

Invasive species impacts on ecosystem structure and function: A comparison of the Bay of Quinte, Canada, and Oneida Lake, USA, before and after zebra mussel invasion

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ABSTRACT

As invasion rates of exotic species increase, an ecosystem level understanding of their impacts is imperative for predicting future spread and consequences. We have previously shown that network analyses are powerful tools for understanding the effects of exotic species perturbation on ecosystems. We now use the network analysis approach to compare how the same perturbation affects another ecosystem of similar trophic status. We compared food web characteristics of the Bay of Quinte, Lake Ontario (Canada), to previous research on Oneida Lake, New York (USA) before and after zebra mussel (*Dreissena polymorpha*) invasion. We used ecological network analysis (ENA) to rigorously quantify ecosystem function through an analysis of direct and indirect food web transfers. We used a social network analysis method, cohesion analysis (CA), to assess ecosystem structure by organizing food web members into subgroups of strongly interacting predators and prey. Together, ENA and CA allowed us to understand how food web structure and function respond simultaneously to perturbation. In general, zebra mussel effects on the Bay of Quinte, when compared to Oneida Lake, were similar in direction, but greater in magnitude. Both systems underwent functional changes involving focused flow through a small number of taxa and increased use of benthic sources of production; additionally, both systems structurally changed with subgroup membership changing considerably (33% in Oneida Lake) or being disrupted entirely (in the Bay of Quinte). However, the response of total ecosystem activity (as measured by carbon flow) differed between both systems, with increasing activity in the Bay of Quinte, and decreasing activity in Oneida Lake. Thus, these analyses revealed parallel effects of zebra mussel invasion in ecosystems of similar trophic status, yet they also suggested that important differences may exist. As exotic species continue to disrupt the structure and function of our native ecosystems, food web network analyses will be useful for understanding their far-reaching effects.

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1. Introduction

Exotic species invasion is a prominent driver of worldwide ecological change (Mills et al., 1994). Exotic species alter ecosystems by disrupting food web dynamics (Madenjian et al., 2002; Mills et al., 2003; Miehls et al., 2009), biogeochemical cycles (Holeck et al., 2004), modifying habitats (Hall and Mills, 2000), and decreasing native biodiversity (Holeck et al., 2004). Invasions in aquatic

systems are particularly harmful, causing negative effects on economically valuable fisheries and damaging nautical structures (Mills et al., 1994; Facon et al., 2005). Invasions by dreissenid mussels, including zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels, are pervasive in North America, multiple European nations, and Russia (Drake and Bossenbroek, 2004). Dreissenid mussels pose a considerable threat to aquatic environments, causing dramatic direct and indirect effects on food webs (Noonburg et al., 2003).

Although dreissenid invasion can lead to pronounced changes in aquatic ecosystems, the severity and scope of impacts varies between ecosystems. In the Great Lakes (Vanderploeg et al., 2002) and some inland waters of North America (MacIsaac, 1996; Idrisi et al., 2001), dreissenid invasion has increased water clarity and light

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penetration, which diverts energy from pelagic to benthic pathways (MacIsaac, 1996; Mayer et al., 2002; Mills et al., 2003). However, in shallow and/or turbulent ecosystems, such as the Hudson River, Saginaw Bay (Lake Huron), and western Lake Erie, resuspension of dreissenid pseudofeces via water column mixing results in lessened effects on water clarity (Vanderploeg et al., 2002). Dreissenid invasion decreases phytoplankton abundance and/or biomass in many ecosystems, including Saginaw Bay (Nalepa et al., 1999), Green Bay (Lake Michigan) (Padilla et al., 1996), western Lake Erie (Leach, 1993), Oneida Lake (New York) (Idrisi et al., 2001), and the Hudson River (Strayer et al., 1999); however, changes in phytoplankton resources do not uniformly affect zooplankton communities in all ecosystems. Zooplankton production and/or density has decreased in Lake Erie, particularly the unstratified regions (Johannsson et al., 2000), and the Hudson River (Strayer et al., 1999). However, in Oneida Lake, zebra mussel effects on zooplankton are marginal (Idrisi et al., 2001). Likewise, modeling studies on Green Bay (Padilla et al., 1996) and mesocosm experiments on the St. Lawrence River (Thorp and Casper, 2003) find similarly small effects on zooplankton.

Dreissenid effects on higher trophic levels, including benthic invertebrates and fish, also vary among systems. Non-mollusca benthic invertebrates declined in the Hudson River subsequent to dreissenid invasion (Strayer et al., 1999), while in Lake Erie (Johannsson et al., 2000) and Saginaw Bay (Nalepa et al., 2003), benthic and macroinvertebrate biomass did not decrease. Yet, zebra mussel effects on unionid clams are consistently negative in the Great Lakes (Vanderploeg et al., 2002), inland lakes (MacIsaac, 1996), and rivers (Strayer et al., 1999). Dreissenid influence on fish varies by ecosystem. Dreissenid introduction might indirectly benefit benthic and littoral fish in Oneida Lake (Rutherford et al., 1999; Jackson et al., 2002; Miehls et al., 2009) and the Hudson River (Strayer et al., 2004); however in Lake Michigan, dreissenids may negatively affect fish through modification of spawning habitat (Marsden and Chotkowski, 2001). Furthermore, young fish, which may directly compete with dreissenids for zooplankton food resources, might be negatively impacted by dreissenid invasion in Lake Michigan (Dettmers et al., 2003), but are less affected in Oneida Lake (Mayer et al., 2000).

These studies indicate the variable nature of dreissenid effects. This variability, in turn, makes it difficult to discern commonalities of dreissenid invasion. To identify commonalities in invaded ecosystems as well as system specific differences, comparative analyses of invaded ecosystems are useful. For example, comparative analyses can be used to examine the effects of dreissenid invasion with ecosystem morphology and size, predator diets (Strayer et al., 2004), and along a trophic gradient (Padilla et al., 1996). Identifying the similarities in invaded ecosystems aids in not only predicting which ecosystems are susceptible to future invasions, but also how those ecosystems might be affected (Drake and Bossenbroek, 2004).

To compare across ecosystems, metrics of ecosystem structure (i.e., components of an ecosystem) and function (i.e., dynamic processes within ecosystems) can be used. Ecosystem structure and function are synthetic concepts, incorporating many aspects of ecosystems. Structural characteristics include measurements of system state, such as biomass and taxonomic composition, and system compartmentalization (i.e., “subgroups” of strongly interacting taxa, e.g., Simon, 1962; Pimm, 1979; Pimm and Lawton, 1980; Krause et al., 2003). Functional characteristics involve rates of change in a system, including measurements of productivity and respiration (Stevenson et al., 1996). Ecosystem structure and function can also explicitly include hierarchical interactions (Simon, 1962) within the ecosystem. For example, structure and function incorporate the interrelationships between populations and communities (i.e., how change at the population

level affects the community, which in turn regulates the population; Gaedke, 1995) as well as the interrelationship between communities within food webs (i.e., how subgroups of tightly linked predators and prey interact within an ecosystem, e.g., benthic and pelagic subgroups in aquatic ecosystems; Krause et al., 2003). Different levels of the ecosystem hierarchy may function at different magnitudes or over different time frames, thus it is advantageous to consider ecosystem structure and function from this hierarchical point of view, especially when dealing with ecosystem response to perturbation (Jørgensen, 2007).

