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Ann E. Krause
University of Toledo, ann.krause@utoledo.edu

Ken A. Frank
Michigan State University

Michael L. Jones
Michigan State University

Thomas F. Nalepa
NOAA, thomas.nalepa@noaa.gov

Richard P. Barbiero
Loyola University Chicago

*See next page for additional authors*

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Authors

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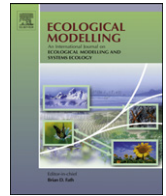
Adaptations in a hierarchical food web of southeastern Lake Michigan

Ann E. Krause[a,*], Ken A. Frank[b,c], Michael L. Jones[c], Thomas F. Nalepa[d], Richard P. Barbiero[e],
Charles P. Madenjian[f], Megan Agy[g], Marlene S. Evans[h], William W. Taylor[c], Doran M. Mason[d],
Nancy J. Leonard[c]

[a] Department of Environmental Sciences, MS#604, University of Toledo, 2801 W. Bancroft, Toledo, OH 43606, USA
[b] Department of Counseling, Educational Psychology, and Special Education, Michigan State University, East Lansing, MI, USA
[c] Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA
[d] NOAA-Great Lakes Environmental Research Laboratory, Ann Arbor, MI, USA
[e] Computer Sciences Corporation and Loyola University Chicago, Chicago, IL, USA
[f] USGS-Great Lakes Science Center, Ann Arbor, MI, USA
[g] Cooperative Institute for Limnology and Ecosystem Research, University of Michigan, Ann Arbor, MI, USA
[h] National Water Research Institute, Environment Canada, Saskatoon, SK, Canada

ABSTRACT

Two issues in ecological network theory are: (1) how to construct an ecological network model and (2) how do entire networks (as opposed to individual species) adapt to changing conditions? We present a novel method for constructing an ecological network model for the food web of southeastern Lake Michigan (USA) and we identify changes in key system properties that are large relative to their uncertainty as this ecological network adapts from one time point to a second time point in response to multiple perturbations. To construct our food web for southeastern Lake Michigan, we followed the list of seven recommendations outlined in Cohen et al. [Cohen, J.E., et al., 1993. Improving food webs. Ecology 74, 252–258] for improving food webs. We explored two inter-related extensions of hierarchical system theory with our food web; the first one was that subsystems react to perturbations independently in the short-term and the second one was that a system's properties change at a slower rate than its subsystems' properties. We used Shannon's equations to provide quantitative versions of the basic food web properties: number of prey, number of predators, number of feeding links, and connectance (or density). We then compared these properties between the two time-periods by developing distributions of each property for each time period that took uncertainty about the property into account. We compared these distributions, and concluded that non-overlapping distributions indicated changes in these properties that were large relative to their uncertainty. Two subsystems were identified within our food web system structure ($p < 0.001$). One subsystem had more non-overlapping distributions in food web properties between Time 1 and Time 2 than the other subsystem. The overall system had all overlapping distributions in food web properties between Time 1 and Time 2. These results supported both extensions of hierarchical systems theory. Interestingly, the subsystem with more non-overlapping distributions in food web properties was the subsystem that contained primarily benthic taxa, contrary to expectations that the identified major perturbations (lower phosphorous inputs and invasive species) would more greatly affect the subsystem containing primarily pelagic taxa. Future food-web research should employ rigorous statistical analysis and incorporate uncertainty in food web properties for a better understanding of how ecological networks adapt.

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1. Introduction

Ecological network theory combines systems theory and network methodology to study ecology. The primary ecological networks studied are food webs, where the nodes of the network are taxonomic populations (taxa) and links between nodes indicate feeding interactions. While much has been learned about food web dynamics through ecological network research, there remain many outstanding issues that need to be addressed for improving future inquiries (Jørgensen, 2007). Two of these issues are (1) how to construct ecological network models and (2) how do entire networks (as opposed to individual species) adapt to changing conditions? In this paper, we present a novel method for constructing an ecological network model for the food web of southeastern Lake Michigan (USA). We identified large changes in key system properties relative to their uncertainty as this ecological network adapts

from one time point to a second time point in response to multiple perturbations.

As the second largest lake by volume of the Laurentian Great Lakes, Lake Michigan is an ecosystem that has gone through profound changes through time (Madenjian et al., 2002). From the early 1980s through the late 1990s, two key disturbances emanating from outside of this system were documented: the invasion and establishment of two exotic invertebrate populations and declines in phosphorous loadings. The two exotic invertebrates are *Bythotrephes longimanus* (cladoceran zooplankter), which was first detected in 1986 (Evans, 1988), and *Dreissena polymorpha* (zebra mussel), which was detected in 1989 (Lauer and McComish, 2001). *Bythotrephes* is a voracious predator on zooplankton, including its native competitor, *Leptodora kindtii*, and competes with small fish (Schulz and Yurista, 1999; Vanderploeg et al., 2002). Although fish in the Great Lakes find *Bythotrephes* difficult to digest because of their long spines (Barnhisel and Harvey, 1995; Parker et al., 2001), *Bythotrephes* are present in fish diets (Pothoven and Madenjian, 2008; Pothoven and Vanderploeg, 2004; Bur and Klarer, 1991). Zebra mussels have a higher filtering rate and broader particle size range than their competitors, the native fingernail clams, resulting in increased water clarity via movement of organic matter from the pelagic to the benthic regions (Vanderploeg et al., 2002). The decline in phosphorous loadings resulted from society's intentional reduction in phosphorus input to return the lake from a eutrophic to an oligotrophic state. Throughout the 1950s, 1960s, and 1970s, phosphorous loading from human activities greatly affected the phytoplankton community by increasing overall biomass and promoting dominance of eutrophic species (Fahnenstiel and Scavia, 1987; Barbiero et al., 2002; Madenjian et al., 2002; Schelske et al., 2006). Then, the Water Quality Agreement in 1972 and other management efforts to reduce human phosphorous loadings were implemented and largely successful in reducing loadings. During this time period, phytoplankton community composition has shifted back to an assemblage more characteristic of a mesotrophic system (Barbiero et al., 2002; Madenjian et al., 2002).

Most studies on Lake Michigan during this time period focus on the dynamics of individual species or taxonomic-group populations but have yet to study how the systems at higher levels, such as communities or food webs, reacted during this time where integrative properties are measured at these higher levels. In this study, we estimated network properties as integrative measures of a food web in southeastern Lake Michigan. There are on-going issues in food web ecology and ecological network research regarding the difficulty of constructing food webs (Cohen et al., 1993; Jørgensen, 2007). It is difficult to construct a new food web model from existing data because the data on taxonomic populations were often collected for other purposes. But it is also difficult to construct a food web from data specifically collected for the construction because it requires extensive fieldwork. To construct our food web for southeastern Lake Michigan, we followed the list of seven recommendations outlined in Cohen et al. (1993) for improving food webs: establish priorities for data collection, provide a precise setting for boundaries, articulate units for defining the nodes of taxonomic populations, define the information used to determine links and provide weight on links where possible, publish the food web in matrix or list format, make the details of the data used to construct the food web available, and produce a food web based on collaboration.

To construct a food web model that followed Cohen et al.'s recommendations for multiple time points, we compiled compatible datasets previously collected by federal and state agencies and university researchers, primarily for monitoring programs of various taxonomic groups. From this, we established two general time periods for our temporal boundaries: the early 1980s (Time 1) and the late 1990s (Time 2). The data sets allowed us to articulate nodes often to the species level for most taxonomic groups, producing almost 200 nodes for each time period. Food web models that are this finely articulated often lack the information needed to calculate measures of interaction strength (see Berlow et al., 2004) or energy flow on links between predators and prey, and our compiled data sets were no exception for links between predator and prey. However, we knew that weighted links are important for constructing food webs to allow for differentiation between strong and weak interactions (Cohen et al., 1993; Bersier et al., 1998; McCann, 2000). Hence, for weighting the links in our food web, we developed a new method to substitute for traditional measures of interaction strength and energy flow. This new method for weighting links takes into account taxa traits that are fairly stable – their prey and habitat preferences – and taxa traits that are more dynamic—their biomass. This method was also flexible in allowing shifts in preferences from one time period to another, including shifts in preferences not related directly to feeding interactions.

To analyze our food web, we turn to hierarchical system theory, which proposes that the evolution of complex systems is dependent on their subsystem structure and thus should be examined at multiple system levels (Simon, 1965). The nearly decomposable subsystems outlined in Simon (1965) have nodes (taxa) that share many or strong interactions among themselves and share few or weak interactions with nodes in other subsystems. In ecology, these subsystems are known as compartments (Pimm, 1979). In this study, we employed a quantitative method for detecting subsystem structure of our food web for the two time points. We then measured quantitative versions for common qualitative properties of food webs at the system level and subsystem level (Bersier et al., 2002): number of links, number of prey, number of predators, and density (also known as connectance). The quantitative versions took into account the resource flow from prey to predators in our food web. Specifically, we used Shannon's equations to measure the distribution of the probabilities in resource flow from prey to predators, which quantified the basic food web properties listed above (Shannon, 1948; Bersier et al., 2002; Zorach and Ulanowicz, 2003). Because the datasets used in this study were collected for other purposes, we also quantified the uncertainty associated these properties.

