



A food web modeling analysis of a Midwestern, USA eutrophic lake dominated by non-native Common Carp and Zebra Mussels



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ABSTRACT

Food web modeling is recognized as fundamental to understanding the complexities of aquatic systems. Ecopath is the most common mass-balance model used to represent food webs and quantify trophic interactions among groups. We constructed annual Ecopath models for four consecutive years during the first half-decade of a zebra mussel invasion in shallow, eutrophic Clear Lake, Iowa, USA, to evaluate changes in relative biomass and total system consumption among food web groups, evaluate food web impacts of non-native common carp and zebra mussels on food web groups, and to interpret food web impacts in light of on-going lake restoration. Total living biomass increased each year of the study; the majority of the increase due to a doubling in planktonic blue green algae, but several other taxa also increased including a more than two-order of magnitude increase in zebra mussels. Common carp accounted for the largest percentage of total fish biomass throughout the study even with on-going harvest. Chironomids, common carp, and zebra mussels were the top-three ranking consumer groups. Non-native common carp and zebra mussels accounted for an average of 42% of the total system consumption. Despite the relatively high biomass densities of common carp and zebra mussel, food web impacts was minimal due to excessive benthic and primary production in this eutrophic system. Consumption occurring via benthic pathways dominated system consumption in Clear Lake throughout our study, supporting the argument that benthic food webs are significant in shallow, eutrophic lake ecosystems and must be considered if ecosystem-level understanding is to be obtained.

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1. Introduction

Lakes are economically and ecologically important ecosystems. In the United States there are over 68,000 bodies of water exceeding 4 ha recognized as lakes for a national lakes assessment (USEPA, 2009). The economic value of lakes and other freshwater bodies in the United States was estimated as \$580 Billion (U.S. dollars) two decades ago (Carson and Mitchell, 1993). A 2006 estimate placed the economic value of fishing alone in lakes in the United States at \$30 Billion (U.S. dollars) (USEPA, 2009). Understanding how these valuable natural resources function is a priority for ensuring their preservation and protecting these significant economic resources.

There are numerous threats to the ecological and economic value of lakes. Impaired physical habitat, eutrophication, non-native nuisance species, and overabundant blue green algae are

among the primary threats to the ecology of lakes (Pimentel et al., 2005; USEPA, 2009; NFHB, 2010). Many of these threats operate synergistically, whereby presence or increase in one factor exacerbates the impacts of others. Interactions among threats complicate our understanding of lake ecological integrity and how to manage their consequences, challenging scientists and managers to adopt approaches that account for these interactions.

The common carp *Cyprinus carpio* is a non-native, nuisance species in the United States (Nico et al., 2014) and throughout much of the world (Lever, 1996). The impacts of common carp on lakes are an example of deleterious synergistic effects (Weber and Brown, 2009). Common carp often become abundant (Nees et al., 1957; Crivelli, 1981), consume large amounts of prey (Richardson et al., 1990; Parkos et al., 2003), excrete large amounts of nutrients (Lamarra, 1975; Qin and Threlkeld, 1990), destroy aquatic vegetation (Crivelli, 1983; Bajer et al., 2009), and suspend large amounts of sediment through their feeding activity (Parkos et al., 2003; Chumchal et al., 2005). Despite decades of effort to control common carp abundance using various strategies, sustained population reductions have proved difficult (Rose and Moen, 1953;

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Roberts and Tilzey, 1996; Schrage and Downing, 2004; Colvin et al., 2012). Because of their persistent and significant impacts, common carp are considered one of the most deleterious non-native aquatic nuisance species worldwide (Koehn, 2004; Weber and Brown, 2009).

Zebra mussels (*Dreissena polymorpha*) are also non-native in the United States and are rapidly expanding their distribution (Benson et al., 2014). Like common carp, zebra mussels also exert multiple effects encompassing habitat, water quality, food availability, and blue green algal abundance (Mayer et al., 2014). Zebra mussels rapidly attain high densities, increase water clarity (Reed-Andersen et al., 2000), reduce phytoplankton (Madenjian, 1995; Caraco et al., 1997), shift phytoplankton ratios toward dominance by blue greens (Vanderploeg et al., 2001; Bierman et al., 2005), enhance benthic algal and macroinvertebrate production (Stewart and Haynes, 1994; Ricciardi et al., 1997), and alter habitat for benthic species (Stewart et al., 1998). They are also responsible for enormous economic and remediation costs resulting from their encrusting and degrading lake and shoreline infrastructure and lowering property values (Connelly et al., 2007; Limburg et al., 2010). Due to their rapid expansion and wide-ranging impacts, zebra mussels are also considered to be one of the most deleterious non-native aquatic nuisance species in North America (Strayer, 2009).

Ecosystem-level modeling is increasingly recognized as fundamental to understanding the complexities of aquatic systems, evaluating alternative environmental and management scenarios, and managing their associated fisheries (Jorgensen, 2011; Bigford, 2014). A subset of ecosystem modeling – food web modeling – is a widely used approach for organizing and describing what is known about the organisms inhabiting a lake and how they relate to each other (Belgrano et al., 2005). Mass-balance food web models have been successfully used to represent major species or groups in food webs and to quantify their trophic interactions (Steele, 2009; van Oevelen et al., 2010). Ecopath, part of the Ecopath with Ecosim (EwE) package of food web analysis software is the most common mass-balance model used to represent food webs and quantify trophic interactions among groups (Christensen and Walters, 2004). Since its introduction by Polovina (1984), Ecopath was extended by Christensen and Pauly (1992) and has become the preeminent tool for modeling food webs (Coll et al., 2009). While Ecopath has primarily been used to understand trophic interactions in marine and estuarine systems, it has also been successfully applied to many freshwater systems (e.g., Fayram et al., 2006; Pine et al., 2007; McGregor, 2014; Rogers et al., 2014).

Clear Lake is an important natural resource for the State of Iowa. Over 432,000 people visit Clear Lake annually with economic value of the lake for vacation and recreational use exceeding \$43 Million (U.S. dollars) annually (CARD, 2008). A recreational fishery, primarily for yellow bass *Morone mississippiensis* and walleye *Sander vitreus*, is valued between \$1 and 2.5 Million (U.S. dollars) annually (S. Grummer, Iowa Department of Natural Resources, personal communication). Clear Lake has a history of non-native species invasions, with common carp inhabiting the lake for roughly a century and zebra mussels inhabiting the lake for the last decade (Johnson, 2008; Washburn, 2009).

The goal of this study was to model the food web of Clear Lake, Iowa, during the early stages of a zebra mussel invasion. The specific objectives of this study were to: (1) construct annual Ecopath models for four consecutive years during the first half-decade of the zebra mussel invasion, (2) evaluate changes in relative biomass and total system consumption among food web groups, (3) evaluate food web impacts of common carp and zebra mussels on food web groups, and (4) interpret food web impacts in light of on-going restoration.

2. Methods

2.1. Study area

Clear Lake is a 1474 ha shallow lake (mean depth = 2.9 m) located in the Western Cornbelt Plains ecoregion of north central Iowa in the Midwestern United States (43°08'N, 93°22'W; Fig. 1). Clear Lake water quality has declined over the past century, transitioning from a historically vegetated, clear-water lake to a eutrophic/hypereutrophic turbid-water state characterized by frequent blue green algal blooms and simplified fish and plant communities (Carlander et al., 2001; Downing et al., 2001; Egertson et al., 2004; Niemeier and Hubert, 1986; Wahl, 2001). A commercial fishery is used to reduce common carp biomass (Colvin et al., 2012), with cumulative yield exceeding 1400 t since 1929. Zebra mussels were first detected in Clear Lake in 2005 (Fig. 1), and lake-wide biomass has increased dramatically since their discovery (Colvin et al., 2010). As of 2010, zebra mussels occupied all types of firm substrate in the lake (e.g., gravel, rock, macrophytes).

2.2. Ecopath models

Annual Ecopath models were used to model food web trophic flows over the 2007 to 2010 study period using a combination of data collected in Clear Lake, data collected from similar lakes, and empirical relationships described below. Ecopath is a mass-balance model that constrains food web group production and consumption by two master equations (Pauly et al., 2000). Ecopath partitions annual group production among losses as:

$$\text{Production} = \text{predation} + \text{net migration} + \text{biomass accumulation} \\ + \text{yield} + \text{other mortality}$$

The model also partitions annual consumption among production, respiration, and feces as:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food}$$

Production and consumption equations are specified in terms of rates for each food web group as:

$$B_i \cdot P/B_i = \sum B_j \cdot Q/B_j \cdot DC_{ij} + NM_i \cdot B_i + BA_i \cdot B_i + F_i \cdot B_i \\ + B_i \cdot P/B_i \cdot (1 - EE_i)$$

where B_i is the biomass of group i , P/B_i is production to biomass ratio of group i , B_j is the biomass of predator j , Q/B_j is the consumption to biomass ratio of consumer i , DC_{ij} is the diet fraction of prey i for predator j , NM_i is the annual net migration (i.e., immigration–emigration) rate of group i , BA_i the biomass accumulation rate for group i , F_i is the annual fishing mortality rate of group i , and EE_i is the ecotrophic efficiency for group i . Ecopath requires B , P/B , Q/B , Y , and DC values for each group in the model to solve Eq. (1) (Christensen and Pauly, 1992). The above equation is subject to the constraint that consumption must equal the sum of production, respiration, and unassimilated food for each group by constraining EE to values of 0 to 1. EE_i is difficult to measure in practice and is estimated by solving the linear equation by generalized linear inverse given previous inputs. Groups with EE exceeding 1 are not balanced (i.e., biomass losses exceeds production). The food web model was constructed by linking groups through group specific consumption of prey items. Prey items and diet fractions required to assemble these trophic linkages were determined from a combination of existing lake-specific data and data from similar systems.

