyclopoid copepodids, *Diacyclops thomasi* and *Mesocyclops edax*
19	Cladocerans herbivorous*	*Bosmina longirostris, Eubosmina coregoni, Daphnia retrocurva* and *Chydorus sphaericus*
20	Micro-zooplankton*	Heterotrophic nanoflagellates and ciliates
21	Macrophytes	*Myriophyllm spicatum* and *Vallisneria americana*
22	Epiphytes	Vegetation between 20 μm and 500 μm
23	Phytoplankton	Cyanophytes, Chlorophytes, Cryptophytes, Chrysophytes, Diatoms and Dinophytes
24	Autotrophic picoplankton	Bacteria and autotrophic picoplankton
25	Pelagic detritus	Suspended organic matter in the water column
26	Sedimented detritus	Decomposed organic matter deposited on benthic sediments

[1]Somers et al., 2003; Young et al., 2010 [2,3]Soupir et al., 2000; Wright and Giles, 1987; Giles et al., 1986; Coker et al., 2001; Froese and Pauly, 2010; DFO, 2010 [4,5]Christensen and Moore, 2007; Aday et al., 2005; Soupir et al., 2000; Coker et al., 2001; Froese and Pauly, 2010 [6]Tyus and Nikirk, 1990; Marsh, 1981; Fitzgerald, 1996; Coker et al., 2001; Froese and Pauly, 2010; DFO, 2010 [7]Gestring, 1991; Danehy and Ringler, 1991; Coker et al., 2001; Johnson et al., 2005; Schaeffer and Margraf, 1986 [8]Andraso, 2005; Fitzgerald, 1996; Coker et al., 2001; Froese and Pauly, 2010 [9]Danehy and Ringler, 1991; Coker et al., 2001; Schaeffer and Margraf, 1986; Munrittrick et al., 1991; Gene et al., 2007; Stewart et al., 2009 [10]Schiller et al., in submission; Johnson et al., 2005 11Pothoven et al., 2009; Hartman et al., 1992; Elser et al., 1995; Keast and Fox,1992; Muth and Busch, 1989; Coker et al., 2001 [12]Marsden, 1997; Coker et al., 2001; Zambrano and Hinojosa, 1999 [13,14]Dormott, 2001 [15]Dormott, 2001; Watanabe, 1984 16Haynes, 1997; David et al., 2005.

* Diet compositions of the Bay of Quinte ecosystem model were adapted during the balancing of the model.

splitting was also used for those two species to reflect the changes in the trophic role and energetic parameters with their life stage. The exotic species, common carp and round goby (*Neogobius melanostomus*), were retained as independent groups to allow assessment of their impacts on the food web of the Harbour. All other fish species were pooled into functional groups based on similarities of habitat, diet and life history characteristics. Channel catfish and brown bullhead were combined together into a group labelled as "toxic tolerant" fish. Yellow perch and white bass (*Morone chrysops*) were labelled as "desired forage" fish. Bluegills (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), and rock bass (*Ambloplites rupestris*) represented the "centrarchids." Alewife, white perch, gizzard shad, and white sucker formed a functional group called "other forage" fish. Emerald shiner (*Notropis atherinoides*), spottail shiner (*Notropis hudsonius*), and golden shiner (*Notemigonus crysoleucas*) were lumped together and labeled as "small pelagic" fish. Fish-eating birds were represented by the "cormorants," which dominate the aquatic birds population in Hamilton Harbour (Somers et al., 2003; Weseloh et al., 2002).

For each functional group, four input parameters were estimated: biomass (*B*), production per unit of biomass (*P*/*B*), consumption per unit of biomass (*Q*/*B*) and diet composition. The biomass for each functional group, expressed as tonnes (t) of wet weight per km^2, was mainly obtained from the Department of Fisheries and Oceans (DFO) field surveys conducted in Hamilton Harbour. The *P*/*B* and *Q*/*B* ratios were taken from published literature or were estimated using empirical equations (Christensen et al., 2005; Pauly, 1980; Randall and Minns, 2000). There are major knowledge gaps with regards to the dietary compositions in Hamilton Harbour, as the corresponding data are available for only a few of the functional groups modeled and the taxonomic resolution is low in the stomach analyses carried out. Thus, the diet composition data were mainly derived from the literature for the same species in similar ecosystems (see references in the footnote of Table 1). Description of the functional groups and their input parameter specifications are provided in the on-line Supplementary Information (SI) (see SI 1).

The parameterization of the Hamilton Harbour ecosystem model was designed to provide a snapshot of the average conditions during the 2004–2008 period. Mass-balance was achieved by iteratively changing the diet matrix, the major source of uncertainty in the model. Diet composition data from the balanced model are presented in Table 2. Trophic levels (TL) were calculated as the biomass weighted average of food items plus 1, and the omnivory index was used to gain insights into the variance of the trophic levels of a consumer's prey groups (Pauly et al., 1993). The network analysis routines of EwE were used to calculate a suite of system property metrics and flow indicators based on theoretical concepts of Odum (1969) and Ulanowicz (1986). A routine proposed by Ulanowicz (1995) was used to aggregate the food web on discrete trophic levels (*sensu* Lindeman, 1942), which were then used to assess the flow distributions and trophic transfer efficiency (TTE) in the system. The mixed trophic index was used to determine direct and indirect trophic impacts among groups (Ulanowicz and Puccia, 1990). Finally, the overall quality of the model was also examined using the pedigree index routine by Christensen et al. (2005). A glossary of terms related to the present Ecopath modeling exercise is provided in SI 2.

Results

The basic input and output parameters for all the groups in the model are shown in Table 3. EwE (version 6.2) was also used to graphically represent trophic flows and trophic levels of the Hamilton Harbour ecosystem (Fig. 2). The highest TL value was assigned to cormorants (TL = 3.66), followed by largemouth bass and northern pike (TL = 3.59 for both). The rest of the fish groups ranged between trophic levels of 2.28 and 3.34. Carnivorous cladocerans had a trophic level of 2.95 and calanoid and cyclopoid copepods had a trophic level of 2.16. All the groups of benthic invertebrates as well as the rest of the zooplankton community (herbivorous cladocerans and micro-zooplankton) had a TL value of 2.0. The values of the respiration to assimilation (*R*/*A*) and production to respiration (*P*/*R*) ratios for all groups were less than one, which was one of the criteria used to accept the balanced solution presented here. The measure of the model quality obtained through the pedigree index routine of EwE was 0.516, indicating that the model foundation is approximately equally based on local and literature-based information. To put this value into a broader context, we note that the Hamilton Harbour ecosystem model falls into the higher pedigree range (0.400–0.599) of Morissette's (2007) categorization, as developed by the evaluation of 50 balanced Ecopath models.

Table 2
Diet compositions of the biotic compartments of the balanced Hamilton Harbour ecosystem model.

No.	Prey	Predator																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Cormorants	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	Adult northern pike	<0.001	<0.001	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	YOY northern pike	<0.001	<0.001	–	<0.001	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	Adult largemouth bass	<0.001	–	–	<0.001	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	YOY largemouth bass	<0.001	<0.001	–	<0.001	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6	Toxic tolerant fish	0.008	0.003	0.001	0.003	0.140	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7	Desired forage fish	<0.001	<0.001	<0.001	<0.001	0.005	0.001	0.005	0.002	–	–	–	–	–	–	–	–	–	–	–	–
8	Centrarchids	0.002	0.005	0.001	<0.001	0.001	0.001	0.001	<0.001	<0.001	–	–	–	–	–	–	–	–	–	–	–
9	Other forage fish	0.028	0.030	0.015	0.002	0.035	0.005	0.080	0.039	0.026	–	–	–	–	–	–	–	–	–	–	–
10	Round goby	0.603	0.364	0.088	0.495	0.034	0.025	0.010	0.027	0.002	–	–	–	–	–	–	–	–	–	–	–
11	Small pelagic fish	0.164	0.203	0.020	0.150	0.030	0.133	0.010	0.003	–	<0.001	–	–	–	–	–	–	–	–	–	–
12	Common carp	0.194	0.395	0.024	0.349	0.010	0.025	0.015	0.017	–	–	–	–	–	–	–	–	–	–	–	–
13	Oligochaetes and Chironomids	–	–	0.140	–	0.555	0.410	0.105	0.205	0.154	0.330	0.305	0.129	–	–	–	–	–	–	–	–
14	Miscellaneous benthos	–	–	–	–	0.091	0.050	0.300	0.341	0.002	0.003	0.001	0.001	–	–	–	–	–	–	–	–
15	Gastropods and bivalves	–	–	–	–	–	0.055	–	0.034	–	0.010	–	0.040	–	–	–	–	–	–	–	–
16	Dreissenids	–	–	–	–	–	0.085	0.020	0.218	–	0.080	–	0.010	–	–	–	–	–	–	–	–
17	Cladocerans carnivorous	–	–	0.200	–	0.029	0.070	0.175	0.037	0.020	0.001	0.020	0.020	–	–	–	–	–	–	–	–
18	Calanoid and cyclopoid copepods	–	–	0.305	–	0.050	0.066	0.175	0.040	0.001	0.001	0.003	0.030	–	–	–	–	0.030	0.050	–	–
19	Cladocerans herbivorous	–	–	0.206	–	0.020	0.075	0.105	0.037	0.249	0.187	0.452	0.020	–	–	–	–	0.390	–	–	–
20	Micro-zooplankton	–	–	–	–	–	–	–	–	0.342	0.078	0.127	0.010	–	–	–	–	0.530	0.100	–	–
21	Macrophytes	–	–	–	–	–	–	–	–	–	–	–	0.150	–	–	–	–	–	–	–	–
22	Epiphytes	–	–	–	–	–	–	–	–	–	0.010	–	0.080	–	–	0.050	0.010	–	0.100	0.150	0.160
23	Phytoplankton	–	–	–	–	–	–	–	–	0.025	–	0.017	0.190	0.200	0.100	0.010	0.420	0.050	0.700	0.850	0.730
24	Autotrophic picoplankton	–	–	–	–	–	–	–	–	0.013	–	0.025	0.010	0.010	0.100	0.040	0.010	–	0.050	–	0.110
25	Pelagic detritus	–	–	–	–	–	–	–	–	0.075	0.150	0.050	0.140	0.300	0.300	0.200	0.140	–	–	–	–
26	Sedimented detritus	–	–	–	–	–	–	–	–	0.091	0.150	–	0.170	0.490	0.500	0.700	0.420	–	–	–	–
	Sum	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**

Table 3
Ecopath outputs (bold fonts) for the Hamilton Harbour ecosystem model. TL is the trophic level, *B* is biomass (t km^{-2}), *P/B* is the production rate (year^{-1}), *Q/B* is the consumption rate (year^{-1}), EE is the ecotrophic efficiency, *P/Q* is the production/consumption ratio, *R/A* is the ratio of respiration to assimilation, *P/R* is the ratio of production to respiration, FD is the flow to detritus (t km^{-2} year^{-1}), NE is the net efficiency, OI is the omnivory index and 0.00 values indicates too few significant digits.

