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Potential Effects of Bigheaded Carps on Four Laurentian Great Lakes Food Webs

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ABSTRACT

Bigheaded carps (Silver Carp *Hypophthalmichthys molitrix* and Bighead Carp *H. nobilis*, collectively 'BHC') are economically and culturally important in Asia and Europe, but are considered highly invasive throughout the Mississippi River watershed and pose a threat to the food web and fisheries of the Laurentian Great Lakes. We used the Ecopath with Ecosim model framework to evaluate potential risk of BHC population growth and food web effects in four Great Lakes habitats, including mesotrophic waters of Saginaw Bay (Lake Huron) and Lake Erie and oligotrophic waters of Lake Michigan's and Lake Huron's main basins. We simulated BHC population growth and food web effects under different scenarios of BHC production rates, prey vulnerability to BHC, and availability of age-0 BHC to predation by salmonines. In the main basins of Lake Michigan and Lake Huron, the projected BHC population growth was low or negative, with a projected final BHC biomass of 0.5 to 1.1 times the initial introductory biomass (2% of total fish biomass for each BHC species), and BHC had negligible effects on most food web groups across all scenarios. In contrast, in Saginaw Bay and Lake Erie, the projected BHC biomass was 2.5 to 12.5 times higher than the initial biomass across all scenarios, and the largest increases occurred under scenarios of high prey vulnerability to BHC and high BHC production rates. High projected BHC biomass in Saginaw Bay and Lake Erie had negative effects on zooplankton and planktivorous fish groups and mixed effects on piscivores, but had relatively negligible effects on most other food web groups across all scenarios. Our results are consistent with reported BHC effects on food webs in the Mississippi River and its tributaries, and inform efforts to prevent the invasion of BHC to the Great Lakes.

INTRODUCTION

Invasive species are a major stressor on terrestrial and aquatic ecosystems, and may profoundly change ecosystem structure, function, and services, and increase management costs (Ciruna et al. 2004). The Laurentian Great Lakes, the world's largest freshwater ecosystem with recreational fisheries valued at $7 billion per year (Southwick Associates 2012), have been particularly vulnerable to introductions of aquatic nonindigenous species with at least 188 species established (Sturtevant et al. 2019). To date, the invasive species that have caused the most harm to the ecosystem include the Sea Lamprey *Petromyzon marinus* (Smith and Tibbles

1980), Alewife *Alosa pseudoharengus* (Madenjian et al. 2015) and *Dreissena* mussels (zebra mussels *D. polymorpha* and quagga mussels *D. bugensis* Vanderploeg et al. 2015). For example, in three of the five Laurentian Great Lakes, the filter-feeding *Dreissena* mussels invaded in the 1990s, and continue to disrupt ecosystem function and services by shifting energy from pelagic to benthic pathways (Hecky et al. 2004) and threatening the sustainability of valuable recreational fisheries (He et al. 2015; Kao et al. 2016). The nationwide environmental damages and losses due to invasion of *Dreissena* mussels alone was estimated at $1 billion per year (Pimentel et al. 2005).

Silver Carp *Hypophthalmichthys molitrix* and Bighead Carp *H. nobilis* (collectively, bigheaded carps or BHC) are economically and culturally important in Asia and Europe, but are considered highly invasive throughout the Mississippi River watershed and pose a threat to the food web and fisheries of the Laurentian Great Lakes. BHC were initially introduced into the USA for water quality control in aquaculture ponds and water treatment plants but escaped into the Mississippi River drainage in the early 1970s (Kelly et al. 2011). Currently, BHC are abundant in the Mississippi River and many of its tributaries, and are moving toward the Great Lakes. The leading edge of the BHC population is in the Illinois River, 74 km away from the Great Lakes, but a Silver Carp and a Bighead Carp have been collected within 11 km of Lake Michigan (https://www.Asiancarp.us). Efforts to reduce the risk of BHC invasion to the Great Lakes have focused on reducing the population in the Illinois River through fisheries harvest and using electric barriers to inhibit movement towards Lake Michigan. Bubble screens, sound and strobe lights also are being evaluated to determine if they deter BHC movements (https://www.Asiancarp.us).

The potential invasion of BHC into the Great Lakes is a major concern for fisheries managers and stakeholders alike (Cudmore et al. 2012, Wittmann et al. 2015). BHC can be highly invasive owing to their high consumption rates of plankton, rapid growth rates, large sizes (up to 130 cm, 50 kg), high fecundities (0.6-2.0 million eggs per female), and paucity of predators on adult carp (Williamson and Garvey 2005, Kolar et al. 2007, Hayer et al. 2014, Zhang et al. 2016). Several studies have shown that at high population densities, BHC consumption can cause shifts in size and abundance of plankton communities (Zhang et al. 2006, Cooke et al. 2009, Sass et al. 2014, Tumolo and Flynn 2017, Li et al. 2017, Collins and Wahl 2018). For example, in the lower Illinois River BHC biomass has reached 45-78% of the total fish biomass (Coulter et al. 2018). Additionally, BHC have caused declines in zooplankton abundance and alteration of existing planktivorous fish communities in floodplain lakes and channels of the Mississippi River and the Missouri River (Phelps et al. 2017) and lower Illinois River (Sass et al. 2014).

Studies have suggested that BHC may find suitable habitats for reproduction and growth, and establish populations in the Great Lakes. Kocovsky et al. (2012) and Currie et al. (2012) found flows and temperatures of several Great Lakes tributaries were suitable for BHC reproduction. Bioenergetics modeling studies by Cooke and Hill (2010), Anderson et al. (2015), and Anderson et al. (2017) suggested BHC could grow in productive areas of Lake Michigan and Lake Erie. By using a bioenergetics model and outputs from a 3-dimensional, spatially explicit biophysical model, Alsip et al. (2019) showed that BHC could grow in productive coastal waters of Lake Michigan, and that Bighead Carp could maintain weight in the less productive open waters of Lake Michigan during summer. Cuddington et al. (2014) and Ivan et al. (2020) suggested that BHC could establish a population in the Great Lakes with a minimal number of spawners, assuming high age-0 survival rates and suitable spawning habitats.

Once established, BHC may reach high biomass levels and disrupt Great Lakes food webs. Model projections of BHC population growth and food web effects in Lake Erie indicate that the carps could reach a third of total fish biomass and have substantial food web effects by causing decreases in biomass of zooplankton and planktivorous fish, and increases in biomass of some piscivores (Zhang et al. 2016). Although suitable habitats for BHC were identified in oligotrophic waters of Lake Michigan (Cooke and Hill 2010, Anderson et al. 2017, Alsip et al. 2019), little is known about BHC effects on the food webs of this lake and other oligotrophic Great Lakes habitats.

The objective of this study was to project BHC population biomass and potential food web effects across Great Lakes habitats that differ in productivity and species composition. With our standardized simulation procedure, we used the Ecopath with Ecosim food web model (EwE, Christensen and Walters 2004) to project population growth and food web effects of BHC in four habitats across three Great Lakes. We hypothesized that BHC biomass and effects will differ among lake habitats and be correlated with productivity.

METHODS

Study Area. We investigated population growth and food web effects of BHC in Saginaw Bay (Lake Huron), Lake Erie, the main basin of Lake Michigan, and the main basin of Lake Huron (Figure 1). Productivity, size and fish species composition differ among these four habitats (Table 1). Saginaw Bay, one of four Lake Huron sub-basins (which also include North Channel, Georgian Bay and the main basin) is mesotrophic (Cha et al. 2016) and has an area of 2,770 km^2 (5% of lake surface) and an average depth of 8.9 m. Conventionally, Lake Erie has been divided into western, central and eastern sub-basins. However, we chose to model BHC effects at the whole-lake scale because the water residence time is relative short (about 2.6 years.), and BHC could migrate extensively throughout the lake (Degrandchamp et al. 2008), just like many native fishes such as Walleye *Sander vitreus* (Wang et al. 2007) and Lake Whitefish *Coregonus clupeaformis* (Oldenburg et al. 2007). Lake Erie has an area of 25,609 km^2 and average depth of 19 m, and is mesotrophic (Table 1). Lake Michigan is divided into two sub-basins: the mesotrophic Green Bay and the oligotrophic main basin (Dove and Chapra 2015; Lin et al. 2016). We modeled BHC food web effects for oligotrophic main basins of Lake Michigan (53,646 km^2, 92% of lake surface, average depth = 91 m) and Lake Huron (37,765 km^2, 63% lake surface, average depth = 73 m). Hereafter, we refer to these four habitats as Saginaw Bay, Lake Erie, Lake Michigan, and Lake Huron.

The four habitats differ with respect to the dominant predators and planktivorous prey fishes that presumably would interact with BHC (Table 1). In Saginaw Bay and Lake Erie, Walleye and Yellow Perch *Perca flavescens* are the dominant predators while Gizzard Shad *Dorosoma cepedianum*, Rainbow smelt *Osmerus mordax* and Emerald Shiner *Notropis atherinoides* are the dominant planktivores (Kao et al. 2014; Zhang et al. 2016). In Lake Michigan and Lake Huron, Lake Trout *Salvelinus namaycush*, Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *O. kisutch*, and Steelhead *O. mykiss* are the dominant predators, while Alewife, Rainbow Smelt and Bloater *Coregonus hoyi* are the dominant planktivores (Kao et al. 2016; Kao et al. 2018).

Food Web Modeling.—We used the EwE models for Saginaw Bay (Kao et al. 2014), Lake Erie (Zhang et al. 2016), Lake Michigan (developed for this study), and Lake Huron (Kao et al. 2016) to project BHC population biomass and potential food web effects among these habitats. Each of these EwE models included (1) an Ecopath model that represents a biomass-balanced food web for a specific time period (Table 1), and provided the initial conditions for Ecosim simulations and (2) a calibrated Ecosim model to simulate time dynamics under different scenarios. Food web groups for each of these models were chosen based on data availability and the research question of the original paper. Two other EwE models exist for Lake Michigan (Rogers et al. 2014; Kao et al. 2018), but we developed a new EwE model that included microbial groups and permitted simulation of mixed reproduced success by wild and hatchery piscivores (i.e. resulting in wild × wild vs wild × hatchery vs hatchery × hatchery spawners). Details of the Lake Michigan EwE model are presented in Supplementary Material 1.