All Ecopath models were constructed in EwE version 6.2.0.620 (Christensen and Walters, 2004). The following sections provide

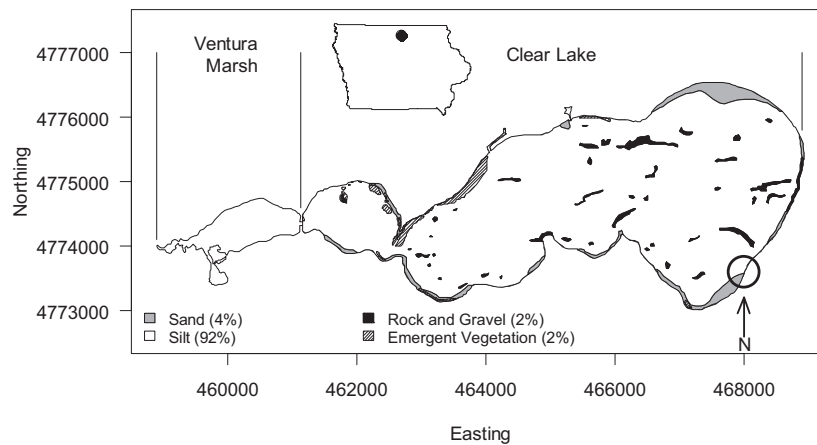


Fig. 1. Map of Clear Lake, with location in north central Iowa (inset). Substrate and vegetation indicated by shading or cross-hatching; percentages of total lake area shown in legend. Ventura Marsh is the major point source of surface water inflow. Circle on southeastern shore is approximate location of first detection of zebra mussels in 2005.

overviews of data sources, quality, and values, but specific details are limited. Further information regarding data used to construct the Ecopath models (e.g., biomass estimates, production, diet compositions) can be found in Appendix S1.

2.3. Data pedigree

Individual parameters used to balance each annual Ecopath model were assigned a data pedigree ranging from 0 (poor) to 1 (excellent) (Christensen et al., 2005). Pedigree index (τ) values represent overall confidence in Ecopath model input parameters, where lower values have greater uncertainty. Data pedigree values are specified in the Ecopath version used for this analysis as: 0 representing parameters that were estimated by Ecopath, borrowed from another model or a guestimate, 0.4 representing parameters that were estimated approximate or indirect methods, 0.7 representing parameters that were estimated by local sampling with low precision, and 1 representing parameters that were estimated by local sampling with high precision. These values correspond to an overall confidence in the parameter value as $\pm 80\%$, $\pm 50\%$, $\pm 30\%$, and $\pm 10\%$, respectively, and provide upper and lower bounds to model mass balancing described below. These confidence levels reflect sources of uncertainty of individual parameters arise from sampling and estimation of biomass density at the lake level and instances where parameters were estimated from empirical relationships or borrowed from similar systems. See (Christensen et al., 2005) for further details regarding data pedigree values.

2.4. Ecopath groups

2.4.1. Consumers

Consumers represented in Ecopath models were aggregated into 32 groups based on taxonomy, diet similarities, and ecological function (Table 1). Fish were represented by 21 groups. Yellow bass, bluegill, black bullhead, and walleye were numerically dominant (Colvin et al., 2010) and two stanzas (i.e., age groupings) were used to capture diet shifts between age 0 (<12 months) and age 1+ (>12 months) fish for these species. Pelagic zooplankton were represented by three groups: cladocerans, copepods, and rotifers. Benthic macroinvertebrates were grouped as chironomids, non-chironomid benthic insects, zebra mussels, other bivalves (e.g., sphaeriidae), snails, two groups of benthic crustaceans, amphipods and non-amphipods (e.g., decapods, ostracods, harpacticoid copepods), and worms (e.g., annelids, turbellarians, nematodes).

2.4.2. Producers and detritus

Producers were organized into five groups based on taxonomy and similar functional ecology (Table 1). Algae were aggregated into 4 groups representing planktonic and benthic sources of edible (e.g., Chlorophyta, Bacillariophyta) and inedible blue green (e.g., Cyanobacteria) groups. An aquatic macrophyte group included submergent, emergent, and floating macroscopic plants. Detritus was represented by a single group and used to accumulate biomass flows from unassimilated food and dead organic matter.

2.5. Ecopath inputs

2.5.1. Biomass (B)

Group-specific biomass (B_i) was estimated using lake- and year-specific information derived from field sampling. A full description of sampling designs and methods of estimating biomass for each group can be found in Colvin et al. (2010) and in Appendix S1. Macrophyte areal cover was monitored by Iowa Department of Natural Resources (IADNR) and macrophyte biomass was estimated using a predictive relationship developed by Hakanson and Bouillon (2002) relating macrophyte coverage to biomass. Biomass values were all assigned a data pedigree of 1 for all years, except macrophytes which were assigned a value of 0.4.

2.5.2. Production (P)

Annual production was estimated for fish and invertebrate groups using published production estimators. Fish production was estimated as:

$$\log_{10}(P) = \log_{10}(0.32) + 0.94 \times \log_{10}(B) - 0.17 \times \log_{10} W_{\max}$$

where P is production in (kg/ha/yr), W_{\max} is the maximum individual weight (g) observed and B is biomass in kg/ha (Downing and Plante, 1993). Annual benthic invertebrate production was estimated using Kalff (2003) modification to Plante and Downing (1989) estimator:

$$\log_{10}(P) = \log_{10}(0.073) + 0.73 \cdot \log_{10}(B)$$

Consumer P/B was calculated by dividing annual production by biomass. Primary producer P/B values were acquired from Jorgensen (2011). Consumer P/B values were assigned a data pedigree value of 0.5 and primary producers were assigned a value of 0.1.

2.5.3. Consumption (input) (Q)

Consumption to biomass ratios (Q/B) were estimated from published predictive relationships and assumed gross growth

Table 1

Taxa included in species or groups for Ecopath models of the food web in Clear Lake, Iowa. Multi-stanza groups indicated by parentheses; 0 in parentheses means young-of-the-year, 1+ in parentheses means one year old and older.

Species or Group	Taxa
Common carp	<i>Cyprinus carpio</i>
Black bass	<i>Micropterus salmoides</i>
Black bullhead (1+)	<i>Ameiurus melas</i>
Black bullhead (0)	<i>Ameiurus melas</i>
Bluegill (1+)	<i>Lepomis macrochirus</i>
Bluegill (0)	<i>Lepomis macrochirus</i>
Channel catfish	<i>Ictalurus punctatus</i>
Other benthivores	<i>Noturus gyrinus</i> <i>Catostomus commersonii</i>
Crappie	<i>Pomoxis nigromaculatus</i> <i>P. annularis</i>
Flathead catfish	<i>Pylodictis olivaris</i>
Darters	<i>Etheostoma nigrum</i> <i>Percina caprodes</i>
Esocids	<i>Esox masquinongy</i> <i>Esox lucius</i>
Walleye (1+)	<i>Sander vitreus</i>
Walleye (0)	<i>Sander vitreus</i>
White bass	<i>Morone chrysops</i>
Bigmouth buffalo	<i>Ictiobus cyprinellus</i>
Small cyprinids	<i>Notemigonus crysoleucas</i> <i>Notropis hudsonius</i> <i>Pimephales promelas</i> <i>Lepomis spp.</i>
Sunfish	<i>Perca flavescens</i>
Yellow perch	<i>Morone mississippiensis</i>
Yellow bass (0)	<i>Morone mississippiensis</i>
Yellow bass (1+)	<i>Morone mississippiensis</i>
Benthic crustaceans (amphipoda)	Amphipoda: Amphipoda
Benthic crustaceans (non amphipoda)	Cladocera: Cladoceran Cladocera: Bosmina Cyclopoida: Cyclopoida Calanoida: Calanoida Harpacticoida: Harpacticoida Isopoda: Asellidae Ostracoda: Ostracod Decapoda: Decapoda Trombidiformes: Hydracarina Coleoptera: Halipidae Diptera: Chaoboridae Diptera: Ceratopogonidae Ephemeroptera: Caenidae Megaloptera: Sialidae Trichoptera: Leptoceridae Trichoptera: Helicopsychidae Trichoptera: Hydroptilidae Lepidoptera: Pyralidae Diptera: Chironomidae
Chironomidae	<i>Dreissena polymorpha</i>
Zebra mussels	<i>Turbellaria</i>
Worms	Hirudinea Veneroida: Sphaeriidae Gastropoda: Ancyliidae Architaenioglossa: Viviparidae Heterostropha: Valvatidae Sorbeoconcha: Hydrobiidae Pulmonata: Physidae Pulmonata: Planorbidae Oligochaeta Nematoda
Copepod	Cyclopoida: Cyclopoida
Cladoceran	Cladocera: Cladoceran Cladocera: Bosmina
Rotifer	Rotifer
Benthic blue green	Cyanobacteria
Planktonic and benthic algae	Chlorophyta Bacillariophyta Dinophyceae Chrysosphyceae Euglenophyta Cryptophyta