Group name	TL	*B*	*P/B*	*Q/B*	EE	*P/Q*	*R/A*	*P/R*	FD	NE	OI
Cormorants	**3.66**	0.219	0.45	50.2	**0.00**	**0.01**	**0.99**	**0.01**	**2.29**	**0.01**	**0.04**
Adult northern pike	**3.59**	0.008	0.21	3.01	**0.07**	**0.07**	**0.91**	**0.10**	**0.01**	**0.09**	**0.07**
YOY northern pike	**3.34**	<0.001	6.65	22.71	**0.04**	**0.29**	**0.63**	**0.58**	**0.00**	**0.37**	**0.15**
Adult largemouth bass	**3.59**	0.086	0.32	6.22	**0.20**	**0.05**	**0.94**	**0.07**	**0.13**	**0.06**	**0.06**
YOY largemouth bass	**3.30**	0.005	5.69	36.68	**0.01**	**0.16**	**0.81**	**0.24**	**0.07**	**0.19**	**0.23**
Toxic tolerant fish	**3.23**	0.177	0.56	12.24	**0.88**	**0.05**	**0.93**	**0.07**	**0.54**	**0.07**	**0.15**
Desired forage fish	**3.29**	0.013	0.55	2.97	**0.98**	**0.19**	**0.77**	**0.30**	**0.01**	**0.23**	**0.16**
Centrarchids	**3.10**	0.014	1.37	4.61	**0.84**	**0.30**	**0.63**	**0.59**	**0.02**	**0.37**	**0.07**
Other forage fish	**2.84**	1.169	0.50	7.77	**0.83**	**0.06**	**0.92**	**0.09**	**2.57**	**0.08**	**0.22**
Round goby	**2.69**	4.190	1.76	7.40	**0.95**	**0.24**	**0.70**	**0.42**	**6.59**	**0.30**	**0.22**
Small pelagic fish	**2.93**	0.887	2.72	27.76	**0.93**	**0.10**	**0.88**	**0.14**	**5.10**	**0.12**	**0.11**
Common carp	**2.28**	3.240	0.78	8.80	**0.69**	**0.10**	**0.88**	**0.14**	**8.01**	**0.13**	**0.25**
Oligochaetes and chironomids	**2.00**	19.02	13.1	62.4	**0.10**	**0.21**	**0.74**	**0.36**	**461.17**	**0.26**	–
Miscellaneous benthos	**2.00**	0.160	5.70	30.2	**0.40**	**0.19**	**0.76**	**0.31**	**1.51**	**0.24**	–
Gastropods and bivalves	**2.00**	0.490	7.30	37.6	**0.52**	**0.19**	**0.76**	**0.32**	**5.42**	**0.24**	–
Dreissenids	**2.00**	2.400	1.35	8.60	**0.79**	**0.19**	**0.76**	**0.31**	**4.95**	**0.24**	–
Cladocerans carnivorous	**2.95**	1.460	18.3	54.8	**0.06**	**0.33**	**0.58**	**0.71**	**41.06**	**0.42**	**0.05**
Calanoid and cyclopoid copepods	**2.16**	7.660	6.91	20.7	**0.22**	**0.33**	**0.58**	**0.71**	**72.99**	**0.42**	**0.14**
Cladocerans herbivorous	**2.00**	24.33	15.4	46.3	**0.14**	**0.33**	**0.58**	**0.71**	**548.94**	**0.42**	–
Micro-zooplankton	**2.00**	4.550	50.0	250.0	**0.30**	**0.20**	**0.75**	**0.33**	**386.60**	**0.25**	–
Macrophytes	**1.00**	33.97	6.80	–	**0.02**	–	–	–	**225.80**	–	–
Epiphytes	**1.00**	14.17	59.8	–	**0.44**	–	–	–	**476.23**	–	–
Phytoplankton	**1.00**	37.39	150.0	–	**0.39**	–	–	–	**3392.60**	–	–
Autotrophic picoplankton	**1.00**	10.39	70.0	–	**0.20**	–	–	–	**579.82**	–	–
Pelagic detritus	**1.00**	359.0	–	–	**0.75**	–	–	–	–	–	–
Sedimented detritus	**1.00**	539.0	–	–	**0.10**	–	–	–	–	–	**0.21**

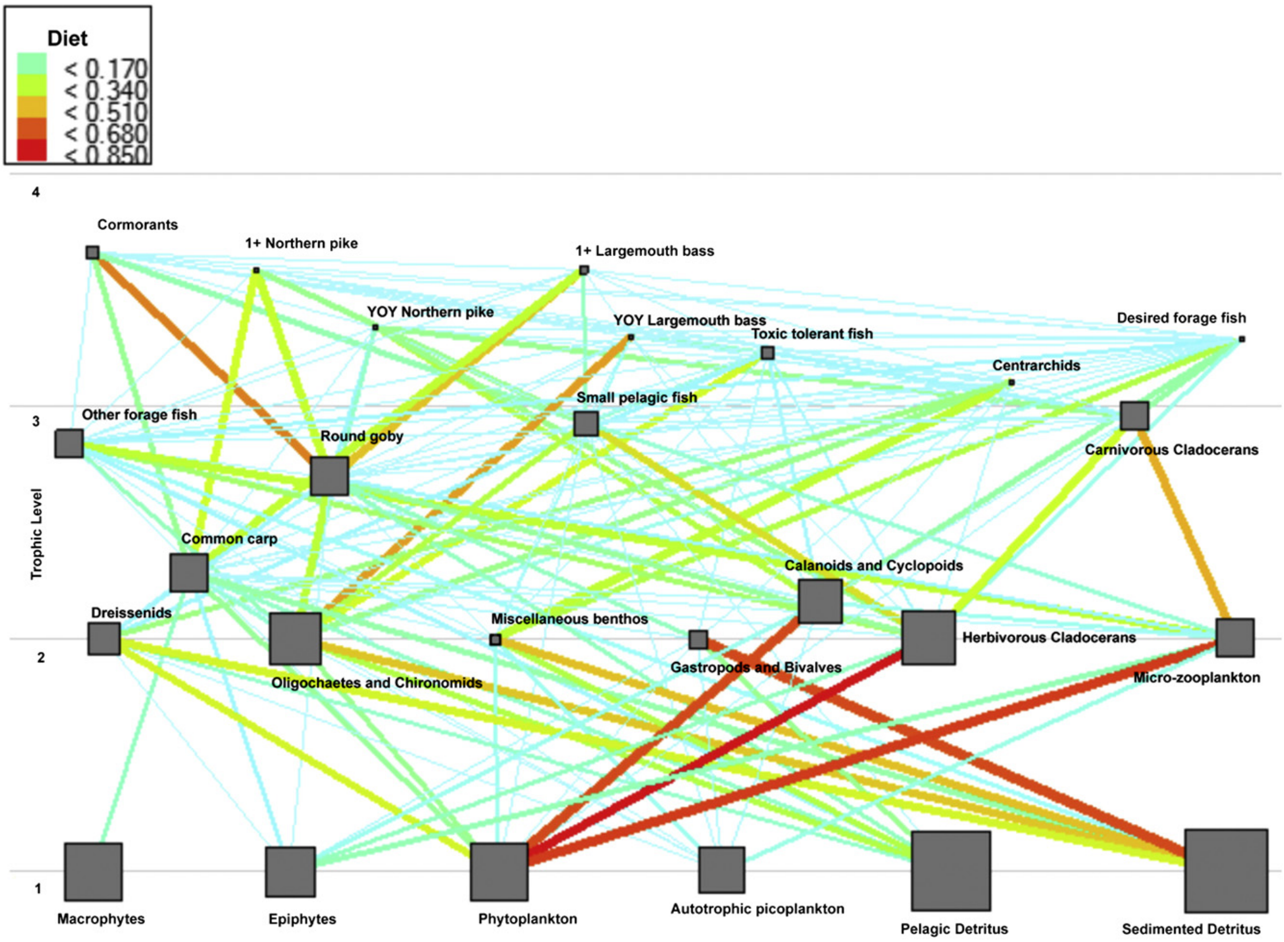

Fig. 2. The Ecopath outputs based on the Hamilton Harbour food web conceptualization. Each functional group is shown as a rectangle and its size is approximately proportional to its biomass. Thickness and colour of the lines illustrate the magnitude of the flow rates. The vertical line demonstrates the functional trophic level of each biotic compartment.

Ecotrophic efficiencies (EE)

An EE value of 0.00 was calculated for cormorants because they have no predators of their own in the Harbour (Table 3). Lower EE values were also calculated for adult northern pike (0.07) and adult largemouth bass (0.20) implying the absence of any commercial or recreational fishing in the Harbour. Likewise, the EE values for the young of the year (YOY) groups were fairly low (northern pike = 0.04, largemouth bass = 0.01), reflecting the absence of substantial predation in the Harbour. The highest EE values were obtained for desired forage (0.98), round goby (0.95), small pelagic fish (0.93), and toxic tolerant fish (0.88), followed by centrarchids (0.84), other forage fish (0.83), and common carp (0.69). Fairly low EE levels were obtained for the majority of the benthic invertebrate groups. Oligochaetes and chironomids were characterized by the lowest value (0.10), suggesting that the predation pressure was particularly low relative to their biomass levels in the system (Table 3). EE values for both carnivorous (0.06) and herbivorous (0.14) cladocerans were also quite low, implying minimal zooplanktivory levels in the system. Similarly, low EE values were assigned to phytoplankton (0.39) and

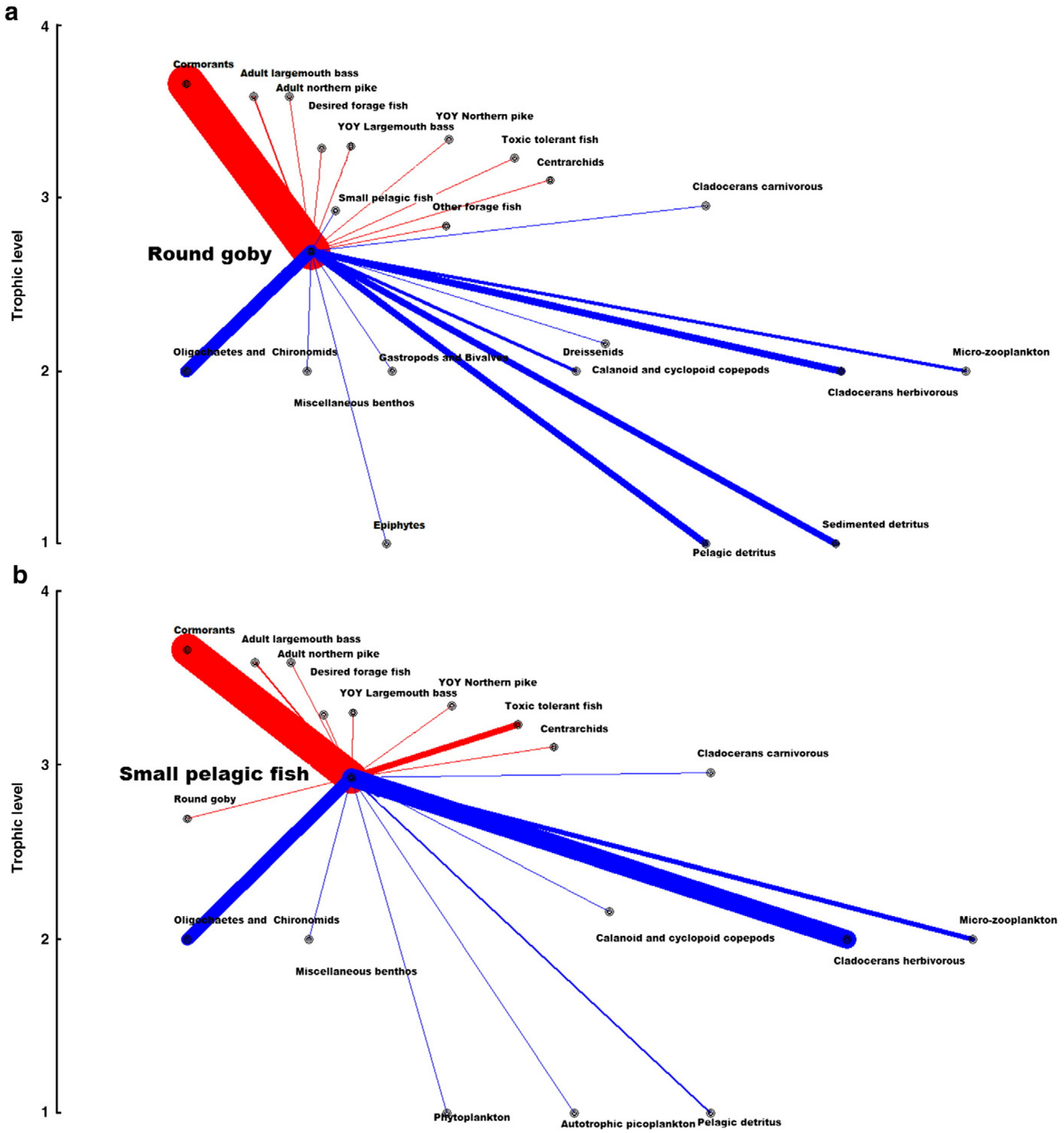

Fig. 3. Trophic interactions of (a) round goby, (b) small pelagic fish, (c) common carp, and (d) dreissenids. The relative width of each connection indicates its magnitude. Blue and red lines indicate prey and predator species, respectively. The trophic level of each group in the model is indicated by the *Y*-axis.