From our network property information, we explored two interrelated extensions of the hierarchical system theory with our food web (Simon, 1965). The first extension is that subsystems within a system react to perturbations independently in the short-term. The second extension is that a system's properties change at a slower rate than its subsystems' properties. These extensions relate to food-web theory, where it has been shown that the presence of these subsystems increase stability in simulated food webs (May, 1973). The weak links between subsystems buffer the effects of perturbations, thus maintaining the stability of the system (Simon, 1965; Pimm, 1979; McCann, 2000; McCann et al., 2005). This stability comes from weak links not transferring the effects of a perturbation as much as strong links. Additionally, they also offer redundancy in the system so that nodes may rely more on their weak links than their strong links in the short term. For example, as mentioned above *Bythotrephes* reduced *Leptodora* populations. *Leptodora* would be a strong resource link for small fish. This reduction would have led fish to have to rely on weaker resource links of smaller, less preferred zooplankton until they learned to replace *Leptodora* with *Bythotrephes* in their diets. The aggregate response of all nodes in the subsystem results in shifts in subsystem properties. System properties are based on the aggregated response of the subsystems, resulting in fewer changes in the overall system if not all subsystems have the same response to the perturbation. In our study, we therefore expected that the changes in subsystem properties from Time 1 to Time 2 would be different among subsystems, and that we would observe fewer changes in system properties from Time 1 to Time 2 than those observed at the subsystem level.
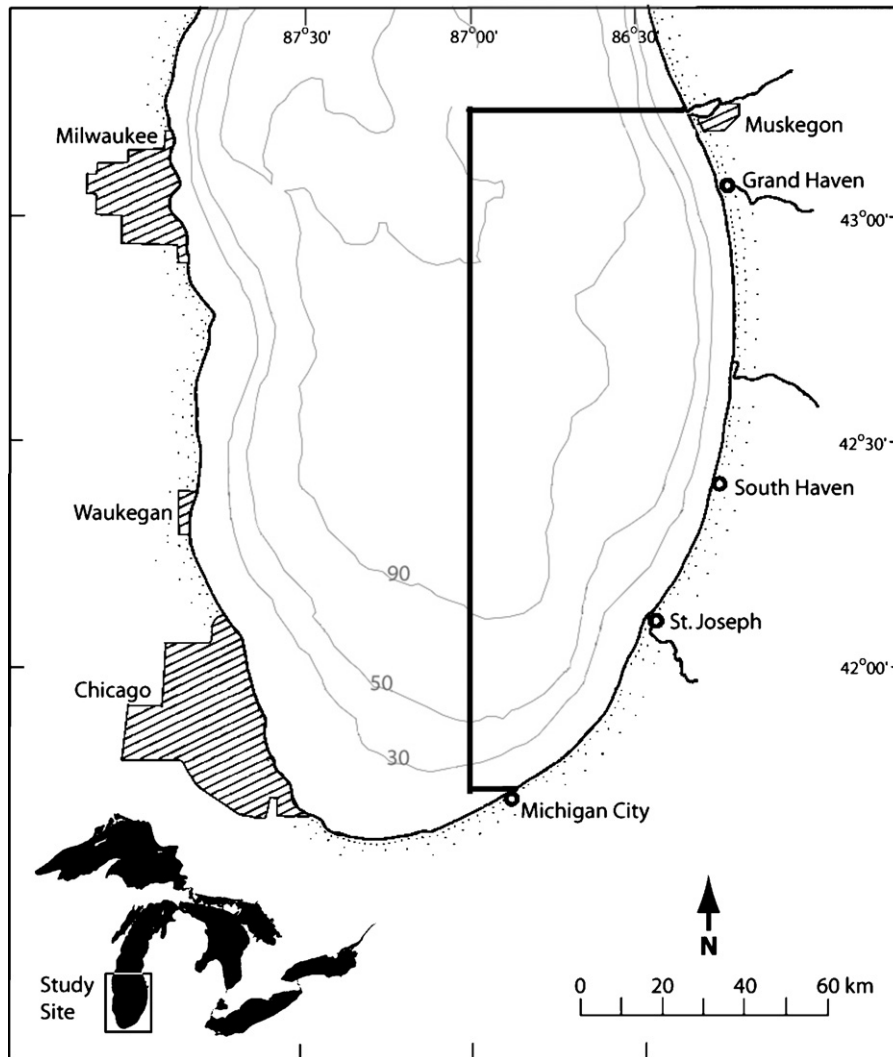
Fig. 1. A map of southern Lake Michigan with the latitude and longitude boundaries of study outlined (figure courtesy of NOAA-Great Lakes Environmental Research Laboratory, Ann Arbor, MI).

2. Methods

We took several steps to construct a food web with weighted links following the recommendations of Cohen et al. (1993). First, we had to identify an area of Lake Michigan where data on the food web were collected consistently in the early-mid 1980s and mid-late 1990s. These datasets defined what taxonomic groups would be assigned as nodes in our network. The collection sites of the data set the boundaries of the spatial area that our food web represented. The collection times set up the seasons that our food web represented. Once we had our nodes identified and the spatial and temporal range defined, we then worked on developing the feeding links between nodes. The feeding links between predator–prey nodes were weighted using a measure of relative probability of interaction. This relative probability of interaction was based on three metrics: selectivity, horizontal space overlap, and vertical space overlap. Selectivity was identified that a predator taxon is thought to eat a prey taxon based on the literature. It had three levels at which it could be set: high, neutral, and low. Horizontal space overlap was based on three bottom depth zones within the identified spatial area. The calculation took into account seasonal preferences and presence. Vertical space overlap was based on four zones in the spring and six zones in the summer. The calculation took into account seasonal preferences and diel vertical migration.

These three measures were multiplied together to generate a relative probability of interaction.

To measure the shifts in network properties of the system, we employed multiple analyses. We used a clustering algorithm to identify subsystems in our food web network where links were weighted by the relative probability of interaction. We then tested whether nodes retained the same subsystem membership in Time 2 as they had in Time 1. We calculated quantitative versions of basic food web or network properties at the system and subsystem level. These quantitative properties were based on the dispersion of weights on links (Shannon's equations), where weights were now a product of the relative probability of interaction and a biomass estimate of the prey node population. Because we had estimates of prey biomass for multiple years within each time period that were not collected together and were collected for other purposes, we produced distributions of the quantitative network properties for each time period. These distributions were based on calculated values of these properties for each possible combination of prey datasets. These distributions represented the uncertainty of each network property was for each time period. We adopted the ad-hoc but reasonable criterion that non-overlapping distributions in properties between Time 1 and Time 2 indicated a large change in that property relative to its uncertainty.

2.1. Study site and data acquisitions

The food web represented southeastern Lake Michigan in spring and summer with a range in bottom depths of 15 to 110 m for the two time periods spanning the years of 1980–1984 (Time 1) and 1995–1999 (Time 2). These temporal and spatial boundaries were selected primarily based on the availability of datasets that were comparable and that represented a broad spectrum of taxonomic groups. During Time 1, phosphorous loadings were relatively high and *Bythotrephes* or zebra mussels had yet to be detected in Lake Michigan waters (Makarewicz et al., 1995; Barbiero et al., 2001; Fleischer et al., 2001; Madenjian et al., 2002). By Time 2, phosphorous loadings were relatively low and both invasive species were firmly established. By 1999, several new exotic species had been detected in the lake, though they had yet to reach high levels of density (Vanderploeg et al., 2002). Thus we assumed these exotic species had a negligible effect on the food web structure and its key system properties in Time 2. Based on our above dataset restrictions, we focused on data collected between the latitudes of 43°15′N and 41°45′N and east of longitude 87°00′W (Fig. 1). We set the seasonal time frame of our food web from April 1 to June 14 for spring and June 15 to September 30 for summer. Most of the datasets only cover spring and summer, important seasons for taxonomic groups with short-lived species, such as phytoplankton and zooplankton. These datasets with short-lived species rarely have autumn or winter data available. The date to separate spring and summer was selected because the lake starts to stratify in June with conditions usually still at the mixing stage at the beginning of June and with the lake usually having set up a thermocline by the end of June. The bottom depth range of 15–110 m was broken into three horizontal depth zones based on previous studies that determined these depth ranges represented different ecological zones: 15–30 m (Zone 1), 31–50 m (Zone 2), and 51–110 m (Zone 3; Nalepa, 1989; Agy, 2001).

The primary information we used from the datasets was taxa presence during the time periods and their associated relative biomass. All datasets had information on taxa groups for multiple years within Time 1 and within Time 2. However, not all of them covered all five years within each time period. The Great Lakes National Program Office (GLNPO) of the US-EPA provided phytoplankton data. GLNPO collected phytoplankton data to monitor water quality and has been consistent in its data collection methods throughout our two time periods (Barbiero and Tuchman, 2001). Although GLNPO collected phytoplankton in only one depth zone, we assumed that their phytoplankton data was representative of all three depth zones. We could not find documentation in the literature that there were large changes in phytoplankton among the chosen depth zones except for *Nitschia* spp. (Munawar and Munawar, 1976; Lowe, 2003). This sampling regime produced more inter-annual variance whereas more comprehensive temporal and spatial sampling would have provided more precise estimates of phytoplankton biomass. This sampling regime will make it more difficult to detect differences in our network properties.

The zooplankton data for the Time 1 food web were collected for the Cook Power Plant study conducted by the University of Michigan, Ann Arbor, MI (Evans, 1986). The Time 2 zooplankton data set was provided by NOAA-Great Lakes Environmental Research Laboratory (GLERL), Ann Arbor, MI and was collected for their Episodic Events in Great Lakes Ecosystems (http://www.glerl.noaa.gov/eegle/data/data.html; Agy, 2001). These two datasets were considered to be comparable in their data collection methods. Collection sites and times gave reasonable coverage for these populations within our spatial and temporal boundaries and in relation to their life-histories (see Krause, 2004 for more detail). Two *Bythotrephes* datasets were collected in a separate, but compatible, sampling program by GLERL (Pothoven et al., 2001) that also provided good spatial and temporal coverage.

The benthic invertebrates were provided by GLERL and collected for a monitoring program using consistent methods (Nalepa, 1989). The data provided good representation of those populations within our spatial and temporal boundaries given the life-histories of benthic invertebrates. This monitoring program did not collect *Mysis relicta* as they require specialized methods for collection. Consistent datasets for *Mysis relicta*, opossum shrimp, were unavailable. However, they are too important as predators and prey within the food web to not be included (Lehman et al., 1990; Eshenroder and Burnham-Curtis, 1999) and thus the following datasets were included in our food web. For Time 1, we used opossum shrimp estimates from Lehman et al. (1990) and McDonald et al. (1990). A comprehensive dataset was available for opossum shrimp from GLERL for Time 2 (Pothoven et al., 2000).

Fish data were available from various state and federal monitoring programs. Forage fish data were from the USGS-Great Lakes Science Center (Ann Arbor, MI) long-term monitoring program (Madenjian et al., 2002). Samples were taken in the fall where the fall populations of fish likely had fewer individuals than those in spring and summer due to mortality and individual fish likely had a higher biomass than in the spring and summer. However, all of the fish species included in our food web only have one cohort per year, as opposed to most of the other taxa, so these data collected once per year provided adequate estimates of relative biomass for the purposes of this food web analysis. Lake whitefish data were available from the Michigan Department of Natural Resources for lake whitefish management unit 8. Salmon and trout data were available from Michigan State University (East Lansing, MI) for salmon management unit 8. While these management units did not perfectly overlap with the latitudinal and longitudinal boundaries, we used them because they were well-developed biomass estimates based on modeling efforts. Sea lamprey data were available from the sea lamprey monitoring program headed by the Great Lakes Fishery Commission (Ann Arbor, MI). For more details on data attributes, see Krause (2004).