Table 1 (Continued)

Species or Group	Taxa
Planktonic and benthic blue green	Cyanobacteria
Macrophytes	Characeae Cyperaceae Hydrocharitaceae Najadaceae Nymphaeaceae Potamogetonaceae Typhaceae Zannichelliaceae
Detritus	Detritus

efficiencies (GGE). Annual consumption (Q) by fish groups was estimated using the empirical consumption estimator for freshwater fish developed by Liao et al. (2005). Fish group Q/B was estimated by dividing the group-specific estimates of Q by B except for age 0 fish. Age 0 fish were assumed to have a GGE of 0.6 to reflect that younger fish have a higher P/Q (Christensen et al., 2005). Invertebrate Q/B was estimated by dividing P/B by P/Q (i.e., gross growth efficiency). P/Q was assumed to be 0.3 for all invertebrate groups except bivalves exclusive of zebra mussels ($P/Q=0.26$), copepods ($P/Q=0.35$), cladocerans ($P/Q=0.27$) and rotifers ($P/Q=0.24$) (Straille, 1997). Invertebrate Q/B estimated from assumed P/Q were compared to Q/B for similar systems to ensure reasonable estimates were used (e.g., Oneida Lake, Jaeger, 2006). A data pedigree value of 0.5 and 0.2 was assigned to each Q/B and P/Q value.

2.5.4. Diet composition

Diet composition (DC) for consumer groups was estimated using lake-specific diet information when available and published diet compositions for groups lacking local information. Fish diet compositions were compiled from a combination of existing studies in Clear Lake, similar nearby lakes, and from published records (e.g., Carlander, 1969; Effendie, 1968; Liao et al., 2002). Diet compositions for benthic invertebrates and zooplankton were compiled from published sources (e.g., Thayer et al., 1997; Thorp and Covich, 2001; Voshell, 2002). Data pedigree values of 0.2 to 0.7 were assigned to each DC to reflect the quality of the data used in estimates. Detailed information on diet composition is in Appendix S1.

2.5.5. Fish yield

Annual commercial and recreational fishery yield values were available for Clear Lake and used in the Ecopath models. Commercial fishery yield of common carp and bigmouth buffalo (*Ictiobus cyprinellus*) biomass was reported directly to IADNR by commercial fishers. An expandable creel survey was used to estimate the annual yield associated with the recreational open water and ice fishery (Colvin et al., 2010; McWilliams, 1984). Commercial and recreational yield was summed within years for Ecopath inputs (i.e., Y_i). A data pedigree value of 1 was assigned to all yield values. Detailed information on fish yield is in Appendix S1.

2.5.6. Import

Data from Clear Lake were used to estimate import of phytoplankton and zooplankton. Phytoplankton and zooplankton flow into the lake from Ventura Marsh and were quantified every 2 weeks during the ice free season in 2008–2010 (Fig. 1). Import to the food web was estimated as the mean biomass (mg wet weight/L) multiplied by the annual inflow to Clear Lake (IADNR TMDL & Water Quality Assessment Section, 2005). Similar data were not available for 2007, so import was assumed to be the average of 2008–2010. Walleye, channel catfish *Ictalurus punctatus*, and esocids (muskel-lunge *Esox masquinongy*, northern pike *Esox lucius*) are imported

into Clear Lake by annual stockings. Annual species-specific stocking biomass was calculated by multiplying the number of fish stocked by the mean weight provided from hatchery records. Values for similar sized fish in [Carlander \(1969\)](#) were used to calculate total biomass when mean weight data were unavailable. Import values are in Appendix S1.

2.5.7. Export

Biomass exported from Clear Lake was estimated for phytoplankton and zooplankton groups based on lake flushing rate. Planktonic phytoplankton and zooplankton loss rates were estimated as the inverse of lake retention time (1.9 years) ([IADNR TMDL & Water Quality Assessment Section, 2005](#); [Scheffer, 1998](#)). Export values are in Appendix S1.

2.6. Ecopath mass-balance

The specific mass-balancing method used is of little consequence to the outcome ([Langseth et al., 2014](#)), so our Ecopath models were mass-balanced by manual iterative adjustment of inputs for groups where EE values were not between 0 and 1. After initial solving of the set of linear equations, groups with the highest ecotrophic efficiencies (EE) were identified and basic inputs were adjusted until EE was between 0 and 1. The process for adjusting problematic groups followed three steps: (1) adjust diet compositions of predators exerting overly high predation, (2) adjust P/B and Q/B values, and (3) adjust B . Attempts were made to keep adjustments within the a priori specified confidence range based on the data pedigree ([Christensen et al., 2005](#)). Once EEs for all groups were between 0 and 1, the Ecopath model was judged to be balanced and used to quantify trophic flows and network indices.

2.7. Consumption (output)

Consumption is a significant component of ecosystem functioning (i.e., cycling of matter). Total annual system consumption was calculated from the mass-balanced Ecopath models as the sum of consumption by all consumer groups within the food web. Consumption by common carp, zebra mussels, and all other groups was calculated and related to total system consumption. Dominant consumers were identified by ranking their proportion of total system consumption, and ranks of important groups were compared among years. Annual consumption of top consumers, common carp, and zebra mussels were compared within each study year.

2.8. Mixed trophic impacts

Impacts of common carp and zebra mussels on other food web groups and the recreational fishery were evaluated using a mixed trophic impact analysis. Mixed trophic impacts (MTI) quantifies the direct and indirect impacts of groups on each other, with values scaled to range from -1 (large negative impact) to 1 (large positive impact). Net impacts are the basis for MTI values and were calculated as the difference of the fraction of prey i in the diet of predator j (i.e., positive impacts), and the fraction of total consumption of i used by predator j (i.e., negative impacts) ([Ulanowicz and Puccia, 1990](#)). MTI values for each group i on group j were calculated as the product of all possible net impacts of group i and group j . Negative MTI values reflect a net negative impact (i.e., direct predation, competition) and positive values reflect a net positive effect (e.g., facilitation, increased prey) ([Christensen and Walters, 2004](#); [Christensen et al., 2005](#); [Janjua and Gerdeaux, 2009](#)). MTI of group i on group j (m_{ij}) was calculated using the network analysis plugin of Ecopath ([Christensen et al., 2005](#); [Ulanowicz and Puccia, 1990](#)). Non-native species' impact on ecosystem components was assessed by examining MTI values for common carp

and zebra mussels. We also examined MTI values for zooplankton and edible phytoplankton groups to identify groups exerting impacts. Mixed trophic impacts of non-native species, zooplankton, and phytoplankton were graphically assessed.

3. Results

3.1. Ecopath models

A total of 38 groups were used to represent consumers, producers, and detritus in the Clear Lake ecosystem ([Table 1](#)). Pedigrees of B , P/B , Q/B , Y , and DC values varied from 0.1 to 1. Total living biomass increased each year of the study, beginning at 191.8 t/km² in 2007, 230.4 in 2008, 242.4 in 2009, and ending at 507.8 t/km² in 2010. The majority of the large increase in total living biomass in 2010 was due to a roughly doubling in planktonic blue green algae biomass, but several other taxa increased as well ([Table 2](#); [Figs. 2 and 3](#)). Despite on-going commercial harvest ([Colvin et al., 2012](#); [Tables S1–S6](#)), common carp accounted for the largest percentage of total fish biomass throughout the study, varying from 55.4% in 2007 to 81.6% in 2010. Zebra mussel absolute and relative biomass increased dramatically over the course of the study. Zebra mussel biomass over the four years was 0.2 t/km² in 2007, 7.1 in 2008, 7.2 in 2009, and 40.8 t/km² in 2010. As a percentage of total benthic invertebrate biomass, zebra mussels accounted for 0.7% in 2007, 38.3% in 2008, 67.3% in 2009, and 89.5% in 2010. Benthic animal biomass was dominated by chironomids, worms, and non-amphipod benthic crustaceans at the start of the study, but by 2010 benthic animal biomass was dominated by zebra mussels ([Figs. 2 and 3](#)). Trophic levels varied from 1 for the primary producer groups to slightly over 4 for flathead catfish and esocids (northern pike and muskellunge), which were primarily piscivorous ([Figs. 2 and 3](#); [Tables S1–S5](#)).