One tool that is useful for analyzing ecosystem structure and function comparatively between systems is network analysis (Gaedke, 1995). Network analysis examines ecosystem processes at multiple scales – including at the level of species–pair interaction, trophic level, subgroup level, and whole system (Heymans et al., 2002; Krause et al., 2003) – via food web analysis. Network analysis depicts food webs as networks of exchange through quantification of feeding interactions and energy flow (Bondavalli et al., 2000). Network analysis has been used to compare ecosystem properties before and after exotic species invasion (Miehls et al., 2009), ecosystem dynamics between seasons (Baird and Ulanowicz, 1989; Bondavalli et al., 2000), differences in marine upwelling and estuarine systems (Baird et al., 1991; Baird and Ulanowicz, 1993), and aquatic ecosystems with and without terrestrial linkages (Heymans et al., 2002).

Network analysis is therefore well suited to address the problem of ecosystem perturbation by dreissenid invasion. Using network analysis, dreissenid invasion can be examined at multiple hierarchical levels both within one food web and between multiple food webs to obtain a system-wide understanding of the effects of their invasion. We use network analysis to compare the effects of zebra mussel invasion within and between two invaded ecosystems. The primary objective of our study is to quantify zebra mussel effects on ecosystem structure and function and to compare these characteristics between ecosystems of similar trophic status, specifically by addressing the following questions:

1. *Structure*: Does zebra mussel invasion alter the membership of food webs and food web subgroups (defined as clusters of strongly interacting predators and prey) in the Bay of Quinte, Lake Ontario, Canada, ecosystem?
2. *Function*: Does the magnitude of carbon flow within food webs and food web subgroups change as a result of zebra mussel invasion in the Bay of Quinte ecosystem?
3. *Comparison*: Do systems of comparable trophic status respond similarly, with respect to direction and magnitude of change, to zebra mussel invasion?

We hypothesized that the Bay of Quinte would respond similarly to Oneida Lake, New York, USA, a system of comparable ecology and trophic status, subsequent to zebra mussel invasion. Previous network analysis examination of the Oneida Lake ecosystem (Miehls et al., 2009) indicates that zebra mussel invasion has pronounced effects throughout entire food webs. Ecosystem activity declines, dissipative flow loss increases, membership of food web subgroups shifts, and energy is shunted from pelagic to benthic pathways (i.e., “benthification”; Mills et al., 2003). Moreover, our Oneida Lake research suggests interactions within fish communities reorganize as food webs adjust to zebra mussel invasion. Given the trophic similarity between Oneida Lake and the Bay of Quinte, we expected to see similar structural and functional changes in the Bay of Quinte.

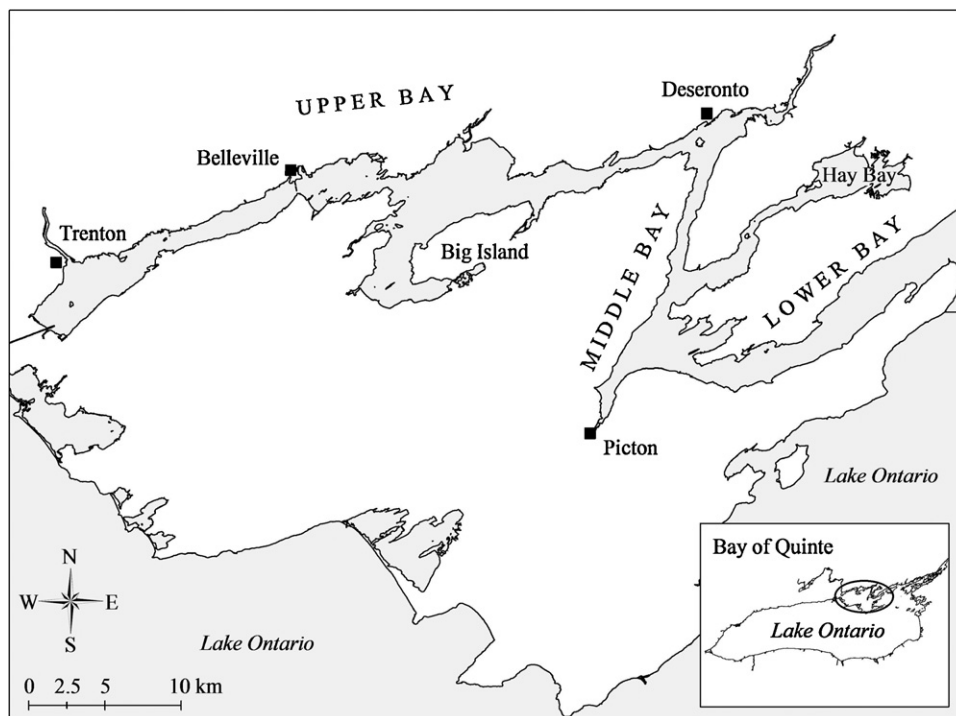


Fig. 1. Map of the Bay of Quinte (Source: Carolyn Bakelaar, Department of Fisheries and Oceans, Canada).

2. Methods

2.1. Study site

The Bay of Quinte is a narrow, Z-shaped inlet on the north-eastern portion of Lake Ontario (Fig. 1). The Bay of Quinte has three distinct morphological regions, known as the upper bay, middle bay, and lower bay, totaling approximately 80 km in length (Diamond et al., 1994) and 257 km² surface area (Minns, 1995). The Bay of Quinte has a strong depth and trophic gradient, ranging from a shallow (mean depth of 3.5 m), eutrophic environment in the upper bay to a deeper (mean depth of 24.4 m), oligotrophic environment in the lower bay (Ridgway et al., 1990; Nicholls et al., 2002), which connects the Bay of Quinte to Lake Ontario. The upper bay is most similar in trophic status and physical characteristics to Oneida Lake (described in Miehls et al., 2009); therefore we use only this region in our analysis. The upper bay has a surface area of 134 km² and stratifies briefly during the summer months (Strus and Hurley, 1992). Zebra mussels colonized the bay in 1993–1994, but were not established until 1995 (Nicholls et al., 2002). Because of the long-term history of limnological research on the Bay of Quinte (e.g., Hurley and Christie, 1977) and Oneida Lake (e.g., Mills et al., 1978), ample data exist throughout the invasion history of zebra mussels to study their effects within and between these systems.

2.2. Network construction

We constructed weighted food web networks for the Bay of Quinte before and after zebra mussel invasion and analyzed the networks using ecological network analysis (ENA) (Ulanowicz, 1986) and a social network analysis method, cohesion analysis (CA) (Frank, 1995; Krause et al., 2003; Miehls et al., 2009). We defined the years 1978–1994 as the pre-zebra mussel invasion time stanza and the years 1995–2002 as the post-invasion time stanza. We created these networks using the same methodology as for Oneida Lake (Miehls et al., 2009) and therefore, do not present details

on network construction here. To make the Bay of Quinte analysis comparable to Oneida Lake, we did not include the microbial food web. The complete list of eighty food web species and aggregate groups are presented in Table 1. Data used to create network flows (i.e., the exchange matrix) were collected from the primary literature, field studies, and expert researchers on the Bay of Quinte. These parameters along with their sources are listed in Appendix 1. Finally, we mass-balanced our networks such that inputs equaled outputs for all taxa (Heymans and Baird, 2000); balanced networks are presented in Appendix 2.

2.3. Ecological network analysis

After we completed network construction, we analyzed Bay of Quinte ecosystem structure (via CA) and function (via ENA) before and after zebra mussel invasion (see Table 2 for a summary of these routines and their relationship to ecosystem properties). We used the EcoNetwrk (<http://www.glerl.noaa.gov/EcoNetwrk/>) software to conduct three ENA routines: (1) input/output analysis, (2) trophic level analysis, and (3) the calculation of ecosystem indices. We provide a brief description of ENA methods below; for greater detail see Ulanowicz (1986,1997).