2.2. Constructing the food web

The taxa that formed the nodes of our food-web network were developed from the available datasets. A total of 164 taxa nodes were found in the datasets of both time periods, 16 taxa were identified in Time 1 datasets but not in Time 2 datasets, and 32 taxa were identified in Time 2 datasets but not in Time 1 for a total of 180 nodes in Time 1 and 196 nodes in Time 2. The food webs of the two time periods shared 74 phytoplankton nodes, 21 zooplankton nodes, 47 benthic invertebrate nodes (including opossum shrimp), and 22 fish nodes. The Time 1 food web had 5 phytoplankton, 5 zooplankton, and 5 benthic invertebrate nodes not found in the Time 2 food web. The Time 2 food web had 22 phytoplankton, 2 zooplankton (including *Bythotrephes*), and 8 benthic invertebrate (including zebra mussel) nodes not found in the Time 1 food web.

Generally, taxa nodes were defined at the species level. We avoided aggregating into higher-level taxonomic groups where possible because of its potential biases, including reduced detection of compartments (Martinez, 1991; Cohen et al., 1993; Gaedke, 1995; Krause et al., 2003). We aggregated beyond the species level in the food web only where sampling was reported at a higher taxonomic level with the exception of phytoplankton. Because of the difficulty in taxonomy at the species-level, potential for misidentification, and large numbers of species within phytoplankton, the 268 species of phytoplankton found in the survey data were aggregated based on their group type (for example, centric diatoms) and on having similar characteristics in size, shape, colonial attributes, motility, toxicity, trophic status (nitrogen-fixing ability, heterotrophic, both hetero and autotrophic), silica, and spatial and temporal presence (Weithoff, 2003). When supported by the datasets, some species of

zooplankton and fish had two nodes associated with them based on ontogenetic shifts in feeding interactions as differences in feeding links from one life-stage to the next can be greater than between species (Gaedke, 1995). In the benthic invertebrate data, we disaggregated a group, the Spheariidae, into three taxonomic groups because the taxa represented by the group were dissimilar in their depth distributions and diets.

Once nodes were identified, the next step for constructing the food web was to identify which nodes linked to each other in a predator–prey interaction and to apply a weight to the link. We developed a method for weighting links based on metrics that included the selectivity of the predator on the prey, predator–prey overlap in horizontal depth across time (seasonally), and predator–prey overlap in vertical depth across time (daily and seasonally). These metrics are often a result of a taxon's characteristics, such as thermal tolerance, depth tolerance, light tolerance, gape size, nutritional requirements, and defense mechanisms. Combining these three metric dimensions provided us with a relative probability of interaction (I_{ij}), where every link had the potential to have the same maximum weight of 1.00. The values used to establish links and calculate weights were documented in a database along with the associated references (over 175 references total; see Supplemental material). This weighting scheme allowed for potential adjustments within each time period if vertical and horizontal distributions were documented as changing for a taxon node, which may be caused by a number of factors, including non-feeding effects of introduced species.

The selectivity of a predator on a prey indicated the preference of a predator for a prey and was set to one of three levels: neutral, high, and low selectivity (sensu Vanderploeg, 1994). First, we linked predators to their possible prey using diet studies for the taxa found in the literature and other sources of information (see supplemental materials for more information). Then, these links were weighted by one of the three selectivity values, which were not affected by the values assigned to other links, unlike diet percentages. We wanted an indicator that had the same potential for obtaining the highest value. If we change the diet percentage on one link from a prey to a predator, we have to change at least one other percentage of another link from a prey to that predator so that the total adds up to 100. The default level for all predator–prey links was a value of 0.50, which indicated neutral selectivity or neutral preference (see Supplemental Materials for diet information and associated citations). If we found evidence in the literature or other sources of diet data that suggested a predator had a strong preference for a prey taxon compared to other prey taxa, then the selectivity of that interaction was assigned a value of 1.00. While perfect selectivity may never occur in nature, the value of 1.00 was selected so there was the potential for a predator–prey pair interaction to have a final weight of 1.00 (the maximum weight) after the spatial overlap adjustment. Otherwise, the maximum weight would be dependant on whatever weight was assigned to high selectivity, as the maximum values for the spatial overlap adjustments were 1.00. If we found evidence that a predator actively selected against a prey taxon that still had the potential to be consumed by the predator (e.g., toxic phytoplankton) or that a prey taxon was rarely found in the diet, then selectivity was given a score of 0.10 to represent a low selectivity or low preference. A value of 0 was not given because that would indicate no selectivity and effectively remove the link between the predator and the prey.

For spatial overlap, we collected information on ranges in taxa presence in vertical and horizontal space from the literature. Three horizontal depth zones were identified based on bottom depths given general biomass distributions observed across taxonomic groups: 1—8–30 m bottom depth, 2—31–50 m bottom depth, and 3—>50 m bottom depth. Because some taxa's horizontal distribution can shift from spring to summer, particularly for the more

mobile fish taxa, each taxon had a separate horizontal depth distribution for each season. Vertical space was divided into depth zones for each season based on thermal structures. Spring had four zones: 1—upper water column (surface to 2 m from sediment surface), 2—lower water column (2 m from sediment surface), 3—sediments surface to 1 cm below, 4—deeper sediments. Summer had six zones: 1—epilimnion, 2—thermocline area, 3—hypolimnion, 4—nephloid area, 5—sediments surface to 1 cm below, 6—deeper sediments. Taxa vertical distributions were determined for spring and summer separately. Vertical depth distributions were also separated into day and night to account for the diel vertical migrations some taxa undertake (e.g., opossum shrimp). For all taxa distributions, we indicated where a taxon's abundance was greater for a given spatial zone relative to the other spatial zones in which they were found. That is, we had the spatial zone of peak abundance for each taxon during spring and summer, and during day and night of each season.

For each predator–prey link, the values for horizontal overlap were calculated in four steps for spring and for summer (see Fig. 2 for example). First, using the scales outlined in the previous paragraph (1–3 for horizontal zones), the higher value of the minimum horizontal depth zones for the pair was subtracted from the lower value of the maximum horizontal depth zones for the pair. One was added to this value to obtain the number of horizontal depth zones in which the taxa pair overlapped in distribution. Second, the maximum range of horizontal depth zones of the predator–prey pair combined was calculated by subtracting the lower value of the minimum horizontal depth zones for the taxa pair from the higher value of the maximum horizontal depth zones for the taxa pair and then adding one to the result. This calculation produces the range of depth zones of that predator–prey pair. Third, to adjust for peak abundances, a percent value was multiplied by this proportion where the adjustment was made for the horizontal overlap values: 100% for predator–prey with horizontal peaks that were the same; 75% peaks were not equal but still within the overlap range; 50% peak for one taxon in the pair was in the overlap range but the peak for the other taxon was not; and 25% if neither peak was in the overlap range. While these percentages are arbitrary, we wanted to reduce the relative probability of interaction to account for non-equal peak abundances and peak abundances outside of the range of horizontal overlap. We could not think of an appropriate non-arbitrary adjustment that would apply to all interactions in the food web. Fourth, the overlap distribution for a predator–prey pair was divided by the distribution range as a pair to obtain the percent overlap within their collective ranges (to normalize their overlap) and multiplied by the peak abundance adjustment. We then took a weighted mean of the spring horizontal value and the summer horizontal value, adjusting for the number of days in spring and summer. If the taxon was only present for a proportion of the time period (e.g., phytoplankton taxa that only bloom in the summer), then the number of days was adjusted accordingly. The maximum horizontal overlap score was 1.00, which indicated that the interacting taxa pair had 100% spatial overlap and 100% temporal overlap in the horizontal range for spring and summer given the spatial boundaries.

We repeated this procedure to calculate vertical overlap only using the vertical zone data rather than the horizontal zone data (1–4 for spring vertical zones, and 1–6 for summer vertical zones). In addition to accounting for spring and summer, we had to account for diel vertical migration. Thus, we had vertical overlap values for spring day, spring night, summer day, and summer night. The mean of these values was calculated, where the values were weighted by the number of days in the same way that the horizontal values for spring and summer were weighted and they were weighted by the number of hours in day and night for spring and for summer (for more detail, see Krause, 2004). Again, the maximum spatial overlap score was 1.00 for the final vertical overlap scores, which indicated

For example, Small Fish species is a prey item for predator Big Fish species. In the spring, Small Fish species is present in horizontal depth zones 1-2 and has peak abundances in zone 1. In the spring, Big Fish species is present in horizontal depth zones 2-3 and has peak abundance in 3.
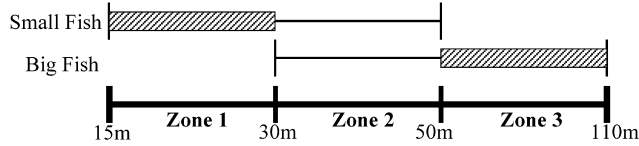
Small Fish Minimum Zone = 1; Maximum Zone = 2
Peak Abundance Zone = 1 (not in Big Fish range)

Big Fish Minimum Zone = 2; Maximum Zone = 3
Peak Abundance Zone = 3 (not in Small Fish range)

Step 1 Overlap of Zones: Small Fish Maximum Zone - Big Fish Minimum Zone + 1
2-2+1=1

Step 2 Range of Zones: Big Fish Maximum Zone - Small Fish Minimum Zone + 1
3-1+1=3

Step 3 Peak abundance overlap adjustment: 25%

**Step 4 Final Calculation of Horizontal Zone Overlap
between Small Fish and Big Fish** = (1/3)*0.25 = 0.08

The value for Small Fish and Big Fish horizontal overlap in the spring is 0.08.