To compare effects of BHC across habitats, we adopted Zhang et al.'s (2016) method to simulate BHC invasion and standardized the simulation procedure. Specifically, in each Ecopath model we added each BHC species as multi-stanza groups, with an age-0 group and an age-1 and older (age-1+) group. We set the total biomass of each BHC species in each Ecopath model at a low level, which represented 2% of the total fish biomass in that food web. Diet fractions of three prey categories (i.e., phytoplankton and protozoa, zooplankton, and detritus) of BHC were from Chen 1982, but within each main prey category (e.g., zooplankton), the diet fractions were proportional to prey availability in each habitat, and weighted with selectivity preference (Chen 1982). We assumed that age-0 carp has the same diet fractions as age-1+ carp of the same species (Table 2). Across the four models, we set the same values for production to biomass ratio (P/B) and production to consumption ratio (P/Q) of age-1+ BHC, and same age-0 BHC diet fractions for each BHC predator (Table 3). We also set the "other mortality rate" (i.e., mortality resulting from starvation, senescence, and disease, etc.) of age-1+ BHC at a low level of 0.08 yr^{-1} by applying an artificial fishing mortality rate on each BHC species in the Ecopath models, and set the other mortality rate of age-0 BHC to 1.6 yr^{-1} by varying the P/B for age-0 BHC (Zhang et al. 2016). Values for the other parameters were calculated using the EwE program software's built-in multi-stanza module (Christensen et al. 2008). In Ecosim, we ran the simulations to model year 2030 and then removed the artificial fishing mortality to allow BHC populations to grow. We ran Ecosim simulations for another 120 years starting from model year 2031 to ensure all modeled food webs reached a new equilibrium.

Scenario Simulations.—To project BHC population biomass and potential food web effects, we used a baseline scenario (with no BHC in the model), together with eight scenarios designed to address several uncertainties associated with BHC production rates, prey vulnerability to BHC, and salmonine (salmon and trout) predation on age-0 BHC (Table 4). In high and low BHC production rate scenarios, we used values of P/B that were from a structured expert judgement solicitation of scientists who work on the Great Lakes and/or study the ecology of BHC (Wittmann et al. 2015; Table 4), and from a meta-analysis of BHC mortality rates (Tsehaye et al. 2013; Table 4). In scenarios of prey vulnerability to BHC, we used values of the vulnerability parameter of a reference planktivore species for age-0 BHC (Table 5). The reference planktivore was the dominant planktivore species in each of the modeled habitats. Values of the prey vulnerability parameter for age-0 and age-1+ reference planktivore groups were used in scenarios of high and low prey vulnerability to age-0 BHC. The two scenarios associated with salmonine predation represented whether the salmonines would consume age-0 BHC, as this was a concern for fisheries managers in previous BHC simulations in Lake Erie (Zhang et al. 2016). In the salmonine predation scenarios, the percent contributions of age-0 BHC to the diet of each salmonine predator group were the same across the modeled habitats. The no-salmonine predation scenario was the same as the salmonine predation scenario except that age-0 BHC were not included in salmonine diets.

The Lake Erie EwE model by Zhang et al. (2016) included piscivorous birds (Double Crested Cormorants *Phalacrocorux auritus*, Red-Breasted Merganser *Mergus serrator*) as potential predators of BHC and other fishes in its dynamic simulations. Because piscivorous birds are highly migratory and their dynamics are not fully determined by the dynamics of the Lake Erie food web, we used a forced biomass time series for piscivorous birds under all BHC scenarios in the Lake Erie food model simulations. The forced biomass time series was generated from the baseline simulation (with no BHC). In the other three modeled habitats, piscivorous birds were not considered to be significant predators of age-0 BHC as their biomass was extremely low.

To compare projected BHC biomass and food web effects across habitats and scenarios, we calculated (1) the percentage of total fish biomass that was comprised of BHC, (2) the change in biomass of each food web group, and (3) the total population consumption and predation mortality rates for selected fish species of interest in each BHC scenario and habitat. These metrics for projected BHC biomass and food web effects were based on simulated biomass, consumption, and mortality rates at equilibrium, which were the averages over the last 10 years of the 120-year simulation period in the baseline scenario, and each of the BHC scenarios in each habitat. The projected change in biomass of a food web group was calculated as the percentage change in the projected biomass in one of the eight BHC scenarios relative to that in the baseline scenario. We considered biomass changes (increases or decreases) of less than 5% as negligible. To visualize how biomass of a food web group could respond to different levels of BHC biomass, we plotted the percent changes in biomass of the food web group (Y-axis) as a function of BHC biomass (X-axis) across all scenarios and habitats.

RESULTS

Projected bigheaded carp biomass.— The projected biomass of BHC varied across habitats and scenarios of prey vulnerability to BHC and BHC production rates (Figure 2). In Saginaw Bay and Lake Erie, the biomass of both age-0 and age-1+ BHC grew substantially across all BHC scenarios. The proportion of total BHC biomass of both age-0 and age-1+ BHC, which comprised 4% of the initial total fish biomass in the Ecopath models, comprised 10–34% and 11–40% of the total fish biomass across all BHC scenarios in Saginaw Bay and Lake Erie, respectively (Figure 3). The highest BHC biomass occurred under scenarios of high prey vulnerability to BHC and high BHC production rates, followed by scenarios of high prey vulnerability to BHC and low BHC production rates. The lowest projected BHC biomass in Saginaw Bay and Lake Erie occurred under scenarios of low prey vulnerability to BHC and low BHC production rates, with BHC contributing about 10% to the total fish biomass. For age-1+ BHC, the biomass in each of the BHC scenarios was higher than the initial BHC biomass in Ecopath, but for age-0 BHC, the biomass was similar to, or lower than its initial biomass under scenarios of low prey vulnerability to BHC and low BHC production rates (Figure 2). Salmonine consumption of age-0 BHC had negligible effects on the projected biomass of age-0 or age-1+ BHC across all scenarios of BHC prey vulnerability and BHC production rates in Saginaw Bay and Lake Erie. Overall, the proportion of total fish biomass that was represented by BHC in Saginaw Bay and Lake Erie ranged from 10 to 44%.

In Lake Michigan and Lake Huron, the increase in BHC biomass was less than was found in Saginaw Bay and Lake Erie across BHC scenarios. In Lake Michigan, while the BHC *proportion* of total fish biomass increased from 4% under initial conditions to about 7–8% (Figure 3), *actual* biomass of age-0 and age-1+ BHC declined from initial levels across all BHC scenarios (Figure 2). In Lake Huron, the contributions of BHC biomass to the total fish biomass ranged from 12 to 15% (Figure 3). Biomass of age-0 BHC declined from initial biomass levels, while age-1+ BHC biomass was relatively similar to, or increased from initial levels under scenarios of high BHC production rates, but declined from initial levels under scenarios of low BHC production rates (Figure 2). Overall, the proportion of total fish biomass from BHC for Lakes Michigan and Huron ranged from 0.5 to 1.1%.

Food web response relative to BHC biomass and across scenarios.— We combined simulation results for all scenarios and habitats together to show how food web groups responded to increases in BHC biomass (Figures 4–8). We also presented biomass changes by food web group in each habitat and across BHC scenarios (Tables 6-9). We focus on reporting results for the food web groups that were projected to have biomass changes from baseline of ≥5% (positive or negative) in response to BHC biomass across BHC scenarios, and give a complete summary of simulated biomass changes for every food web group in each habitat across BHC scenarios in Supplementary Material 2. Note that we considered a <5% biomass change as negligible.

As we hypothesized, food web groups had mixed responses to BHC biomass across habitats and BHC scenarios. In relatively more productive Saginaw Bay and Lake Erie, the biomass response of food web groups often was greatest under scenarios of high prey vulnerability to BHC, regardless of scenarios of BHC production rates, and often showed (positive or negative) trends with respect to BHC biomass. In relatively less productive Lake Michigan and Lake Huron, the biomass response by food web groups to BHC biomass was negligible in most BHC scenarios.

Relatively few piscivorous fishes showed increases in biomass in response to BHC biomass across BHC scenarios (Figures 4, 5). For Walleye in Saginaw Bay, biomass of larvae, age-0, age-1, and adult groups decreased from baseline by up to 16%, 13%, 11%, and 6%, respectively (Figure 4a) under scenarios of high prey vulnerability to BHC. For Lake Erie Walleye, biomass of larvae and age-0 groups decreased from baseline by up to 6% and 9%, respectively, while the biomass of the adult group increased from baseline by up to 19% under scenarios of high prey vulnerability to BHC (Figure 4a). In Lake Michigan, the biomass of the adult Walleye group increased from baseline by 7–11% across all BHC scenarios. Note that biomass of Lake Huron Walleye was not simulated because its biomass is controlled by the food web dynamics in Saginaw Bay (Kao et al. 2016).

Response of Yellow Perch groups to BHC scenarios differed among habitats (Figure 4b). In Saginaw Bay, biomass of Yellow Perch larval and age-0 groups decreased from baseline by up to 24% and 17%, respectively, under scenarios of high prey vulnerability to BHC, but the biomass of age-1–2 and age-2+ groups increased by up to 9% and 29%, respectively, under scenarios of high prey vulnerability to BHC. In Lake Erie, Yellow Perch biomass of larval, age-0, and age 1–2 groups decreased from baseline under scenarios of high prey vulnerability to BHC by up to 10%, 23%, and 20%, respectively, but the biomass of the age-2+ group increased from baseline by up to 6%. In Lake Huron, biomass of the Yellow Perch age-0 group decreased by up to 6%, while the biomass of the age-3+ group increased from baseline by up to 16% across all BHC scenarios. In Lake Michigan, biomass change responses of Yellow Perch life stages to BHC scenarios were negligible (Figure 4b).

While projected biomass changes of the other piscivorous and omnivorous fish groups differed among BHC scenarios, the largest biomass changes from baseline occurred under scenarios of high prey vulnerability to BHC across habitats (Figure 5, Table 6). In Saginaw Bay, projected biomass increased from baseline by up to 9% for salmonines (modeled as an "Outer Bay predator" group) and by up to 10% for Spottail Shiner *Notropis hudsonius*, but decreased from baseline by up to 49% for White Perch *Morone americana* and by up to 8% for the "Other prey fishes" group that was dominated by sunfishes *Lepomis* spp. (Supplementary Material 2). For piscivorous fishes in Lake Erie, projected biomass decreased from baseline by up to 9% for Lake Trout, by up to 19% for Steelhead, by up to 18% for Burbot *Lota lota*, and by up to 14% for White Bass *Morone chrysops*, but increased from baseline by up to 20% for Smallmouth Bass *Micropterus dolomieu* (Figure 5, Table 6). For the omnivorous White Perch in Lake Erie, projected biomass increased from baseline by up to 40% under high prey vulnerability to BHC scenarios but decreased slightly from baseline by up to 5% under low prey vulnerability to BHC and production scenarios (Table 6). Note that White Perch was not modeled in Lake Michigan and Lake Huron due to low biomass.