3.2. Consumption

The temporal trend in total annual system consumption was the opposite of total living biomass and was dominated by detritus and algae consumers. Total system consumption was 301.9, 279.1, 264.2, and 190.5 t/km²/yr in 2007 to 2010, respectively. Chironomids, common carp, and zebra mussels were the top-three ranking consumer groups in all four study years, although their relative order varied ([Fig. 4](#)). Together these three groups accounted for an average of 72.6% of the total system consumption over the course of the study. Annual consumption by chironomids varied from 39.7 to 129.8 t/km²/yr, or 18.8 to 43% of total system consumption. Annual common carp consumption varied from 42.1 to 58.9 t/km²/yr, representing 15.9 to 30.9% of total system consumption. Annual zebra mussel consumption varied from 23.9 to 120.3 t/km²/yr, ranging from 7.9 to 45.5% of total system consumption. Together, non-native common carp and zebra mussels accounted for an average of 42.1% of the total system consumption over the course of the study. Consumption by other individual groups was small compared with chironomids, common carp and zebra mussels ([Fig. 4](#)).

3.3. Mixed trophic impacts

Common carp trophic impacts were greatest on groups with which they compete, groups they consume, and the commercial fishery ([Fig. 5](#)). As expected, common carp positively impacted the commercial fishery. Common carp impacts were negative for prey groups, and for bigmouth buffalo, which was likely due to an indirect impact of commercial fishery by-catch.

Zebra mussel trophic impacts increased over the study period with increasing zebra mussel biomass ([Fig. 5](#)). Negative trophic impacts of zebra mussels were observed for groups competing

Table 2

Basic estimates for mass-balanced Ecopath models of the food web in Clear Lake, Iowa, 2007–2010. Species and groups defined in Table 1. *B* is biomass, *P/B* is the production to biomass ratio, *Q/B* is the consumption to biomass ratio, *EE* is ecotrophic efficiency, and *P/Q* is the production to consumption ratio (gross food conversion efficiency).

Species or group	Trophic level	<i>B</i> (t/km ²)	<i>P/B</i> (year ⁻¹)	<i>Q/B</i> (year ⁻¹)	<i>EE</i>	<i>P/Q</i> (year ⁻¹)
2007						
Common carp	2.281	15.23	0.409	3.485	0.901	0.117
Black bass	3.699	0.01	0.92	3.567	0.235	0.258
Black bullhead (1+)	2.824	0.6	0.75	1.083	0.005	0.693
Black bullhead (0)	3.048	0.023	2.1	3.7	0.353	0.568
Bluegill (1+)	3.018	0.04	1.3	1.742	0.548	0.746
Bluegill (0)	3.035	0.005	2.271	4.87	0.138	0.466
Channel catfish	3.209	0.152	0.683	3.526	0.544	0.194
Other benthivores	2.634	0.296	0.661	3.517	0.003	0.188
Crappie	3.084	0.043	0.948	3.543	0.917	0.268
Flathead catfish	4.046	0.2	0.7	3	0.006	0.233
Darters	3.048	0.008	1.846	3.566	0.357	0.518
Esocids	4.059	0.216	0.8	3.5	0.009	0.229
Walleye (1+)	3.068	0.942	0.88	1.251	0.911	0.703
Walleye (0)	3.197	0.038	1.2	3.8	0.542	0.316
White bass	3.225	0.123	0.95	3.529	0.602	0.269
Bigmouth buffalo	3.056	1.6	0.454	3.496	0.336	0.13
Small cyprinids	3.05	0.02	2.5	3.557	0.765	0.703
Sunfish	3.03	0.007	1.9	3.595	0.758	0.529
Yellow perch	2.964	0.022	1.3	3.552	0.883	0.366
Yellow bass (0)	3.027	0.9	2.2	4.667	0.125	0.471
Yellow bass (1+)	3.059	6.996	1.35	1.703	0.143	0.793
Worms	2.063	4.341	0.9	3	0.484	0.3
Chironomidae	2.054	21.633	1.8	6	0.913	0.3
Amphipods	2	0.04	8.85	29.5	0.603	0.3
Benthic crustaceans	2	2.528	1.422	4.741	0.333	0.3
Benthic insects	2.01	0.221	2.745	9.151	0.578	0.3
Snails	2	0.09	4.073	13.575	0.955	0.3
Zebra mussels	2	0.199	36	120	0.011	0.3
Other bivalves	2	0.103	3.376	12.966	0.392	0.26
Copepod	2.116	0.74	5.12	14.629	0.977	0.35
Cladoceran	2	0.815	7.33	27.166	0.987	0.27
Rotifer	2	0.06	15	63.149	0.174	0.238
Benthic blue green	1	8.571	85	0	0.054	0
Benthic algae	1	14.43	113	0	0.057	0
Planktonic blue green	1	108.516	86	0	0.001	0
Planktonic algae	1	1.834	113	0	0.192	0
Macrophytes	1	0.259	8	0	0.073	0
Detritus	1	14,357.15	0	0	0.004	0
2008						
Common carp	2.213	13.8	0.5	3.484	0.842	0.144
Black bass	3.699	0.005	1.053	3.573	0.016	0.295
Black bullhead (1+)	2.82	0.912	1.12	1.488	0.012	0.753
Black bullhead (0)	3.048	0.068	1.65	4.23	0.291	0.39
Bluegill (1+)	3.018	0.065	1.2	1.507	0.556	0.797
Bluegill (0)	3.035	0.006	2.117	4.3	0.329	0.492
Channel catfish	3.2	0.07	0.9	3.537	0.921	0.254
Other benthivores	2.634	0.002	2.8	3.594	0.68	0.779
Crappie	3.084	0.015	2.3	3.56	0.836	0.646
Flathead catfish	4.042	1.25	0.436	3	0.008	0.145
Darters	3.048	0.006	2.45	3.584	0.499	0.684
Esocids	4.07	0.166	0.629	3.525	0	0.178
Walleye (1+)	3.08	1.222	1.1	1.516	0.631	0.726
Walleye (0)	3.197	0.085	1.504	4.3	0.668	0.35
White bass	3.225	0.336	0.6	3.516	0.671	0.171
Bigmouth buffalo	3.056	2.898	0.415	3.487	0.803	0.119
Small cyprinids	3.05	0.01	3	4	0.512	0.75
Sunfish	3.03	0.002	2.6	3.624	0.7	0.717
Yellow perch	2.964	0.015	1.9	3.563	0.448	0.533
Yellow bass (0)	3.027	0.476	2.3	4.87	0.27	0.472
Yellow bass (1+)	3.059	3.117	1.45	1.815	0.675	0.799
Worms	2.063	1.591	3	10	0.358	0.3
Chironomidae	2.054	8.4	3.96	13.2	0.893	0.3
Amphipods	2	0.08	3.875	12.918	0.645	0.3
Benthic crustaceans	2	1.136	3	10	0.416	0.3
Benthic insects	2.01	0.2	3.362	11.206	0.404	0.3
Snails	2	0.02	5.678	18.927	0.646	0.3
Zebra mussels	2	7.125	1.075	3.584	0.008	0.3
Other bivalves	2	0.044	4.236	16.271	0.083	0.26
Copepod	2.116	1.3	2.8	8	0.846	0.35
Cladoceran	2	1.3	3.4	12.601	0.971	0.27
Rotifer	2	0.604	3.2	13.472	0.126	0.238
Benthic blue green	1	1	98	0	0.354	0
Benthic algae	1	0.95	132	0	0.662	0

Table 2 (Continued)