Fig. 2. An example of how to calculate a spatial overlap value for a predator–prey pair for 1 season. Little Fish is a prey taxon to the predator taxon Big Fish. Each taxon has its own horizontal depth distribution and preferences for the spring. The steps in the calculation are outlined. This procedure was followed to calculate horizontal overlap values for spring and summer and vertical overlap values for night and day in spring and summer.

that the interacting taxa pair had 100% spatial overlap and 100% temporal overlap for spring and summer and for day and night given the spatial boundaries.

The three scores of selectivity, horizontal depth overlap, and vertical depth overlap were then multiplied together for each predator j–prey i pair for a final link weight ($I_{i,j}$). This weight represented a relative probability of interaction. If a predator node had high selectivity for a prey and maximum spatial and temporal overlap with a prey node, their relative probability of interaction was 1.00, the highest value attainable. We set the lower limit for a relative probability of interaction at 0.01, where any interaction lower than 0.01 was removed as it was deemed an unlikely interaction. Of the removed interactions, 95% involved a phytoplankton taxon node as a prey and 95% of those interactions involved a benthic invertebrate taxon node as a predator. Based on our diet citations (see supplemental materials), there was a very small likelihood for many benthic invertebrate groups to be preying on phytoplankton freshly deposited on the sediment surface. That most of the removed interactions involved benthic predator–phytoplankton prey seemed to support our decision for removing the more unlikely interactions. For predator–prey links present for both Time 1 and Time 2, this weight was kept the same across time except for those links associated with five nodes of benthic invertebrate taxa. There was evidence in the benthic invertebrate dataset that horizontal peak abundance shifted between Time 1 and Time 2. Their links reflected this change between the two time periods. The Time 1 and Time 2 food web can be found in Supplemental Materials.

2.3. Quantifying subsystems

To detect subsystems, we analyzed the food webs for both time periods using the odds ratio method employed by KliqueFinder (Frank, 1995, 1996). This method seeks subsystems within a network structure by iteratively reassigning taxa to subsystems to maximize the odds that links occur within subsystems versus links between subsystems (Table 1). The method sums up all of weights (I_{ij}) associated with the links between taxon i and taxon j present in the food web ($\Sigma_i\Sigma_j I_{ij}$). This sum is separated into two values based on two categories: one category containing links that occur within subsystems (cell D in Table 1) because taxon i and taxon j are in the same subsystem and are linked together and one category containing links that occur between subsystems (cell B in Table 1) because taxon i and taxon j are in different subsystems and are linked together. The potential number of links (P) that can occur between all taxa pairs in a network [$n \times (n-1)$ where n = total number of taxa] are assigned the maximum weight (I_{max}, in this study maximum weight = 1.00). The difference between the total weight that could potentially occur in the system [$n \times (n-1) \times I_{max}$] and the sum of the weights that actually occur or are present in the system ($\Sigma_i\Sigma_j I_{ij}$) provides the weight associated with links that have the potential to be in a system but are absent (not present, no link occurring between a taxa pair). This difference is divided among the two categories the same as the sum of the weights: one category containing links that are absent within subsystems (cell C in Table 1) because taxon i and taxon j are in the same subsystem and

Table 1
The calculation of the odds ratio based on link occurrences between taxa pairs.

		Link occurring		
		No	Yes	
Subsystem membership	Different	A	B	$n(n-1)I_{max} - [\Sigma_g n_g(n_g-1)]I_{max}$
	Same	C	D	$[\Sigma_g n_g(n_g-1)]I_{max}$
		$n(n-1)I_{max} - \Sigma_i\Sigma_j I_{ij}$	$\Sigma_i\Sigma_j I_{ij}$	$n(n-1)I_{max}$

For the symbols: I_{ij} represents the weight of a link between taxon i and taxon j, I_{max} represents the maximum weight out of all I_{ij}, n represents the number of taxa in the food web, and n_g represents the number of taxa in subsystem g.

are not linked together and one category containing links that occur between subsystems (cell A in Table 1) because taxon i and taxon j are in different subsystems and are not linked together. The algorithm starts with an initial assignment of taxa to subsystems based on selecting an initial triad. After the initial subsystem assignment, the algorithm calculates the odds that a link occurs within a subsystem versus between subsystems. This odds ratio takes into account on the weights assigned to present and absent links where the odds ratio is calculated as [(AxD)/(BxC)]. The algorithm then reassigns taxa to subsystems iteratively until a local maximum of the odds ratio is found (Frank, 1995). From this algorithm, we obtain an odds ratio associated with the assignments of taxa to subsystems. Two advantages of this method are that a taxon can only be assigned to one subsystem, not multiple subsystems, and the number of subsystems are not defined *a priori* to the analysis. This method has previously been shown to successfully identify subsystems in food webs (Krause et al., 2003) and has been shown to be effective in Monte Carlo simulations (Frank, 1995).

We tested for significant subsystems by conducting a Monte Carlo simulation (Frank, 1995, 1996). Links and their weights were randomly assigned to taxa pairs to generate 500 random food webs. The constraints for the generated food webs were that the sum of weights for each row was equal to the row marginal of the original food web (row represented predators and columns represented prey; Frank, 1995; Krause et al., 2003). The odds ratio was calculated after applying the clustering algorithm to each random food web to generate a distribution of odds ratios for a probability estimate that the odds ratio found for Time 1 and Time 2 was different from a random distribution ($\alpha = 0.05$).

Similarity in subsystem assignment between Time 1 and Time 2 was tested to determine if subsystem assignment changed across time. This analysis tested our expectation of a stable subsystem assignment across time because our weights were based on stable characteristics of taxa. The primary change from Time 1 and Time 2 was the difference in whether taxa were present in one time period but not in the other time period (e.g., zebra mussels were present in Time 2 but not Time 1). We did not expect that to have a significant influence on a taxon's subsystem assignment. To test our expectations, we summed the number of taxa pairs where both taxa were members of the same subsystem in Time 1 and Time 2 (E), summed the number of taxa pairs where taxa were members of different subsystem in Time 1 and Time 2 (H), summed the number of taxa pairs that where the taxa pair were members of the same subsystem in Time 1 and members of different subsystems in Time 2 (G), and summed the number of taxa pairs where taxa were members of different subsystems in Time 1 and members of the same subsystem in Time 2 (F). We calculated the odds ratio as follows: [(E × H)/(G × F)]. This is the increase in the odds that two taxa will be in the same subsystem in Time 2 given that they were in the same subsystem in Time 1.

2.4. Shannon's equations for quantitative food web properties

The most basic of structural properties for food webs are the number of feeding links between prey and predators, number of prey taxa, and number of predator taxa. Most commonly these properties are measured qualitatively, that is, without taking into account weights on links to differentiate between strong and weak links. However, qualitative food web properties have a tendency for inaccurately reproducing the structure of food webs (Bersier et al., 2002; Krause et al., 2003).

Quantitative measures are those derived from the weights assigned to links in the food web. Shannon's equations (1949) provided us with quantitative measures of these basic food web properties. Specifically, Shannon's equations characterize the disorder or uncertainty in the probability of the transfer of information,

such as resources, across pathways from sources (prey) that send the information to the sinks (predators) that receive the information (Shannon and Weaver, 1949). As the disorder or uncertainty increases, the more resource flow becomes evenly distributed across links. The greatest level of disorder or uncertainty occurs when there are equal weights across links leading to an equal probability for resources to flow across any link in the food web. The more uneven weights and their resulting probabilities become, the more certainty we have about what links resources will be flowing across. With Shannon's equations, we measured temporal changes in basic food web properties for Lake Michigan by quantifying how the distribution of resource flow from prey to predators changed from Time 1 to Time 2.

Our primary focus was on how the distribution of resource flows across links changed across time at our two system levels not in how the size of the system changed. Therefore, we normalized the quantitative basic food web properties relative to their maximum values. These maximum values depended on whether the property was measured for Time 1 or for Time 2 and measured for the system or subsystem level. The maximum Shannon value that can be reached through equal probabilities is equal to the log of a basic food web property's corresponding qualitative value (Ulanowicz and Wolff, 1991; Zorach and Ulanowicz, 2003). The normalized value allowed us to see how quantitative versions of properties changed relative to their qualitative counterpart. If the normalized value declined over time, then we knew that the decline in the quantitative property was the result of a less even distribution in resource flows not a result of a decline in the qualitative property. For example, a decline in normalized links from Time 1 to Time 2 would indicate that resource flows were concentrating onto fewer of the available links in Time 2 than in Time 1.

To approximate resource flow in our food web, we multiplied the relative probability of interaction weight associated with a feeding link between a prey and predator pair (see section on constructing a food web for calculation) and the mean biomass estimate of the prey taxon in that predator–prey pair. Mean biomass was estimated for each taxon for each year available within Time 1 and Time 2 where all taxa had more than one estimate within each time period (see Supplemental Material for biomass estimates and Krause, 2004 for more detail). Biomass estimates were all converted to a common unit of mg of dry weight/m^2 and were based on the spatial area defined in the food web. These estimates were not assumed to be absolute values of biomass but rather were assumed to be reasonable relative indices to aid in quantifying basic network properties because the collection methods were consistent across time periods. The biomass estimate for prey i for a given year within Time 1 was multiplied by the relative probability of interaction ($I_{i,j}$) for Time 1 for each predator (j)–prey (i) pair to give us a new weight, $w_{i,j}$, for each link in the food web. The calculation of this weight is comparable to energy food webs where the consumption rate of a predator is multiplied by the amount of carbon in the population of its prey. The primary difference between these two measures is that, in an energy food web, the amount of carbon transferred is assumed to be an absolute value and carbon is a proxy for energy, whereas our weights ($w_{i,j}$) simply represent an index of general resource flow.

Shannon's first equation quantifies the number of links in a network. First, we calculated the probability of resource flowing from prey i to predator j [$p(i,j)$] from our weight of resource flow $w_{i,j}$:

$$p(i,j) = \frac{w_{i,j}}{\sum_{i,j} w_{i,j}} \tag{1}$$

Next we calculated the Shannon's first equation $H(x,y)$, which is the measure of the evenness of the probabilities of resource flow between prey i and predator j across all prey (x) and predator (y)

pairs with links:

$$H(x, y) = -\sum_{i,j} p(i,j) \log p(i,j) \qquad (2)$$

If we transform the $H(x,y)$ by taking its exponential function, it provides us with a quantitative measure of links (Lq) in a food web (Zorach and Ulanowicz, 2003). Here, the maximum of $e^{H(x,y)}$ is equal to its qualitative counterpart, the number of links (L) in a food web. The maximum occurs when there is an equal probability of resource flow across all links; that is, the weights on the links are all even or equal. Uneven weights result in uneven probabilities, where the more uneven they are, the smaller the value for quantitative links. Low normalized values indicate most of the resources are flowing across only a few of all of the available links (a few strong and many weak links).