Biomass of most planktivorous fish groups declined from baseline with increases in BHC biomass in Saginaw Bay and Lake Erie across BHC scenarios (Figure 6, Table 7). Under scenarios of high prey vulnerability to BHC in Saginaw Bay, biomass decreased from baseline by up to 14% for Gizzard Shad and by up to 46% for Emerald Shiner (Figure 6, Table 7). In Lake Erie, under scenarios of high prey vulnerability to BHC, biomass of Rainbow Smelt and Alewife decreased from baseline by up to 8%, while biomass of Emerald Shiner decreased from baseline by up to 70% (Figure 6, Table 7). In Lake Huron, biomass of Alewife also decreased by up to 8% under high BHC production rate scenarios (Figure 6, Table 7). Note that biomass of Alewife and Rainbow Smelt was not simulated in Saginaw Bay as their dynamics were controlled by the food web dynamics in Lake Huron main basin (Kao et al. 2014), and Gizzard Shad and Emerald Shiner were not modeled in Lake Michigan (Supplementary Material 1) or Lake Huron (Kao et al. 2016) due to low biomass.

The biomass changes from baseline of benthivorous fish groups, including Common Carp *Cyprinus carpio*, Freshwater Drum *Aplodinotus grunniens*, Round Goby *Neogobius melanostomus*, Deepwater Sculpin *Myoxocephalus thompsonii*, Slimy Sculpin *Cottus cognatus*, and panfish *Lepomis* spp., in response to BHC biomass were nearly all negligible under BHC scenarios in all lake habitats (see Supplementary Material 2 for complete results). The exceptions were Round Goby and the “other prey fishes” group (dominated by Lepomis spp.) in Saginaw Bay, whose biomass decreased from baseline by up to 11 and 8%, respectively, and the “other fishes” group (Silver Chub *Macrhybopsis storeriana*, Trout-Perch *Percopsis omiscomaycus*, and Logperch *Percina caprodes*) in Lake Erie whose biomass decreased from baseline by up to 13% under scenarios of high prey vulnerability to BHC. Note that Trout-Perch and Log-Perch were not modeled in Lake Michigan and Lake Huron due to low biomass.

Response of zooplankton groups to BHC biomass varied across taxa in Saginaw Bay and Lake Erie, but was negligible across all BHC scenarios in Lake Michigan and Lake Huron (Figure 7, Table 8). Under scenarios of high prey vulnerability to BHC in Saginaw Bay, biomass increased from baseline by up to 5% for copepods and by up to 20% for rotifers, but decreased from baseline by up to 42% for herbivorous cladocerans and by up to 32% for predaceous cladocerans. Similarly, under scenarios of high prey vulnerability to BHC in Lake Erie, biomass decreased from baseline by up to 13% for herbivorous cladocerans and by up to 8% for predaceous cladocerans (Figure 7, Table 8).

With few exceptions, biomass changes of phytoplankton and microbial groups were negligible in response to BHC biomass within all lake habitats and under all scenarios (Figure 8, Table 9). However under scenarios of high prey vulnerability to BHC in Saginaw Bay, biomass increased from baseline by up to 14% for protozoa, by up to 5% for non blue-green algae, but decreased by up to 11% for blue-green algae (Table 9).

The biomass response of most benthic groups changed less than 4% over the entire range of BHC biomass (Supplementary Material 2). However in Lake Erie, biomass of the "other benthos" group (mainly insect larvae) decreased from baseline by up to 6% under scenarios of high prey vulnerability to BHC.

Consumption by fishes

Consumption by BHC.—Consumption by BHC (g m^{-2} yr^{-1}) varied among age groups and lake habitats. Age-0 BHC consumed less than adult BHC, and both age groups consumed less in Lake Michigan and Lake Huron than in Saginaw Bay or Lake Erie (Figures S3.1a–d in Supplementary Material 3). In Lake Erie and Saginaw Bay, BHC consumption was higher under scenarios of high prey vulnerability to BHC than under scenarios of low prey vulnerability to BHC, while within these prey vulnerability scenarios, BHC consumption was higher under scenarios of high BHC production rates than low BHC production rates (Figures S3.1a, 1b). In Lake Michigan and Lake Huron, simulated BHC consumption was higher under scenarios of high BHC production rates than under low BHC production rates (Figures S3.1c, d).

Silver Carp consumed more phytoplankton than zooplankton, while the converse was true for Bighead Carp. Simulated BHC diet compositions also varied among lake habitats. In Saginaw Bay, Silver Carp consumed mainly non blue-green algae, in-water detritus, and blue-green algae (Figure S3.1a) while Bighead Carp consumed mainly cladocerans, non blue-green algae, and in-water detritus. In Lake Erie, the top three prey items consumed by Silver Carp were blue-green algae, non blue-green algae, and detritus, while Bighead Carp consumed mostly cladocerans, blue-green algae, and detritus (Figure S3.1b). In Lake Michigan, Silver Carp consumed mainly diatoms, detritus, and other phytoplankton (excluding blue-green algae), while Bighead Carp consumed copepod nauplii, diatoms, and detritus (Figure S3.1c). In Lake Huron, Silver Carp consumed mainly non blue-green algae, pelagic detritus, and blue-green algae, while Bighead Carp mainly consumed herbivorous cladocerans, calanoid copepods, and non blue-green algae (Figure S3.1d).

Consumption by piscivores.—In Saginaw Bay, consumption by adult Walleye decreased from baseline under scenarios of high prey vulnerability to BHC, primarily owing to the reduction of age-0 Gizzard Shad biomass in its diet (Figure S3.2a). In contrast, in Lake Erie, consumption by adult Walleye increased from baseline, primarily owing to the addition of age-0 BHC to its diet (Figure S3.2b). In Lake Michigan and Lake Huron, consumption by adult Walleye increased under all BHC scenarios through addition of age-0 BHC to the diet (Figures S3.2c, d).

Consumption by other predators varied among habitats and BHC scenarios. In Lake Erie, consumption by Lake Trout, Burbot, Steelhead, and White Bass each declined from baseline only under scenarios of high prey availability to BHC. Compared to a baseline scenario, Lake Trout, Steelhead, and Burbot had reduced consumption of Emerald Shiner, Burbot also had reduced consumption of Round Goby, and White Bass had reduced consumption of Rainbow Smelt (Figure S3.2b). Consumption by Smallmouth Bass increased from baseline under scenarios of high prey vulnerability to BHC, primarily owing to the addition of age-0 BHC to its diet (Figure S3.2b). In Lake Michigan and Lake Huron, there were negligible changes from baseline in consumption by Chinook Salmon, Lake Trout, or Burbot across all BHC scenarios (Figures S3.2c, d).

Consumption by planktivores.—In Saginaw Bay, consumption by most planktivores decreased from baseline under scenarios of high prey vulnerability to BHC, primarily owing to the reduction of herbivorous cladoceran biomass available for planktivore consumption (Figure S3.3a). In Lake Erie, consumption by Rainbow Smelt, Alewife, and Emerald Shiner all declined under scenarios of high prey vulnerability to BHC, with greatest reductions in prey consumption by Emerald Shiner (Figure S3.3b). Gizzard Shad showed negligible changes from baseline in prey consumption under BHC scenarios. With only one exception, consumption by every planktivore in Lake Michigan and Lake Huron showed negligible changes across all BHC scenarios (Figure S3.3c). The lone exception was Alewife in Lake Huron, whose prey consumption decreased from baseline under scenarios of high BHC production rates, owing to decreases in consumption of copepod nauplii and herbivorous cladocerans (Figure S3.3d).

Consumption by omnivores.—Consumption by adult Yellow Perch in Saginaw Bay increased, especially under scenarios of high prey vulnerability to BHC, primarily owing to the addition of age-0 BHC to its diet (Figure S3.4a). In Lake Erie and Lake Michigan, consumption by adult Yellow Perch showed negligible change across BHC scenarios, but in Lake Erie its consumption of age-0 BHC replaced consumption of other prey under scenarios of high prey vulnerability to BHC (Figures S3.4b, c). In Lake Huron, consumption by adult Yellow Perch increased from baseline in all BHC scenarios primarily through increased consumption of oligochaetes (Figure S3.4d).

Changes from baseline in prey consumption by other omnivores were mostly negligible in response to BHC scenarios (Figures S3.4a–d). However, in Saginaw Bay, consumption by White Perch decreased from baseline under scenarios of high prey vulnerability to BHC, owing to reduced consumption of herbivorous cladocerans (Figure S3.4a). In Lake Erie, consumption by White Perch increased from baseline under scenarios of high prey vulnerability scenarios to BHC through addition of age-0 BHC to its diet (Figure S3.4b).

Predation Mortality

Predation mortality on age-0 BHC.— Predation mortality on age-0 BHC varied among BHC scenarios in Saginaw Bay (Table 10). In Lake Erie, predation mortality was lower under scenarios of high age-0 BHC production rates, but higher under scenarios of low BHC production rates. In Lake Michigan and Lake Huron, predation mortality on age-0 BHC was lower under scenarios of high age-0 BHC production rates and salmonine consumption of age-0 BHC compared to scenarios with low age-0 BHC production rates (Table 10).

Predation mortality on planktivores.—There was very little change from baseline in predation mortality on planktivores across BHC scenarios. In Saginaw Bay, predation mortality on Emerald Shiner and Gizzard Shad declined from baseline only under scenarios of low prey vulnerability to BHC (Table S3.2). In Lake Erie, predation mortality on Rainbow Smelt and Alewife decreased from baseline under all BHC scenarios, while predation mortality on Emerald Shiner and Gizzard Shad decreased from baseline under scenarios of high prey vulnerability to BHC (Table S3.2). In Lake Michigan and Lake Huron, there were negligible changes from baseline in predation mortality on planktivores under all BHC scenarios.

Predation mortality on omnivores.—In Saginaw Bay, predation mortality on age-0 Yellow Perch decreased from baseline under all BHC scenarios, but for age-1 and age-2+ Yellow perch predation mortality decreased from baseline most under scenarios of high prey vulnerability to BHC. In Lake Erie, Lake Michigan, and Lake Huron, there were negligible changes from baseline in predation mortality on Yellow Perch under any BHC scenario (Table S3.2). There were negligible changes from baseline in predation mortality on White Perch in Saginaw Bay or Lake Erie under any BHC scenario.