Species or group	Trophic level	B (t/km ²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	P/Q (year ⁻¹)
Planktonic blue green	1	174.208	85	0	0.002	0
Planktonic algae	1	7.604	113	0	0.047	0
Macrophytes	1	0.35	8	0	0.065	0
Detritus	1	18,369.53	0	0	0.003	0
2009						
Common carp	2.03	13.8	0.311	3.05	0.456	0.102
Black bass	3.698	0.001	1.774	3.59	0.009	0.494
Black bullhead (1+)	2.82	0.099	0.946	1.267	0	0.746
Black bullhead (0)	3.048	0.004	1	3.7	0.564	0.27
Bluegill (1+)	3.018	0.011	1.3	1.751	0.674	0.742
Bluegill (0)	3.035	0.001	2.2	4.87	0.869	0.452
Channel catfish	3.199	0.247	0.589	3.52	0.848	0.167
Other benthivores	2.634	0	2.054	3.606	0.057	0.57
Crappie	3.084	0.016	1.381	3.56	0.782	0.388
Flathead catfish	4.04	0.001	0.907	3.594	0.004	0.252
Darters	3.048	0.002	2.19	3.585	0.37	0.611
Esocids	4.066	0.001	0.789	3.594	0	0.219
Walleye (1+)	3.073	1.647	0.594	1.089	0.254	0.545
Walleye (0)	3.197	0.029	1.126	3.8	0.253	0.296
White bass	3.225	0.14	0.809	3.527	0.204	0.229
Bigmouth buffalo	3.056	1.1	0.77	3.594	0.879	0.214
Small cyprinids	3.05	0.022	1.819	3.552	0.246	0.512
Sunfish	3.03	0.001	1	3.594	0.88	0.278
Yellow perch	2.964	0.042	1.245	3.543	0.086	0.351
Yellow bass (0)	3.027	0.205	2.3	4.87	0.087	0.472
Yellow bass (1+)	3.056	1.344	1.45	1.815	0.988	0.799
Worms	2.063	0.82	2.113	7.043	0.424	0.3
Chironomidae	2.054	1.75	8.5	28.333	0.665	0.3
Amphipods	2	0.35	5.121	17.069	0.079	0.3
Benthic crustaceans	2	0.2	4.8	16	1	0.3
Benthic insects	2.01	0.232	5.6	18.667	0.125	0.3
Snails	2	0.087	3.53	11.767	0.186	0.3
Zebra mussels	2	7.217	5	16.667	0.002	0.3
Other bivalves	2	0.07	3.135	12.042	0.166	0.26
Copepod	2.116	0.5	4.4	12.571	0.596	0.35
Cladoceran	2	0.516	6.5	24.09	0.562	0.27
Rotifer	2	0.02	15	63.149	0.4	0.238
Benthic blue green	1	13.441	113	0	0.01	0
Benthic algae	1	4.49	113	0	0.086	0
Planktonic blue green	1	190.856	85	0	0.002	0
Planktonic algae	1	2.777	113	0	0.353	0
Macrophytes	1	0.363	9	0	0.523	0
Detritus	1	15,577.46	0	0	0.002	0
2010						
Common carp	2.031	16.9	0.385	3.487	0.136	0.11
Black bass	3.698	0.001	1.551	3.59	0.011	0.432
Black bullhead (1+)	2.82	0.2	0.6	3.551	0.013	0.169
Black bullhead (0)	3.048	0.007	3	14.043	0.436	0.214
Bluegill (1+)	3.018	0.008	1.403	3.565	0.835	0.394
Bluegill (0)	3.035	0.001	2.1	9.556	0.88	0.22
Channel catfish	3.199	0.26	0.617	3.519	0.274	0.175
Other benthivores	2.634	0.069	0.916	3.537	0.008	0.259
Crappie	3.084	0.069	0.859	3.537	0.256	0.243
Flathead catfish	4.037	0.15	0.557	3	0.004	0.186
Darters	3.048	0.002	2.322	3.592	0.954	0.646
Esocids	4.066	0.084	0.612	3.534	0	0.173
Walleye (1+)	3.073	0.4	0.591	3.2	0.687	0.185
Walleye (0)	3.197	0.008	1.62	11.523	0.996	0.141
White bass	3.225	0.087	0.798	3.534	0.278	0.226
Bigmouth buffalo	3.053	1.3	0.595	3.532	0.506	0.168
Small cyprinids	3.05	0.01	1.632	3.563	0.78	0.458
Sunfish	3.03	0.002	2.8	3.611	0.865	0.775
Yellow perch	2.964	0.044	1.196	3.543	0.111	0.338
Yellow bass (0)	3.027	0.104	1.75	9.457	0.379	0.185
Yellow bass (1+)	3.056	1	1.3	3.505	0.98	0.371
Worms	2.063	1.657	1.916	6.385	0.359	0.3
Chironomidae	2.054	2.291	5.2	17.333	0.972	0.3
Amphipods	2	0.063	5.7	19	0.476	0.3
Benthic crustaceans	2	0.437	3.853	12.844	0.497	0.3
Benthic insects	2.01	0.124	3.355	11.184	0.639	0.3
Snails	2	0.055	4.096	13.654	0.434	0.3
Zebra mussels	2	40.784	0.673	1.122	0.003	0.6
Other bivalves	2	0.135	3.135	12.042	0.153	0.26
Copepod	2.116	0.25	4.64	13.257	0.918	0.35
Cladoceran	2	0.3	6.5	24.09	0.975	0.27
Rotifer	2	0.013	7.5	31.575	0.905	0.238
Benthic blue green	1	13.525	113	0	0.009	0

Table 2 (Continued)

Species or group	Trophic level	<i>B</i> (t/km ²)	<i>P/B</i> (year ⁻¹)	<i>Q/B</i> (year ⁻¹)	EE	<i>P/Q</i> (year ⁻¹)
Benthic algae	1	19.181	113	0	0.016	0
Planktonic blue green	1	404.599	85	0	0.003	0
Planktonic algae	1	3.454	113	0	0.12	0
Macrophytes	1	0.259	9	0	0.435	0
Detritus	1	17,432.33	0	0	0.002	0

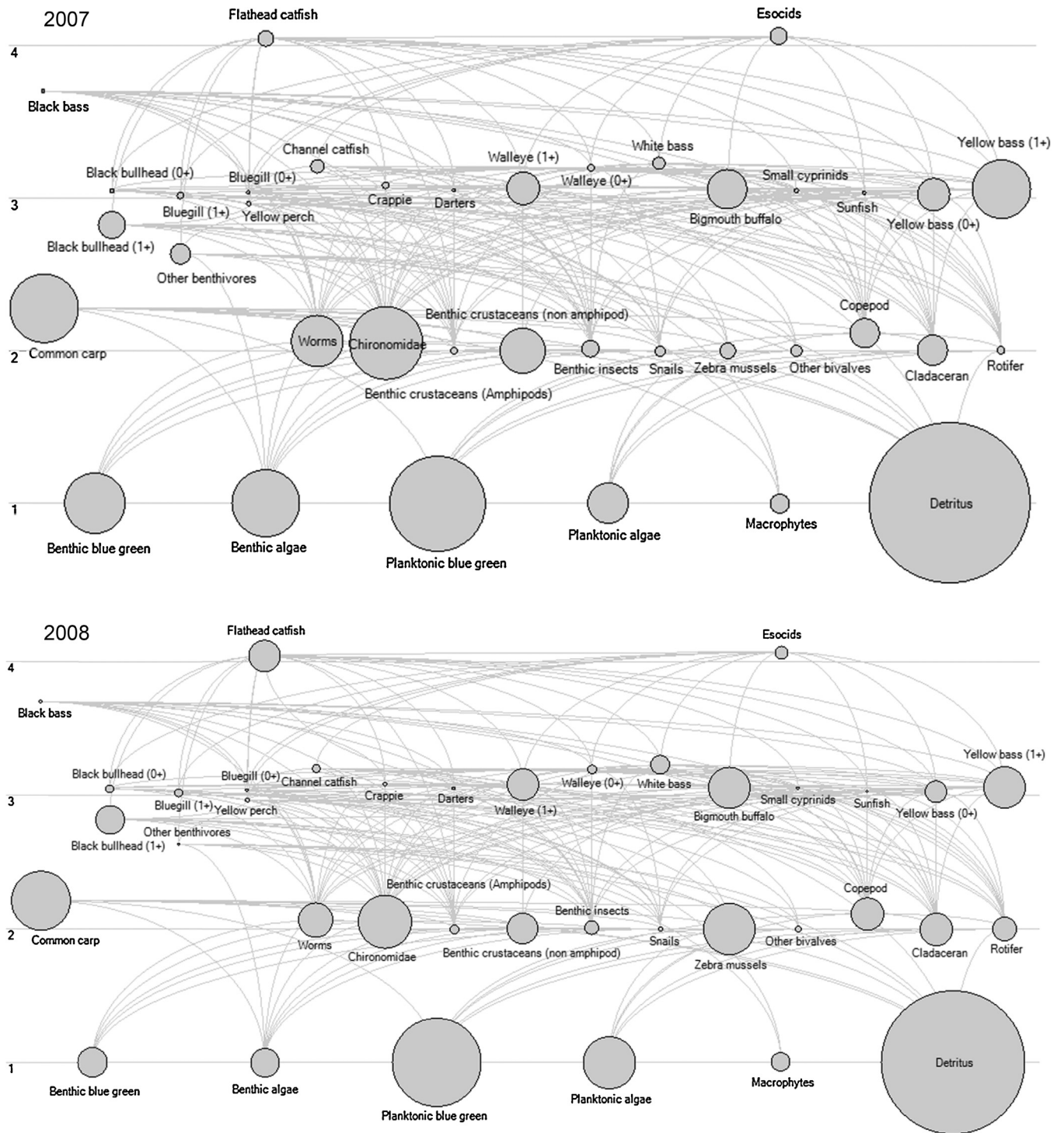


Fig. 2. Trophic flow diagrams of the food web in Clear Lake, Iowa, 2007 (upper panel) and 2008 (lower panel). Size of circles indicates relative biomass of groups. Curved lines indicate trophic pathways. Trophic levels indicated by vertical position (gray horizontal lines) and labeled along left sides of panels.