Shannon's modification of Eq. (2) (Shannon, 1948) helps us to quantify the distribution of resource flow from prey and the distribution of resource flow to predators. In the equation for prey, the log of the probability of resource flow between prey i and predator j is replaced by log of the sum of probabilities $p(i,j)$ associated with prey i. This is equivalent to taking the probability of the amount of resource flow from prey i:

$$H(x) = -\sum_{i,j} p(i,j) \log \sum_j p(i,j) \qquad (3)$$

$H(x)$ is the measure of the evenness in the probabilities associated with resources flowing from prey. The probabilities associated with predators, $H(y)$, is similarly measured by replacing the summed probabilities across prey i by the summed probabilities across predator j. $H(y)$ calculated the evenness in the probabilities of resources flowing to predators. Quantitative measure of prey nodes (Xq) was calculated as $e^{H(x)}$ and quantitative measure of predator nodes (Yq) was calculated as $e^{H(y)}$. The maximum value of $e^{H(x)}$ is always equal to the qualitative counterpart of the property, number of prey nodes (X) in a food web. To reach the maximum, there would have to be an equal amount of resource flow from every prey node in the food web. Similarly, the maximum value of $e^{H(y)}$ is its qualitative counterpart of the property, the number of predator nodes (Y), which is reached when there is an equal amount of resource flow going to every predator node. The smaller the quantitative measures, the more uneven the resource flow from prey nodes and the more uneven the resource flow to predator nodes. Low normalized values or prey nodes indicate that a few of the prey nodes are dominating the resource flows given all of the prey nodes that send or provide resources. A similar interpretation can be made for low normalized values of predator nodes, where a few predators dominate resource flows given all of the predator nodes that to receive resources.

Density, also known as connectance, is an important food web property because it is prominent in the diversity versus stability debate (May, 1973; Bersier et al., 2002). The qualitative version of density is calculated as $L/(X \times Y)$, the proportion of realized links to potential links in the network. Quantitative versions of links, prey, and predators can be substituted for their qualitative counterparts to calculate quantitative measure of density for the network [Dq = Lq/(Xq × Yq)]. Algebraically, this calculation is equivalent to $e^{H(x,y) - [H(x) + H(y)]}$. The maximum value for Dq is 1, the same as the qualitative version, because the links that are realized in a network cannot exceed the potential links for a network. Thus, there is no need for normalization. Higher Dq can be interpreted as high evenness of resource flow across links relative to the evenness of resource flow from sources and evenness of resource flow to sinks. The less even resource flow across links with respect to resource flow from sources and resource flow to sinks indicates that resource flow is more constrained

in what sink resources flows to when it is known what source resources flowed from. In other terms, the smaller the proportion, the less uncertainty there is in resource flow from sources to sinks. It is directly related to the measure of the mutual information, a concept from information theory (Cover and Thomas, 1991), where quantitative density is the inverse of mutual information.

To determine large changes in food web structure through time, we calculated the uncertainty in these normalized network properties (NXq, NYq, NLq) and Dq for the higher system level for resource flows within the overall food web and for the lower system level for resource flows within the subsystems and resource flows between subsystems. Because not all collections had data for all five years and were sampled independently in the field, we calculated the normalized network properties for every possible combination of the biomass data sets for that time period as our measure of the uncertainty we had for each property. The biomass data sets were divided by collection and year (see Supplemental Materials). For example, the benthic invertebrate biomass estimates were based on the same samples taken during the same collecting trips for years 1980 and 1981 in Time 1, providing two data sets. Some collections were species specific, such as *Bythotrephes*. Samples of *Bythotrephes* were collected in years 1995, 1996, 1997, 1998, and 1999 for Time 2, providing five data sets. For Time 1, there were a total of 2000 combinations of data sets for a total of 2000 estimates for each normalized property. Time 2 had 24,000 combinations for a total of 24,000 estimates for each normalized property, primarily because of the addition of the *Bythotrephes* data set and the addition of three more years for phytoplankton data in Time 2 compared to Time 1. To determine if the differences in properties between time periods were large relative to their uncertainty, we compared the minimum and maximum values in their distributions between Time 1 and Time 2. If there was no overlap in the distributions, then the normalized property was considered to have exhibited a large change between Time 1 and Time 2. That is, none of our estimated Time 1 values of a normalized property were found in the Time 2 distribution of values for that property. We developed distributions of the network properties for both the higher and lower system levels in Time 1 and Time 2 giving us 5 distributions per network property (4) per time period (2) for a total of 40 distributions and 20 comparisons in all.

We had two primary assumptions with this analysis of uncertainty. Our first assumption was that we considered the observed inter-annual variation in biomass estimates was a plausible measure of uncertainty regarding the true value of the normalized property for each time period. As noted before, the relative probability of interaction was based on fairly stable taxonomic characteristics, thus we did not incorporate uncertainty related to that measure. However, biomass is a population characteristic, which can carry much inter-annual variability (see Madenjian et al., 2002). We did not consider intra-annual variability because the datasets were collected at different time and space intervals and using different gear, so intra-annual variability would not be comparable among the datasets. That is, intra-annual variability would be highly influenced by how the data were collected. Our second assumption for uncertainty was that each dataset varies independently of all other datasets whereas the biomass estimates within a dataset are not independent of the other biomass estimates within that dataset. This assumption likely yields an overestimate of the actual uncertainty because there are likely dependencies among datasets across time with those taxa whose populations covary. For example, zooplankton populations may decrease when there is an increase in the number of larval fish or there may be declines in the populations of phytoplankton, zooplankton, and fish larvae from a delayed spring and cooler summer. Because this method would combine datasets from different years inde-

Table 2
Time 1 node subsystem assignment, taxa identification number, and scientific name.

Subsystem 1	
ID #	Name
Phytoplankton—Centric Bacillariophyceae	
83	*Aulacoseria subarctica*
84	*Stephanodiscus* spp.
85	*Cyclostephanos* spp. and *Cyclotella* spp.
86	*Rhizosolenia* spp.
87	*Stephanodiscus hantzschii f. tenuis*
88	*Melosira islandica*
89	*Stephanodiscus alpinus*
90	*Actinocyclus* sp. and *Cyclotella* sp.
91	*Stephanodiscus* spp.
92	*Stephanodiscus niagarae*
93	*Stephanodiscus hantzschii*
94	*Cyclotella comensis*
95	*Cyclotella* spp.
96	*Cyclotella pseudostelligera*
175	*Cyclotella* spp.
Phytoplankton—Pennate Bacillariophyceae	
24	*Achnanthes* spp.
23	*Fragilaria* spp.
25	*Nitzschia* spp.
26	*Fragilaria* spp. and *Synedra* sp.
27	*Amphora* sp. and *Navicula* spp.
28	*Nitzschia* spp.
29	*Diatoma* spp.
30	*Fragilaria* spp.
31	*Nitzschia* spp.
32	*Nitzschia* spp.
33	*Tabellaria fenestrata*
34	*Asterionella* sp. and *Tabellaria* sp.
35	*Nitzschia* spp.
36	*Fragilaria* sp. and *Synedra* sp.
37	*Cymatopleura solea*
38	*Synedra* spp.
39	*Nitzschia* spp.
41	*Synedra* spp.
42	*Fragilaria pinnata*
170	*Meridion circulare*
171	*Gomphonema olivaceum*
172	*Cymbella microcephala*
Phytoplankton—Dinophyceae	
79	*Amphidinium* sp.
80	*Gymnodinium* sp. and *Peridinium* sp.
81	*Peridinium* sp.
82	*Ceratium hirundinella*
Crustacean Zooplankton	
1	*Bosmina longirostris*
2	*Daphnia galeata mendotae*
3	*Daphnia retrocurva*
4	*Diaphanosoma* spp.
5	*Eubosima coregoni*
6	*Leptodora kindti*
7	*Polyphemus pediculus*
8	*Cyclops* spp.
9	*Diacyclops thomasi*
10	*Mesocyclops edax*
11	*Tropocyclops prasinus mexicanus*
12	*Epischura lacustris*
13	*Eurytemora affinis*
14	*Leptodiaptomus ashlandi*
15	*Leptodiaptomus minutus*
16	*Leptodiaptomus sicilis*
17	*Diaptomus* spp. copepodites
18	*Limnocalanus macrurus* copepodites
19	*Limnocalanus macrurus* adults
20	*Skistodiaptomus oregonensis*
21	Nauplii
165	*Alona* spp.
166	*Chydorus spaericus*
167	*Holopedium gibberum*
168	*Acanthocyclops vernalis*
169	*Ceriodaphia* spp.
Opposum shrimp	
22	*Mysis relicta*

