

Modeling Lake Michigan's Suitability for Bigheaded Carps: The Importance of Diet Flexibility and Subsurface Habitat

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Abstract

As Bighead and Silver Carp (bigheaded carps [BHC]) arrive at Lake Michigan's doorstep, questions remain as to whether there is sufficient food for these invasive filter-feeding fishes to grow and survive in the upper Great Lakes. Previous studies suggest that suitable BHC habitat in Lake Michigan is limited to a few productive, nearshore areas, but these studies have not considered how BHC's diet plasticity or the availability of subsurface prey influences the ability of these fishes to grow in the lake. This study builds previous models by using simulated outputs of prey biomass (phytoplankton, zooplankton, and detritus) and water temperature from a three-dimensional biophysical model of Lake Michigan to evaluate growth rate potential (GRP, quantitative index of habitat suitability) of adult BHC throughout the entire volume of the lake. We defined suitable habitat as habitats that can support $GRP \geq 0 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$. Consistent with previous studies, our results revealed that habitats with the highest quality were concentrated in eutrophic areas of Green Bay and other nearshore areas influenced by tributary phosphorous loads. However, in contrast to previous studies, we found suitable offshore habitat owing to our added consideration of BHC diet plasticity and subsurface prey resources. Feeding on all three types of prey throughout the water column extended suitable habitat throughout much of the lake for Bighead Carp, but not for Silver Carp. Our vertical analysis along the nearshore-offshore gradient near Muskegon, MI indicates that subsurface temperature and prey biomass are not only sufficient to support Bighead Carp growth, but provide maximum habitat quality during late summer stratification. Overall, our study demonstrates that BHC are capable of surviving and growing in much larger areas of Lake Michigan than predicted by previous studies, and thus indicates that the risk of establishment is not sufficiently mitigated by low plankton concentrations.

Introduction

The ecological history of the Laurentian Great Lakes post-European settlement is arguably best known for the intentional and unintentional introduction of aquatic non-indigenous species. However, of the 180+ established non-native species in the Great Lakes, only a few have become invasive. The undesirable, system-altering effects of the most notorious invaders, i.e. the Sea Lamprey (*Petromyzon marinus*) and the dreissenid mussels, have imposed significant socioeconomic burdens and caused ecological change at an unprecedented rate (Rosaen, Grover & Spencer, 2012; Pagnucco *et al.*, 2015). As a result, stakeholders ranging from the general public (Michigan Sea Grant, 2016) to high-ranking government officials have become acutely aware of the next major invaders sitting on Lake Michigan's door step: Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *H. molitrix* (hereafter collectively referred to as bigheaded carp [BHC]).

Introduced in the US in the 1970s to control eutrophication in reservoirs and sewage treatment lagoons (Kolar *et al.*, 2007), these high-volume filter-feeders have since spread throughout the Mississippi River basin following their escape and are progressing towards Lake Michigan via the Chicago Area Waterway System: the man-made connection between the Illinois River and Lake Michigan (ACRCC, 2016). BHC are capable of consuming substantial amounts of plankton, which allows them to out-compete native planktivores and larval fish (Sampson, Chick & Pegg, 2009). Their voracious consumption habits exert significant competitive pressure upon the zooplankton community, particularly on *Daphnia* spp. (Radke & Kahl, 2002; Cooke, Hill & Meyer, 2009; Sass *et al.*, 2014), and they are capable of altering phytoplankton species composition by promoting the dominance of taxa that are able to resist digestion (Görgényi *et al.*, 2016). If BHC invade Lake Michigan, they would compete with an already-declining population of planktivorous prey fishes (Madenjian *et al.*, 2012) for a

limited prey supply (Vanderploeg *et al.*, 2010, 2012) and could become a trophic choke point that reduces the flow of energy to higher trophic levels (Irons *et al.*, 2007).

The magnitude of potential BHC impacts in Lake Michigan is contingent upon their ability to establish successfully. Establishment is a multi-faceted stage in the invasion process and a variety of approaches have been used to address the probability of BHC establishment in the Great Lakes (Cooke & Hill, 2010; Kocovsky, Chapman & McKenna, 2012; Cuddington, Currie & Koops, 2014; Anderson *et al.*, 2015). Previous modeling efforts have determined that BHC establishment would not be limited by hydrologic and climatic conditions (Chen, Wiley & Mcnyset, 2007; Herborg *et al.*, 2007), and several Great Lakes tributaries would be viable spawning habitats (Kolar *et al.*, 2007; Kocovsky *et al.*, 2012; Murphy & Jackson, 2013). However, the capacity of the oligotrophic offshore waters of Lake Michigan to support invasive planktivores has generated skepticism around the likelihood of BHC establishment (Cooke & Hill, 2010).