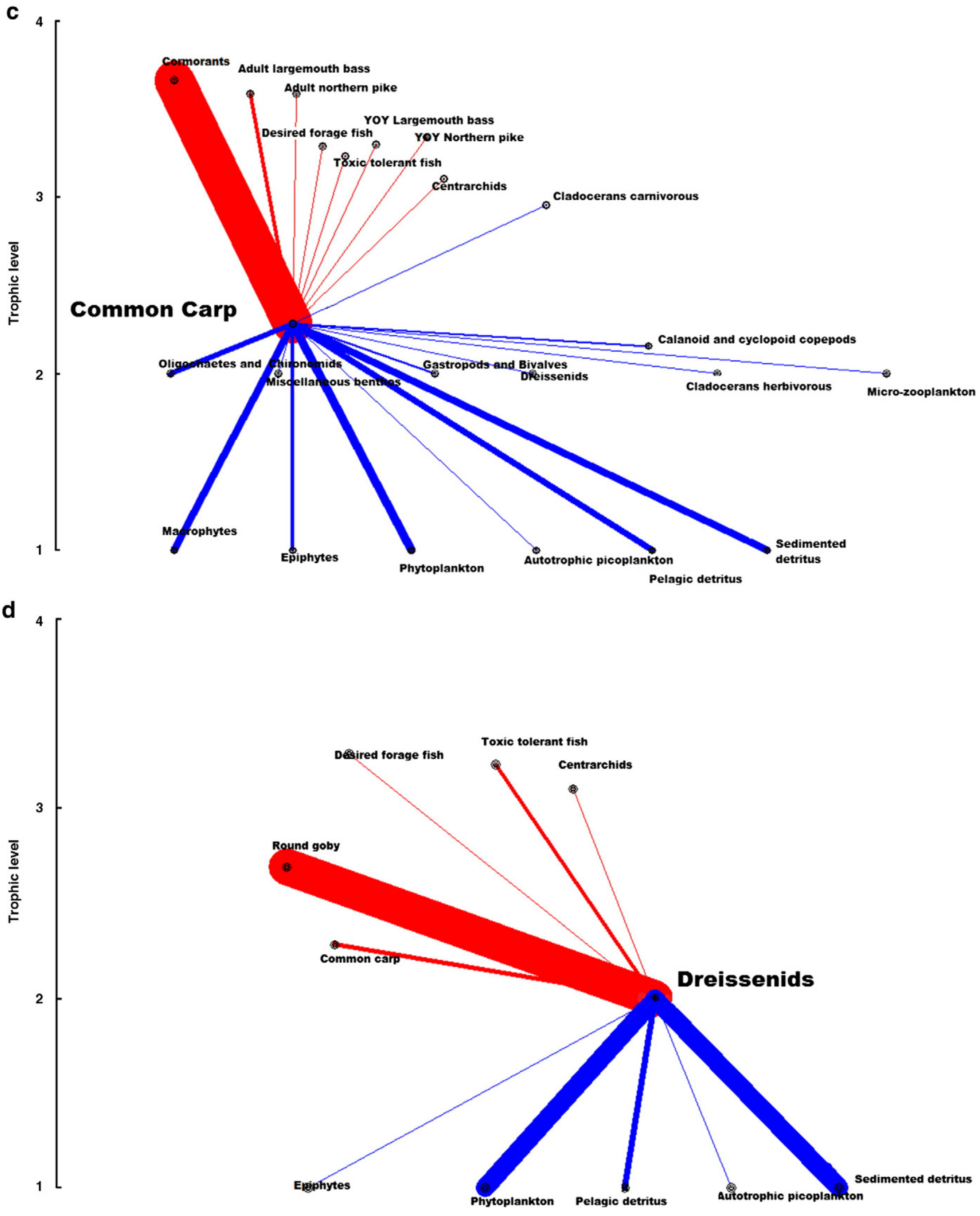

Fig. 3 (*continued*).

epiphytes (0.44), reflecting limited grazing pressure from herbivorous zooplankton and therefore a largely unexploited algal standing stock. The EE values calculated for pelagic (0.75) and sedimented (0.10) detritus indicated that a substantial fraction of the particulate matter settling onto the bottom sediments remains largely unutilized until buried by newly deposited material. Notably, the ratios between production and consumption (*P*/*Q*) – often referred to as gross food conversion efficiency – for the consumer groups were between 0.05

and 0.33. These values suggest that the consumption of most groups is about 3–20 times higher than their production, which provides support for the basic assumptions underlying the Hamilton Harbour ecosystem model (Christensen et al., 2005). In particular, longer-lived and slower-growing groups (e.g., cormorants, northern pike, largemouth bass, channel catfish, brown bullhead, and common carp) were plausibly characterized by the lowest P/Q ratios (<0.10), whereas the high P/Q value for centrarchids reflects a high P/B relative to the Q/B value assigned (Table 3).

Omnivory indices and trophic interactions

Cormorants have a nearly zero omnivory index (*OI*) value (0.04), as these aquatic birds exclusively feed upon fish (Table 3). The highest *OI* value was calculated for common carp (0.25), followed by YOY largemouth bass (0.23), round goby (0.22), and other forage fish (0.22), indicative of flexible dietary patterns that encompass both plant/detrital and animal food sources. Round goby, small pelagic fish, common carp, and dreissenids play a key role in the transfer of energy through the Hamilton Harbour food web, and the trophic linkages of these ecologically significant groups are provided in Fig. 3. In the case of round goby, oligochaetes and chironomids represent their strongest trophic linkage, followed by herbivorous cladocerans, detritus, and dreissenids (Fig. 3a). Likewise, herbivorous cladocerans and oligochaetes/chironomids are the main staples of the diet of small pelagic fish (Fig. 3b). For common carp, the largest food sources are the oligochaetes/chironomids, phytoplankton, macrophytes, and detritus (Fig. 3c). In contrast, cormorants appear to exert much of the predation pressure upon round goby, small pelagic fish, and carp populations. The latter finding requires empirical evidence (especially the causal link between juvenile carp and cormorants) to rule out the possibility that it is not an artifact stemming from the model balancing exercise. Round goby, common carp, and toxic tolerant fish represent the main predators of dreissenids, which in turn have strong feeding reliance upon algae and detritus (Fig. 3d).

Trophic transfer efficiency

The aggregation of the ecosystem into discrete trophic levels primarily suggests that most of the trophic flows were concentrated in TLs I–II and were practically insignificant at the higher TLs (Table 4). Further, the breakdown of the trophic flows by groups overwhelmingly stresses the importance of phytoplankton and sedimented detritus on the ecosystem functioning, as our model predicts that 83.6% of the total flows from the first trophic level are associated with the two compartments. Oligochaetes and chironomids (32.22%) along with micro-zooplankton (30.91%) and herbivorous cladocerans (30.61%) were predominantly responsible for the flows at the herbivore/detritivore level (II). The trophic flows at the first-order carnivore level (TL III) mainly originated from carnivorous cladocerans (47.47%), followed by small pelagic fish (13.69%), round goby (13.37%), calanoid and cyclopoid copepods (10.46%), and other forage fish (5.87%). Not surprisingly, cormorants profoundly dominated the flows at the higher trophic levels (IV and V). The geometric means of the transfer efficiencies of the flows originating from detritus and the primary producers through the trophic levels II–IV, calculated as the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from the trophic level to the next, and the throughput on that trophic level, were approximately 2.0% and 3.8%, respectively (Table 5).

Network analysis

To characterize the structure and size of the system, we examined the key ecosystem attributes derived from the model (Table 6). The sum of all consumption and all respiratory flows in the system were estimated to be 3851 and 2126 t km^{-2} $year^{-1}$, respectively. The total production from all the primary producers considered was 8310 t km^{-2} $year^{-1}$, while the total system throughput was 18431 t km^{-2} $year^{-1}$. The net system production was particularly high (5230 t km^{-2} $year^{-1}$), suggesting that the Harbour ecosystem is fairly immature (Odum, 1969). Likewise, the calculated ratio of total primary production to total respiration was

Table 4
Trophic transfer matrix of the Hamilton Harbour ecosystem model showing the distribution of flows (t km^{-2} $year^{-1}$) by groups and trophic levels.

Group	Trophic level					
	I	II	III	IV	V	VI
Cormorants	–	–	3.86	6.994	0.122	0.0008
Adult northern pike	–	–	0.01	0.013	–	–
YOY northern pike	–	–	0.01	0.003	–	–
Adult largemouth bass	–	–	0.23	0.301	0.006	–
YOY largemouth bass	–	–	0.15	0.044	0.007	0.0001
Toxic tolerant fish	–	–	2.02	0.571	0.010	–
Desired forage fish	–	–	0.03	0.012	–	–
Centrarchids	–	–	0.07	0.007	–	-
Other forage fish	–	2.6	9.38	0.256	0.001	–
Round goby	–	9.6	21.36	0.035	–	–
Small pelagic fish	–	2.3	21.88	0.474	0.002	–
Common carp	–	25.7	8.25	0.766	0.002	–
Oligochaetes and chironomids	–	1186.0	–	–	–	–
Miscellaneous benthos	–	4.8	–	–	–	–
Gastropods and bivalves	–	18.4	–	–	–	–
Dreissenids	–	20.6	–	–	–	–
Cladocerans carnivorous	–	4.0	75.85	0.253	–	–
Calanoid and cyclopoid copepods	–	142.1	16.71	–	–	–
Cladocerans herbivorous	–	1127.0	–	–	–	–
Micro-zooplankton	–	1138.0	–	–	–	–
Macrophytes	231	–	–	–	–	–
Epiphytes	847	–	–	–	–	–
Phytoplankton	5550	–	–	–	–	–
Autotrophic picoplankton	727	–	–	–	–	–
Pelagic detritus	500	–	–	–	–	–
Sedimented detritus	6223	–	–	–	–	–
Total	14079	3681.0	159.80	9.730	0.150	0.0009

Table 5
Transfer efficiency at various *TLs* showing the contribution of detritus and primary production to the Hamilton Harbour trophic network.

Sources	TL					
	II	III	IV	V	VI	VII
Producer	4.9	4.9	2.2	0.6		
Detritus	2.7	12.1	0.2	0.1		
All flows	4.3	6.1	1.5	0.6	0.2	0.1

Note: Proportion of total flow originating from detritus: 0.45
Transfer efficiencies (calc. as geometric mean for TL II–IV):
Primary producers: 3.8%
Detritus: 2.0%
Total: 3.4%

also greater than one (3.46), which also indicates that the system production exceeds respiration and thus the system is in its early developmental stage (Odum, 1969). The relatively high values of the primary production/biomass ≥ 44.11 year^{-1} (i.e., accumulation of biomass over time) and the biomass/total throughput <0.01 (high available energy flow used to support the total system biomass) are indicative of a system that undergoes its early developmental stages. The low values of the connectance (0.296) and system omnivory (0.080) indices also suggest a linear rather than a “web-like” food chain structure.