Subsystem 1 (continued)	
ID #	Name
Phytoplankton—Chlorophyceae	
43	*Planktonema lauterbornii*
44	*Crucigenia* sp. and *Gloeocystis* sp.
45	*Dictyosphaerium* spp. and *Chlamydocapsa* sp.
46	*Scenedesmus* spp.
47	*Stichococcus* spp.
48	*Elakatothrix* spp. and *Kirchneriella* sp.
49	*Nephrocytium* sp. and *Oocystis* sp.
50	*Monoraphidium* spp.
51	*Ankistrodesmus* spp.
52	*Monoraphidium* spp.
53	*Crucigenia* spp.
54	*Oocystis* spp.
55	*Oocystis* spp.
173	*Sphaerellocystis* spp.
Phytoplankton—Chrysophyceae	
56	Protozoa
57	*Chromulina* sp. and *Ochromonas* spp.
58	*Dinobryon* spp.
59	Haptophyceae
60	*Bitrichia* sp. and *Rhizochrysis* sp.
61	*Kephyrion* spp. and *Pseudokephyrion* spp.
62	*Dinobryon* spp.
63	*Mallomonas* spp.
64	*Kephyrion* spp.
65	*Dinobryon* spp.
66	*Paraphysomonas* sp.
Phytoplankton—Cryptophyceae	
67	*Chroomonas* and *Rhodomonas* spp.
68	*Cryptomonas* spp.
69	*Rhodomonas* spp.
70	*Cryptomonas* spp.
71	*Cryptomonas* spp.
72	*Cryptomonas* spp.
Phytoplankton—Cyanophyceae	
73	*Agmenellum* sp., *Anacystis* spp., *Aphanothece* spp., *Aphanocapsa* spp. & *Gomphosphaeria* spp.
74	*Anacystis* sp. and *Synechoccus* sp.
75	*Microcystis* spp.
76	*Anabaena* spp.
77	*Oscillatoria* spp.
78	*Oscillatoria limnetica*
Phytoplankton—Euglenophyceae	
174	*Euglena* sp.
Fish	
142	*Petromyzon marinus*
143	*Alosa pseudoharengus* larvae
144	*Alosa pseudoharengus* adult
145	*Notropis hudsonius*
146	*Osmerus mordax* larvae
147	*Osmerus mordax* adult
148	*Coregonus clupeaformis*
149	*Coregonus hoyi* larvae
150	*Coregonus hoyi* adult
151	*Oncorhynchus kisutch*
152	*Oncorhynchus mykiss*
153	*Oncorhynchus tshawytscha*
154	*Salmo trutta*
155	*Salvelinus namaycush* juvenile
156	*Salvelinus namaycush* adult
158	*Lota lota*
159	*Pungitius pungitius*
160	*Cottus cognatus*
161	*Myoxocephalus thompsonii*
162	*Etheostoma nigrum*
163	*Perca flavescens*
Isopods	
176	*Caecidotea racovitzai*
Snails	
97	*Valvata sincera*
Amphipod	
101	*Diporeia hoyi*
Dipteran Larvae	
107	*Chironomus anthracinus*

Table 2 (*Continued*)

Subsystem 2			Subsystem 2 (continued)	
ID #	Name		ID #	Name
Phytoplankton—Pennate Bacillariophyceae			**Oligochaetes**	
40	*Nitzschia lauenburgiana*		127	*Aulodrilus americanus*
Fish			128	*Aulodrilus pluriseta*
157	*Percopsis omiscomaycus*		129	*Ilyodrilus templentoni*
Snails			130	*Varichaetadrilus angustipenis*
179	*Amnicola limnosa*		131	*Limnodrilus claparedianus*
180	*Pseudosuccinea columnella*		132	*Limnodrilus hoffmeisteri*
Fingernail clam			133	*Limnodrilus profundicola*
99	*Pisidium henslowanum*		134	*Limnodrilus udekemianus*
100	*Pisidium* spp.		135	*Quistrodrilus multisetosus*
Leech			136	*Spirosperma nikolskyi*
164	*Helobdella stagnalis*		137	*Tasserkidrilus superiorensis*
Dipteran Larvae			138	*Potamothrix moldaviensis*
102	*Procladius* sp.		139	*Potamothrix vejdovskyi*
103	*Potthastia cf. longimanus*		140	*Tasserkidrilus americanus*
104	*Monodiamesa tuberculata*		141	*Tubifex tubifex*
105	*Heterotrissocladius changi*		119	*Enchytraeidae* spp.
106	*Heterotrissocladius oliveri*		120	*Stylodrilus heringianus*
108	*Chironomus fluviatilis*		121	*Arcteonais lomondi*
109	*Chironomus* sp.		122	*Chaetogaster* sp.
110	*Cryptochironomus* sp.		123	*Piguetiella michiganensis*
111	*Cladopelma* sp.		124	*Stylaria lacustris*
112	*Paracladopelma winnelli*		125	*Uncinais uncinata*
113	*Paracladopelma undine*		126	*Vejdovskyella intermedia*
114	*Polypedilum scalaenum*		178	*Limnodrilus spiralis*
115	*Polypedilum tuberculum*			
116	*Robackia cf. demeijerei*			
117	*Micropsectra* sp.			
118	*Tanytarsus* sp.			
177	*Cryptochironomus cf. fulvus*			
191	*Cryptochironomus cf. digitatus*			
192	*Demicryptochironomus* sp.			
193	*Paracladopelma camptolabis*			
194	*Polypedilum nereis*			

pendently, the combinations likely resulted in a distribution of normalized properties that was greater (that is, more variable) than what might have been observed had the datasets been amenable for calculating normalized properties for each of the five years within each time period. With an overestimate of uncertainty, we are confident that the detected differences in a property are probably valid. Conversely, we may be overestimating the variance, thus, there may be changes in properties we were unable to detect.

3. Results

The Time 1 and Time 2 food webs had significant subsystem structures where the odds ratios for links within versus between subsystems were 23.63 and 31.12, respectively ($p < 0.001$). Two subsystems were detected in both Time 1 and Time 2 food webs, where many of the phytoplankton taxa, zooplankton taxa, and fish taxa were assigned to subsystem 1 and benthic invertebrate taxa were assigned to subsystem 2 (Tables 2 and 3). The odds were high (odds = 20.69) that two taxa in the same subsystem in Time 1 were also in the same subsystem in Time 2. This high odds ratio implies that subsystem assignments were similar across the two time periods. Subsystem 1 had 12 taxa nodes detected in Time 1 but not detected in Time 2. It also had 25 taxa nodes not detected in Time 1 but detected in Time 2, including the invasive taxa of *Bythotrephes* and zebra mussels. Subsystem 2 had four taxa nodes detected in Time 1 but not detected in Time 2. As well, it had seven new taxa nodes not detected in Time 1 but detected in Time 2. Five taxa were assigned to subsystem 1 in Time 1 but then were assigned to subsystem 2 in Time 2 (*Myoxocephalus thompsonii*, *Notropis hudsonius*, and *Pungitius pungitius*—fish, *Chironomus anthracinus*—benthic invertebrate, and a centric diatom group—phytoplankton). No taxa

assigned to subsystem 2 in Time 1 were assigned to subsystem 1 in Time 2.

We found that the subsystem level had seven normalized network properties with large changes relative to its respective uncertainty from Time 1 to Time 2 (non-overlapping distributions) whereas the overall food web had none (that is, the higher system level; Table 4). At the lower system level, the subsystem with pelagic taxa (subsystem 1) had an increase in its normalized prey (NXq) from Time 1 to Time 2 based on resource flow within its subsystem. There was also an increase in the normalized links (NLq) from subsystem 1 to subsystem 2 from Time 1 to Time 2. The subsystem with benthic taxa (subsystem 2) had more large changes relative to uncertainty in food web properties over time than subsystem 1. Normalized prey (NXq) and normalized links (NLq) declined from Time 1 to Time 2 based on resource flow within subsystem 2. In addition, there was an increase in density (Dq) for resource flows within subsystem 2 from Time 1 to Time 2. For resource flow across links from subsystem 2 as prey to subsystem 1 as predators, normalized prey (NXq) and normalized links (NLq) declined from Time 1 to Time 2 based on outgoing resource flow from subsystem 2 to subsystem 1. A table with the minimum value, 5% value, 95% value, and maximum value of each food web property can be found in the supplemental material.

4. Discussion

Our food web fit within the hierarchical system theory, where we successfully identified subsystems within our food web system structure (Simon, 1965; Krause et al., 2003). As with the Chesapeake Bay food web based on interaction strength (Krause et al., 2003), the subsystem 1 represented a pelagic biotic habitat and subsystem 2

Table 3
Time 2 node subsystem assignment, taxa identification number, and scientific name.