Input/output analysis (Hannon, 1973; Patten et al., 1976; Szyrmer and Ulanowicz, 1987) quantifies the amount of carbon (or other elements, e.g., nitrogen or phosphorus, or energy, e.g., calories, depending on the goal of the analysis) supplied to any one taxon by another taxon in the food web. The analysis includes a routine called IMPACTS that quantifies the relative effect of one taxon on another over all food web paths, including direct and indirect routes (Ulanowicz and Puccia, 1990; Heymans and Baird, 2000). Indirect paths are especially important as the net indirect effect may overwhelm direct interactions in food webs (Patten, 1984). Thus, the IMPACTS analysis is a rigorous method to trace the far-reaching effects of zebra mussel perturbation. Importantly, the IMPACTS analysis is conducted using only one network, the post-zebra mussel invasion network; a comparison of networks is not used in the IMPACTS analysis. As such, the IMPACTS analysis pro-

Table 1
List of food web taxa.^a

No.	Common name	Taxonomic classification	No.	Common name	Taxonomic classification
1	Cormorants	<i>Phalacrocorax auritus</i>	41	Isopods	Isopoda order
2	Walleye Age 4+	<i>Sander vitreus</i>	42	Leeches	Hirudinea class
3	Walleye Age 1–3	<i>Sander vitreus</i>	43	Oligochaetes	Oligochaeta class
4	Walleye Age-0	<i>Sander vitreus</i>	44	Snails	Gastropoda class
5	Yellow Perch Age 1+	<i>Perca flavescens</i>	45	Zebra Mussels	<i>Dreissena polymorpha</i>
6	Yellow Perch Age-0	<i>Perca flavescens</i>	46	<i>Alona</i> spp.	<i>Alona</i> spp.
7	White Perch Age 1+	<i>Morone americana</i>	47	<i>Bosmina longirostris</i>	<i>Bosmina longirostris</i>
8	White Perch Age-0	<i>Morone americana</i>	48	<i>Ceriodaphnia</i> spp.	<i>Ceriodaphnia</i> spp.
9	Black Crappie 1+	<i>Pomoxis nigromaculatus</i>	49	Chydoridae family	Chydoridae family
10	Bluegill Age 1+	<i>Lepomis macrochirus</i>	50	<i>Daphnia mendotae</i>	<i>Daphnia mendotae</i>
11	<i>Lepomis</i> spp. Age 1+	<i>Lepomis</i> genus	51	<i>Daphnia pulicaria</i>	<i>Daphnia pulicaria</i>
12	Pumpkinseed Age 1+	<i>Lepomis gibbosus</i>	52	<i>Daphnia retrocurva</i>	<i>Daphnia retrocurva</i>
13	Rock Bass Age 1+	<i>Ambloplites rupestris</i>	53	<i>Eubosmina coregoni</i>	<i>Eubosmina coregoni</i>
14	Centrarchids Age 1+	Centrarchidae family	54	Sididae family	Sididae family
15	Centrarchids Age-0	Centrarchidae family	55	Large-bodied Cladocerans	Large-bodied Cladocerans
16	Alewife	<i>Alosa pseudoharengus</i>	56	<i>Cercopagis pengoi</i>	<i>Cercopagis pengoi</i>
17	American Eel	<i>Anguilla rostrata</i>	57	<i>Leptodora kindtii</i>	<i>Leptodora kindtii</i>
18	Brook Silverside	<i>Labidesthes sicculus</i>	58	<i>Acanthocyclops vernalis</i>	<i>Acanthocyclops vernalis</i>
19	Brown Bullhead	<i>Ameiurus nebulosus</i>	59	<i>Diacyclops thomasi</i>	<i>Diacyclops thomasi</i>
20	Channel Catfish	<i>Ictalurus punctatus</i>	60	<i>Eucyclops</i> spp.	<i>Eucyclops</i> spp.
21	Common Carp	<i>Cyprinus carpio carpio</i>	61	<i>Mesocyclops</i> spp.	<i>Mesocyclops</i> spp.
22	Emerald Shiner	<i>Notropis atherinoides</i>	62	<i>Tropocyclops extensus</i>	<i>Tropocyclops extensus</i>
23	Freshwater Drum	<i>Aplodinotus grunniens</i>	63	Cyclopoida copepodites	Cyclopoida copepodites
24	Gizzard Shad	<i>Dorosoma cepedianum</i>	64	Diaptomidae family	Diaptomidae family
25	Johnny Darter	<i>Etheostoma nigrum</i>	65	Temoridae family	Temoridae family
26	Largemouth Bass	<i>Micropterus salmoides</i>	66	Calanoida copepodites	Calanoida copepodites
27	Log Perch	<i>Percina caprodes</i>	67	Harpacticoida	Harpacticoida
28	Longnose Gar	<i>Lepisosteus osseus</i>	68	Nauplii	Nauplii
29	Northern Pike	<i>Esox lucius</i>	69	Rotifers	Rotifers
30	Round Goby	<i>Neogobius melanostomus</i>	70	Blue-green Algae	Cyanophyceae
31	Smallmouth Bass	<i>Micropterus dolomieu</i>	71	Diatoms	Bacillariophyceae
32	Spottail Shiner	<i>Notropis hudsonius</i>	72	Flagellates	Cryptophyceae & Dinophyceae
33	Trout-perch	<i>Percopsis omiscomaycus</i>	73	Golden Algae	Chrysophyceae
34	White Bass	<i>Morone chrysops</i>	74	Green Algae	Chlorophyceae
35	White Sucker	<i>Catostomus commersonii</i>	75	Epiphytes	Epiphytes
36	Amphipods	Amphipoda order	76	Macrophytes	Macrophytes
37	Chironomids	Chironomidae family	77	Periphytes	Periphytes
38	Clams	Sphaeriidae family	78	Pelagic Detritus	Pelagic Detritus
39	Crayfish	<i>Orconectes</i> spp.	79	Sedimented Detritus	Sedimented Detritus
40	Insects	Arthropoda phylum	80	DOC	DOC

^a Brook silverside, emerald shiners, largemouth bass, round gobies, zebra mussels, and *Cercopagis pengoi*, were present in the post-zebra mussel time stanza, but not the pre-zebra mussel time stanza.

vides a snapshot of trophic effects (e.g., trophic cascades) involving zebra mussels.

Trophic analysis reinterprets the web of predator-prey transfers in terms of the Lindeman trophic chain concept (Lindeman, 1942; Ulanowicz, 1995). Trophic analysis apportions the feeding activities of taxa among a series of hypothetical integer trophic levels to create the Lindeman spine which is used to evaluate the efficiency of carbon flow in the system (Heymans and Baird, 2000).

Ecosystem indices quantify system level properties such as growth and development, and assess the vulnerability and resilience of an ecosystem to perturbation (Ulanowicz, 1997). These indices are: total system throughput (TST), average mutual information (AMI), ascendancy (A), overhead (O), and development capacity (C).