DISCUSSION

Our model results suggest that biomass of BHC would be greater in Saginaw Bay and Lake Erie, where productivity is higher, than in either Lake Michigan or Lake Huron. The percentage of total fish biomass represented by BHC also was greatest in Saginaw Bay and Lake Erie. Our simulated values of BHC biomass as a percentage of total Lake Erie fish biomass are similar to prior estimates generated by Zhang et al. (2016) and are consistent with prey productivity trends in other habitats where they occur. For example, the percentage of total fish biomass represented by BHC in Saginaw Bay (10–34%) and Lake Erie (11–40%) was lower than those (45–78%) reported in 2010 for the highly productive Illinois River (Coulter et al. 2018) where average spring total phosphorus and chlorophyll *a* concentrations are higher (360 µg L^{-1} and 27.2 µg L^{-1}, respectively) (Johnson and Hagerty 2008) than concentrations found in the Great Lakes habitats (Table 1). In contrast, in Lake Qiandaohu, China, where BHC do not reproduce successfully and are heavily stocked, a BHC biomass of 6.3 g m^{-2} was reported which represented approximately 46% of the total fish biomass despite a relatively low chlorophyll *a* value of 2.4 µg L^{-1} (Liu et al. 2007) that is lower than chlorophyll *a* values for Saginaw Bay and Lake Erie, but higher than values in Lake Michigan and Lake Huron. In Lake Balaton, Hungary, biomass of stocked BHC hybrids ranged from 2.1–2.8 g m^{-2} and comprised approximately 25% of the total fish biomass (Specziar 2010). Average phosphorus concentration in Lake Balaton is 64 µg L^{-1} and chlorophyll *a* biomass is 12 µg L^{-1} (General Directorate of Water Management of Hungary, http://www.ovf.hu/).

In our model projections, Bighead Carp reached a similar equilibrium biomass as Silver Carp in all modeled habitats. This is more likely a function of the way we configured the Ecopath models than it is reflective of prey biomass available to each species in each lake. For example, we set initial biomass and consumption of each carp species to be the same values, and set proportional composition of age-0 BHC in predators' diets to be the same. The only differences were in the initial conditions for Bighead Carp and Silver Carp in the von Bertalanffy growth parameters, diet compositions (e.g., Bighead Carp eat more zooplankton than Silver Carp; Silver Carp eat more phytoplankton than Bighead Carp), and P/B values under low BHC production rates scenarios. Most other studies have reported that Silver Carp reach higher biomass levels than Bighead Carp in productive habitats where the two species co-occur. For example, in the lower Illinois River in 2005, Silver Carp comprised 85% of total BHC biomass (Irons et al. 2007). In Lake Poyang, China in 2000, Silver Carp comprised 58% of total BHC biomass (Wang et al. 2019). Possible explanations for the dominance of Silver Carp where the two species co-occur include higher predator preference for Bighead Carp (Sanft et al. 2018), and that Silver Carp feed more on phytoplankton and thereby can access a more abundant food resource. However, in less productive lakes like Lake Qiandaohu, China, biomass of Bighead Carp was greater (76% of total BHC biomass) than that of Silver Carp, possibly due to higher stocking levels (Dr. Q. Liu, Shanghai Ocean University, personal communication). Alsip et al. (2019) simulated growth potential of BHC in Lake Michigan, and found Bighead Carp would have positive growth in more areas than would Silver Carp. This model outcome may be a function of lower energy density for Bighead Carp compared to Silver Carp used in the model, allowing Bighead Carp to achieve positive growth in areas of low prey density (Alsip et al. 2019). Based on these studies, we would expect that Silver Carp also would reach a higher biomass in productive areas in the Great Lakes if both BHC species become established.

Differences in projected BHC biomass among scenarios were driven by differences in BHC production rates and vulnerability of prey to BHC, and less so by variation in predation mortality on age-0 BHC by salmonines. The greatest biomass of BHC in any lake occurred under scenarios of high prey vulnerability to BHC. Projected BHC biomass was highest in Saginaw Bay and Lake Erie because of the high vulnerability and biomass density of their prey, and to a lesser extent on BHC production rates. The prey vulnerability coefficient in the Ecosim model is a parameter in the foraging arena concept (Ahrens et al. 2012) that determines the availability of prey to predators, with higher values of vulnerability indicating that a higher proportion of prey production is available to predators. A comparison of the percentage of zooplankton production consumed in Great Lakes Ecopath models reveals that approximately 40% of the available zooplankton production is utilized by resident fish and invertebrate planktivores in our study habitats (Kao et al. 2014; Kao et al. 2018; Kao et al. 2016; Zhang et al. 2016), which leaves nearly 60% potentially available to invasive planktivores such as BHC. Owing to the difference in lake depths (Table 1), although the total areal density of zooplankton biomass (g m^{-2}) was highest in Lake Michigan and Lake Huron, the volumetric biomass density (g m^{-3}) was lower in those lakes than in Saginaw Bay or Lake Erie. As an outcome of model calibration, the vulnerability coefficients of zooplankton as prey available to native planktivores were higher for the mesotrophic and shallower Saginaw Bay and Lake Erie than for the oligotrophic and deeper basins of Lake Michigan and Lake Huron. This suggests that spatial overlap between planktivorous fish and zooplankton may be higher in Saginaw Bay and Lake Erie compared to Lake Michigan and Lake Huron, and implies that Saginaw Bay and Lake Erie would be more vulnerable to BHC invasion compared to the other deeper and more oligotrophic habitats across the Great Lakes.

Food Web Response to BHC across lake habitats

Results of our model simulations suggest that BHC would have some negative effects on many food web groups in relatively more productive Saginaw Bay and Lake Erie (5–25% projected changes in biomass from baseline values), and negligible effects (<5% projected changes in biomass from baseline values) on food web groups in oligotrophic Lake Michigan and Lake Huron. The greatest effects of BHC biomass were projected to be on planktivorous fish and zooplankton, and less so on piscivores, benthos, phytoplankton and the microbial groups. Larger decreases in biomass also were projected for Emerald Shiner in Lake Erie. The declines in planktivore biomass were more related to declines in biomass and consumption of zooplankton, given their predation mortality was lower than baseline (i.e., without BHC in the habitat) values. In Saginaw Bay, BHC consumption caused large decreases in biomass of cladocerans and planktivores, which released food competition and/or predation mortality on copepods, rotifers, protozoa, bacteria and non blue-green algae and led to biomass increases of these groups (Supplementary Material 3). In the other three modeled habitats, the lack of response by phytoplankton and microbial groups to BHC consumption may be attributable to an indirect effect of reduced filtration pressure from lowered zooplankton biomass. Large increases in biomass also were projected for invasive White Perch in Lake Erie, owing to consumption of age-0 BHC and reduced predation from sub-adult Walleye and other piscivores.

Studies of BHC effects on food webs in the Mississippi-Illinois River system are largely consistent with our model results. In the Illinois River, biomass of large and small size groups of zooplankton and chlorophyll α declined after BHC introduction (DeBoer et al. 2018; Irons et al. 2007). Irons et al. (2007) indicated density and condition of planktivorous Gizzard Shad and Bigmouth Buffalo (*Ictiobus cyprinellus*) declined after BHC invaded the river, and Pendleton et al. (2017) showed declines in biomass of planktivorous fish in off-channel habitats after bigheaded carp introduction. However, DeBoer et al. (2018) reported increases in age-0 fish biomass and negligible changes in adult fish biomass in the main channel habitat of lower Illinois River over the period from 2002–2017. They speculated the increase in age-0 fish biomass may have resulted from piscivores switching from feeding on less abundant native prey fish to feeding on more abundant Silver Carp juveniles. In contrast, Phelps et al. (2017) analyzed long-term (20-year) data from the Mississippi River, short-term (5-month) data from backwater lakes, and conducted laboratory experiments to demonstrate negative effects of high densities of Silver Carp on the fish community. They found that densities of Gizzard Shad and piscivorous Bowfin *Amia calva* declined in the Mississippi River after the introduction and irruption of the Silver Carp population, while their laboratory results with age-0 stages of Silver Carp, Gizzard Shad, and Bigmouth Buffalo showed reduced survival of Gizzard Shad and reduced growth of Bigmouth Buffalo in the presence of high densities of Silver Carp (Phelps et al. 2017). The negative effects of Silver Carp on density and condition of native planktivorous fishes were confirmed by other studies that suggest competition with Silver Carp for plankton has negatively affected native planktivore condition and growth (Minder and Pyron 2018, Fletcher et al. 2019).

Our model results suggest that age groups of some fish species may experience different trends in abundance in response to BHC carp invasion. Although adult Walleye biomass was projected to increase slightly in Lake Erie as BHC biomass increased, biomass of younger Walleye life stages declined because their planktivorous prey biomass declined, and the addition of age-0 BHC as prey could not compensate for the loss of their existing planktivorous prey. Walleye biomass in Saginaw Bay was negatively affected even with the addition of age-0 BHC to its diet. In Lake Michigan, age-0 BHC biomass was projected to have a minor but positive effect (<10% increase) as prey for Walleye, but we consider this a relatively minor change because the baseline Walleye biomass was extremely low (0.00017 g m^{-2}).

The response of other predators to BHC biomass was mixed. In Lake Erie, Lake Trout, Burbot, Steelhead and White Bass biomass decreased owing to a decrease in biomass of their planktivorous prey (Alewife, Rainbow Smelt, Emerald Shiner), and did not benefit from availability of age-0 BHC as was observed for White Bass in the Illinois River drainage (Anderson 2016). There was no significant change in Lake Trout biomass in the other habitats, or in Pacific salmonine biomass in either Lake Michigan or Lake Huron. In contrast, biomass of fishes that consumed age-0 BHC increased, including Smallmouth Bass in Saginaw Bay and Lake Erie, and White Perch in Lake Erie.

Higher BHC biomass in Saginaw Bay and Lake Erie led to greater effects on zooplankton and planktivores within these habitats but differences existed between habitats in the food web response to BHC. For example, decreases in herbivorous cladoceran biomass were larger in response to BHC invasion in Saginaw Bay than in Lake Erie. As a consequence, Gizzard Shad consumption and biomass decreased in Saginaw Bay, while in Lake Erie, Gizzard Shad consumption and biomass was less affected by BHC introduction. Also, copepod biomass increased in Saginaw Bay in response to BHC introduction, but decreased in Lake Erie. This is consistent with the decline of Emerald Shiner in Lake Erie, which declined by a much greater amount in scenarios with high prey vulnerability to BHC than in Saginaw Bay as a result of more direct competition for zooplankton prey.