Subsystem 1		Subsystem 1 (continued)	
ID #	Name	ID #	Name
Phytoplankton—Centric Bacillariophyceae		**Crustacean Zooplankton**	
83	*Aulacoseria subarctica*	1	*Bosmina longirostris*
84	*Stephanodiscus* spp.	2	*Daphnia galeata mendotae*
85	*Cyclostephanos* spp. and *Cyclotella* spp.	3	*Daphnia retrocurva*
86	*Rhizosolenia* spp.	4	*Diaphanosoma* spp.
87	*Stephanodiscus hantzschii f. tenuis*	5	*Eubosima coregoni*
88	*Melosira islandica*	6	*Leptodora kindti*
89	*Stephanodiscus alpinus*	7	*Polyphemus pediculus*
90	*Actinocyclus* sp. and *Cyclotella* sp.	8	*Cyclops* spp.
91	*Stephanodiscus* spp.	9	*Diacyclops thomasi*
93	*Stephanodiscus hantzschii*	10	*Mesocyclops edax*
94	*Cyclotella comensis*	11	*Tropocyclops prasinus mexicanus*
95	*Cyclotella* spp.	12	*Epischura lacustris*
96	*Cyclotella pseudostelligera*	13	*Eurytemora affinis*
185	*Melosira* spp.	14	*Leptodiaptomus ashlandi*
186	*Stephanodiscus* spp.	15	*Leptodiaptomus minutus*
187	*Thalassiosira weisflogii*	16	*Leptodiaptomus sicilis*
188	*Rhizosolenia* spp.	17	*Diaptomus* spp. copepodites
Phytoplankton—Pennate Bacillariophyceae		18	*Limnocalanus macrurus* copepodites
24	*Achnanthes* spp.	19	*Limnocalanus macrurus* adults
23	*Fragilaria* spp.	20	*Skistodiaptomus oregonensis*
25	*Nitzschia* spp.	21	Nauplii
26	*Fragilaria* spp. and *Synedra* sp.	165	*Bythotrephes cederstroemii*
27	*Amphora* sp. and *Navicula* spp.	166	*Daphnia pulicaria*
28	*Nitzschia* spp.	**Phytoplankton—Chlorophyceae**	
29	*Diatoma* spp.	43	*Planktonema lauterbornii*
30	*Fragilaria* spp.	44	*Crucigenia* sp. and *Gloeocystis* sp.
31	*Nitzschia* spp.	45	*Dictyosphaerium* spp. and *Chlamydocapsa* sp.
32	*Nitzschia* spp.	46	*Scenedesmus* spp.
33	*Tabellaria fenestrata*	47	*Stichococcus* sp.
34	*Asterionella* sp. and *Tabellaria* sp.	48	*Elakatothrix* spp. and *Kirchneriella* sp.
35	*Nitzschia* spp.	49	*Nephrocytium* sp. and *Oocystis* sp.
36	*Fragilaria* sp. and *Synedra* sp.	50	*Monoraphidium* spp.
37	*Cymatopleura solea*	51	*Ankistrodesmus* spp.
38	*Synedra* spp.	52	*Monoraphidium* spp.
39	*Nitzschia* spp.	53	*Crucigenia* spp.,
41	*Synedra* spp.	54	*Oocystis* spp.
42	*Fragilaria pinnata*	55	*Oocystis* spp.
167	*Cocconeis placentula var. euglypta*	171	*Eudorina elegans*
168	*Surirella augusta*	172	*Microspora* sp. and *Ulothrix* sp.
169	*Amphipleura pelliucdia*	173	*Franceia* sp., *Monoraphidium* spp., *Tetraedron* spp. *Treubaria* sp. and *Golenkinia* spp.
170	*Synedra delicatissima*	174	*Carteria* and *Chlamydomonas* spp.
Phytoplankton—Cyanophyceae		175	*Closteriopsis longissima*
73	*Agmenellum* sp., *Anacystis* spp., *Aphanothece* spp., *Aphanocapsa* spp. and *Gomphosphaeria* spp.	**Phytoplankton—Chrysophyceae**	
74	*Anacystis* sp. and *Synechoccus* sp.	56	Protozoa
75	*Microcystis* spp.	57	*Chromulina* sp. and *Ochromonas* spp.
76	*Anabaena* spp.	58	*Dinobryon* spp.
77	*Oscillatoria* spp.	59	Haptophyceae
78	*Oscillatoria limnetica*	60	*Bitrichia* sp. and *Rhizochrysis* sp.
182	*Chroococcus* spp.	61	*Kephyrion* spp. and *Pseudokephyrion* spp.
Phytoplankton—Dinophyceae		62	*Dinobryon* spp.
79	*Amphidinium* sp.	63	*Mallomonas* spp.
80	*Gymnodinium* sp. and *Peridinium* sp.	64	*Kephyrion* spp.
81	*Peridinium* sp.	65	*Dinobryon* spp.
82	*Ceratium hirundinella*	66	*Paraphysomonas* sp.
183	*Glenodinium* sp.	176	*Stichogloea* sp.
184	*Gymnodinium helveticum var. achroum*	177	*Hyalobryon* sp.
Opposum shrimp		178	*Chrysosphaerella* sp. and *Spiniferomonas* sp.
22	*Mysis relicta*	179	*Bicoeca* spp.
Snails		180	*Chrysococcus* sp.
97	*Valvata sincera*	181	*Chrysolykos* sp.
Amphipod		**Phytoplankton—Cryptophyceae**	
101	*Diporeia hoyi*	67	*Chroomonas* and *Rhodomonas* spp.
Fingernail clam		68	*Cryptomonas* spp.
98	*Sphaerium* spp.	69	*Rhodomonas* spp.
Zebra Mussel		70	*Cryptomonas* spp.
189	*Dreissena polymorpha*	71	*Cryptomonas* spp.
		72	*Cryptomonas* spp.

Table 3 (*Continued*)

Subsystem 1		Subsystem 1 (continued)	
ID #	Name	ID #	Name
Fish		**Fish (continued)**	
142	*Petromyzon marinus*	152	*Oncorhynchus mykiss*
143	*Alosa pseudoharengus larvae*	153	*Oncorhynchus tshawytscha*
144	*Alosa pseudoharengus adult*	154	*Salmo trutta*
146	*Osmerus mordax larvae*	155	*Salvelinus namaycush juvenile*
147	*Osmerus mordax adult*	156	*Salvelinus namaycush adult*
148	*Coregonus clupeaformis*	158	*Lota lota*
149	*Coregonus hoyi larvae*	160	*Cottus cognatus*
150	*Coregonus hoyi adult*	162	*Etheostoma nigrum*
151	*Oncorhynchus kisutch*	163	*Perca flavescens*

Subsystem 2		Subsystem 2 (continued)	
ID #	Name	ID #	Name
Phytoplankton—Centric Bacillariophyceae		117	*Micropsectra* sp.
92	*Stephanodiscus niagarae*	118	*Tanytarsus* sp.
Phytoplankton—Pennate Bacillariophyceae		191	*Cryptochironomus cf. digitatus*
40	*Nitzschia lauenburgiana*	192	*Demicryptochironomus* sp.
Fish		193	*Paracladopelma camptolabis*
145	*Notropis hudsonius*	194	*Polypedilum nereis*
157	*Percopsis omiscomaycus*	**Oligochaetes**	
159	*Pungitius pungitius*	127	*Aulodrilus americanus*
161	*Myoxocephalus thompsonii*	128	*Aulodrilus pluriseta*
Amphipod		129	*Ilyodrilus templentoni*
190	*Gammarus* sp.	130	*Varichaetadrilus angustipenis*
Fingernail clam		131	*Limnodrilus claparedianus*
99	*Pisidium henslowanum*	132	*Limnodrilus hoffmeisteri*
100	*Pisidium* spp.	133	*Limnodrilus profundicola*
Leech		134	*Limnodrilus udekemianus*
164	*Helobdella stagnalis*	135	*Quistrodrilus multisetosus*
Dipteran Larvae		136	*Spirosperma nikolskyi*
102	*Procladius* sp.	137	*Tasserkidrilus superiorensis*
103	*Potthastia cf. longimanus*	138	*Potamothrix moldaviensis*
104	*Monodiamesa tuberculata*	139	*Potamothrix vejdovskyi*
105	*Heterotrissocladius changi*	140	*Tasserkidrilus americanus*
106	*Heterotrissocladius oliveri*	141	*Tubifex tubifex*
107	*Chironomus anthracinus*	119	Enchytraeidae spp.
108	*Chironomus fluviatilis*	120	*Stylodrilus heringianus*
109	*Chironomus* sp.	121	*Arcteonais lomondi*
110	*Cryptochironomus* sp.	122	*Chaetogaster* sp.
111	*Cladopelma* sp.	123	*Piguetiella michiganensis*
112	*Paracladopelma winnelli*	124	*Stylaria lacustris*
113	*Paracladopelma undine*	125	*Uncinais uncinata*
114	*Polypedilum scalaenum*	126	*Vejdovskyella intermedia*
115	*Polypedilum tuberculum*	195	*Isochaetides freyi*
116	*Robackia cf. demeijerei*	196	*Orthocladius* sp.

represented a benthic biotic habitat given taxa node assignment (Tables 2 and 3; Krause et al., 2003). These subsystems are considered biotic habitats rather than physical habitats because a few taxa nodes that physically reside in one habitat were assigned to the other habitat based on their feeding interactions. For example, *Diporeia* spp., a benthic invertebrate, was assigned to subsystem 1 because it is an important prey item for some of the fish taxa in subsystem 1 and it consumes high quantities of freshly settled diatoms (Nalepa et al., 2000b). While the terms niche or guild may seem appropriate, niche refers to an individual taxon and not a group of taxa within a subsystem and guild refers to functionally similar taxa, such as fish that eat other fish in the pelagic region.

Our results supported the extension of hierarchical systems theory because the two subsystems adapted differently across time indicating that they were reacting independently in the short-term (Fig. 3). Internally, subsystem 1 exhibited a shift in the flow of resources so that they were more evenly flowing from prey nodes (within NXq) from Time 1 to Time 2, that is, less dominance in resource flows among prey. In contrast, subsystem 2 exhibited resource flow shifts from prey nodes (within NXq) that were more uneven in distribution over the same time period, indicating more

dominance in resource flow by a few prey. In addition, subsystem 2 had two more significant property shifts in resource flow within its subsystem. Its resource flow across links within its subsystem (Within NLq) declined indicating that resource flow was concentrated on few links in Time 2 than in Time 1 (more uneven distribution across links). Essentially, subsystem 2 had resource flow concentrated on fewer links and fewer prey nodes over time. Also, subsystem 2 experienced an increase in its specialization in resource flows from prey to predators within its subsystem from Time 1 to Time 2 as indicated by its increase in density (Dq; Cover and Thomas, 1991). Overall, subsystem 2 appeared to experience more changes in network properties than subsystem 1 plus it had an opposite reaction in one of those properties, normalized quantitative prey nodes, in comparison to the reaction of subsystem 1.

When we look at how the two subsystems relate to each other, more changes emanated from shifts in resource flows from prey in subsystem 2. Subsystem 2 saw a decrease in evenness not only in resources flowing across links to subsystem 1 (Outgoing NLq) but also in the evenness of resources from prey (Outgoing NXq). Just like its internal changes, subsystem 2 had fewer links and fewer prey

Table 4
Normalized network properties compared between Time 1 and Time 2 for the higher and lower system levels. For the lower system, the properties are measured for links that occur within subsystems and links that are outgoing from subsystems.

System Level	Time	Mean Normalized Links (NLq)	Mean Normalized Prey (NXq)	Mean Normalized Predators (NYq)	Mean Density (Dq)
Higher	1	0.11	0.14	0.51	0.25
	2	0.16	0.21	0.58	0.21
Lower					
Subsystem 1 (Pelagic)					
Within	1	0.12	0.17[a]	0.62	0.29
	2	0.21	0.28	0.71	0.26
Outgoing	1	0.03[a]	0.05	0.19	0.64
	2	0.12	0.15	0.47	0.47
Subsystem 2 (Benthic)					
Within	1	0.11[a]	0.14[a]	0.38	0.77
	2	0.06	0.08	0.32	0.84[a]
Outgoing	1	0.17[a]	0.19[a]	0.54	0.53
	2	0.06	0.08	0.31	0.54

[a] Non-overlapping distributions between the network property in Time 1 and the property in Time 2.

nodes controlling resource flow over time related to its outgoing links to subsystem 1. Its shifts in prey biomass also contributed to a decline in the evenness of resources flow to predators (Outgoing NYq) in subsystem 1. Conversely, resources subsystem 1 provided to subsystem 2 through predator–prey interactions increased in its evenness of resource flow across links (Outgoing NLq) from Time 1 to Time 2.