The total ascendency of the system (26108 flow bits) primarily consists of the internal flows (10127 flow bits or 14.5% of the total fluxes in the system), followed by exports (12.3%), respiration (6.9%), and imports (3.7%) (Table 7). Importantly, the internal redundancy (or the overhead on the internal flow) and the system overhead are fairly high ($>62\%$ of the development capacity). The latter result is not surprising, given that the system has been regularly subjected to anthropogenic disturbances and thus highly organized flow is unlikely to develop. Further, if we compare the values typically reported in the literature (Fayram et al., 2006; Hossain et al., 2010; Liu et al., 2007; Villanueva et al., 2008; Yunkai-Li et al., 2009), we infer that the amount of recycled throughput excluding detritus (8.26 t km^{-2} year^{-1}), the Finn's cycling index (1.58%), and the values of Finn's mean (2.35) and straight-through path length without detritus (2.21) are also on par with our earlier findings that the Hamilton Harbour is probably an immature and fairly simple system (Table 8).

Mixed trophic impact (MTI)

The MTI routine provides a trophic interaction matrix, which illustrates how a change in the biomass of a functional group listed in the left of the rows would impact the biomass of the groups listed in the top of the columns (Fig. 4). Namely, cormorants have a negative impact on all the fish groups that constitute a substantial portion of their diet, such as round goby, common carp, small pelagic and other forage fish. Consequently, the benthic community (oligochaetes and chironomids, gastropods/bivalves, miscellaneous benthos, and dreissenids) appears to capitalize on the biomass reduction of the aforementioned groups due to the alleviation from the predation pressure. Interestingly, species that represent a very small portion of the cormorant diet (i.e., northern pike and largemouth bass) are very sensitive to any perturbations exerted from the top predators. This somewhat unexpected result presumably stems from their low biomass levels, and thus emphasizes how fragile the two targeted species are in their current ecological state. Among the trophic relationships considered by the Hamilton Harbour ecosystem model, our analysis highlights the impact of the round goby on a number of functional groups at both higher and lower trophic levels in the Harbour. In particular, round goby competes with other residents of the fish community for the same food resources and habitats, while having a strong trophic linkage with the dreissenids (see also Fig. 3). Common carp has a significant negative impact on macrophytes, because of its characteristic benthic foraging pattern of uprooting the macrophytes in the system. Because of their relative low abundance, some fish groups such as desired forage fish, centrarchids, largemouth bass, and northern pike have almost no impact on the rest of the food web. We also note the negative impact of carnivorous zooplankton on the herbivorous residents of the zooplankton community, which subsequently cascades as an increase of the algal standing biomass due to the diminished grazing pressure. Herbivorous cladocerans and microzooplankton compete for the same food sources and exert negative control on the primary producers of the system. Detritus and phytoplankton appear to have a direct positive impact on the benthic invertebrates, which in turn should be propagated throughout the food web.

Table 6
Ecosystem indicators describing the Hamilton Harbour ecosystem structure.

Parameter	Values	Units
Sum of all consumption	3851	t km^{-2} year^{-1}
Sum of all exports	5731	t km^{-2} year^{-1}
Sum of all respiratory flows	2126	t km^{-2} year^{-1}
Sum of all flows into detritus	6723	t km^{-2} year^{-1}
Total system throughput	18431	t km^{-2} year^{-1}
Sum of all production	8310	t km^{-2} year^{-1}
Calculated total net primary production	7356	t km^{-2} year^{-1}
Net system production	5230	t km^{-2} year^{-1}
Total biomass (excluding detritus)	166.75	t km^{-2}
Total primary production/total biomass	44.11	yr^{-1}
Total primary production/total respiration	3.46	
Total biomass/total throughput	0.009	yr^{-1}
Connectance index	0.296	
System Omnivory index	0.080	

Table 7
Totals of flux indices for the Hamilton Harbour ecosystem model.

Source	Ascendency		Overhead		Capacity	
	Flowbits	%	Flowbits	%	Flowbits	%
Imports	2593	3.7	23	0.0	2616	3.7
Internal flow	10127	14.5	35367	50.6	45493	65.1
Export	8564	12.3	1959	2.8	10523	15.1
Respiration	4825	6.9	6448	9.2	11272	16.1
Total	26108	37.3	43796	62.7	69904	100.0

Discussion

In the Great Lakes, the growing appreciation of the complex policy decisions required to restore and maintain the ecological integrity along with the need to address the cumulative effects of the multitude of tightly intertwined stressors has triggered a shift from the historical water quality/fisheries exploitation paradigms to the ecosystem management paradigm (Minns and Kelso, 2000). Yet, while the concept of a holistic ecosystem management makes sense as a pragmatic means to address the multifaceted environmental problems, sceptical viewpoints caution that this approach entails an accommodation of the ecological complexity through a multi-causal way of thinking, which in

Table 8
Cycling and path lengths for the Hamilton Harbour ecosystem model.

Cycles and pathways	Values	Units
Throughput cycled (excluding detritus)	8.26	t km^{-2} year^{-1}
Predatory cycling index	0.17	% of throughput without detritus
Throughput cycled (including detritus)	291.25	t km^{-2} year^{-1}
Finn's cycling index	1.58	% of total throughput
Finn's mean path length	2.35	
Finn's straight-through path length (without detritus)	2.21	
Finn's straight-through path length (with detritus)	2.31	

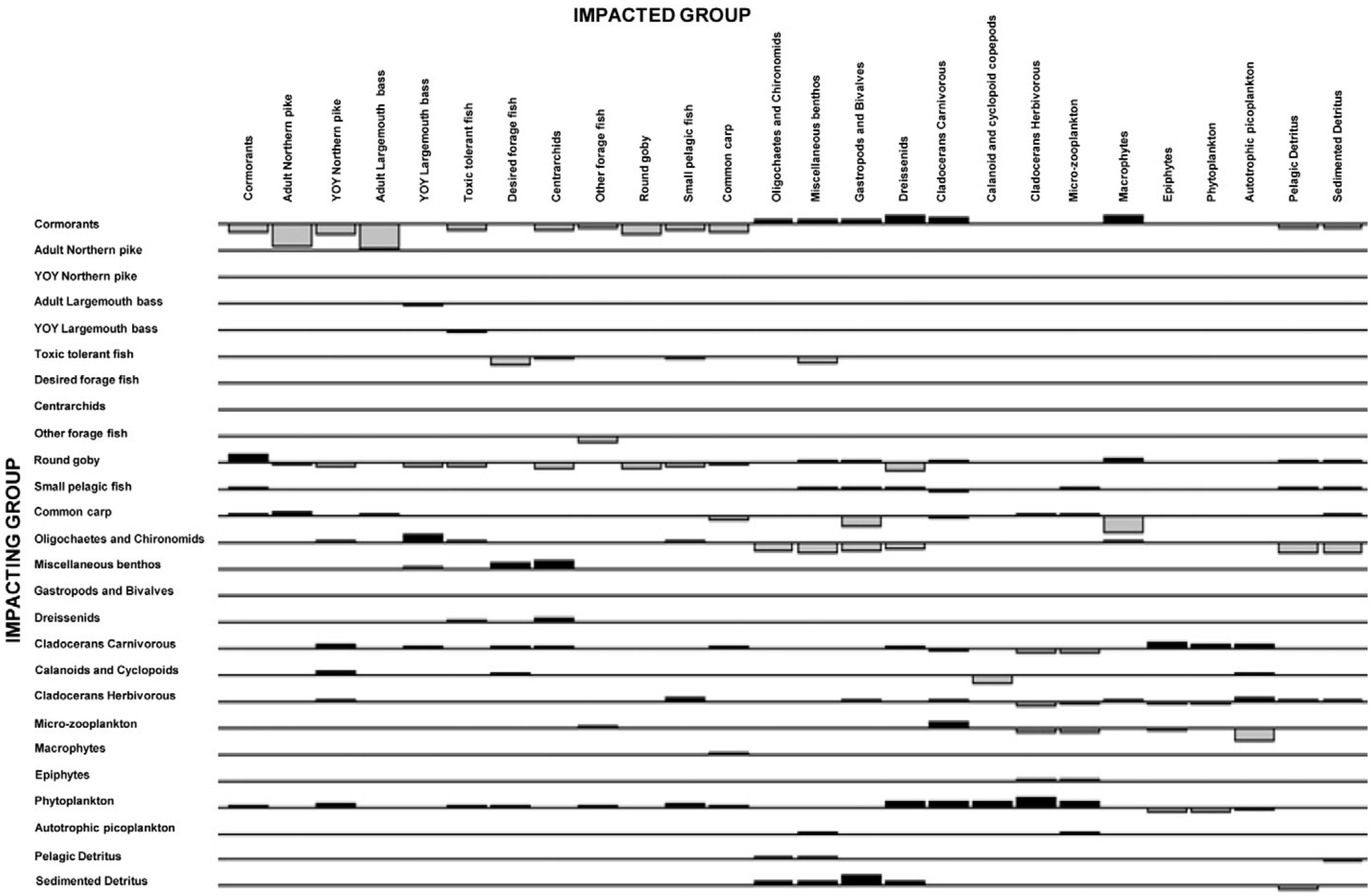

Fig. 4. The mixed trophic impact analysis of the Hamilton Harbour ecosystem model. Impacting and impacted groups are placed along the vertical and horizontal axis, respectively. Grey and black bars represent direct and indirect relative impact. The bars pointing upwards indicate positive impacts, while the bars pointing downwards show negative impacts.

turn can be a major impediment for eliciting the straightforward scientific answers required from the regulatory agencies to employ the provisions of the Great Lakes Water Quality Agreement (Bowerman et al., 1999; Krantzberg, 2004; Zhang and Arhonditsis, 2008). In this study, we recognise that the ecosystem approach has indeed made compelling the adoption of more sophisticated scientific methodologies, suitable for elucidating causal mechanisms, complex interrelationships, direct and indirect ecological paths of the Great Lakes basin ecosystem. Yet, the critical evaluation of the inference drawn and the impartial differentiation between real knowledge gained and existing knowledge gaps can be the only thrusts for coping with the ubiquitous uncertainty pertaining to the emerging complex modelling constructs. In this regard, we believe that the key findings of our ecosystem model should be critically evaluated against the existing empirical information from the Harbour in order to put the postulated ecological structure into perspective as well as to guide future model refinements.

Ecosystem attributes

The relative values of metrics that characterize community energetics and structure, life histories, nutrient cycling, selection pressure, and overall homeostasis can potentially offer insights into the stage of ecosystem development (mature or immature) and subsequently into the system stability (Odum, 1969). In our study, several of the ecosystem metrics such as the primary production/biomass, primary production/respiration, and the biomass/total throughput provided evidence that the Hamilton Harbour is a system in its early developmental stage. Given the current eutrophic status of the Harbour, this finding may seem to contradict the classical limnological theory, which suggests that ecosystems tend to progress in time from the less productive (oligotrophic) to the more productive (eutrophic) state. Odum's (1969) conceptual model of ecological succession refers to maturity changes brought about by biological processes within the ecosystem, whereas the cultural eutrophication experienced in the Harbour is related to anthropogenic activities that act as an external stimuli pushing the system back (in successional terms) to a “younger” state. To put some of the metrics presented herein into perspective, the ratio between total primary production and total respiration falls within the second highest range (3.2–6.4) of Christensen and Pauly's (1993) classification scheme. Yet, we caution that the high primary production/respiration value in conjunction with the fairly high ratio between the total export and the system throughput (>0.3) may also stem from the omission of bacterial respiratory activity from our model. Namely, our model assumes that the entire detritus pool is exported out of the system, and therefore downplays the likelihood of a substantial portion of detritus to be respired (reutilized) by bacteria (Christensen et al., 2005). When the configuration of our “autotrophic picoplankton” group was modified to account for the role of heterotrophic bacteria (see SI 1), both the primary production/respiration (1.9) and total export/system throughput (0.25) ratios were significantly decreased.