TST quantifies ecosystem size as the sum of all carbon (or other elemental or energetic currency) flows in the system and has units of production ($\text{g C m}^{-2} \text{ year}^{-1}$). AMI is an information theoretic index (Shannon, 1948; McEliece, 1977) that quantifies the organization of a network based on pathway flow constraints. Using conditional probabilities, AMI quantifies the average amount of information known about the pathways a unit of material (e.g., carbon) can follow upon entering a system. The more constrained the system is (i.e., the fewer the flow paths), the more information there is on pathways and the higher the AMI. Likewise, the AMI is higher when the amount of material (e.g., carbon) transferred is concentrated on a few pathways, while other path-

ways carry comparatively little. Ascendancy quantifies the growth, development, and efficiency of ecosystem function (Ulanowicz, 1986) and is calculated by scaling AMI with TST: $A = \text{TST} \times \text{AMI}$. To give an example of how AMI and ascendancy interact, a food web network with a few highly concentrated flows between taxa has more constraints on flow and thus has a higher AMI value than a network with a large number of similarly weighted flows between taxa. Ascendancy then takes into account the total amount of carbon flowing (i.e., throughput) over each of those paths: a food web network with few flows between taxa but large amounts of carbon (i.e., throughput) traveling over those flows has a higher ascendancy value than a food web network with many flows between taxa, each of which carry a small amount of carbon.

Overhead quantifies the system's functional inefficiencies (Heymans et al., 2002) as well as the resiliency of a system to perturbation (Heymans and Baird, 2000). There are four primary contributors to overhead: imports (i.e., immigrations) and exports (i.e., emigrations and fisheries harvest), respirative flow loss, and redundant food web flows (i.e., multiple flow paths connecting taxa). Overhead is calculated by scaling the system's conditional entropy (Ulanowicz, 1986), a measure of network disorganization, by TST: $O = \text{TST} \times \text{Conditional Entropy}$. Conditional entropy quantifies the uncertainty remaining after the flow structure is determined and is complimentary to AMI (Ulanowicz, 1986). Development capacity is the upper bound on ecosystem growth and

Table 2
Summary of network analysis routines and their relationships to ecosystem properties.

Network analysis routine	Ecosystem property
Ecological network analyses:	Ecosystem function
Input/output analysis	Direct and indirect effects
Trophic level analysis	Trophic flow efficiency
Ecosystem indices:	Quantification of whole system function
Total system throughput (TST)	Ecosystem size and growth
Average mutual information (AMI)	Ecosystem flow organization
Ascendency (A)	Ecosystem growth and development
Overhead (O)	Ecosystem inefficiencies and flow redundancy
Development capacity (C)	Upper bound on ecosystem growth and development
Social network analysis:	Ecosystem structure
Cohesion analysis	Subgroup structure

Table 3
Association between common subgroup membership and the occurrence of ties between predators and prey (adapted from Frank, 1995). The odds ratio method maximizes the ratio AD:BC.

	Tie occurring		
	No	Yes	
Subgroup			
Different	A	B	Possible relations between predators and prey in different subgroups
Membership			
Same	C	D	Possible relations between predators and prey in the same subgroup
	Unrealized interactions	Realized interactions	Total possible relations

development, and is calculated through the addition of ascendency and overhead: $C = A + O$.

2.4. Cohesion analysis

Cohesion analysis identifies subgroups in food webs based on strengths of feeding relationships (Krause et al., 2003), where the maximization of an odds ratio is used as a criterion to assign subgroup membership.¹ CA uses an algorithm to iteratively reassign taxa to subgroups to maximize the odds that strong predatory interactions occur within subgroups, versus between subgroups (Frank, 1996). The intent of CA is to determine the network structure that maximizes the number of (strong) predator–prey interactions (realized interactions) within subgroups while minimizing predator–prey interactions between subgroups and taxa without connecting flows (unrealized interactions) within subgroups (Table 3). Using the software Kliqfinder (Frank, 1995), we identified subgroups within the Bay of Quinte food web networks. We tested the statistical significance of our subgroups against 1000 randomly generated re-combinations of our data (Frank, 1996) and inspected the structure of significant subgroups. Although our ENA required balanced networks, our CA did not. In order to avoid intro-

¹ Our use of the term “subgroup” is analogous to the Pimm and Lawton (1980) definition of food web “compartment”. We use the term “subgroup” to avoid confusion between Pimm and Lawton (1980) and Ulanowicz (1986) uses of the term “compartment”.

ducing uncertainty from ENA balancing procedures, we used the unbalanced networks for CA. As a result, we could not include detrital groups in our CA because we derived detrital diet via balancing. Furthermore, our CA required us to adjust the network data to meet the data input range of Kliqfinder. We encountered this problem in our Oneida Lake analysis and used the same method as presented in Miehls et al. (2009) to parsimoniously adjust data.

We summarized results of the CA as “crystallized sociograms” using multidimensional scaling (Frank, 1996) in SAS System for Windows. In these diagrams, proximity of subgroups corresponds to: (1) the strength of predator–prey relationships spanning subgroups (i.e., closely spaced subgroups are connected by relatively stronger interactions than distant subgroups); (2) the similarity of connections to other subgroups; and (3) the subgroup’s importance to overall food web structure (i.e., centrally located subgroups are more important to food web structure than peripherally located subgroups). Similarly, location of taxa within a subgroup indicates the strength of connections between taxa and the importance of taxa to the subgroup.

After we identified network subgroups, we performed ENA on the largest subgroup (in terms of TST and number of taxa) to evaluate functional linkages. We maintained the same mass-balance in the subgroup analysis as the full food web by treating all flows to and from non-subgroup taxa as imports and exports to the subgroup. Because detrital groups were not assigned to subgroups, detritus could not be explicitly incorporated into the subgroup ENA. Nevertheless, flow to detritus was implicitly included by treating detrital flow as an export from the subgroup.

3. Results

3.1. Ecological network analysis – entire network

3.1.1. Input/output analysis

Zebra mussel effects on the Bay of Quinte food web were predominantly negative (Fig. 2). Cormorants (taxon 1 in Fig. 2; hereafter numbers in parentheses refer to taxa numbers in Fig. 2) were positively affected, while effects on fish (2–35) were mixed. Benthic fish (e.g., ictalurids, carp and freshwater drum, 19–20, 21, and 23, respectively) and benthic-associated fish (e.g., adult centrarchids, 9–14) exhibited positive impacts, while pelagic fish (e.g., white perch, alewife and shiners, 7–8, 16, and 22 and 32, respectively) and some sportfish (e.g., walleye and smallmouth bass, 2–4 and 31, respectively) were negatively affected. Round gobies (30) showed the greatest positive effects throughout the entire food web. Effects on benthic invertebrate taxa (36–44) were equally positive and negative, with zebra mussels strongly negatively affecting themselves (45). Effects on zooplankton (46–69) and phytoplankton (70–74) taxa were wholly negative and benthic plants (75–76) were marginally affected. Finally, zebra mussels positively influenced sedimented detritus (79), while negatively influencing other detrital groups (78 and 80).

3.1.2. Lindeman trophic analysis

Total production (i.e., flow between predators and prey plus the usable exports from the system) was $425.3 \text{ g C m}^{-2} \text{ year}^{-1}$ before zebra mussel invasion and $624.3 \text{ g C m}^{-2} \text{ year}^{-1}$ after, a 47% increase. Total flow loss due to respiration was $534.1 \text{ g C m}^{-2} \text{ year}^{-1}$ pre-invasion, and $510.9 \text{ g C m}^{-2} \text{ year}^{-1}$ after invasion, a 4% decrease. We were unable to create the Lindeman trophic spine for the full Bay of Quinte food web networks due to the complexity of trophic interactions in our networks (computations ran for over 6 months when an extended power outage stopped the analysis). Therefore, we could not analyze efficiency of flow between trophic levels.