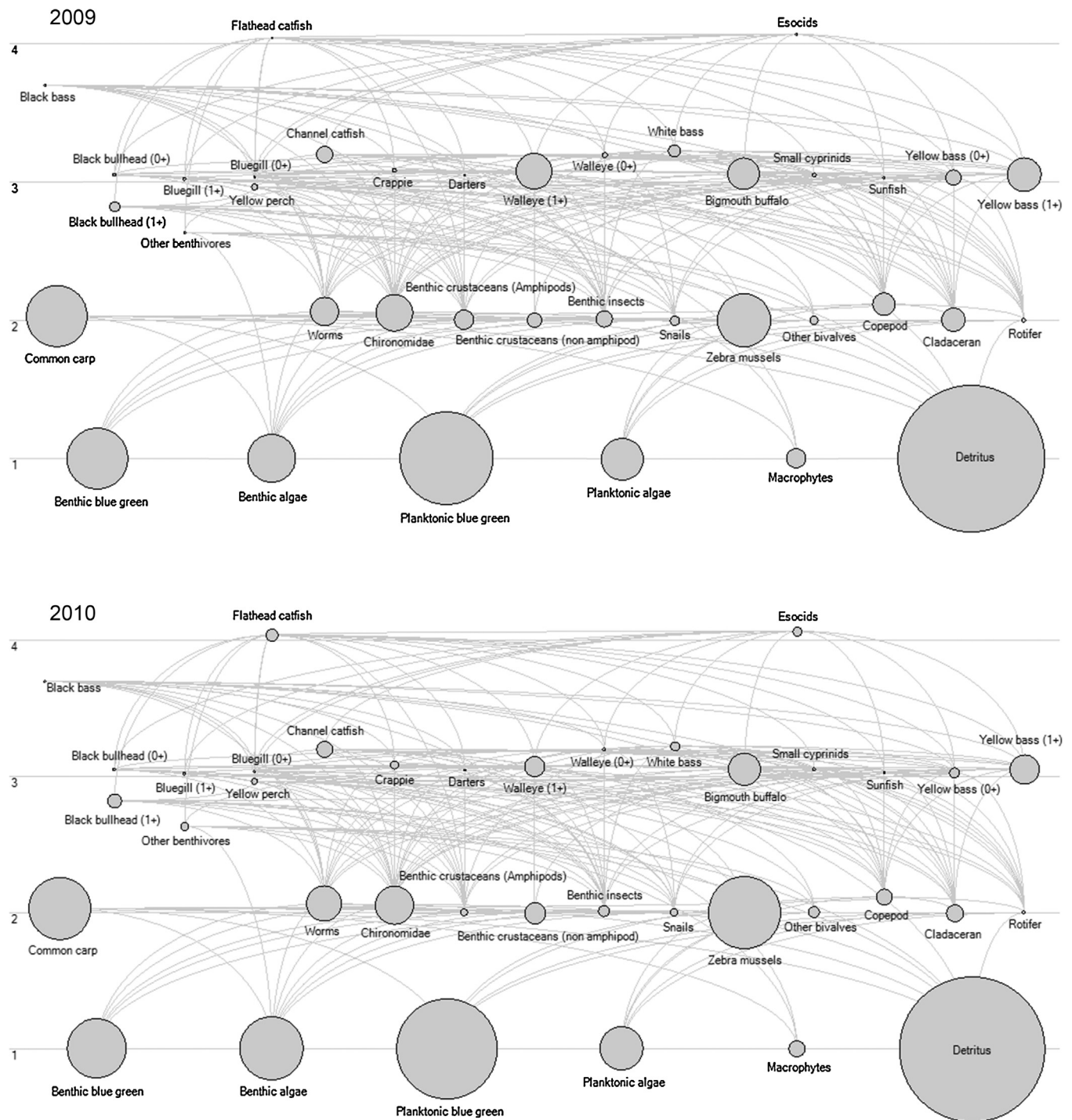


Fig. 3. Trophic flow diagrams of the food web in Clear Lake, Iowa, 2009 (upper panel) and 2010 (lower panel). Size of circles indicates relative biomass of groups. Curved lines indicate trophic pathways. Trophic levels indicated by vertical position (gray horizontal lines) and labeled along left sides of panels.

with zebra mussels for pelagic phytoplankton, such as zooplankton and other bivalves. Zebra mussels also exhibited indirect negative impacts on age 0 yellow bass and lower trophic level fish groups via competition with zooplankton for edible planktonic algae.

Food web groups impacting edible planktonic algae and zooplankton groups were consistent among years (Fig. 6). Zebra mussels had the largest negative impact on edible planktonic algae. Relative to zebra mussels, zooplankton groups had a negligible impact on edible planktonic algae. Predation by age 0 yellow bass and bigmouth buffalo exhibited negative impacts on both

copepods and cladocerans. Zebra mussels had a negative impact on both copepods and cladocerans. Planktonic algae was the only group that exhibited a consistent positive impact of sizable magnitude on zooplankton groups.

Adult yellow bass had a consistently strong positive affect on the recreational fishery (Fig. 6). Adult walleye had a strong positive impact on the recreational fishery in 2007 and 2008, but a much smaller positive impact in 2009 and 2010 as yield declined. Chironomids had a positive effect on the recreational fishery throughout the study, highlighting the importance of this group as sport fish prey.

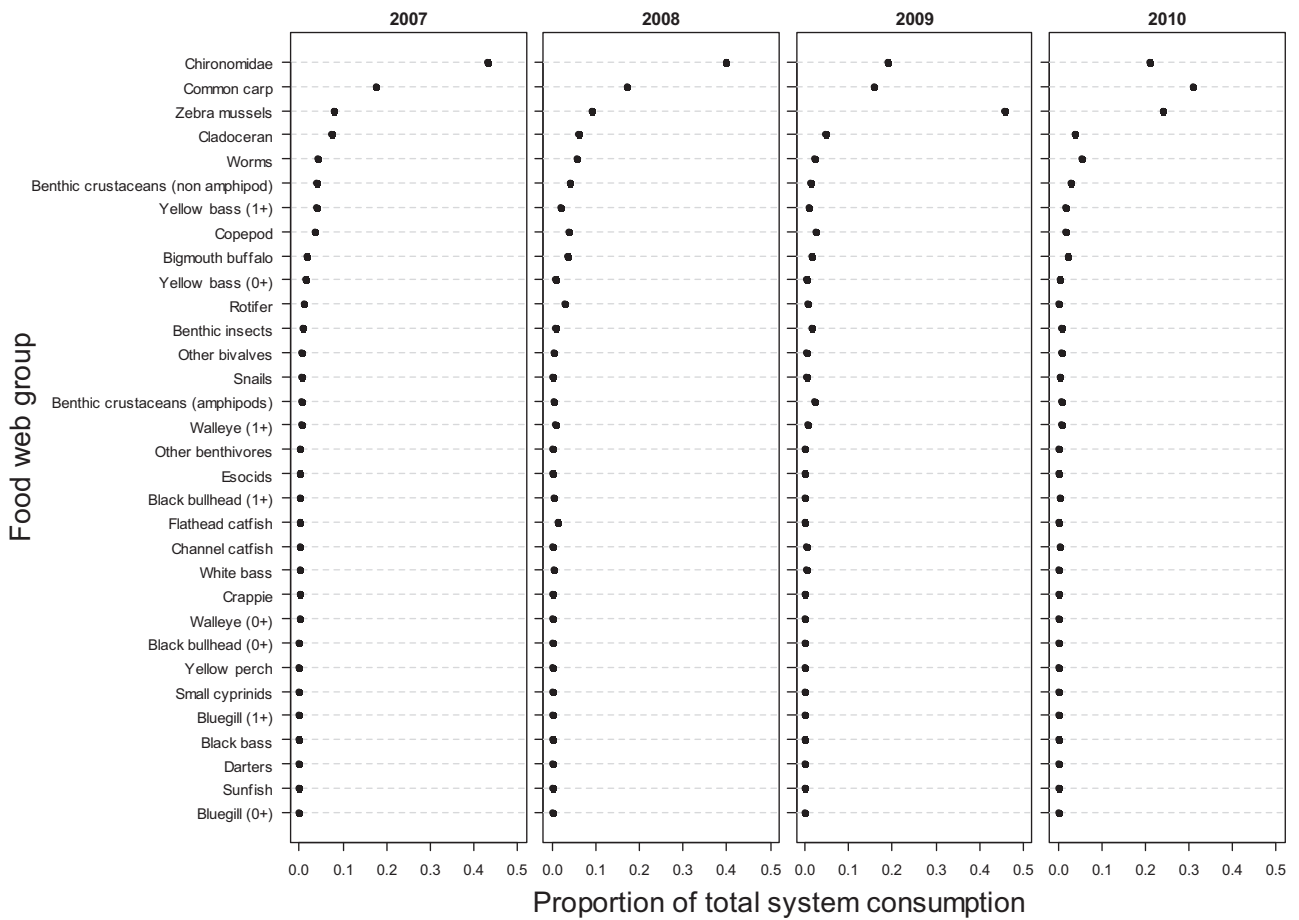


Fig. 4. Proportion of total system consumption for food web groups in Clear Lake, Iowa, 2007–2010. Groups ranked on the y-axis by decreasing proportion in 2007.