The connectance and system omnivory indices suggest a relatively high degree of consumer specialization in the Harbour and lack of aptitude to feed upon various trophic levels. Earlier Ecopath applications showed that both indices tend to be loosely associated with the ecosystem maturity (Christensen, 1995; Christensen and Pauly, 1993), but Odum (1969) expected a linear food chain structure in the form of “plant-herbivore-carnivore sequences” during the early stages of succession, as a result of low biodiversity. However, our results appear to contradict Ryman's (2009) empirical finding that several fish species in the Harbour, typically categorized as specialists, are characterized by large variation of their isotopic signatures indicative of feeding upon both littoral sources with high carbon signatures and pelagic sources with low carbon signatures. The same study also casts doubt on the applicability of the general classification between generalists and specialists in the Harbour, asserting that the inadequate food quantity/quality in the system may force fish to eat "whatever they can, whenever they can" (Ryman, 2009). Keeping in mind that Ryman's (2009) analysis represents a relatively short time (6-month) window of the food web dynamics in the Harbour, a possible explanation for the discrepancy between our EwE analysis and Ryman's (2009) stable isotope study may be related to the diet compositions assumed. Although the model was balanced by iteratively adjusting the diet matrix, the lack of fish diet data from the Harbour is admittedly one of the major sources of uncertainty of our analysis.

Another important trend in the maturation process is the increase in the capacity to recycle nutrients within the ecosystem; i.e., the effective closing of the nutrient biogeochemical cycles (Odum, 1969; Vasconcellos et al., 1997). In a similar manner, the number of pathways that a unit of energy or nutrient flow will be passing through on its way from inflow to outflow is also expected to increase in mature systems. Our Finn's cycling index and mean path length suggest a very low fraction of the total system throughput recycled as well as a low number of nodes (or compartments) that an inflow or outflow passes through. Our estimates fall within the areas delineated by the relationships of the Finn's cycling index against the primary productivity/respiration and mean path length in Christensen and Pauly (1993; see SI 2). The Ecopath model also predicts a moderately high system overhead ($\approx$62%) suggesting that the system possesses a decent amount of reserves to overcome external disturbances. Given that immature systems are usually assumed to demonstrate lower stability, the latter finding seems somewhat counterintuitive and differs from what was reported by Aoki (1995) and Fayram et al. (2006). However, our study is not the first to report a relatively high system overhead ratio that negates the general evidence of an immature and relatively simple system (e.g., see Yunkai-Li et al., 2009; Hossain et al., 2010). In congruence with our results, Perez-Espana and Arreguin-Sanchez (2001) study asserted that ecosystem maturity and stability are related but in inverse way of what has been historically perceived, i.e., immature systems are more stable and ecosystems become more fragile as they mature. Moreover, our predictions for the system overhead-Finn's cycling index pair are consistent with the Christensen and Pauly's (1993) parabolic relationship (Fig. 6, p. 343; see also SI 2), although the Harbour falls within the lower end of its steepest segment where the system overhead increases rapidly with the cycling until it levels off at an approximate cycling value of 15%. This non-linear (and probably non-monotonic) pattern was interpreted as evidence that only intermediate levels of recycling are optimal from a stability point of view, whereas systems with low recycling rates may be less stable because of their dependence on rapid energy flow through the various ecosystem compartments, thereby increasing their vulnerability to external nutrient pulses. On the other hand, systems experiencing high recycling levels may be more sensitive to external perturbations due to their strong reliance upon a pattern of tightly intertwined energy flows (Christensen and Pauly, 1993).

Our model estimates that approximately 291 t km^{-2} $year^{-1}$ of the detrital material is being recycled within the system, although this amount represents a small portion of the total system throughput. This prediction is on par with recent empirical evidence that the microbial community (bacteria, autotrophic picoplankton, heterotrophic nanoflagellates, and ciliates) of the Hamilton Harbour constitutes an important vector of autochthonous energy transfer to higher trophic levels (e.g., Fitzpatrick et al., 2007; Munawar et al., 2005). Furthermore, the microbially mediated mineralization is likely to be an important supplier of bioavailable nutrients in the Harbour mixed layer and can largely determine the compliance of the system with the targeted water quality goals as the subsidies of phosphate associated with rapid nutrient turnover rates significantly modulate the epilimnetic phytoplankton dynamics and can conceivably cast doubt on the projected efficacy of the on-going restoration efforts (Gudimov et al., 2010, 2011). An intense nutrient regeneration can also explain the relatively small fraction of dissolved inorganic phosphorus relative to the contemporaneous total phosphorus or epilimnetic phytoplankton levels (Burley, 2007). Importantly, the microbial loop is likely to exert greater control as we gradually shift from eutrophic to meso- or oligotrophic conditions (Biddanda et al., 2001; Cotner and Biddanda, 2002; Legendre and Rassoulzadegan, 1995), and thus this component of the food web could potentially be an indispensable pathway in advancing our understanding of the Harbour ecosystem functioning and effectively tracking its transition to a new "restored" state (Munawar and Fitzpatrick, 2007).

Trophic interactions in the lower food web

The fairly low ecotrophic efficiency values ($<$0.30) for all the herbivorous zooplankton groups are surprising and seemingly contradict recent work by Gerlofsma et al. (2007), who reported relatively high chlorophyll *a*/total phosphorus ratios (0.41–0.62) in the Harbour. This pattern was interpreted as an indicator of an odd-link system characterized by strong predation of herbivorous zooplankton by fish. Evidence in support of their conclusion was also provided by the smaller mean length of cladocerans (320–425 μm) in the system relative to the Bay of Quinte (see their Fig. 7; pg 88), as fish preferentially consume larger zooplankton individuals and the mean zooplankton community length can reflect the balance between piscivores and planktivores within the fish community (Mills et al., 1987). While these contradictory findings pinpoint a knowledge gap with regards to the zooplankton capacity to effectively suppress the epilimnetic algal biomass, Munawar and Fitzpatrick (2007) offered a somewhat different perspective supporting the notion of a predominant bottom-up forcing of the herbivorous community in the system. Namely, it was argued that the existing pelagic autochthonous production is unlikely to meet the zooplankton energy requirements, and thus allochthonous sources may account for a substantial portion of their diet. Yet, even if seston abundance is not critical in the Harbour, the likelihood of a zooplankton community primarily driven by bottom-up factors cannot be ruled out, as the nutritional/biochemical quality of the available food may be equally important (Brett and Müller-Navarra, 1997). Apparently, allochthonous organic matter represents the inferior quality component of zooplankton's diet and primarily supports the energetic demands of the animals through the pathways of catabolism, whereas phytoplankton is the component of their diet that is actually used for production of new somatic material (Brett et al., 2009). The extremely low transfer efficiency from the first to the upper trophic levels and the pyramid-like food web predicted by our ecosystem model are consistent with the idea that nutritional/biochemical factors (e.g., polyunsaturated fatty acids) modulate the trophodynamics in the Harbour (Perhar and Arhonditsis, 2009).

Consistent with Gerlofsma et al.'s (2007) top-down hypothesis, Ramin et al. (2011) identified the structural shift towards a zooplankton community dominated by large and fast growing daphnids (and not necessarily the abundance itself) as the most efficient lower food web configuration to achieve compliance with the existing water quality goals. In this regard, the present analysis paints a different picture with regards to the nature of the top-down control exerted on the herbivorous community. Namely, instead of planktivorous fish, the carnivorous zooplankton (*Leptodora kindtii, Polyphemus pediculus, Cercopagis pengoi*) appears to have the strongest direct association with the herbivorous zooplankton community and therefore dominates the flows of mass/energy in the third trophic level. The likelihood of carnivorous zooplankton to be a primary regulatory factor was also proposed by Munawar and Fitzpatrick (2007), who noted that the proportion of carnivorous to herbivorous zooplankton is relatively high, frequently accounting for 25–50% of the zooplankton biomass. The predicted linear food chain structure is also on par with this conceptualization of the lower food web, while the patterns derived from the mixed trophic impact analysis showed that any increases in biomass of carnivorous zooplankton can alleviate the autotrophic community from the grazing pressure exerted by the herbivores. On the other hand, aside from the desired forage fish (yellow perch and white bass) and the YOY northern pike, our model parameterization suggests that none of the residents of the fish community demonstrates strong feeding reliance upon carnivorous zooplankton. Given that biomass of the YOY northern pike is currently fairly limited in the Harbour, the extremely low ecotrophic efficiency (0.06) resulting from the present food web configuration seemingly suggests an underutilization of carnivorous zooplankton in the system. Yet, we caution that this assertion requires further investigation for two basic reasons: (i) we completely lack zooplankton diet data from the Harbour and thus diet compositions of the Bay of Quinte ecosystem model were used and subsequently adapted during the balancing of the model, and (ii) a careful inspection of Munawar and Fitzpatrick's (2007) data indicates that the proportion of carnivorous zooplankton undergoes sharp declines to lower than 10% of the total zooplankton biomass for most of the summer period (see their Figs. 6–9) which may in turn reflect stronger control from its fish predators.

Fish community

Round goby became established in the Harbour in 1998 and has been detected in higher numbers at various locations in Hamilton Harbour (Balshine et al., 2005; Vélez-Espino et al., 2010). Generally, existing evidence suggests that the rapid proliferation and aggressive behaviour of round goby can alter benthic communities and nutrient cycles (Janssen and Jude, 2001; Kuhns and Berg, 1999), displace native species through shelter monopolization (Balshine et al., 2005), and voraciously consume eggs of native fishes (Chotkowski and Marsden, 1999; Jude, 2001). Likewise, our analysis highlights the relative importance of their competition patterns with other specialists (planktivores, insectivores or invertivores) on the system trophodynamics, while the variability associated with their predation pressure indirectly affects the abundance and composition of the benthic community (i.e., miscellaneous benthos, gastropods/bivalves, and dreissenids). Generally, the abundance of offshore specialists (alewife, white perch, gizzard shad, white sucker) is higher in the Harbour than elsewhere, although their amount relative to the total fish biomass varies over time. In particular, alewife abundance has experienced a distinct decline in the area, which was mainly attributed to a causal link with cormorant predation (Somers et al., 2003) or the increase in natural reproduction of Chinook salmon (O'Gorman et al., 2004).

We also note that the importance of round goby may even be downplayed by our analysis due to the underestimation of their biomass in electrofishing data (Brousseau and Randall, 2008). Another possible source of uncertainty about the capacity of the Hamilton Harbour ecosystem model to depict their functional role in the system is the cormorant predation. Our diet matrix allots approximately 60% of the cormorant diet to round goby, which is in line with the empirical evidence provided by Somers et al. (2003). Further, Weseloh et al. (2002) documented the expansion of cormorant colonies over an 11-year period between 1989 and 2000, and noted that the Hamilton Harbour has one of the three largest populations in Lake Ontario. Thus, if we also consider their opportunistic feeding patterns in conjunction with the substantial goby density, it is reasonable to assume that the cormorants may drive the round goby year-to-year variability in the system (Stapanian, 2002).

Several studies have shown that fish biomass in the Harbour is dominated by generalists, such as common carp and brown bullhead (Bowlby et al., 2007; Brousseau and Randall, 2008; Minns et al., 1994). Carp abundance in the system has been subjected to wide fluctuations with a peak in the mid-1990s, when the operation of the carp barrier resulted in a substantial reduction in their population at the Cootes Paradise (Lougheed et al., 2004). Despite recent declines in the common carp biomass, this generalist species is still one of the top contributors of the total fish biomass in the Harbour. Further, brown bullhead is another key generalist characterized by increasing trends of its percentage contribution to the total fish biomass in the system (Bowlby et al., 2007). In our model conceptualization, brown bullhead has been grouped together with channel catfish ("toxic tolerant" fish) and the resulting omnivory index was somewhat lower (0.15) than the one derived for carp (0.25). Yet, Bowlby et al.'s (2007) asserted that channel catfish may be the Harbour's top predator and as such should be categorized as a piscivore rather than a generalist. If this hypothesis holds true, future updates of our model should divide this group and examine its impact on the characterization of the system.