Biologically, we were surprised that subsystem 2, the benthic biotic habitat, demonstrated more changes over time than subsystem 1, the pelagic biotic habitat, given our two primary external
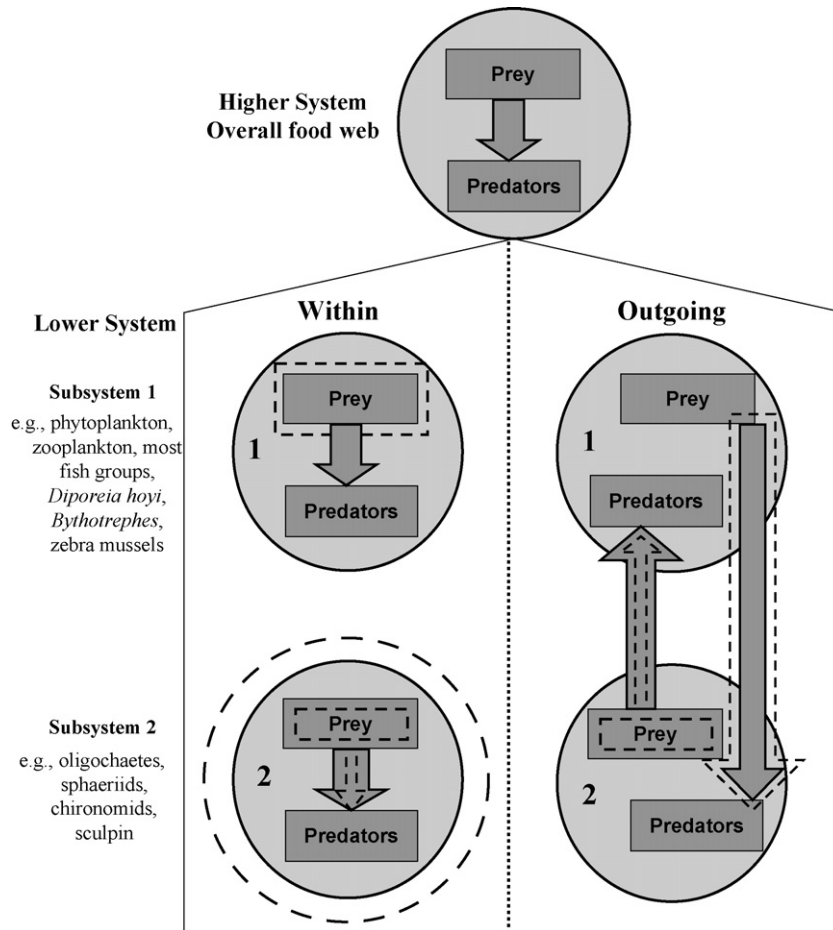

Fig. 3. Conceptual diagram of the changes in food web properties for the higher system level (overall food web) and lower system level (subsystems). Circles represent the food web property of density (Dq). Rectangles represent the food web properties of normalized prey (NXq) or normalized predators (NYq). Arrows represent the food web property of normalized links (NLq). Solid lines represent Time 1 and dashed lines represent Time 2. If dashed lines are outside of the solid, which indicates a large increase in the food web property from Time 1 to Time 2 relative to its uncertainty (non-overlap in property distributions between Time 1 and Time 2). If the dashed line is inside the solid line, that indicates a large decrease in the food web property from Time 1 to Time 2 relative to its uncertainty.

perturbations, nutrient loading and introduced species, are thought to impact pelagic taxa more. The reduction of phosphorous loading would impact phytoplankton, which were primarily located in subsystem 1. The two invading species were assigned to subsystem 1 as well. With both of these external perturbations directly impacting subsystem 1, we expected this subsystem to experience more changes in its food web properties. The reduction in phosphorous loadings is thought to have changed phytoplankton communities from population dominance of eutrophic species to mesotrophic, including the increase the diatom populations in the summer as a result of less silica depletion in the spring (Fahnenstiel and Scavia, 1987; Barbiero et al., 2002; Madenjian et al., 2002; Schelske et al., 2006). *Bythotrephes* have been implicated in the decline in zooplankton species richness (Barbiero and Tuchman, 2004). Zebra mussels have the potential to affect phytoplankton through consumption at high filtering rates (Vanderploeg et al., 2002). All of these factors could have lead to changes in the distribution of resource flow across links and to predators. They likely all contributed to the increase observed in the normalized prey (NXq) for resource flows within subsystem 1 and going to subsystem 2. Particularly, zebra mussels have been implicated in the decline of *Diporeia* spp., a major prey item for a few of the fish species found in subsystem 1 (Nalepa et al., 2000b; Vanderploeg et al., 2002). *Diporeia* spp. biomass was very high in the early 1980s, thus, they may have been dominating resource flow as a prey item in Time 1 and their decline then helped to increase resource flow evenness from prey in subsystem 1 to predators in subsystems 1 and 2. However, phytoplankton and zooplankton nodes represented most of the prey nodes so *Diporeia* spp. are not likely to be the sole explanation for these large temporal changes in network properties relative to their uncertainty.

While these two perturbations were not directly associated with subsystem 2, there are two important ways in which they may have had a large enough influence to move network properties of this subsystem. The network properties of subsystem 2 all indicate a simpler system in time 2 than in time 1 with a dominance in prey and links and less specialization (as indicated by higher density). Oligochaete and sphaeriid taxa found in subsystem 2 were multiple prey nodes with declining biomass implicated by nutrient reductions (Nalepa et al., 2000a). Zebra mussels changed the physical space on the sediment surface that may have benefited multiple prey nodes taxa: amphipods, turbellarians, chironomids, and gastropods (Vanderploeg et al., 2002). This benefit may have resulted in increases in biomass for some of these prey nodes. The decline of some taxa biomasses with smaller relative probabilities of interaction with their predators and increase in other taxa biomasses with higher relative probabilities of interaction with their predators may have led to greater disparity in biomass distributions creating a more uneven distribution of resource flows across links and from prey. This shift in resource flow would account for the decline we observed in the food web properties associated with subsystem 2. The reassignment of three fish taxa nodes from subsystem 1 in Time 1 to subsystem 2 in Time 2 may have also contributed to the shift in resource flow distribution. The shift in subsystems for these three fish taxa was most likely a result of the new taxa that were added to subsystem 1 in Time 2 (primarily introduced taxa and phytoplankton). After the algorithm placed many of these new taxa into subsystem 1, it then moved these three fish taxa from subsystem 1 to subsystem 2 to increase the odds that interactions were occurring within subsystems rather than between subsystems. While we could try to relate patterns in network properties of subsystems based on how a subset of their components (taxa nodes) reacted to the perturbations, the reality is these network properties are influenced by multiple processes occurring within the subsystem that are not well-understood. In addition, we would need to look at the patterns in relation to the uncertainty,

which could become quite complex in this analysis with almost 200 nodes.

The higher-level system, that is, the overall food web, had no large changes in network properties relative to their uncertainty (no non-overlapping distributions). This pattern supported the second extension of hierarchical system theory, where we expected to detect fewer changes in higher-level properties of the system properties from Time 1 to Time 2 than those observed at the subsystem level. We are not aware of other studies in ecology that have examined system adaptation at both of the system and subsystem levels in relation to hierarchical system theory.

Taking into account the uncertainty in the biomass within our time periods allowed us to perform a rigorous analysis of how our system changed through time. The largest difference in network properties between Time 1 and Time 2 were found in the normalized quantitative predators (NYq) for both subsystems (Table 1), yet the distributions for these properties overlapped between the two time periods indicating that the shifts were not large relative to their uncertainty. This result along with the smaller differences between Time 1 and Time 2 properties that had non-overlapping distributions demonstrate how it can be misleading to interpret changes over time without taking into account the uncertainty of the properties. Properties derived from Shannon's equations, such as Ulanowicz's capacity and ascendancy (1997), are sometimes compared across systems or across time for the same system without taking account the uncertainty in these measures (e.g., Monaco and Ulanowicz, 1997; Pérez-España and Arreguín-Sánchez, 1999). This study highlights the importance of taking into account biomass variability for taxa nodes when weights on links incorporate a biomass estimate and when making comparisons of network properties across time or across systems. In addition, the subsystem analysis was also statistically rigorous by testing the clustering parameter (odds ratio) against a distribution of odds ratios from random food webs.

We presented in detail a novel method for constructing a food web given the datasets available, primarily from long-term monitoring programs. In addition, we applied the recommendations outlined in Cohen et al. (1993) to generate a well-constructed food web. When choosing which data to include in our food web, we laid out explicit setting guidelines including the temporal boundaries of season and year and spatial boundaries of latitude and longitude and bottom depth boundaries that collections must have been made in to be included in the analysis. We chose datasets within taxonomic groups that we thought were the most comparable within our boundaries. A taxon node was defined to the species level except in cases where aggregation or disaggregation was warranted. The links between predators and prey were based on inferences from prior publications and expert opinions. Full documentation for constructing the food web has been provided in the supplemental materials, including references of where values were obtained. The last recommendation from Cohen et al. (1993) is for creating food webs through collaboration, which our food web meets as demonstrated by our author list and acknowledgements section. We have demonstrated that a well-constructed food web model developed from empirical data can test system and ecological theories in real-world ecological systems (e.g., Dunne et al., 2002).

Even with choosing the most data rich time periods and spatial area for comparability, there were still components within the food web that were not included for lack of data. The most glaring omissions in our food web are the taxonomic groups of picoplankton, benthic plankton, rotifers, microbial groups including bacteria, and most larval fish, the lack of representation of fall and winter seasons, and the lack of nearshore information. These areas of the food web were not monitored at a level that would allow us to follow all of the recommendations of Cohen et al. (1993) or to conduct the uncer-

tainty analysis for changes in key network properties. Although our food web does not completely capture the entire food web, it is one of the few large, well-constructed food webs published, where there are also weights on links. As such, we would expect this food web to be used by other researchers in future studies on systems and ecological network theory. However, we recognize that our results are confined to the system as described in this study based on the boundaries, nodes, and links that were included within the system.

Our study only touches on how ecological networks adapt by supporting two extensions of hierarchical systems theory. To fully explore implications of this theory and its extensions on the adaptations of ecological networks, we suggest more research employing rigorous analyses on the trajectories of quantitative network properties. The quantitative network properties should be derived from ecological networks that are well constructed and these properties should include measure of their uncertainty.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.07.021.

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