Response of zooplankton and microbes to BHC biomass varied among habitats and showed strong interspecific interactions. In Saginaw Bay, the decline in herbivorous cladoceran biomass due to BHC consumption led to higher biomass of copepods, rotifers, protozoa, and bacteria because of reduced competition for algae. In Lake Erie, biomass of both copepods and cladocerans decreased in response to BHC, but to a less degree than in Saginaw Bay, and led to negligible changes in rotifer and microbe biomass in Lake Erie. These results are consistent with observations from Lake Donghu China, which has been continuously stocked with BHC since the 1970s. By 1991 in Lake Donghu, large cladocerans decreased, copepods and rotifers had minor changes, while protozoa increased compared to before BHC stocking (Yang et al. 2005).

Simulated changes in phytoplankton biomass in response to BHC biomass were observed only in Saginaw Bay. Biomass of non blue-green phytoplankton (diatoms, green algae) increased, while biomass of blue-green algae decreased. Non blue-green phytoplankton biomass likely increased owing to decreases in macrozooplankton, and because of competitive release from blue-green algae whose projected decline was attributed to BHC consumption. Studies suggest that blue-green algae form a large part of BHC diet composition when the algae is abundant (Chen 1982, Cooke et al. 2009). BHC were introduced into the United States to control algae in aquaculture and waste ponds, and whether BHC can control blue-green algae, particularly *Microcystis*, is of great interest to water quality management in China (Miura 1990, Ke et al. 2007, Ma et al. 2012). Estimates of the minimum BHC biomass needed to control *Microcystis* were 92–100 g m^{-2} in Lake Donghu (Liu and Xie 2002) and 55 g m^{-2} in Lake Shichahai (Zhang et al. 2006), while a BHC biomass of approximately 20 g m^{-2} was estimated to be too low to control *Microcystis* (Ke et al. 2007). These BHC biomass levels are much higher than those projected to occur in the Great Lakes habitats we have modeled (up to 9.2 g m^{-2} in Saginaw Bay, and 7.4 g m^{-2} in Lake Erie), which may explain why our model simulations projected only minor decreases in blue-green algae biomass with introductions of BHC. Also, we may have underestimated the projected effects of BHC consumption on blue-green algae biomass in the Great Lakes because *Microcystis* blooms only occur in nearshore areas during two to three months in summer or fall, while our input parameters and simulation drivers in EwE models were based on growing-season averages across the whole habitats.

Changes in biomass of benthic organisms were relatively minor in response to BHC. We anticipated that invasion of BHC would have significant negative effects on *Dreissena* mussels as they would both compete for phytoplankton, but effects on *Dreissena* mussels were negligible in Lake Erie and Lake Michigan, likely because the projected biomass of *Dreissena* was so large. Changes in projected biomass of other benthic groups that mainly fed on detritus were negligible. Zhang et al. (2016) also reported little change in benthos biomass in response to a simulated BHC invasion in Lake Erie.

In Lake Michigan and Lake Huron, biomass of food web groups changed little in response to BHC biomass, which did not increase above the low introductory levels under most BHC scenarios. This result suggests that the habitats in these lakes, while not productive enough to support high production of BHC, still are adequate to sustain a low population size of BHC which is consistent with the findings in Alsip et al. (2019). As we simulated the food web at the whole lake level, organism biomass more reflected the oligotrophic conditions of the larger main basin and not the smaller, more mesotrophic nearshore areas.

Scenario simulations

Scenario simulations allowed us to evaluate consequences of previously documented sources of uncertainty for BHC biomass and food web effects. These included variability in prey vulnerability to BHC, BHC production rates, and predation on age-0 BHC by salmonines (Wittmann et al. 2015; Zhang et al. 2016). By far the most important factor explaining potential for BHC populations to grow was vulnerability of their prey, followed by variability in BHC production rate. Predation by salmonines on age-0 BHC did not appear to affect BHC population biomass. As with prior scenario simulations of BHC in Lake Erie, BHC biomass did not change with vulnerability to predators (Zhang et al. 2016). In reality, it is unlikely that salmonines would be able to prey on age-0 BHC because their habitats would not overlap. In the Mississippi River drainage, age-0 carp spend much of their first year in shallow side-channel and wetland habitats (eg. Kolar et al. 2007, Chick et al. 2020) that are not inhabited by salmonines in the Great Lakes.

Model simulations of BHC effects on food webs in other freshwater ecosystems were consistent with results in this analysis. In Lake Ontario, which is less productive than Lake Erie or Saginaw Bay, but more productive than Lake Michigan or Lake Huron, Currie et al. (2012) used an Ecopath biomass balance approach to project that at high biomass levels, BHC could have significant negative effects on Alewife, the dominant planktivore species. Kramer et al. (2019) simulated food web response to invasion by BHC in currently uninvaded areas of the Mississippi River, and found that biomass of all members of the food web would decline by 10–30%. Liu et al. (2007) used an Ecopath model to analyze trophic flows of Lake Qiandohu in China, and found that aggressive BHC stocking practices and elimination of piscivores allowed BHC to reach a biomass of 6.3 g m^{-2}, which was sufficient to reduce phytoplankton biomass and eliminate algal blooms.

Model biases

The Ecopath models used in this study were developed by different groups using data from different time periods, which could have confounded the comparisons among the four habitats. Kao et al. (2014, 2016) developed the Lake Huron main basin and Saginaw Bay models, while Zhang et al. (2016) developed the Lake Erie model and the Lake Michigan model in this study. Yet, by running the simulations to model year 2031 without releasing BHC populations to grow, all simulations were consistent with current observations from each lake, and had experienced recent food web changes. For example, decreases in productivity of the lower food web resulted from declining nutrient inputs and *Dreissena* mussel filtration in both Lake Michigan and Lake Huron. This gives us confidence that the relative direction and magnitude of food web response to BHC scenarios would be similar across habitats of similar productivity.

Our model projections of BHC effects on lake food webs are likely underestimated. We averaged biomass of food web groups across all habitats and growing seasons, and ignored the connectivity and movement of nutrients and fish between productive nearshore habitats in Lake Huron and Lake Michigan with less productive offshore habitats. In Lake Erie, we averaged biomass of food web groups that occur in the productive western basin and the more oligotrophic eastern basin. Some fish species in Saginaw Bay move seasonally to Lake Huron main basin and back again, and in Lake Erie, fish in the more productive western basin migrate seasonally to the central and eastern basins (Wang et al. 2007), so BHC effects occurring within these more productive areas likely will reverberate to adjacent habitats. In Lake Michigan, early life stages of key fish species that occur in drowned river mouth lakes were not included in our simulations, but likely would be affected by BHC consumption of their zooplankton prey (Fletcher et al. 2019). We also may have underestimated the effect of BHC planktivory on age-0 fish (besides Walleye and Yellow Perch) by simulating their average prey consumption over their first year. Barthelmes (1984) found densities of larval percids declined with heavy stocking of Silver Carp, possible because of competition with fish larvae for plankton prey (Ivan et al. 2020) or through direct consumption of larvae. We did not evaluate the possibility that BHC could consume native fish larvae, which, if it occurred, could cause population collapse (Zhang et al. 2016).

Since BHC are not yet established in the Great Lakes, and because the vulnerability of Great Lakes plankton to BHC is unknown, we assumed BHC would have the same feeding efficiency for plankton as the planktivore species we identified as reference species in each lake and vice versa. If BHC are more efficient at eating plankton than the reference species we used (Cuthbert et al. 2019), then we likely underestimated BHC's potential biomass and effects on Great Lakes food webs. Similarly, the vulnerability parameters of existing species in all of our

Ecosim models were estimated by fitting predicted biomass to observed biomass time series. Therefore, these values of vulnerability parameters, as well as our simulations, did not account for behavioral effects of BHC on existing species. We did run two scenarios to evaluate the sensitivity of BHC biomass to vulnerability of their plankton prey, and found BHC biomass was highly sensitive to vulnerability of its prey. Further work should quantitatively measure and compare foraging efficiency of BHC on plankton with that of existing planktivores.

Another potential bias resulting from our model approach was to use the same values of consumption and production for BHC across all lake habitats. In reality, Lake Erie has warmer temperatures and should favor higher consumption and production rates of BHC compared to colder, more oligotrophic lake habitats. Thus, we may have overestimated effects in Lake Huron and Lake Michigan relative to Lake Erie and Saginaw Bay, although projected BHC biomass and effects in these lakes were low. Further use of bioenergetics models to quantify BHC potential consumption rates in Great Lakes habitats (Cooke and Hill 2010, Anderson et al. 2015, Anderson et al. 2017, Alsip et al. 2019) would refine risk assessments of BHC establishment, growth and potential effects (Ivan et al. 2020).

Conclusions and Recommendations for future work

Our food web model projections provide support for previous risk assessments of BHC in the Great Lakes. Cudmore et al. (2012) also reported that productive areas of the Great Lakes would provide adequate prey and habitat for BHC, and effects on the food web would be negative for crustacean zooplankton, planktivorous fishes, and piscivores that may feed on them. Our model results may inform predictions of BHC effects in other Great Lakes. The results imply that productive nearshore areas will be most vulnerable, such as Lake St. Clair, Bay of Quinte in Lake Ontario, drowned river mouth lakes of Lake Michigan, southern Green Bay, and the North Channel of Lake Huron. Food web effects will be greatest on macrozooplankton and planktivores, and to a lesser degree on piscivores.

Although our results help define potential risk of BHC to food webs in these Great Lakes habitats, additional studies are needed to reduce the uncertainty. We recommend using models to project the population growth and consumption of BHC in spatially heterogeneous Great Lakes habitats. It would be important to simulate the entire life cycle of BHC in tributary and nearshore habitats of the Great Lakes, including spawning, early life history, movement and feeding. Use of individual-based bioenergetics models, or whole ecosystem models (the Atlantis Ecosystem model; Fulton et al. 2011) will facilitate such projections for nearshore and offshore zones of Lake Ontario, Green Bay, and Lake Superior. Finally, we recommend testing model skill by testing the ability of the model to predict BHC dynamics and food web effects in well-studied ecosystems that already have been invaded by BHC (e.g., the Illinois River), where the history of BHC invasion and effects is relatively well known and food web effects are well documented.

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Table 1. Area, average depth, spring total phosphorus (TP) and chlorophyll *a* (Chl), trophic state, dominant piscivorous and planktivorous fishes, and initial bigheaded carp (BHC) biomass used in the Ecopath with Ecosim model for each lake habitat. Also given are time periods of data used to configure Ecopath models. TP and Chl values for each lake habitat were averages from 2008–2010.