Notwithstanding the promising trends of the northern pike biomass in the Hamilton Harbour, the numbers of other piscivores (walleye, largemouth and smallmouth bass) still remain low compared to the Bay of Quinte (Bowlby et al., 2007). In particular, while piscivores should contribute at least 20% of the total biomass in a balanced system (Minns et al., 1994), the average biomass of piscivores is less than 10% in the Harbour (Brousseau and Randall, 2008). Degraded water quality conditions and the lack of high quality habitat (fine substrates and dense macrophytes) still appear to be an impediment towards the establishment of a diverse fish community that can effectively support top predators and subsequently mitigate the impact of invasive species (Minns et al., 1999). In the Hamilton Harbour, simple macrophyte assemblages (i.e., grass-like with long narrow leaves) dominate over more complex forms (i.e., branching stems with various leaf forms), while the two dominant macrophytes species, *Vallisneria americana* and *Myriophyllum spicatum*, are able to tolerate low light conditions and higher levels of turbidity (Borman et al., 2001). Thus, the system still lacks an essential feature of habitat quality for both fish and their prey populations (LaPointe et al., 2007). Increases in macrophyte growth and diversity will create more spawning and nursery habitat for certain native species, which in turn may be another regulatory factor (along with the reduction of the exogenous nutrient loading) to influence the duration of the transient phase and the future resilience of the system. The bottom-up approach historically followed in the Harbour was sufficient to bring the system to its present state, but any further improvements should be viewed in the context of a combined bottom-up and top-down control (Gudimov et al., 2010, 2011; Ramin et al., 2011).

In conclusion, we developed an ecosystem model to illuminate the main attributes and trophic relationships underlying the Hamilton Harbour food web. Several ecosystem properties (e.g., primary production/biomass, biomass/total throughput, system omnivory index, amount of recycled throughput, Finn's cycling index) provide evidence that the Hamilton Harbour is an immature and fairly simple system with linear food chain structure. Yet, we caution that this ecosystem characterization may partly stem from some of the assumptions made during the conceptual design of the model (e.g., functional fish groups considered, original omission of bacterial respiratory activity). The extremely low transfer efficiency from the first to the upper trophic levels and the pyramid-like food web predicted may reflect the importance of nutritional/biochemical quality factors on the trophodynamics in the Harbour. The fairly low ecotrophic efficiency values for both carnivorous and herbivorous cladocerans are indicative of low zooplanktivory levels in the system. Among the trophic relationships considered by the Hamilton Harbour ecosystem model, our analysis highlights the relative importance of round goby that demonstrates a wide range of trophic interactions with a number of functional groups at different trophic levels.

Model-based approaches to fisheries management are intended either for heuristic purposes, illuminating trophic interrelationships and pinpointing unexpected ramification of management actions, or for predictive uses, aiming to offer a formal examination of policy-relevant responses of the fish community (e.g., stock biomass, maximum sustainable yield) (Essington, 2007). While the Hamilton Harbour ecosystem model could ultimately be used for the latter type of questions, the substantial uncertainty associated with several critical inputs (biomass estimates, diet compositions) poses constraints on its use and also invites a rigorous assessment of some of the assumptions made during its development. After all, we should bear in mind that the large number of input parameters entails multiple ways to balance our ecosystem model, and thus multiple (and often contradictory) inferences can be drawn from the same initial data (Arhonditsis and Brett, 2004). Acknowledging the knowledge gaps from the system as well as the uncertainties associated with any modeling endeavour, the present exercise should rather be viewed as the beginning of our efforts towards the development of a credible ecosystem model for the Hamilton Harbour.

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Appendix A. Supplementary data

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SUPPLEMENTARY INFORMATION 1

DESCRIPTION OF GROUP-SPECIFIC PARAMETERIZATION

This section provides the information used and the assumptions made for the derivation of the group-specific biomass (*B*), production to biomass (*P/B*), consumption to biomass (*Q/B*), and diet compositions of the biotic compartments included in the Hamilton Harbour Ecosystem Model.

Cormorants: We assumed that cormorants (*Phalacrocorax auritus*) are the main fish-eating birds at the Hamilton Harbour. Cormorants typically arrive in the system around late March and reach their maximum population in May. The birds usually leave the area in September. A cormorant biomass of 218.65 kg km^{-2} $year^{-1}$ was obtained by multiplying the average annual number of individuals present in the Harbour with the average individual weight (Somers *et al.*, 2007; Seefelt and Gillingham, 2008). A *P/B* value of 0.45 $year^{-1}$ was estimated by assuming an annual survival rate for adult cormorants of 80%, while incidental mortality was assumed to be very negligible (Grèmillet, 1997). We assumed that the daily consumption is 550 g wet weight per individual per day for half a year, which resulted in a *Q/B* level of 50.19 $year^{-1}$ (Seefelt and Gillingham, 2008). We originally assumed that cormorants mainly feed upon small pelagic fish (50%), round goby (20%), other forage (20%), desired forage fish (5%) and common carp (5%) (Somers *et al.*, 2003; Young *et al.*, 2010); this diet specification was modified to achieve a mass-balanced solution.

Fish community: The model contains eleven (11) fish groups. Both northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) were separated into two stanzas. We used a 150 mm length value to distinguish between northern pike young of the year (YOY) and adults, respectively. Likewise, individuals of largemouth bass with length smaller (or larger) than 45 mm were classified as YOY (or adults). All other fish species, except round goby (*Neogobius melanostomus*) and common carp (*Cyprinus carpio*), were pooled into functional groups based on the similarity of the habitat, diet and life history characteristics. Channel catfish (*Ictalurus punctatus*) and brown bullhead (*Ameiurus* *nebulosus*) were combined together into a group labelled as “toxic-tolerant” fish. Yellow perch (*Perca flavescens*) and white bass (*Morone chrysops*) were labelled as “desired-forage” fish. Bluegills (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), and rock bass (*Ambloplites rupestris*) represented the “centrarchids”. Alewife (*Alosa pseudoharengus*), white perch (*Morone Americana*), gizzard shed (*Dorosoma cepedianum*), and white sucker (*Catostomus commersonii*) formed a functional group called “other forage” fish. Emerald Shiner (*Notropis atherinoides*), spottail shiner (*Notropis hudsonius*), and golden shiner (*Notemigonus crysoleucas*) were lumped together and labeled as “small pelagic” fish.

Hamilton Harbour was divided into three depth-based habitat types to accommodate the different preferences from the fish functional groups considered: (*1*) littoral habitat (0-5 m), (*2*) middle offshore habitat (5-15 m), and (*3*) deepest offshore habitat (>15 m). Fish biomass estimation was based upon the results of various surveys conducted by the Department of Fisheries and Oceans (*DFO*) in the Harbour during the 2004-2008 period. Fish biomass for the nearshore zone was calculated from the electrofishing data reported by Brousseau and Randall (2008). The biomass estimates for the middle offshore habitat were calculated from the bottom trawl (concurrently to the acoustic) survey (Kathy Leisti, unpublished data), whereas the estimates for the deepest offshore habitat were solely based on acoustic survey data (Kathy Leisti, unpublished data).

Littoral habitat: Brousseau and Randall (2008) provided annual species-specific biomass estimates, based on an electrofishing survey conducted in the nearshore zone of the Hamilton Harbour. We used the average of their biomass data for three years (2006-2008) to depict the recent average fish standing biomass in the system. The calculation of the average biomass per unit area was also based on the assumption that an effective fishing field was developed to a depth of 5 m and about 4 m long in either side of the boat, and thus the transects examined were about 10 m wide and 100 m long (Randall and Minns, 2000).

Middle offshore (western and northern sector): Acoustic and bottom trawl surveys in the middle offshore area were conducted simultaneously by DFO in 2006 (Kathy Leisti, unpublished data). About fourteen (14) fish species were found in the trawl hauls, but alewife (40%), emerald shiner (23%), round goby (15%), white perch (11%), spottail shiner (5%) and brown bullhead (4%) constitute most of the total fish biomass caught. Our species-specific biomass values account for the catch per unit effort (CPUE), using existing estimates of the catch record of bottom trawl hauls, and were then standardized as number of fish caught per hectare of area swept by trawling. Assuming a catchability coefficient equal to one, the numbers of individuals were converted to species-specific biomass by multiplying with the average weight of a single individual. We also assumed that the proportion of each species (by number and weight) in the bottom trawl catch represents the composition of the fish assemblages sampled acoustically. We took the average of the trawl and acoustic fish biomass values to represent the species-specific biomass in the middle offshore zone of Harbour.

Deepest offshore (south-central sector): The acoustic survey conducted by DFO in 2006 was used to estimate the fish biomass in the deepest offshore section of the Hamilton Harbour (Kathy Leisti, unpublished data). We again assumed the proportion of each species (by number and weight) in the bottom trawl catch represents the composition of the fish assemblages sampled acoustically. For smaller fish species (< 300 mm), we used the species composition of the bottom trawl catch in the middle offshore zone to partition total acoustic biomass by species, whereas the composition of the electrofishing catch was used for large fish species (> 300 mm). In a similar manner, we used the composition of the bottom trawl catch to partition the total acoustic schooling fish biomass. We summed up all different biomass estimates (small, large, and schooling fish) by species to obtain aggregated species-specific (acoustic) biomass for the Hamilton Harbour. Finally, the species-specific biomass values for the three habitats were pooled together to obtain areal-weighted aggregated estimates (biomass per unit area).

For the majority of the fish functional groups, the *P/B* values were adapted from Randall and Minns (2000). For round goby, we originally used an average annual survival of 0.60 to derive an instantaneous mortality rate (or *P/B* value) of 0.51 year^{-1} (Velez-Espino *et al.*, 2010), which was subsequently increased to achieve $EE < 1$. While the final estimate (1.76) is quite high relative to our starting point, we note that it is very close to the value derived from the Bay of Quinte ecosystem model (1.33). Adults and YOY northern pike were assigned *P/B* values of 0.21 and 6.65 year^{-1} (Minns *et al.*, 1996), respectively. For largemouth bass adults, a *P/B* value of 0.32 year^{-1} was adapted from Randall and Minns (2000), while the corresponding value for their YOY counterparts was set equal to 5.69 year^{-1} (Hoffman and Bettoli, 2005). Using information from the Fishbase (Froese and Pauly, 2010), the curvature parameter *K* of the von Bertalanffy Growth Function was set equal to 0.22 and 0.25 for northern pike and largemouth bass, respectively, while the corresponding $W_{\text{maturity}}/W_{\text{infinity}}$ ratios were 0.152 and 0.21 (Randall and Minns, 2000).

Consumption rates (*Q/B*) for all fish species were estimated using the following empirical relationship (Palomares and Pauly, 1998):

$$\log (Q/B) = 7.964 - 0.204 \log W_{\infty} - 1.965\, T' + 0.083 A + 0.532 h + 0.398 d \qquad \textbf{(1)}$$

where W_{∞} is a parameter of the von Bertalanffy weight growth function; *T* is an expression for the mean annual temperature of the water body, expressed using $T' = 1000/\text{Kelvin}$ (Kelvin = ^{o}C + 273.15); *A* is the aspect ratio of the caudal fin which is closely related to the average level of activity and is calculated from $A = l^2/s$, where *l* is the height of the caudal fin and *s* is the surface area; *h* and *d* are dummy parameters, where $h = 1$ for herbivorous group and $d = 1$ for detritus feeder; otherwise *h* and *d* were set equal to zero. The values of the asymptotic weight (W_{∞}) for all the species were adapted from Randall and Minns (2000). The mean water temperature of Hamilton Harbour was set equal to 12.1 $^{\circ}$C. The aspect ratios for all the species were assumed to be equal to that of the default values provided in Fishbase (Froese and Pauly, 2010).