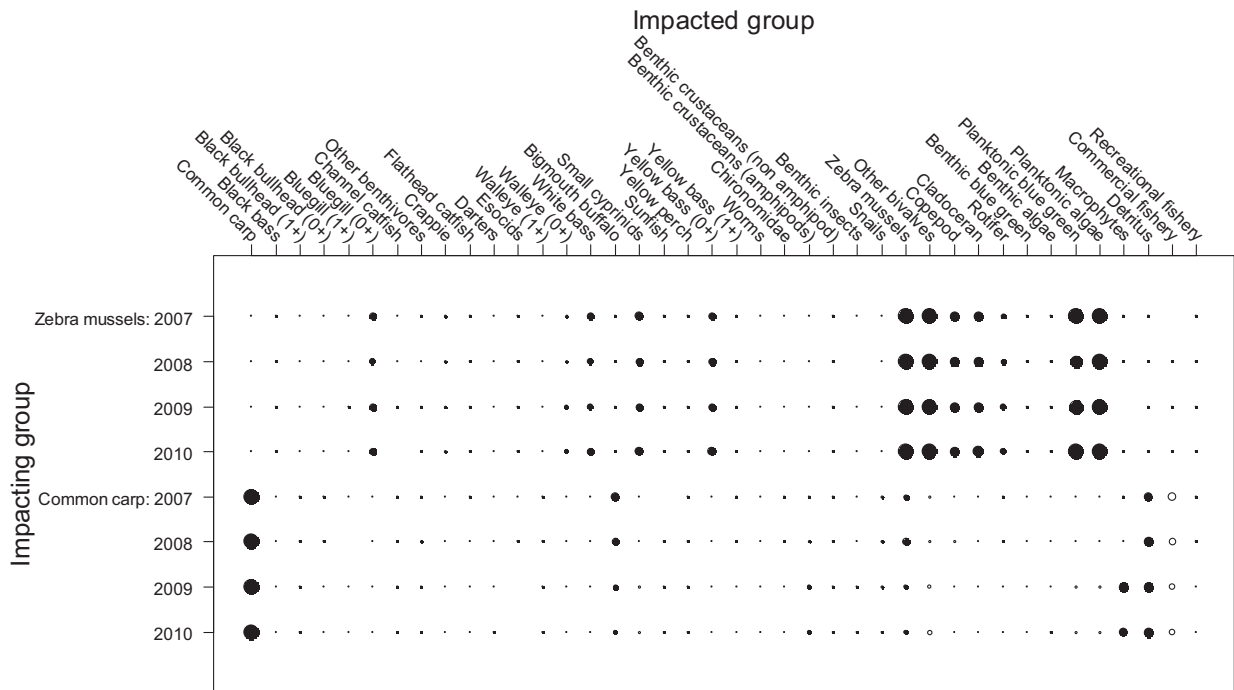


Fig. 5. Mixed trophic impacts of common carp and zebra mussels on food web groups in Clear Lake, Iowa, 2007–2010. Open circles represent positive impact; closed circles represent negative impact. Circle diameter proportional to magnitude of impact.

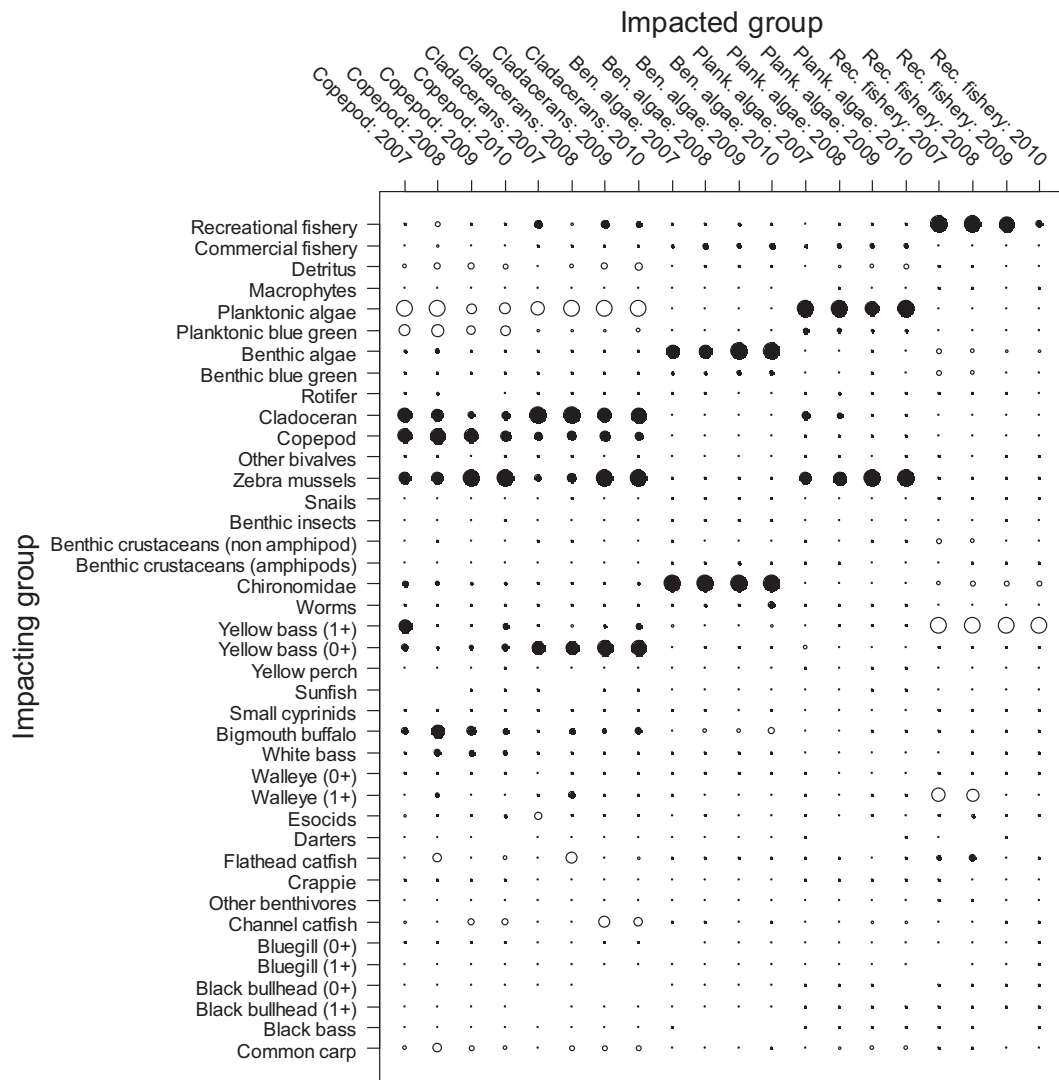


Fig. 6. Mixed trophic impacts of food web groups on zooplankton, algae, and the recreational fishery in Clear Lake, Iowa, 2007–2010. Open circles represent positive impact; closed circles represent negative impact. Circle diameter proportional to magnitude of impact.

4. Discussion

4.1. Model scope

Our Ecopath models successfully represented the food web structure and interrelationships in Clear Lake over a four year period during which a newly invading species increased dramatically in abundance. This study represents a unique approach to modeling changes in a freshwater food web undergoing a zebra mussel invasion. Relative to lakes in which previous food web-based studies of zebra mussel impacts have been conducted (e.g., Jaeger, 2006; Miehl et al., 2009; Yu and Culver, 1999), Clear Lake is smaller, shallower, more eutrophic, and thus representative of systems predicted to be at high risk of zebra mussel invasion (Whittier et al., 2007). Previous studies have focused on pre- and post-invasion food webs, an approach which averages over many years in each model, whereas our study reflects annual changes in the food web of Clear Lake. We believe the temporal resolution of our approach relative to other studies enabled important insights into food web dynamics during the Clear Lake zebra mussel invasion, and suggests evaluating invasion dynamics will be useful for understanding and mitigating future invasions in similar systems.