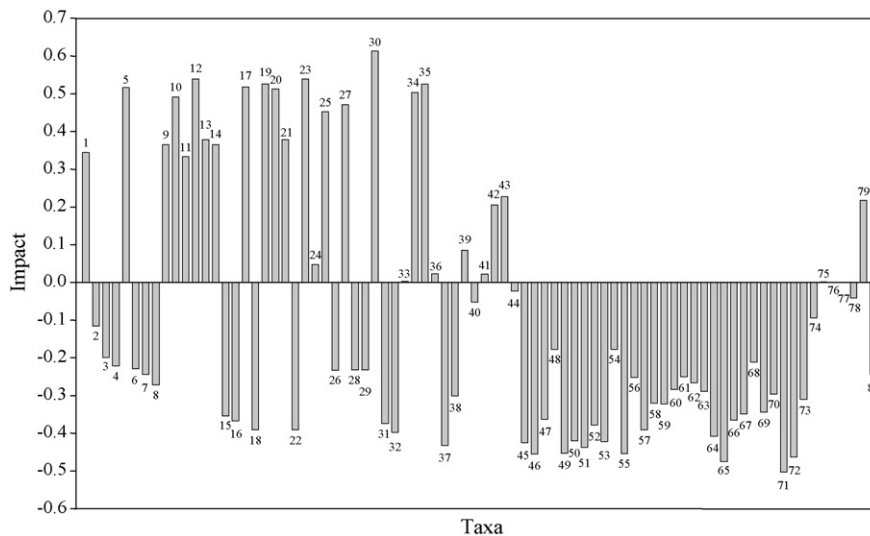


Fig. 2. Zebra mussel impacts on the Bay of Quinte food web. The scale is relative: impacts above the zero line are positive impacts of zebra mussels and impacts below the zero line are negative impacts of zebra mussels. Taxa numbers are placed above or below each bar. See Table 1 for taxa codes.

3.1.3. Ecosystem indices

The ecosystem analysis indicated that zebra mussel invasion caused moderate-to-strong changes to ecosystem function (Table 4, Panel A). TST (i.e., ecosystem growth) increased 9%, as did development capacity (i.e., ecosystem complexity) by 11%. Concomitantly, ascendancy (i.e., organization) increased (47%) while overhead (i.e., disorganization) decreased slightly (1%). In part, changes in capacity, ascendancy, and overhead were driven by increased TST. To remove the effects of TST scaling on capacity, we simply divided capacity by TST (this process yields a quantity equivalent to the Shannon flow diversity index for ecosystems; Ulanowicz, 1997) which revealed a 2% increase after invasion. To remove TST scaling on ascendancy and overhead and look at the proportion of organized flow relative to disorganized flow in the ecosystem, we divided ascendancy and overhead by development capacity which yields “relative ascendancy” and “relative overhead”, respectively (ascendancy, overhead, and capacity are scaled by TST, thus TST is removed through division; Heymans and Baird, 2000). Relative ascendancy increased 8% following zebra mussel invasion, while relative overhead decreased 8%. Finally, considering the contributors to relative overhead, overhead on imports, exports, and dissipative overhead decreased between 10 and 28%, while redundancy increased 9%.

3.2. Cohesion analysis

We identified six subgroups in the pre-invasion network and eight subgroups in the post-invasion network. Even though the odds ratio was greater post-invasion (odds ratio = 14.6) than pre-invasion (odds ratio = 12.7), the pre-invasion subgroups were marginally statistically significant ($p < 0.07$) and post-invasion subgroups were clearly not statistically significant ($p > 0.5$) (see Appendix 3 for a discussion of these results; the odds ratio describes the likelihood of predator-prey interactions falling within the same subgroup versus between subgroups; high odds ratios indicate predators and prey are clustered in common subgroups while taxa that do not interact are in different subgroups). Therefore, only results for the pre-invasion network (Table 5) are described below. We identified three subgroups containing mixed taxa: (1) a planktivorous food web subgroup (subgroup 1); (2) a subgroup of benthic-associated taxa (subgroup 2); and (3) a subgroup of centrarchids and zooplankton (subgroup 3; note that subgroup names were based on ecological descriptions that represent the major-

ity of taxa in each subgroup; some taxa may not fit the subgroup name). The remaining subgroups were largely composed of piscivorous (subgroup 5) and invertivorous (subgroup 6) fish (subgroup 4 contained both piscivorous and invertivorous fish). Interactions among (Panel A) and within (Panel B) subgroups were summarized in a crystallized sociogram (Fig. 3). The planktivorous food web subgroup (subgroup 1) was fundamental to Bay of Quinte structure, sharing close interactions with all subgroups (Fig. 3, Panel A). Zooplankton and phytoplankton were central to this subgroup and interactions were closely knit (Fig. 3, Panel B). The remaining subgroups illustrated less dense interactions (Fig. 3, Panel B) and more peripheral roles in the food web (Fig. 3, Panel A).

3.3. Ecological network analysis – grouped network

Since the post-invasion subgroups had non-statistically significant odds ratios, we could not conduct the input/output analysis at the subgroup level. Below we analyze the functional characteristics of the planktivorous food web subgroup (subgroup 1; pre-invasion) with the remaining ENA methods. This subgroup dominated ecosystem structure (in terms of number of taxa) and size (as quantified by TST) (Table 4, Panel B). As discussed below, an analogous subgroup in Oneida Lake was also analyzed.

3.3.1. Lindeman trophic analysis

The Lindeman trophic analysis identified twelve trophic levels in the planktivorous food web subgroup before zebra mussel invasion (Fig. 4). Adult yellow perch, subadult, and juvenile walleye were the top predators in this subgroup. Flow in the grazer chain decreased as trophic level increased, as did flow to detritus and flow loss due to respiration. Efficiency was greatest at trophic level I (51%), similar for trophic levels II and IV (4–6%), and lowest for trophic levels V and higher. Total production of the subgroup was $414.7 \text{ g C m}^{-2} \text{ year}^{-1}$ (97% of full food web) while total respiration was $198.3 \text{ g C m}^{-2} \text{ year}^{-1}$ (37% of full food web).

3.3.2. Ecosystem indices

Similar to the full food web analysis, the planktivorous food web subgroup before zebra mussel invasion was largely composed of disorganized flow (i.e., overhead and relative overhead; Table 4, Panel C). Throughput in this subgroup amounted to $1192.4 \text{ g C m}^{-2} \text{ year}^{-1}$, constituting 52% of total food web flow. Ascendancy represented 32% of development capacity, while over-