Till to date, stomach content analyses were carried out only for brown bullhead and pumpkinseed (Fitzgerald, 1996), and round goby (Schiller *et al.*, in submission) within the Hamilton Harbour. When no information was available, literature information, qualitative data, and expert knowledge was used to determine the diet compositions of the different functional groups (see references in the footnote of Table 1). The original diet matrix was then iteratively modified to achieve mass-balance.

Benthic invertebrate groups: Biomass values of the benthic invertebrate groups were estimated using data from the *DFO* survey (Dermott *et al.*, 2007). We used values for five different depth zones which were then summed up to obtain areal-weighted annual average biomass estimates (tonnes of shell-free wet weight km^{-2}) for the entire Harbour. *P/B* and *Q/B* values were assumed to be equal to those of the Bay of Quinte, which suggests an implicit assumption that the community structure and composition is similar between the two systems (Ron Dermott, pers. comm.). For benthic invertebrate groups, the diet compositions of oligochaetes, chironomids and miscellaneous benthos were adapted from Dermott (2001). Diets of gastropods and bivalves were based on Dermott (2001) and Watanabe (1984), while the diets of dreissenids were derived from Haynes (1997) and David *et al.* (2005).

Zooplankton groups: Gerlofsma *et al.* (2007) provided the distribution of zooplankton seasonal biomass and the production of different zooplankton groups in Hamilton Harbour during the growing season (May 1-October 31, 2002-2004). Despite the spatiotemporal variability characterizing the Hamilton Harbour zooplankton community, Gerlofsma et al. (2007) noted a structural shift to a more diverse community less dominated by rotifers, which in turn may reflect an improvement of the integrity of the food web structure, and increase in the energy flow to higher trophic levels. However, the present zooplankton community still indicates that Hamilton Harbour is eutrophic, being dominated by cladocerans and cyclopoids (*Diacyclops thomasi*, *Cyclops vernalis*) compared to calanoids (*Leptodiaptomus siciloides*). Cladocerans mainly include the *Bosmina longirostris,* species from the

Daphnia and *Ceriodaphnia* genera, and the carnivorous species *Leptodora kindtii* and *Cercopagis pengoi.* Areal-weighted annual average biomass and production rates were estimated by taking the biomass averages and production rates over all the sampling stations during the entire study period. The *Q/B* values of the zooplankton species were assumed to be equal to those of the Bay of Quinte, postulating a similar zooplankton community structure and composition between the two systems. The diet of carnivorous cladocerans comprises micro-zooplankton, herbivorous cladocerans, calanoid and cyclopoid copepods, phytoplankton, and carnivorous cladocerans. The diet assumed for calanoid and cyclopoid copepods was dominated by phytoplankton, epiphytes, micro-zooplankton, autotrophic picoplankton, calanoid and cyclopoid copepods. For herbivorous cladocerans, their diet composition is primarily dominated by phytoplankton and epiphytes.

Microbial loop: The microbial food web of the system consists of bacteria, autotrophic picoplankton, heterotrophic nanoflagellates, and ciliates (Azam *et al.*, 1983). Bacteria and autotrophic picoplankton were lumped together and labeled as “autotrophic picoplankton”. Heterotrophic nanoflagellates and ciliates represent the biotic compartment labeled as “micro-zooplankton”. Biomass values of the two groups were derived from surveys conducted in Hamilton Harbour from May to November, 2002-2004 (Munawar and Fitzpatrick, 2007). Biomass was calculated in the littoral and offshore zones. Areal-weighted average biomass values (mg m^{-3}) were then calculated based on a littoral to offshore area ratio of 0.33:0.67. For micro-zooplankton, the *P/B* and *Q/B* values were assumed equal to 50 and 250 $year^{-1}$, respectively (Taylor and Johannsson, 1991). A *P/B* value of 70 $year^{-1}$ was also assumed for autotrophic picoplankton. The diet composition assigned to micro-zooplankton was dominated by phytoplankton, epiphytes, and autotrophic picoplankton. Finally, we examined the robustness of the model parameterization to the omission of bacterial respiratory activity. In particular, the role of heterotrophic bacteria was reproduced by assigning *Q/B*=250 $year^{-1}$ to the autotrophic picoplankton group, while the rest model specification remained unaltered.

Macrophytes: Macrophyte biomass was estimated from the macrophyte cover of the system using an ArcMap GRID layer along with the following empirical relationship, originally developed for the Bay of Quinte (Kathy Leisti, unpublished data):

$$\arcsin\sqrt{\%\text{cover}} = 369.03x - 12.013 \qquad R^2=0.5159 \tag{2}$$

where %cover represents the percentage of submerged macrophyte cover per grid cell, and x is the submerged macrophyte biomass (g/m^2). The macrophyte biomass per unit area were then multiplied by the cell area (25 m^2) and then summed up over the entire grid, resulting in a final biomass estimate of 33.94 gm^{-2}. A *P/B* value of 6.80 was also adopted from the Bay of Quinte ecosystem model (Leisti *et al.*, 2006).

Epiphytes: Epiphyton biomass was estimated from data of the *DFO* macrophyte survey in 2006 (Kathy Leisti, unpublished data). An annual average biomass of 14.17 g wet weight m^{-2} was estimated using a macrophyte: epiphyte ratio of 0.41. We assumed that the epiphyton community structure in Hamilton Harbour appears to be similar to that of the Bay of Quinte, and thus a *P/B* of 59.80 year^{-1} was assigned (Leisti *et al.*, 2006).

Phytoplankton: Munawar and Fitzpatrick (2007) reported average phytoplankton biomass values of 20.92 t km^{-2} and 45.28 t km^{-2} for two sites in the Hamilton Harbour (see Fig. 2 in Dermott *et al.*, 2007). We assumed that their station 908 represents the littoral zone (includes the area of 0-5m depth zone plus half of the area corresponding to the 5-15 m zone), while their station 258 represents the offshore zone (and therefore includes half of the area of the 5-15 m zone plus the area corresponding to depths greater than >15 m). We then used the percentage contribution of the two zones (i.e., littoral to offshore area is approximately equal to 0.33: 0.67) to derive an annual average biomass of 37.39 g m^{-2}. A phytoplankton *P/B* value of 150 year^{-1} was also assigned, assuming that the primary production mainly occurs during the growing season.

Detritus: Detritus represents the dead organic material, dying phytoplankton cells, and faecal pellets. The fraction of the detritus that remains suspended in the water column "pelagic detritus" was separated from the fraction sinking out of the euphotic zone and ultimately settling down to the bottom sediments "sedimented detritus". Detritus biomass was estimated using the following empirical relationship that relates detritus biomass to primary productivity and the euphotic depth (Pauly *et al.*, 1993):

$$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E \qquad \textbf{(3)}$$

In equation (3), if we assume a seasonal areal photosynthesis rate of 245 g C/m^2 (or primary production rate of 159.25 g C m^{-2} $year^{-1}$) along with a euphotic depth of 6.75 m, we estimate a detritus biomass of 0.406 g C m^{-2} $year^{-1}$. Using Cushing *et al.*'s (1958) carbon to wet weight ratio of 42, we then derive an average autochthonous detritus biomass of 107.08 t ww km^{-2} $year^{-1}$. On the other hand, the exogenous particulate organic carbon was estimated to be 252 t ww km^{-2} $year^{-1}$ (Burley, 2007), and thus the total annual pelagic detritus biomass was set equal to 359.08 t ww km^{-2}. Finally, the annual average biomass of sedimented detritus was assumed 1.5 times greater than the pelagic detritus biomass.

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SUPPLEMENTARY INFORMATION 2

GLOSSARY OF TERMS USED FOR ECOPATH ANALYSIS

Ascendency: Ascendency is a measure of how well an ecosystem is processing material and energy. It is often used to quantify ecosystem growth and development (Ulanowicz, 1986).

Assimilation: Assimilation is the part of the food intake that is assimilated. Assimilation is a flow expressed, e.g., in $t \cdot km^{-2} \cdot year^{-1}$.

Biomass in habitat area: Biomass in habitat area is the average biomass per unit area in the habitat where the group resides.

Connectance index (*CI*): The connectance index (*CI*) for a given food web is the ratio of the number of actual links to the number of possible links.

Consumption (*Q*): Consumption is the intake of food by a group over the time period considered. Consumption = production + respiration + unassimilated food.

Detritus import: Detritus import is the entry or import of detritus into the system.

Development capacity: The upper bound on ecosystem growth and development (i.e., the upper limit of the size of the ascendency) is called the ‘development capacity’.

Ecotrophic efficiency (*EE*): The ecotrophic efficiency (*EE*) is the fraction of the production that is used in the system, i.e., either passed up the food web, used for biomass accumulation, migration or export.

Flow to detritus: Flow to detritus consists of what is egested (the non-assimilated food) and those elements of the group, which die of old age, diseases, etc., (i.e., sources of 'other mortality', expressed by 1 - *EE*). The flow to detritus, expressed, e.g., in $t \cdot km^{-2} \cdot year^{-1}$, should be positive for all groups.

Mixed trophic impact (*MTI*): The Mixed trophic impact for living groups is calculated by constructing an *n* x *n* matrix, where the i, j^{th} element representing the interaction between the impacting group *i* and the impacted group *j* is $MTI_{i,j} = DC_{i,j} - FC_{j,i}$, where $DC_{i,j}$ is the diet composition term expressing how much *j* contributes to the diet of *i*, and $FC_{j,i}$ is a host composition term giving the proportion of the predation on *j* that is due to *i* as a predator.

Net efficiency (*NE*): The net food conversion efficiency is calculated as the production divided by the assimilated part of the food, i.e., *Net efficiency = P/B / (Q/B · (1 - GS))* where *P/B* is the production / biomass ratio, *Q/B* is the consumption / biomass ratio, and *GS* is the proportion of the food that is not assimilated.

Net system production: Net system production is the difference between total primary production and total respiration. As can be inferred from the discussion of ecosystem maturity, system production will be large in immature systems and close to zero in mature ones. Systems with large imports may have a negative system production. Systems production is expressed at $t \cdot km^{-2} \cdot year^{-1}$.

Omnivory index (*OI*): The 'omnivory index' is calculated as the variance of the trophic level of a consumer's prey groups. When the value of the omnivory index is zero, the consumer in question is specialized, i.e., it feeds on a single trophic level. A large value indicates that the consumer feeds on many trophic levels. The omnivory index is dimensionless.

Path length: The path length is defined as the average number of groups that an inflow or outflow passes through. It is calculated as: Path length = Total System Throughput / (Σ Export + Σ Respiration). As diversity of flows and recycling is expected to increase with maturity, so is the path length.

Production/Biomass (*P/B*): The Production/Biomass (*P/B*) ratio is equivalent to the instantaneous rate of total mortality (*Z*) used by fisheries biologists.

Production/Consumption (*P/Q*): Production/consumption is the ratio between production (*P*) and consumption (*Q*) of a system and is a dimensionless parameter.

Production/Respiration (*P/R*): The (dimensionless) ratio of production/respiration expresses the fate of the assimilated food. Computationally, this ratio can take any positive value, though thermodynamic constraints limit the realized range of this ratio to values lower than 1.

Production: Production refers to the elaboration of tissue (whether it survives or not) by a group over the period considered. Total mortality, under the condition assumed for the construction of mass-balance models, equal to production over biomass. Therefore, estimates of total mortality (*Z*) can be used as input values for the production over biomass ratio (*P/B*). Production includes fishery yield plus predation, net migration, biomass change and other mortality.

Respiration/Assimilation (*R/A*): This is a (dimensionless) ratio of respiration to assimilation that cannot exceed 1.