4.2. Common carp

Despite on-going commercial harvest targeting their removal as a nuisance species (Colvin et al., 2012), common carp had the highest biomass of any fish species over all four years of our study yet trophic impacts were small relative to other consumers. Common carp ranked first, second or third in total system consumption in all four study years. It is interesting that despite such dominance of total system biomass and consumption, less dramatic overall system impact was suggested by MTI. This apparent contradiction is explained by common carp having the highest proportional representation of detritus in their diets of any group (exceeding 73%) in our models, with the remainder of their diets consisting of benthic organisms, including macrophytes. Eutrophic systems like Clear Lake support ample detritus and benthic primary and secondary production which are used by benthic omnivores like common carp. High consumption rates by benthivorous fishes can influence nutrient cycling in lake ecosystems (Sereda et al., 2008). This is especially true for common carp, where high biomass and a diet dominated by benthic foods can alter lake nutrient levels via excretion (Lamarra, 1975; Schrage and Downing, 2004). In particular, benthivorous fish excrete phosphorous at higher rates than piscivorous fishes due to differences in elemental stoichiometry of

their diets (Jobling, 1994; Sereda and Hudson, 2010). Common carp excretion is a function of consumption, which in turn is a function of biomass (Jobling, 1994; Liao et al., 2005; Sereda and Hudson, 2010). However, Ecopath food web analyses do not take nutrient cycling into account, which can have significant bottom up effects on phytoplankton production in freshwater systems (Conroy et al., 2005; Schaus et al., 1997; Schrage and Downing, 2004). Detailed examination of nutrient flows to evaluate potential bottom up effects will be needed to fully evaluate common carp effects in Clear Lake.

A final indicator of potential strong impacts of common carp in Clear Lake is their biomass in relation to the 100 kg/ha (10 t/km²) threshold suggested as a biomass level above which common carp have deleterious effects on lakes (Bajer et al., 2009). Our predicted yearly mean biomass estimates, which were used as inputs in our Ecopath models, were all well above the 100 kg/ha threshold. This empirical value implies no particular mechanism, but reflects observations from a number of studies. Our food web analysis suggests some potential mechanisms of impact, but there are other potentially important mechanisms (e.g., bioturbation, excretion, uprooting macrophytes) that operate outside the scope of food web analysis.

4.3. Zebra mussels

Decades of eutrophication have created favorable trophic conditions for invading zebra mussels in Clear Lake (Egerton et al., 2004). Extremely high external nutrient loading (Knoll, 2011) has resulted in abundant phytoplankton production that can be utilized by filter-feeding zebra mussels, supporting their rapid rise from discovery in 2005 to one of the dominant food web groups by 2010. Despite biomass and associated consumption increases over the study period, there was a lack of trophic impact on the system. This was due to excess phytoplankton production in this system due to eutrophication where ecotrophic efficiencies for phytoplankton groups did not exceed 35%. The extent of future zebra mussel impacts in Clear Lake will depend on their capacity to expand beyond the limited hard substrate (<2% of lake area)—their preferred habitat (Coakley et al., 2002). However, zebra mussels have shown the ability to expand beyond preferred habitat by attaching to shells of both living and dead conspecifics (Mortl and Rothaupt, 2003). Zebra mussel reefs can grow by gregarious recruitment until large aggregations break off creating a slow outward expansion from areas with hard substrates to normally unsuitable soft substrates (Coakley et al., 1997). Zebra mussels can also conglomerate using byssal strands to facilitate soft sediment colonization (Berkman et al., 1998). However, these expansion processes are slow relative to the initial zebra mussel invasion and the extent to which they will occur in and their consequences for Clear Lake are uncertain.

As phytoplanktivorous filter feeders, zebra mussels divert energy from the pelagic to benthic portion of the food web, a process called “benthification” (Mayer et al., 2014), reducing trophic support for pelagic consumers and to some extent, recreational fisheries. Zebra mussels occupy a similar trophic niche as zooplankton in lake ecosystems and both groups can improve water quality by reducing phytoplankton abundance through grazing. However, in other respects zebra mussels and zooplankton function differently within the system. Zooplankton move energy “up” the pelagic food web, providing support for higher trophic levels, whereas zebra mussels shunt energy away from pelagic food webs by converting phytoplankton into pseudofeces (Berg et al., 1996; Vanderploeg et al., 2001) and into their own biomass which is then utilized by benthic consumers (e.g., amphipods, insects, benthivorous fishes) (Magoulick and Lewis, 2002; Stewart and Haynes, 1994; Stewart et al., 1998). Shunting energy away from the pelagic food web can reduce abundance and growth of sport fishes (Mayer

et al., 2000; Miehl et al., 2009; Rutherford et al., 1999; Thayer et al., 1997). However, some fish species can prey directly on zebra mussels and invertebrates associated with zebra mussel colonies, potentially enhancing those populations and fisheries they support (Magoulick and Lewis, 2002; Watzin et al., 2008).

Zebra mussels are selective filter feeders, preferring diatoms and green algae (the planktonic algae group in our models) and rejecting blue green algae, which has been shown to result in increasing dominance of blue green algae over other forms in lakes with zebra mussel populations (Vanderploeg et al., 2001; Bierman et al., 2005). Planktonic blue green algae increased roughly 4-fold over the course of the study while zebra mussels increased by over two orders of magnitude. The (non-blue green) planktonic algae group also increased in biomass over the four years, but at a slower rate such that the ratio of planktonic blue green to non-blue green algae biomass increased from 59 in 2007 to 117 in 2010. These trends are similar to those in previous studies (Budd et al., 2002; Nicholls et al., 2002), and although our study was not designed to test hypotheses, the similarity of our findings suggests that zebra mussels may have played a role in the increasing absolute abundance of planktonic blue green algae and its increase relative to non-blue green algae in Clear Lake. Nutrient dynamics, including both external and internal sources and fluxes, regulate phytoplankton dynamics, and are not considered in a food web analysis. A more comprehensive model of the Clear Lake ecosystem encompassing nutrient dynamics as well as food web dynamics would be necessary to partition effects of zebra mussels on phytoplankton dynamics with confidence.

4.4. Food web and lake restoration

Because of their importance as phytoplankton grazers, predation on zooplankton potentially limits long term success of lake restoration (Sondergaard et al., 2007). Our MTI analysis indicated that zooplankton were negatively impacted by age 0 yellow bass. Consumption by age 0 yellow bass was 12 to 47% of annual zooplankton production, likely limiting zooplankton abundance. This is similar to other shallow lake systems where zooplanktivorous fish (e.g., age 0 yellow perch) suppress zooplankton, thereby limiting lake restoration success, (Perrow et al., 1995, 1996). In Clear Lake, zebra mussels may increase the likelihood of successful lake restoration by compensating for reduced zooplankton abundance due to age 0 yellow bass predation. Despite the fact that long-term lake restoration success may be limited by age 0 yellow bass, managing this abundant and popular sport fish to minimize negative zooplankton impacts will pose a significant ecological and social challenge.

The majority of past research in lake ecosystems has focused on pelagic food webs. The disparity of pelagic versus benthic research was so notable that Vadeboncoeur et al. (2002) found that the number of published papers referencing benthic or benthic and pelagic systems were at most 20% of those referencing pelagic systems only. Whole-lake food webs are comprised of both benthic and pelagic pathways. Within lake ecosystems, consumption is a critical function to cycle biomass and nutrients. Consumption occurring through benthic pathways in Clear Lake dominated system consumption throughout our study, supporting the argument that benthic food webs are significant in whole-lake ecosystems and must be considered if ecosystem-level understanding is to be obtained (Vadeboncoeur et al., 2002). The fact that zebra mussels are now a dominant component of the Clear Lake ecosystem supports this assertion (Mayer et al., 2014). These results advance the understanding of lake ecosystems by incorporating benthic and pelagic foodwebs, providing evidence that pathways of energy and nutrient flow within the benthic component of the food web have important implications for the entire ecosystem.

This food web analysis was done as part of a larger, more comprehensive effort to model the entire Clear Lake ecosystem, including nutrient dynamics and the physical environment (Colvin et al., 2012). The comprehensive ecosystem model, of which the Ecopath food web models presented here are a major component, is analogous to the end-to-end (E2E) models (Rose, 2010; Steele, 2012; Steele et al., 2012) becoming prominent in the marine literature to integrate climate effects and other abiotic factors with food web dynamics. While the findings of our study and other capabilities of EWE such as time dynamic simulation modeling in Ecosim (Christensen and Walters, 2004) illustrate the power of food web analysis, we acknowledge limitations of food web analysis where factors such as external nutrient loading, internal nutrient dynamics, light availability, physical resuspension of sediments and other factors outside the food web are important. We believe that food web analyses such as we have presented here can provide many important insights into functions and interrelationships in ecosystems like Clear Lake, and limitations resulting from considering only the food web and its interactions can be overcome by extending the scope of ecosystem models beyond the food web. Our Clear Lake Ecosystem Simulation Model (CLESM) is such a model (Colvin et al., 2012), with a food web model as its foundation but with other important processes represented as integrated modules, and outputs representing food web interactions plus several other important ecosystem-level phenomena.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.05.016>

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