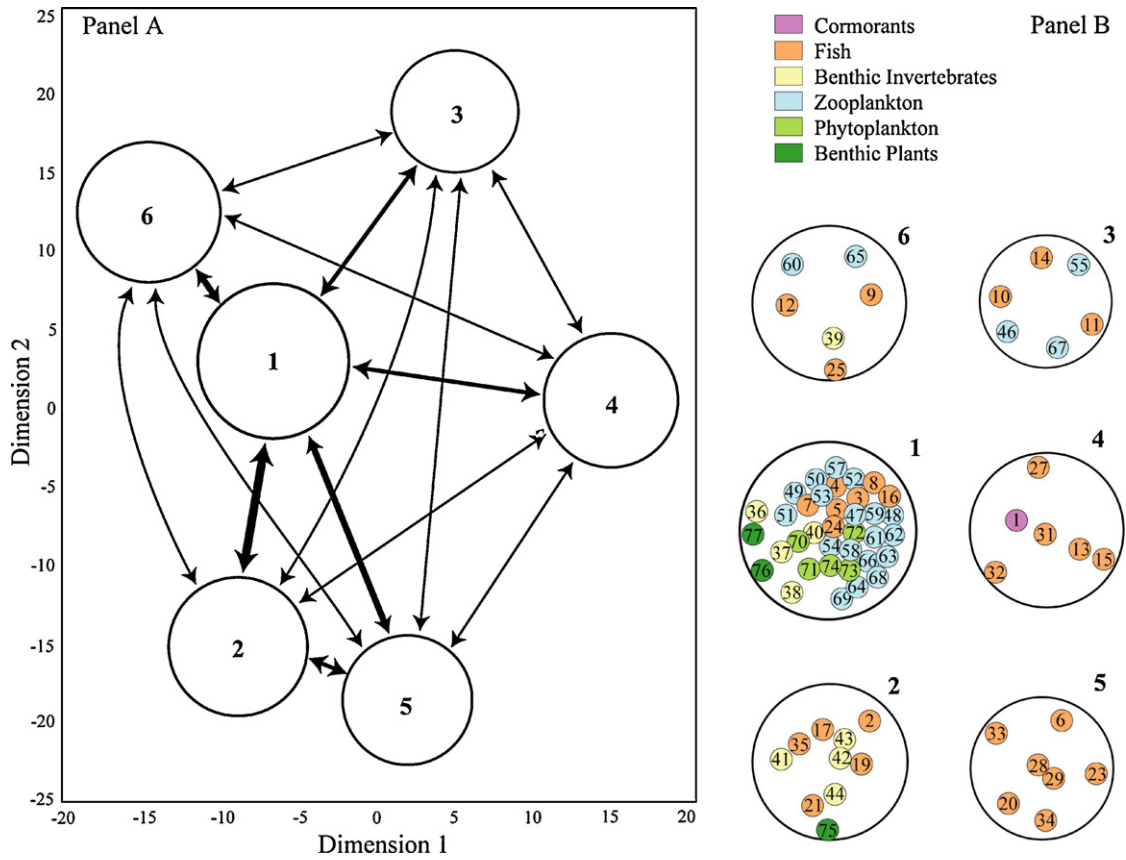


Fig. 3. Panel A: Crystallized sociogram for the pre-zebra mussel invasion time stanza. Units are relative distances based on the inverse of the density of interactions (see Frank, 1996). Subgroups 1–6 are plotted with the direction of feeding relationships represented by arrows; thickness of arrows indicates weight of feeding relationships. Panel B: Placement of taxa within subgroups. Circles indicate subgroup boundaries and colors represent general groupings of taxa. Subgroup numbers are located to the upper right of all subgroups.

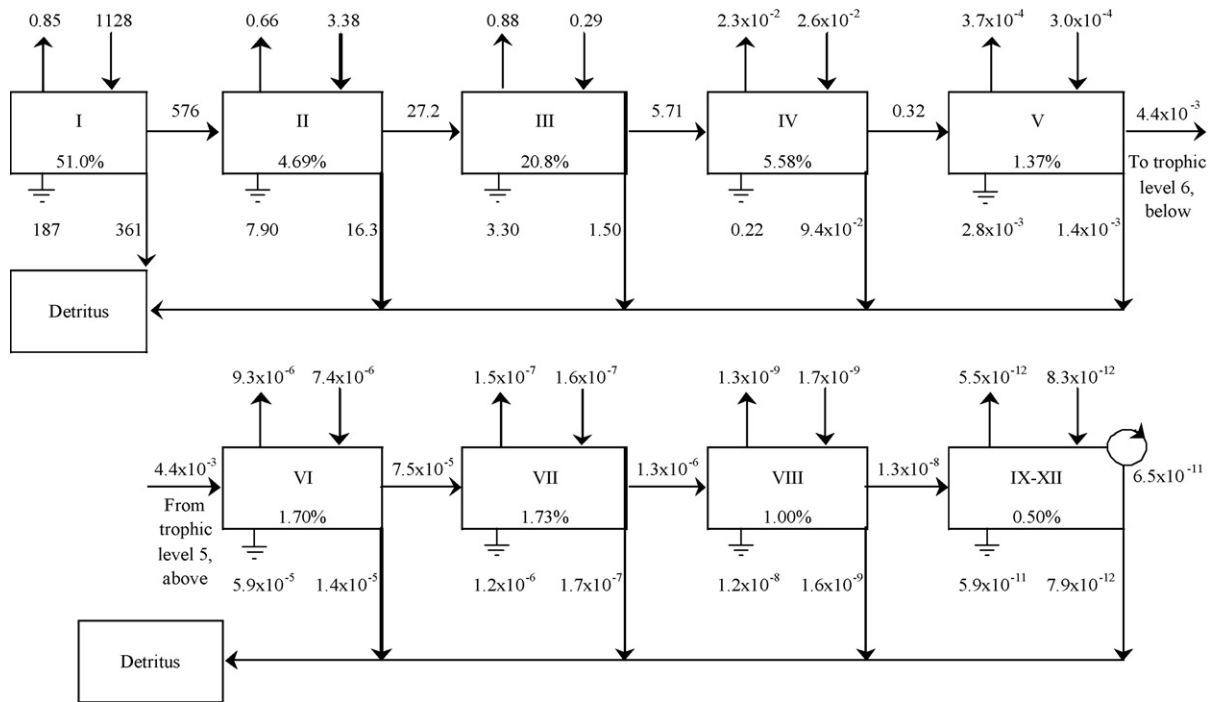


Fig. 4. Lindeman trophic spine for the planktivorous food web subgroup (subgroup 1) in the pre-zebra mussel invasion time stanza. Boxes with roman numerals represent the integer trophic levels; the number within each trophic box is the percent efficiency of that trophic level at processing carbon. Arrows between the trophic boxes are flows in the grazer food chain, arrows leaving the top of trophic boxes are exports, arrows entering the top of trophic boxes are imports, and arrows leaving the bottom of trophic boxes are flows to detritus, represented by the detrital box. The ground symbol from electronic circuitry represents flow loss due to respiration. All flows are in $g\ C\ m^{-2}\ year^{-1}$.

Table 4Ecosystem indices for the full food web (Panel A), subgroup throughput (Panel B), and ecosystem indices for subgroup 1 (Panel C).^a

Index	Pre-zebra mussels value	Post-zebra mussels value	% Difference value
Panel A: full food web			
Total system throughput (g C m ⁻² year ⁻¹)	2304.2	2505.4	8.7
Development capacity (g C bits m ⁻² year ⁻¹)	10 160.5	11 281.2	11.0
Ascendency (g C bits m ⁻² year ⁻¹)	2541.1	3726.8	46.7
Total overhead (g C bits m ⁻² year ⁻¹)	7619.3	7554.4	-0.9
Overhead on imports (g C bits m ⁻² year ⁻¹)	2594.2	2591.3	-0.1
Overhead on exports (g C bits m ⁻² year ⁻¹)	893.7	711.7	-20.4
Dissipative overhead (g C bits m ⁻² year ⁻¹)	2096.5	1787.7	-14.7
Redundancy (g C bits m ⁻² year ⁻¹)	2034.9	2463.7	21.1
Unscaled capacity (bits)	4.4	4.5	2.1
Ascendency/capacity (%)	25.0	33.0	32.1
Total overhead/capacity (%)	75.0	67.0	-10.7
Overhead on imports/capacity (%)	25.5	23.0	-10.0
Overhead on exports/capacity (%)	8.8	6.3	-28.3
Dissipative overhead/capacity (%)	20.6	15.8	-23.2
Redundancy/capacity (%)	20.0	21.8	9.0
TST (g C m ⁻² year ⁻¹)			
Panel B: subgroup TST			
Subgroup 1	1192.4		
Subgroup 2	16.45		
Subgroup 3	0.20		
Subgroup 4	0.03		
Subgroup 5	0.08		
Subgroup 6	0.06		
Panel C: subgroup 1 indices			
Development capacity (g C bits m ⁻² year ⁻¹)	4041.3		
Ascendency (g C bits m ⁻² year ⁻¹)	1282.1		
Total overhead (g C bits m ⁻² year ⁻¹)	2759.2		
Overhead on imports (g C bits m ⁻² year ⁻¹)	914.1		
Overhead on exports (g C bits m ⁻² year ⁻¹)	838.8		
Dissipative overhead (g C bits m ⁻² year ⁻¹)	727.2		
Redundancy (g C bits m ⁻² year ⁻¹)	279.2		
Unscaled capacity (bits)	3.4		
Ascendency/capacity (%)	31.7		
Total overhead/capacity (%)	68.3		
Overhead on imports/capacity (%)	22.6		
Overhead on exports/capacity (%)	20.8		
Dissipative overhead/capacity (%)	18.0		
Redundancy/capacity (%)	6.9		