	Saginaw Bay	Lake Erie	Lake Michigan (main basin)	Lake Huron (main basin)
Area (km^2)	2,770	25,609	53,646	37,765
Depth (m)	8.9	19	91	73
TP (μg L^{-1})	15.91[a]	21.24[b]	3.20[b]	2.03[b]
Chl (μg L^{-1})	7.19[a]	5.75[b]	0.80[b]	0.65[b]
Trophic state	Mesotrophic[c]	Mesotrophic[d]	Oligotrophic[d]	Oligotrophic[d]
Initial BHC biomass (g m^{-2})	0.074–0.078	0.056–0.059	0.041–0.042	0.050–0.052

Dominant piscivores	Percids	Percids	Salmonines	Salmonines
Dominant planktivores	Gizzard Shad, Emerald Shiner	Gizzard Shad, Emerald Shiner, Rainbow Smelt	Alewife, Rainbow Smelt, Bloater	Alewife, Rainbow Smelt, Bloater
Ecopath period	1988–1990	1999–2001	1994–1998	1981–1984

[a] Stow and Hook (2013)

[b] US EPA Great Lakes National Program Office (available at https://cdx.epa.gov/)

[c] Cha et al. (2016)

[d] Dove and Chapra (2015)

Table 2. Diet composition (%) of Bighead Carp (BCP) and Silver Carp (SCP) in each Ecopath model. Age-0 and age-1+ carp of the same species had the same diet composition. Note that food web groups were different among models, and "-" indicates those groups were not explicitly included in the model.

	Saginaw Bay		Lake Erie		Lake Michigan		Lake Huron	
	BCP	SCP	BCP	SCP	BCP	SCP	BCP	SCP
Blue-green algae	4.6	9.2	22.0	44.7	3.2	6.2	4.0	8.1
Non blue-green algae	26.6	53.9	9.2	18.7	-	-	27.1	54.7
Diatoms	-	-	-	-	17.8	34.9	-	-
Other phytoplankton	-	-	-	-	9.7	18.9	-	-
Protozoa	0.8	4.9	0.8	4.6	1.4	8.0	0.9	5.2
Rotifers	0.1	0.2	0.8	1.4	0.2	0.3	3.4	4.5
Copepod nauplii	9.8	2.5	-	-	47.1	10.3	1.3	0.3
Calanoids	11.6	2.9	-	-	1.8	0.4	2.5	0.5
Cyclopoids	5.2	1.3	-	-	1.3	0.3	2.4	0.5
Copepods	-	-	6.1	1.6	-	-	-	-
Predaceous cladocerans	0.3	0.1	1.4	0.3	0.2	0.04	0.1	0.01
Herbivorous cladocerans	28.0	5.1	46.7	8.7	4.4	0.7	45.2	6.3
Detritus	13.0	20.0	13.0	20.0	13.0	20.0	13.0	20.0

Table 3. Percent composition of age-0 bigheaded carps in predators' diets in each Ecopath model. Note that food web groups were different among models, and "-" indicates those groups were not explicitly included in the model.

Group (age stanza)	Saginaw Bay	Lake Erie	Lake Michigan	Lake Huron
Walleye (0)	0.5	0.5	-	-
Walleye (1)	2.5	-	-	-
Walleye (1–2)	-	2.5	-	-
Walleye (2+)	1.5	-	-	-
Walleye (3+)	-	1.5	-	-
Walleye (all)	-	-	1.5	1.5
Yellow Perch (1)	-	1.0	-	1.0
Yellow Perch (1–2)	1.0	-	1.0	-
Yellow Perch (2+)	-	1.0	-	1.0
Yellow Perch (3+)	1.0	-	1.0	-
Steelhead	0.25	0.25	0.25	0.25
Burbot	0.1	0.1	0.1	0.1
White Bass	0.5	0.5	0.5	0.5
White Perch	0.1	0.5	0.5	0.5
Smallmouth Bass	-	1.5	-	-
Freshwater Drum	0.1	0.1	0.1	0.1
Lake Trout	0.05	0.05	0.05	0.05
Catfish	0.5	0.5	-	-
Outer Bay predators	0.25	-	-	-
Inner Bay predators	1.5	-	-	-
Chinook salmon (1+)	-	-	0.25	0.25
Coho Salmon (1+)	-	-	0.25	-
Other salmonines	-	-	-	0.25

Table 4. Simulation scenarios used to investigate potential food web effects of bigheaded carps (BHC). Scenarios include a baseline scenario with no BHC (BaseL) and eight combinations of high or low production rates of BHC (HZ, LZ), high or low prey vulnerability to age-0 BHC (HP, LP), and whether salmonines feed on age-0 BHC (Y, N). For example, a scenario of high

BHC production rates (HZ), high prey vulnerability to BHC (HP), and predation by salmonines (Y) would be denoted as HZHPY.

Scenario	Bighead Carp production	Silver Carp production	Prey vulnerability to BHC	Predation by salmonines
BaseL				
HZLPY	High[a]	High[a]	Low	Yes
HZHPY	High[a]	High[a]	High	Yes
HZLPN	High[a]	High[a]	Low	No
HZHPN	High[a]	High[a]	High	No
LZLPY	Low[b]	Low[c]	Low	Yes
LZHPY	Low[b]	Low[c]	High	Yes
LZLPN	Low[b]	Low[c]	Low	No
LZHPN	Low[b]	Low[c]	High	No

[a] The production to biomass ratio (P/B) for age-1+ group was set to 1.08 yr^{-1}

[b] P/B for age-1+ group was set to 0.654 yr^{-1}

[c] P/B for age-1+ group was set to 0.631 yr^{-1}

Table 5. Reference planktivore fish groups in each lake habitat that were used in simulation scenarios of high or low prey vulnerability (HP or LP, respectively) to bigheaded carps.

Habitat	Age stanza of bigheaded carps	Reference group (age stanza)	Vulnerability		
			Calibrated	HP	LP
Saginaw Bay	0	Emerald Shiner (0–0.5)	1.214	10.000	1.214
	1+	Emerald Shiner (0.5+)	10.000	10.000	10.000
Lake Erie	0	Gizzard Shad	11.000	11.000	1.214[a]
	1+	Gizzard Shad	11.000	11.000	11. 000
Lake Michigan	0	Alewife (0)	8.553	8.553	1.242
	1+	Alewife (1+)	1.242	1.242	1.242
Lake Huron	0	Alewife (0)	1.956	1.956	1.833
	1+	Alewife (1+)	1.833	1.833	1.833

[a] used Saginaw Bay value because age-0 Gizzard Shad was not included in the model explicitly.

Table 6. Projected percent changes in biomass of selected piscivorous and omnivorous fishes from a baseline scenario (no bigheaded carps) to each of the eight bigheaded carp invasion scenarios in Saginaw Bay, Lake Erie, Lake Michigan, and Lake Huron. Values in bold font are ≥ 5% and considered significant. Refer to Table 4 for the explanation of bigheaded carp invasion scenarios.

	Bigheaded carp invasion scenario							
	HZLPY	HZHPY	HZLPN	HZHPN	LZLPY	LZHPY	LZLPN	LZHPN
Saginaw Bay								
White Perch	**−5.53**	**−45.74**	**−5.28**	**−49.18**	−4.82	**−34.66**	−4.82	**−34.66**
Inner Bay predators	−0.02	3.57	0.35	3.02	−0.90	−1.47	−0.90	−1.47
Lake Erie								
Lake Trout	−0.90	**−7.79**	−0.90	**−8.48**	−0.81	**−5.46**	−0.81	**−5.98**
Steelhead	−0.74	**−14.51**	−1.01	**−18.64**	−1.09	**−11.22**	−1.36	**−14.26**
Burbot	−1.75	**−18.05**	−1.73	**−17.99**	−1.91	**−13.47**	−1.89	**−13.42**
Smallmouth Bass	0.94	**20.37**	0.94	**20.37**	0.54	**13.44**	0.54	**13.46**
White Bass	3.05	**−13.75**	3.04	**−13.88**	2.27	**−11.03**	2.25	**−11.12**
White Perch	−2.46	**35.35**	−2.44	**35.83**	−5.33	**19.65**	−5.32	**20.05**
Lake Michigan								
Chinook Salmon	0.85	0.89	−0.28	−0.04	0.83	0.79	−0.16	0.17
Lake Trout	0.03	0.07	−0.05	0.01	0.04	0.10	−0.02	0.07
Steelhead	0.31	0.29	−0.03	0.06	0.27	0.27	0.01	0.12
Burbot	0.60	0.59	0.65	0.63	0.55	0.48	0.59	0.51
Coho Salmon	0.18	0.16	−0.07	0.00	0.20	0.16	−0.03	0.06
Lake Huron								
Chinook Salmon	−1.93	−1.96	−2.65	−2.61	−0.97	−0.93	−1.31	−1.27
Lake Trout	−1.54	−1.55	−1.65	−1.65	−0.95	−0.93	−0.88	−0.86
Burbot	0.31	0.31	0.21	0.22	0.28	0.27	0.20	0.20
Other salmonines	1.00	1.01	−0.38	−0.39	0.83	0.82	−0.18	−0.18

Table 7. Projected percent changes in biomass of selected planktivorous fishes from a baseline scenario (no bigheaded carps) to each of the eight bigheaded carp invasion scenarios in Saginaw

Bay, Lake Erie, Lake Michigan, and Lake Huron. Values in bold font are ≥ 5% and considered significant. Refer to Table 4 for the explanation of bigheaded carp invasion scenarios.

	Bigheaded carp invasion scenario							
	HZLPY	HZHPY	HZLPN	HZHPN	LZLPY	LZHPY	LZLPN	LZHPN
Saginaw Bay								
Gizzard Shad	−1.21	**−14.33**	−1.21	**−13.08**	−1.13	**−8.82**	−1.13	**−8.82**
Emerald Shiner	−3.61	**−45.93**	−3.12	**−43.21**	−2.96	**−28.72**	−2.96	**−28.72**
Lake Erie								
Rainbow Smelt	−0.69	**−7.59**	−0.68	**−7.58**	−0.80	**−5.71**	−0.79	**−5.70**
Alewife	−0.21	**−7.62**	−0.21	**−7.62**	−0.43	**−5.92**	−0.43	**−5.92**
Gizzard Shad	0.74	−0.20	0.60	−0.34	1.20	1.40	1.06	1.24
Emerald Shiner	−1.98	**−69.55**	−1.96	**−69.52**	−3.16	**−52.70**	−3.16	**−52.70**
Lake Michigan								
Rainbow Smelt	0.57	0.87	0.15	0.43	0.67	1.10	0.27	0.65
Alewife	−0.29	−0.06	−0.23	−0.01	−0.16	0.18	−0.12	0.18
Lake Huron								
Rainbow Smelt	−1.46	−1.46	−1.79	−1.85	−0.38	−0.37	−0.90	−0.89
Alewife	−5.49	−5.62	−7.61	−7.37	−3.30	−3.15	−3.61	−3.49

Table 8. Projected percent changes in biomass of selected zooplankton groups from a baseline scenario (no bigheaded carps) to each of the eight bigheaded carp invasion scenarios in Saginaw Bay, Lake Erie, Lake Michigan, and Lake Huron. Values in bold font are ≥ 5% and considered significant. Refer to Table 4 for the explanation of bigheaded carp invasion scenarios.

