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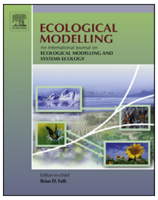

A food web modeling analysis of a Midwestern, USA eutrophic lake dominated by non-native Common Carp and Zebra Mussels

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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.

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 (Neess 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:

$$B_i \cdot P/B_i = \sum B_j \cdot Q/B_j \cdot \mathrm{DC}_{ij} + \mathrm{NM}_i \cdot B_i + \mathrm{BA}_i \cdot B_i + F_i \cdot B_i \\ + B_i \cdot P/B_i \cdot (1 - \mathrm{EE}_i)$$

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_i 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