Respiration/Biomass (*R/B*): The *R/B* ratio can be seen as an expression of the activity of the group. The higher the activity-level is for a given group, the higher the ratio. The *R/B* ratio is strongly impacted by the assumed fraction of the food that is not assimilated. The ratio of respiration/biomass can take any positive value, and has the unit dimension time^{-1}.

Respiration: In Ecopath, respiration is calculated as the difference between the assimilated part of the consumption and that part of production that is not attributable to primary production.

The respiration of any living group (*i*) can be expressed as,

$$Resp_i = (1 - GS_i) \cdot Q_i - (1 - TM_i) \cdot P_i$$

where $Resp_i$ is the respiration of group i, GS_i is the fraction of *i*'s consumption that is not assimilated, Q_i is the consumption of *i*, and TM_i is the proportion of the production that can be attributed to primary production. Respiration is used, in Ecopath, only for balancing the flows between groups. Respiration is a non-negative flow expressed, e.g., in $\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$.

System biomass/throughput: The total system biomass that is supported by the available energy flow in a system can be expected to increase to a maximum for the most mature stages of a system. For the estimation of this ratio, total system throughput is used as a measure consistent with other Ecopath outputs. The system biomass/throughput ratio can take any positive value, and has time^{-1} as dimension.

System omnivory index: The system omnivory index is defined as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake. The system omnivory index is a measure of how the feeding interactions are distributed between trophic levels.

System overhead: The difference between the development capacity and the ascendency is called system overhead. It is used to quantify ecosystem flow inefficiencies and redundancies. The overhead provides a limit on how much the ascendency can increase and reflects the system's "strength in reserve" from which it can draw to overcome unexpected perturbations.

System primary production/Biomass: The ratio between a system's primary production (P_p) and its total biomass (B) is expected to be a function of its maturity. In immature systems, production exceeds respiration for most groups, and as a consequence, one can expect the biomass to accumulate over time. Its dimension is time^{-1} and it can take any positive value.

System primary production/Respiration: This is the ratio between total primary production (P_p) and total respiration (R) in a system. It is considered to be an important ratio for description of the maturity of an ecosystem. The P_p/R ratio can take any positive value and is dimensionless.

System respiration/Biomass: In an ecosystem, the ratio of total respiration (R) to total biomass (B) can be seen as a thermodynamic order function. The ratio has the unit dimension time^{-1}, and can take any positive value.

Total primary production: Total net primary production is calculated as the summed primary production from all producers. Primary production is a flow expressed, e.g., in t · km^{-2} · year^{-1}.

Total system biomass: Total system biomass is simply the sum of the group biomasses available in the system. They have the unit of t · km^{-2}.

Total system throughput: The total system throughput is the sum of all flows in a system, expressed, e.g., in t · km^{-2} · year^{-1}. Total system throughput represents the size of the entire system in terms of flow. It is estimated as the sum of four components of the flows, i.e., Total system throughput = Total consumption + Total export + Total respiration + Total flows to detritus.

Trophic level (*TL*): In Ecopath, the trophic levels are not necessarily integers (1, 2, 3...), but can be fractional (e.g., 1.3, 2.7, etc.). The trophic level is a dimensionless index. A routine assigns definitional trophic levels (TL) of 1 to producers and detritus and a trophic level of 1 + [the weighted average of the preys' trophic level] to consumers.

Cited results from the Christensen and Pauly (1993) study:

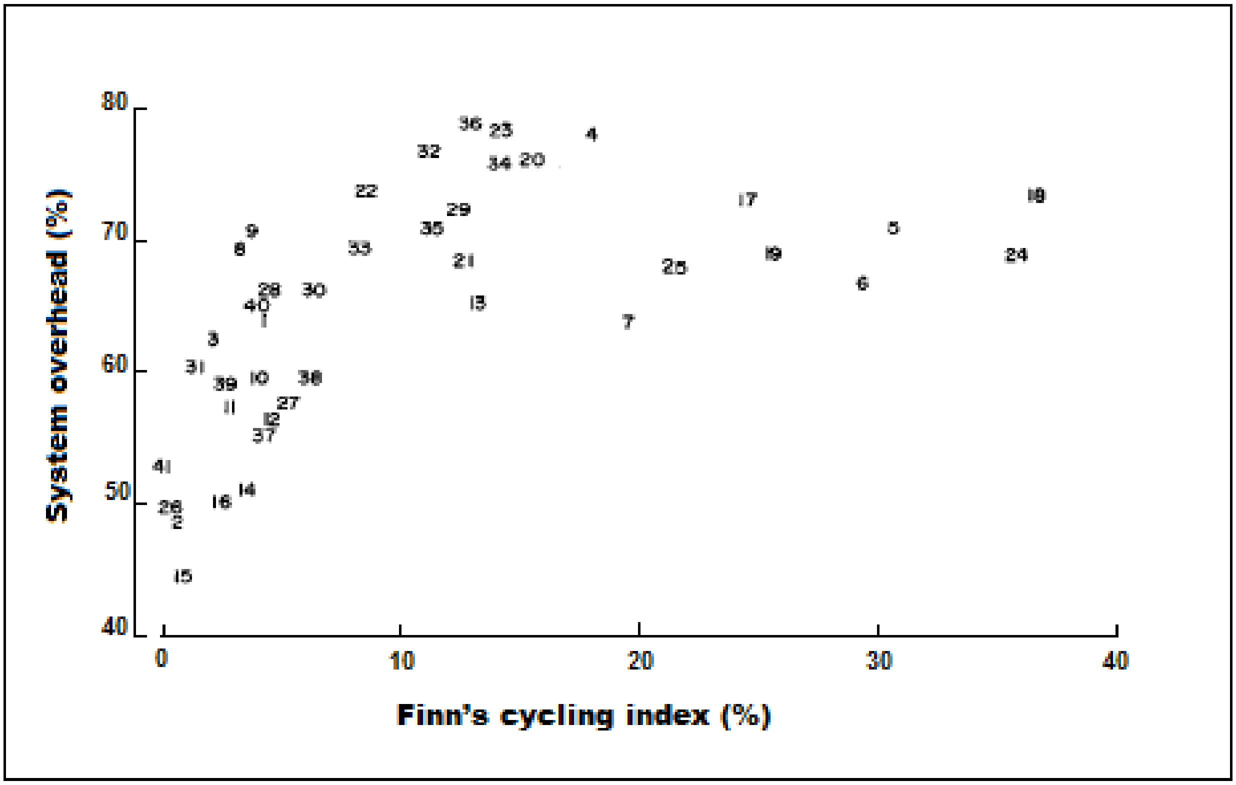

Figure 1: Relationship between system overhead and Finn's cycling index: The parabolic pattern suggests that only intermediate levels of recycling are optimal from a stability point of view, whereas systems with low recycling rates may be less stable because of their dependence on rapid energy flow through the various ecosystem compartments which increases their vulnerability to external nutrient pulses or systems experiencing high recycling levels may be more sensitive to external perturbations due to their strong reliance upon a pattern of tightly intertwined energy flows (modified from Christensen and Pauly, 1993) . [Numbers correspond to the 41 ecosystems analyzed by the Christensen and Pauly (1993) study (see also their Table 1).]

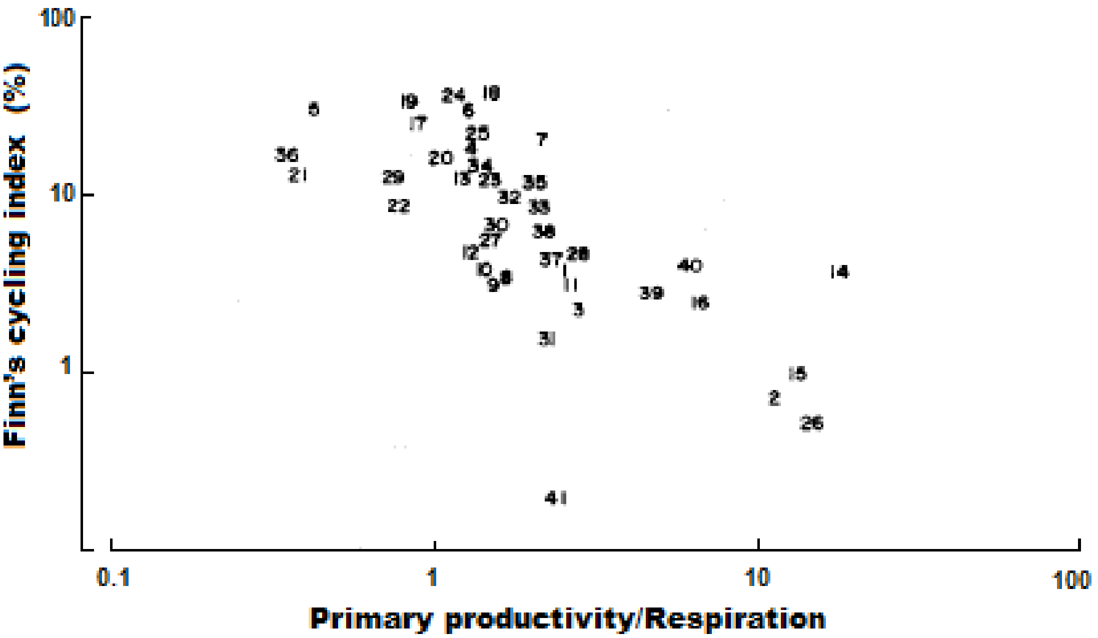

Figure 2: Relationship between Finn's cycling index and the primary productivity/respiration ratio, suggesting that systems with very high primary productivity/respiration values demonstrate a low degree of recycling (modified from Christensen and Pauly, 1993).

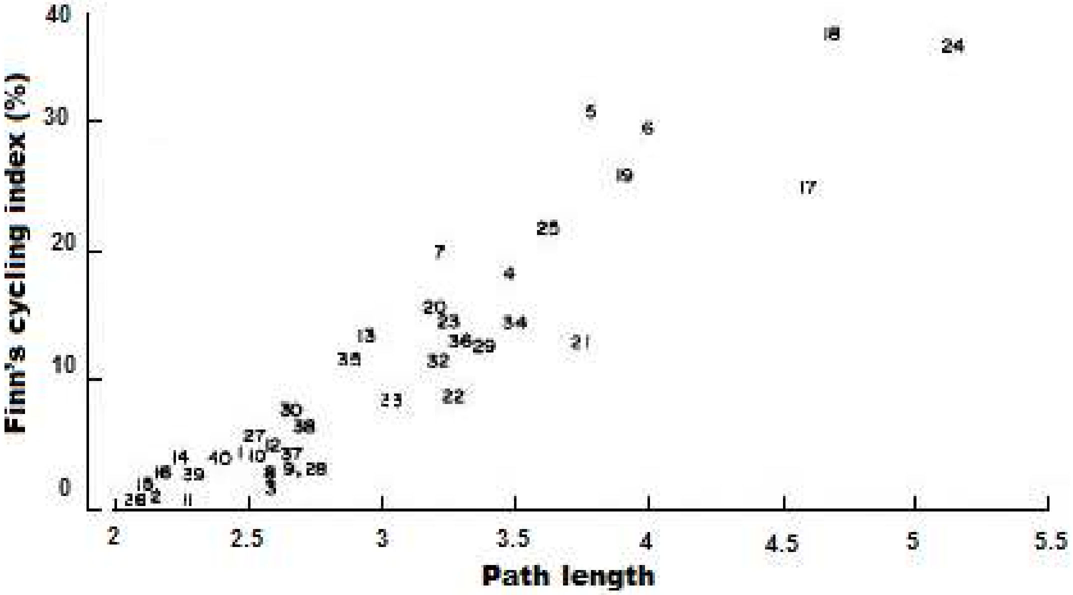

Figure 3: Relationship between Finn's cycling index and the average path length, suggesting a strong correlation between the two ecosystem descriptors (modified from Christensen and Pauly, 1993). The path length is defined as the average number of groups that a flow passes through and is calculated as the total throughput divided by the sum of the exports and respiration.

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