	Bigheaded carp invasion scenario							
	HZLPY	HZHPY	HZLPN	HZHPN	LZLPY	LZHPY	LZLPN	LZHPN
Saginaw Bay								
Copepods	0.45	4.78	0.42	**5.13**	0.41	3.57	0.41	3.57
Herbivorous cladocerans	−4.99	**−42.18**	−4.69	**−38.93**	−4.37	**−27.21**	−4.37	**−27.21**
Predaceous cladocerans	−3.86	**−31.80**	−3.63	**−29.44**	−3.37	**−20.70**	−3.37	**−20.70**
Rotifers	2.06	**20.46**	1.89	**18.51**	1.87	**12.84**	1.87	**12.84**

Lake Erie								
Copepods	−0.09	−1.95	−0.09	−1.95	−0.17	−1.55	−0.17	−1.55
Herbivorous cladocerans	−0.46	**−13.12**	−0.46	**−13.12**	−0.89	**−10.32**	−0.89	**−10.32**
Predaceous cladocerans	−0.33	**−8.71**	−0.33	**−8.71**	−0.85	**−7.23**	−0.85	**−7.23**
Rotifers	−0.09	−3.20	−0.09	−3.20	−0.18	−2.47	−0.18	−2.47
Lake Michigan								
Copepods	0.01	0.06	−0.04	0.01	0.03	0.11	−0.02	0.05
Herbivorous cladocerans	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.02
Predaceous cladocerans	−0.27	−0.21	−0.28	−0.22	−0.22	−0.09	−0.23	−0.12
Rotifers	−0.01	−0.02	0.01	0.00	−0.01	−0.03	0.01	−0.01
Lake Huron								
Copepods	−0.34	−0.34	−0.42	−0.40	−0.24	−0.24	−0.22	−0.21
Herbivorous cladocerans	−0.18	−0.19	−0.62	−0.62	−0.32	−0.31	−0.35	−0.34
Predaceous cladocerans	−1.38	−1.41	−1.28	−1.29	−0.38	−0.33	−0.16	−0.12
Rotifers	−0.13	−0.12	−0.10	−0.10	0.00	0.00	−0.01	−0.01

Table 9. Projected percent changes in biomass of protozoa, bacteria, and phytoplankton groups from a baseline scenario (no bigheaded carps) to each of the eight bigheaded carp invasion scenarios in Saginaw Bay, Lake Erie, Lake Michigan, and Lake Huron. Values in bold font are ≥ 5% and considered significant. Refer to Table 4 for the explanation of bigheaded carp invasion scenarios.

	Bigheaded carp invasion scenario							
	HZLPY	HZHPY	HZLPN	HZHPN	LZLPY	LZHPY	LZLPN	LZHPN
Saginaw Bay								
Protozoa	1.31	**13.89**	1.19	**12.27**	1.18	**8.45**	1.18	**8.45**
Bacteria	1.71	**13.20**	1.63	**11.93**	1.52	**8.21**	1.52	**8.21**
Non blue-green algae	0.49	**5.38**	0.45	4.90	0.43	3.40	0.43	3.40
Blue-green algae	−1.57	**−11.33**	−1.48	**−10.43**	−1.32	**−7.31**	−1.32	**−7.31**
Lake Erie								
Protozoa	−0.03	2.25	−0.03	2.25	0.09	1.79	0.09	1.79
Bacteria	−0.03	−3.47	−0.02	−3.47	−0.14	−2.67	−0.14	−2.67
Non blue-green algae	0.00	0.45	0.00	0.45	0.01	0.35	0.01	0.35

Blue-green algae	−0.14	−3.07	−0.14	−3.07	−0.22	−2.36	−0.22	−2.36
Lake Michigan								
Protozoa	0.17	0.15	0.18	0.17	0.17	0.17	0.19	0.18
Bacteria	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
Non blue-green algae	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02
Blue-green algae	0.00	0.01	0.00	0.01	0.01	0.03	0.01	0.03
Lake Huron								
Protozoa	−1.88	−1.86	−1.42	−1.51	−0.14	−0.15	−0.27	−0.28
Bacteria	−0.20	−0.20	−0.20	−0.20	0.03	0.03	−0.01	−0.01
Non blue-green algae	−0.10	−0.09	−0.10	−0.10	−0.01	−0.02	−0.02	−0.03
Blue-green algae	−0.20	−0.21	−0.28	−0.26	−0.25	−0.24	−0.24	−0.23

Table 10. Projected predation mortality rates (yr^{-1}) on age-0 bigheaded carps under the eight bigheaded carp invasion scenarios in Saginaw Bay, Lake Erie, Lake Michigan, and Lake Huron. Values in bold font are ≥ 5% and considered significant. Refer to Table 4 for the explanation of bigheaded carp invasion scenarios.

	Bigheaded carp invasion scenario							
	HZLPY	HZHPY	HZLPN	HZHPN	LZLPY	LZHPY	LZLPN	LZHPN
Saginaw Bay								
Bighead carp	**7.98**	**6.57**	**5.84**	**5.02**	**7.84**	**7.15**	**7.74**	**7.06**
Silver carp	**7.51**	**6.13**	**5.52**	4.71	**7.31**	**6.7**	**7.22**	**6.61**
Lake Erie								
Bighead carp	**5.02**	4.44	4.99	4.43	**7.15**	**6.19**	**7.14**	**6.18**
Silver carp	4.73	4.15	4.71	4.13	**6.61**	**5.80**	**6.62**	**5.80**
Lake Michigan								
Bighead carp	0.44	0.44	0.19	0.20	1.00	1.02	0.48	0.49
Silver carp	0.38	0.38	0.17	0.16	0.93	0.91	0.44	0.41
Lake Huron								
Bighead carp	1.97	1.96	1.90	1.89	3.38	3.39	3.26	3.27
Silver carp	1.81	1.80	1.74	1.74	3.05	3.06	2.95	2.95

Figure 1. The four Great Lakes habitats (shaded) that were modeled for bigheaded carp impacts on food webs.

Figure 2. Initial and Ecosim projected biomass of age-0 and age-1+ bigheaded carps under each of the eight bigheaded carp invasion scenarios in Saginaw Bay (SB), Lake Erie (LE), Lake Michigan (LM), and Lake Huron (LH). Refer to Table 4 for the explanation of bigheaded carp invasion scenarios.

Figure 3. Initial and Ecosim projected percent composition of total fish biomass that was comprised of bigheaded carps (BHC) under each of the eight BHC invasion scenarios in each of Saginaw Bay (SB), Lake Erie (LE), Lake Michigan (LM), and Lake Huron (LH). Refer to Table 4 for the explanation of BHC invasion scenarios.

Figure 4. Projected percent changes from a baseline scenario (no bigheaded carps) in biomass (**A**) Walleye and (**B**) Yellow Perch age classes in response to bigheaded carp biomass under each of the bigheaded carp invasion scenarios in each modeled habitat. Refer to Table 4 for the explanation of BHC invasion scenarios.

Figure 5. Projected percent changes from a baseline scenario (no bigheaded carps) in biomass of selected piscivorous fishes in response to bigheaded carp biomass across bigheaded carp invasion scenarios in the four modeled habitats: Saginaw Bay (SB), Lake Erie (LE), Lake Michigan (LM), and Lake Huron (LH). Note that each fish might not be explicitly modeled in one or more habitats and Smallmouth Bass in Saginaw Bay was simulated as “Inner Bay predators”.

Figure 6. Projected percent changes from a baseline scenario (no bigheaded carps) in biomass of selected planktivorous fishes in response to bigheaded carp biomass across bigheaded carp invasion scenarios in the four modeled habitats: Saginaw Bay (SB), Lake Erie (LE), Lake Michigan (LM), and Lake Huron (LH). Note that each fish might not be explicitly modeled in one or more habitats.

Figure 7. Projected percent changes from a baseline scenario (no bigheaded carps) in biomass of zooplankton groups in response to bigheaded carp biomass across bigheaded carp invasion scenarios in the four modeled habitats: Saginaw Bay (SB), Lake Erie (LE), Lake Michigan (LM), and Lake Huron (LH).

Figure 8. Projected percent changes from a baseline scenario (no bigheaded carps) in biomass of protozoa, bacteria, and phytoplankton groups in response to bigheaded carp biomass across bigheaded carp invasion scenarios in the four modeled habitats: Saginaw Bay (SB), Lake Erie (LE), Lake Michigan (LM), and Lake Huron (LH).