^a The percent difference was calculated as: %Difference = ((Post - Pre)/Pre) × 100%.

head composed 68% of capacity. Relative overhead on imports and dissipative flow ranged between 18 and 23%, similar to the full food web. However, relative overhead on exports (21%) was greater in the subgroup; whereas relative overhead on redundant flows (7%) was less in the subgroup.

4. Discussion

Exotic species invasion is a pervasive threat to aquatic ecosystems. As invasion rates escalate (Holeck et al., 2004), it is essential that researchers understand ecosystem response to invasion to forecast and prevent further spread (Drake and Bossenbroek, 2004). In this study, we investigated exotic species perturbation on the Bay of Quinte through a rigorous inspection of ecosystem properties. Our use of network analyses allows for objective, quantifiable, and ecosystem level insight into the effects of zebra mussel invasion. Our analysis indicates that zebra mussels exert considerable influence in the Bay of Quinte by altering ecosystem structure (question 1) and function (question 2). Below we begin our discussion with the CA structural findings, and then place those results within the ENA functional context. Furthermore, we compare (question

3) zebra mussel effects in the Bay of Quinte to previous research on Oneida Lake (Miehls et al., 2009).

4.1. Cohesion analysis – structure

Structural effects of zebra mussel invasion on the Bay of Quinte are pronounced, as evidenced by a complete disruption of food web subgroup structure. Before invasion, the planktivorous food web subgroup (subgroup 1; a primarily pelagic subgroup) dominated ecosystem structure. The centrality of this subgroup (Fig. 3) parallels findings on Oneida Lake where we identified a planktivorous subgroup constituting the majority of structure. The prominence of these subgroups is expected as both systems were eutrophic and largely comprised of pelagic pathways before invasion. In Oneida Lake, zebra mussels established in the planktivorous subgroup, linking this subgroup to the benthos. However, in the Bay of Quinte, zebra mussel introduction entirely removed subgroup structure. In effect, zebra mussel invasion homogenized the structure of Bay of Quinte food web interactions.

The greatest effects of zebra mussel invasion in Oneida Lake are restricted to taxa within the planktivorous subgroup. Our method

Table 5

Subgroups identified for the pre-zebra mussel invasion time stanza. We loosely named subgroups based on ecological descriptions that represent the majority of taxa within each subgroup; however, not all taxa fit the subgroup name.

No.	Subgroup 1: planktivorous food web
3	Walleye Age 1–3
4	Walleye Age-0
5	Yellow Perch Age 1+
7	White Perch Age 1+
8	White Perch Age-0
16	Alewife
24	Gizzard Shad
36	Amphipods
37	Chironomids
38	Clams
40	Insects
47	<i>Bosmina longirostris</i>
48	<i>Ceriodaphnia</i> spp.
49	Chydoridae family
50	<i>Daphnia galeata mendotae</i>
51	<i>Daphnia pulicaria</i>
52	<i>Daphnia retrocurva</i>
53	<i>Eubosmina coregoni</i>
54	Sididae family
57	<i>Leptodora kindtii</i>
58	<i>Acanthocyclops vernalis</i>
59	<i>Diacyclops thomasi</i>
61	<i>Mesocyclops</i> spp.
62	<i>Tropocyclops extensus</i>
63	Cyclopoida copepodites
64	Diaptomidae family
66	Calanoida copepodites
68	Nauplii
69	Rotifers
70	Blue-green Algae
71	Diatoms
72	Flagellates
73	Golden Algae
74	Green Algae
76	Macrophytes
77	Periphytes
No.	Subgroup 2: benthic-associated
2	Walleye Age 4+
17	American Eel
19	Brown Bullhead
21	Common Carp
35	White Sucker
41	Isopods
42	Leeches
43	Oligochaetes
44	Snails
75	Epiphytes
No.	Subgroup 3: centrarchids and zooplankton
10	Bluegill Age 1+
11	<i>Lepomis</i> spp. Age 1+
14	Centrarchids Age 1+
46	<i>Alona</i> spp.
55	Large-bodied Cladocerans
67	Harpacticoida
No.	Subgroup 4: piscivores and invertivores
1	Cormorants
13	Rock Bass Age 1+
15	Centrarchids Age-0
27	Log Perch
31	Smallmouth Bass
32	Spottail Shiner
No.	Subgroup 5: piscivores
6	Yellow Perch Age-0
20	Channel Catfish
23	Freshwater Drum
28	Longnose Gar

Table 5 (Continued)

No.	Subgroup 5: piscivores
29	Northern Pike
33	Trout-perch
34	White Bass
No.	Subgroup 6: invertivores
9	Black Crappie 1+
12	Pumpkinseed Age 1+
25	Johnny Darter
39	Crayfish
60	<i>Eucyclops</i> spp.
65	Temoridae family

of subgroup identification concentrates strong predator-prey interactions within subgroups, leaving only weak interactions between subgroups. According to food web stability theory, weak interactions are important for promoting community persistence and stability by dampening oscillations between interacting species (McCann et al., 1998; McCann et al., 2005; but see Emmerson and Yearsley, 2004). Strong interactions often involve strong feedbacks, which can lead to oscillatory behavior (e.g., as seen in two species predator-prey cycles). When additional interactions (i.e., additional predators, prey, or competitors) are added to the system, interactions strengths weaken (feedbacks become more diffuse) and community dynamics stabilize. For instance, weak interactions provide alternatives such that a species can mitigate the effects of a disturbance by shifting to its weak ties for resources when strong ties are no longer providing the resources it needs. In a similar manner, strong interactions propagate effects of a disturbance (due to strong feedbacks), such as invasion by exotic species, while weak interactions localize effects of disturbance (through weak feedbacks). In the context of subgroup structure, perturbations affect subgroup members which are connected by strong ties but may not affect taxa in other subgroups which are connected through weak ties (Krause et al., 2003). In a sense, subgroup structure provides a buffer against ecosystem perturbation (Simon, 1962; Pimm, 1979; McCann, 2000; Krause et al., 2003). Thus, our results for Oneida Lake corroborate the subgroup buffering effect. However, as described above, zebra mussel invasion overwhelmed subgroup structure in the Bay of Quinte. This result has two implications: (1) the effects of zebra mussel invasion must be more severe in the Bay of Quinte than Oneida Lake to overcome the buffering effect of subgroup structure; and (2) zebra mussel influence is more expansive in the Bay of Quinte without the confines of subgroup structure.