Figure 1

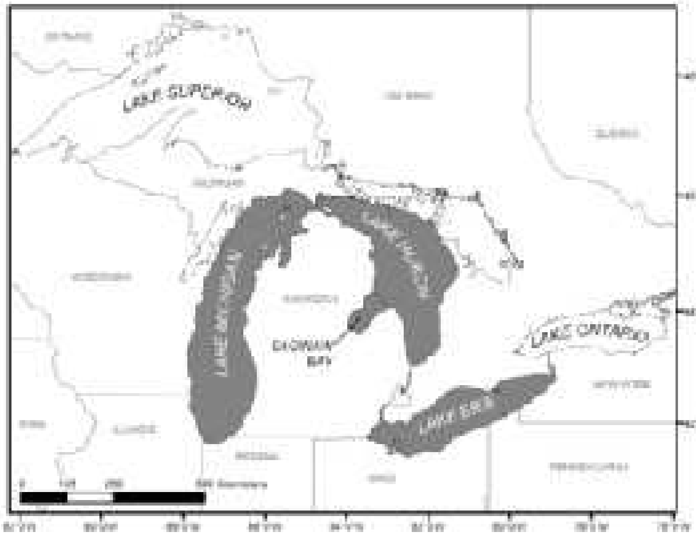

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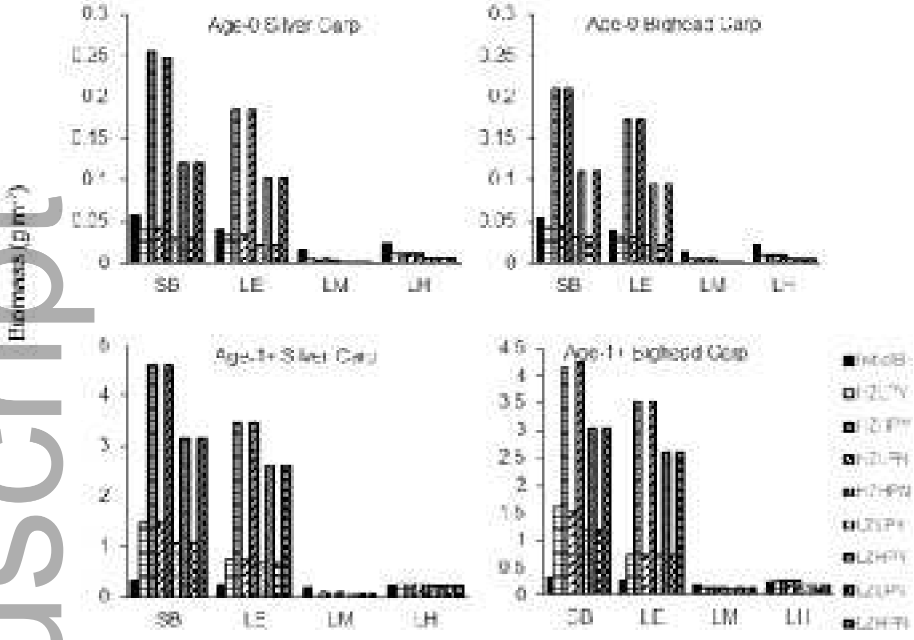
Figure 2



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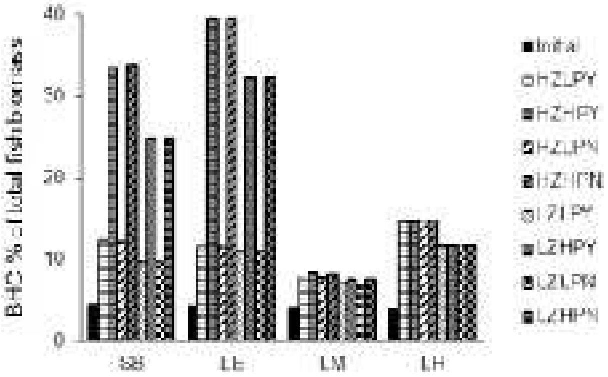

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Figure 4a

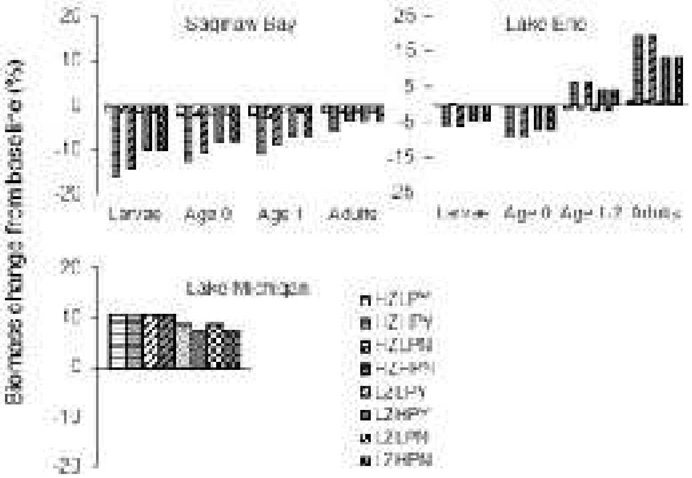

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Figure 4b

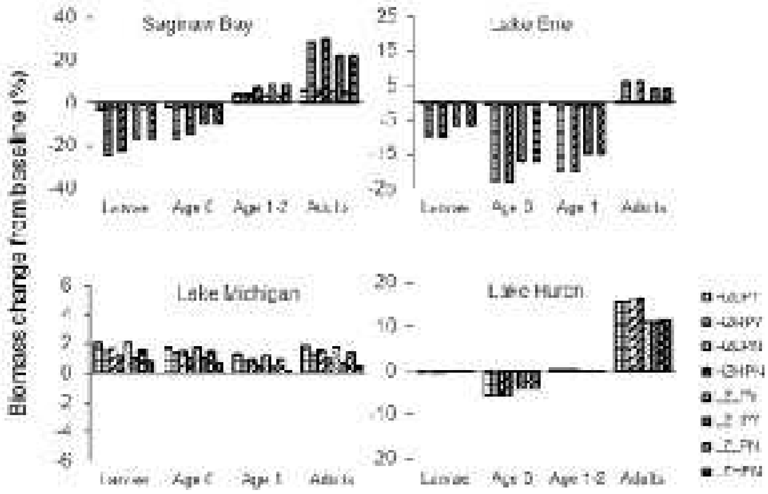

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Figure 5

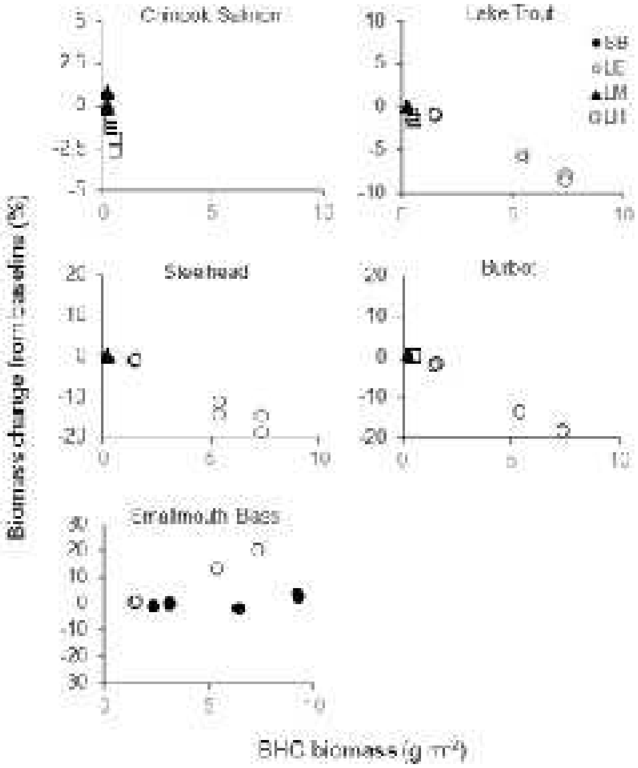

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Figure 6

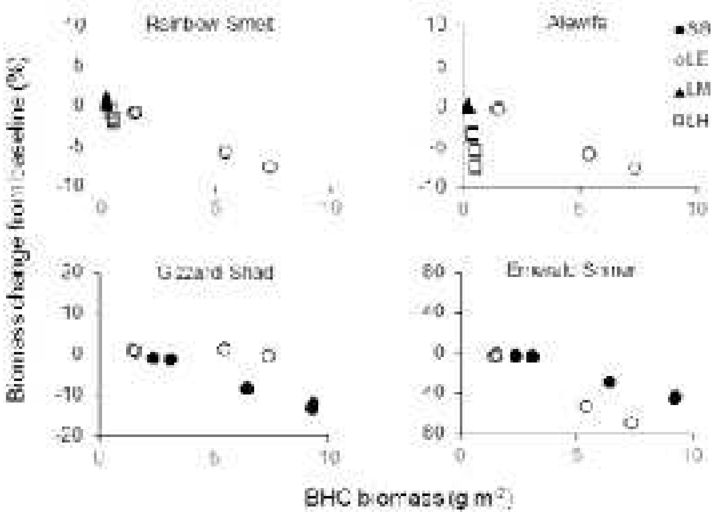

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Figure 7

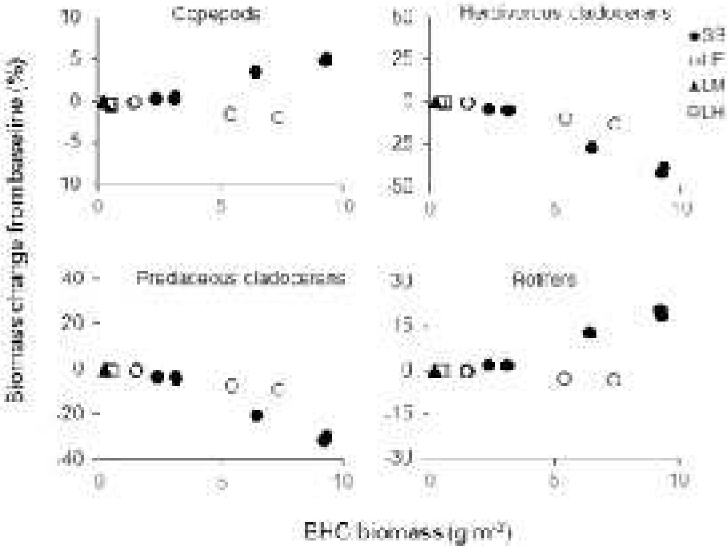

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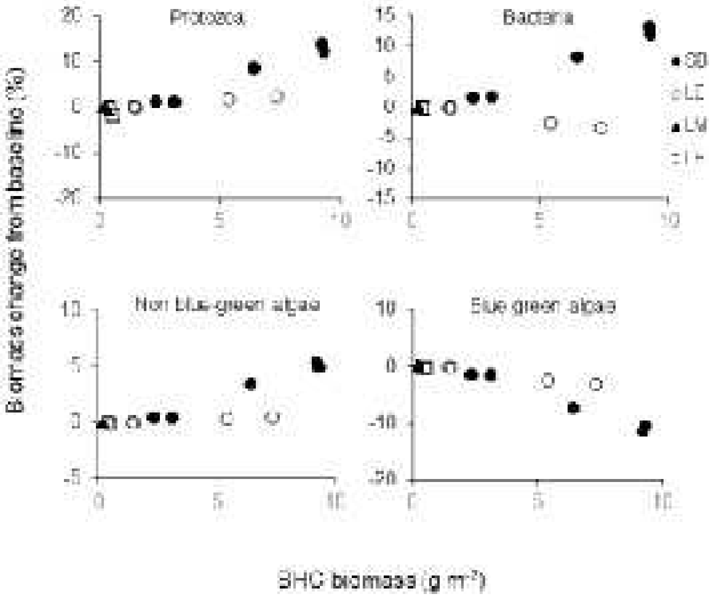
Figure 8



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