4.2. Ecological network analysis – function

Our IMPACTS analysis indicates parallel food web response to zebra mussel invasion in the Bay of Quinte and Oneida Lake. The Bay of Quinte analysis suggests that zebra mussels have negative effects via feeding interactions on most taxa, yet zebra mussels positively affect some taxa, especially fish. In both the Bay of Quinte and Oneida Lake, benthic fish and centrarchids garner positive impacts, although these effects are more pronounced in the Bay of Quinte. Potentially the effects are greater in the Bay of Quinte due to the disruption of subgroup structure and the associated loss of subgroup buffering effects resultant from zebra mussel invasion. Walleye, which declined during the 1990s in both systems, show negative effects for all life stages in both analyses. In Oneida Lake, the decline of walleye is likely attributable to double-crested cormorant predation and not zebra mussel interactions (Rudstam et al., 2004); however, cormorant predation pressure on walleye is not as intense in the Bay of Quinte (J.A. Hoyle, personal communication, 2005; Appendix 2). Therefore, declines in walleye abundance are

more ascribable to zebra mussel influence in the Bay of Quinte than Oneida Lake, although commercial and recreational fisheries may also contribute to declines of walleye in the Bay of Quinte (Appendix 2). The strongest positive impact in the Bay of Quinte belongs to round gobies, a recent Ponto-Caspian invader not present in Oneida Lake. Our Bay of Quinte research corroborates a facilitative interaction between zebra mussels and round gobies (Simberloff and Von Holle, 1999; Ricciardi, 2001) and suggests that Oneida Lake may be susceptible to round goby establishment due to its similarity in fish community response to zebra mussel invasion. Considering the lower trophic levels, benthic invertebrate (mixed impacts), zooplankton (all negative impacts), and phytoplankton (all negative impacts) taxa exhibit similar responses to invasion in both systems.

When considering the results of the IMPACTS analysis, it is important to note that positive and negative effects found in the IMPACTS analysis do not necessarily indicate a realized effect occurred on, e.g., biomass or production, of a species in the system. The IMPACTS analysis quantifies the net effect of zebra mussels transmitted via feeding interactions (e.g. trophic cascades), but does not suggest that realized responses in the food web were causally related to zebra mussels.

Changes in flow efficiency are similar in the Bay of Quinte and Oneida Lake and reveal a shift in the primary paths of flow. Production increased in the Bay of Quinte (47%) after invasion, and decreased slightly in Oneida Lake (5%). The increase in Bay of Quinte production is largely due to greater primary production in benthic pathways, providing evidence for benthification. Macrophyte production increased from 2.9 to 33.4 g C m⁻² year⁻¹ (1048% increase) while detrital production increased from 4.5 to 70.2 g C m⁻² year⁻¹ (1462% increase). Oneida Lake macrophyte and detrital production also increased (13% and 460%, respectively). Respiration decreased in both the Bay of Quinte (4%) and Oneida Lake (23%) after invasion. Moreover, trophic chains for the planktivorous food web subgroup were similar in both systems pre-invasion. Although the trophic spine for the Bay of Quinte (12 levels) was longer than Oneida Lake (6 levels), flow efficiency by trophic level generally decreased with increased trophic level in both systems (with the exception of flow at trophic level II), and was greatest at trophic level I (51% – Bay of Quinte; 53% – Oneida Lake), indicating the importance of lower trophic levels to these systems before zebra mussel invasion.

Zebra mussels exhibit an overwhelming presence in the Bay of Quinte. After invasion, total system throughput and ascendancy increased, with zebra mussels garnering over 15% of throughput and comprising 89% of living biomass. Perhaps the food web exhibits increased organization due to this considerable flow asymmetry: focused flow through zebra mussels increases AMI, which in turn increases ascendancy. Ecosystem organization responded similarly in Oneida Lake where zebra mussels also dominate flow (10% of TST) and living biomass (67%). Moreover, both systems are predominantly comprised of disorganized flow (66–75% overhead), potentially indicative of frequent perturbation, such as exotic species invasion (Prout et al., 1990) and changes in nutrient loading (Mills et al., 2003). Finally, removing the effects of TST scaling reveals that zebra mussel invasion increased development capacity in both systems (i.e., unscaled capacity increased), adding a layer of functional complexity. Complexity benefits ecosystems by promoting flow diversity, which can buffer future ecological change (Pérez-España and Arreguín-Sánchez, 1999) in these systems. Finally, unscaled capacity is consistently larger in Oneida Lake than in the Bay of Quinte before and after zebra mussel invasion; thus, Oneida Lake has a greater overall potential for system development (and due to the equivalency of unscaled capacity and Shannon's flow diversity index, Oneida Lake also has a greater diversity of flows).

Comparing these results to ecological theory suggests that zebra mussel invasion perturbed the Bay of Quinte and Oneida Lake

ecosystems in an unexpected manner. Drawing from Odum's (1969) theory of ecosystem development, Ulanowicz (1996) suggests that perturbed ecosystems exhibit decreased system throughput and food web organization (i.e., increased overhead) due to an interruption of the ecological processes that optimize efficient functioning. Moreover, Ulanowicz (1997) predicts that frequently perturbed systems would harbor greater overhead values as a "strength in reserve" which the system uses to adapt to a new threat (Bondavalli et al., 2000). Given these theoretical predictions of ecosystem response to perturbation, we were surprised that ecosystem organization increased in both the Bay of Quinte and Oneida Lake. We attribute these unexpected ecosystem responses to the enormity of zebra mussel influence in these systems. Zebra mussel invasion overwhelmed both ecosystems, yielding increased organization through dominance of ecosystem function.

A limitation of ENA is that the analysis does not incorporate variability in flow estimates. Therefore, we cannot discern statistical significance in our ENA findings. However, in the case of the whole system analysis, ecosystem indices are based on log-scaled measures (Ulanowicz, 1986) and thus even small percent changes represent larger ecological changes. Additionally, ENA assumes mass-balance in food webs for some routines. As aquatic ecosystems are dynamic in space and time, this assumption is rarely met. Balancing introduces a degree of uncertainty into ENA, which makes careful choice of balancing methods and inspection of results for ecological plausibility essential. The final assumption of this research is that differences in food web structure and function between the time stanzas are attributable to zebra mussel invasion. Round gobies and *Cercopagis pengoi* also invaded the Bay of Quinte during our time periods, and cormorant biomass increased substantially. Although these changes may alter food web structure and function, we believe zebra mussel introduction far outweighs all other ecological change during our time periods, as evidenced by the dominance of zebra mussel flow and biomass. Therefore, we are confident in the robustness of our results.

In conclusion, zebra mussel invasion exerts a far-reaching influence on ecosystems. Although whole-system analysis is a formidable task due to the complexity of ecosystem structure and function and paucity of long-term data in many systems (Gaedke, 1995), the extensive history of data collection by Bay of Quinte researchers and our application of network analysis methods allows us to decipher the effects of zebra mussel invasion at the ecosystem level. Zebra mussel introduction not only causes substantial changes to food web subgroup structure, but also alters food web function by shunting energy from pelagic to benthic pathways, affecting ecosystem production and respiration. Moreover, zebra mussel effects are similar in Oneida Lake, a system of comparable trophic status. Therefore, these findings have implications for the prediction of zebra mussel effects in other eutrophic systems. Finally, these findings highlight the value of making network analysis comparisons across invaded ecosystems. As exotic species invasion becomes an ever-increasing threat to aquatic ecosystems worldwide, understanding ecosystem dynamics is of paramount importance.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.07.013.

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