The oligotrophication of Lake Michigan that has occurred over the past 50 years has been linked to several factors including climatic variation, reduced phosphorous loads, and, perhaps most notably, the proliferation of the invasive quagga mussel *Dreissena rostriformis bugensis* (Warner & Lesht, 2015; Rowe *et al.*, 2017). The filtering activity of the dreissenid mussels (*D. r. b.* and *D. polymorpha*) has contributed to major changes in Lake Michigan's lower trophic levels (Fahnenstiel *et al.*, 2010). Some of the more impactful effects include the disappearance of the spring phytoplankton bloom (Vanderploeg *et al.*, 2010), the redirection of nutrients and the flow of energy to the nearshore (Hecky *et al.*, 2004), and changes in size structure and species composition in zooplankton and phytoplankton communities (Vanderploeg *et al.*, 2012; De Stasio, Schrimpf & Cornwell, 2014). The dreissenid invasion also has altered energy dynamics in alewives *Alosa pseudoharengus* and contributed to the declining biomass of planktivorous prey fishes in Lake Michigan (Madenjian *et al.*, 2006, 2012). The

reductions in plankton and planktivorous fish biomass suggests that BHC would likely be food-limited in most pelagic habitats of Lake Michigan. While the cold, less productive waters of Lake Michigan are likely not as conducive for BHC growth than the productive rivers in their native and introduced ranges, the degree to which their establishment and spread are limited by these factors has only recently been investigated.

Recent evaluations of BHC habitat suitability have used bioenergetics models to determine Lake Michigan's capacity to support the growth of these invasive fishes (Cooke & Hill, 2010; Anderson *et al.*, 2017). Bioenergetics models are particularly useful in this application because they can translate prey abundance and water temperatures into growth potential of BHC, thus highlighting where in Lake Michigan there is sufficient food and thermal conditions for an individual fish to maintain weight or grow. Cooke & Hill (2010) and Anderson *et al.* (2017) found that suitable habitat for BHC growth is limited to a few productive, nearshore areas, but they did not account for the fishes' flexible diet and modeled growth only at surface conditions. While BHC typically feed on phytoplankton or zooplankton, they are also opportunistic feeders that have the flexibility to feed on organic detritus and bacteria (Chen, 1982; Kolar *et al.*, 2007; Anderson, Chapman & Hayer, 2016). Understanding how a BHC's diet plasticity influences their growth potential is vital to understanding establishment risk.

Consideration of the temporal and three-dimensional spatial complexities of Lake Michigan is also essential for quantifying habitat suitability. For example, a thermally stratified pelagic environment like Lake Michigan may offer opportunities for growth at depths that have yet to be assessed. Maximum growth rate at lower temperatures is attained when feeding at reduced rations (Hanson *et al.*, 1997), and the presence of a deep chlorophyll layer (DCL) during summer stratification suggests that BHC may find sufficient food abundance below Lake Michigan's surface (Pothoven & Fahnenstiel, 2013; Bramburger & Reavie, 2016). Given the potential energetic benefits of the DCL, it

seems likely that BHC could reside there to optimize their growth. Improving our understanding of establishment risk requires that all potential habitats in the lake be investigated, and therefore, habitat suitability assessments need to evaluate spatially explicit growth potential throughout the water column as well as across the entire extent of the lake.

We approached the question of establishment by evaluating the growth rate potential (GRP) (Brandt, Mason & Patrick, 1992) of BHC given habitat conditions (i.e. prey biomass and water temperatures) present in Lake Michigan. We used simulated prey abundance and temperature values from a three-dimensional biophysical model of Lake Michigan (Rowe *et al.*, 2015, 2017). Our GRP model builds upon the foundational work of Anderson *et al.* (2015, 2017) and Cooke & Hill (2010) by evaluating Lake Michigan's habitat quality based on the biomass of three prey resources (phytoplankton, zooplankton, detritus) throughout the water column in Lake Michigan. Our research objectives were to: 1) elucidate how a flexible diet and the availability of subsurface prey influence the extent and quality of suitable BHC habitat in Lake Michigan; 2) characterize the spatiotemporal dynamics of suitable habitat across the lake as well as vertically throughout the water column along a nearshore-offshore transect. We hypothesized that suitable habitat for BHC would increase in response to increases in the types of prey items in their diet and the availability of subsurface resources. We also hypothesized that the extent and quality of suitable habitat would fluctuate seasonally and that suitable habitat existed beneath the surface (>1 m).

Methods

Study Site

Lake Michigan is a meso-oligotrophic lake at temperate latitudes (Figure 1). Lake Michigan has a surface area of about 57,800 km², a mean depth of 85 m, a maximum depth of 282 m, and average summer surface temperatures that reach 21-22 °C (<https://coastwatch.glerl.noaa.gov/>). The lake is dimictic—mixing in the spring and fall and thermally stratifying in the summer and winter—and demonstrates great spatial heterogeneity in its abiotic and biotic environment (Rowe et al., 2017).

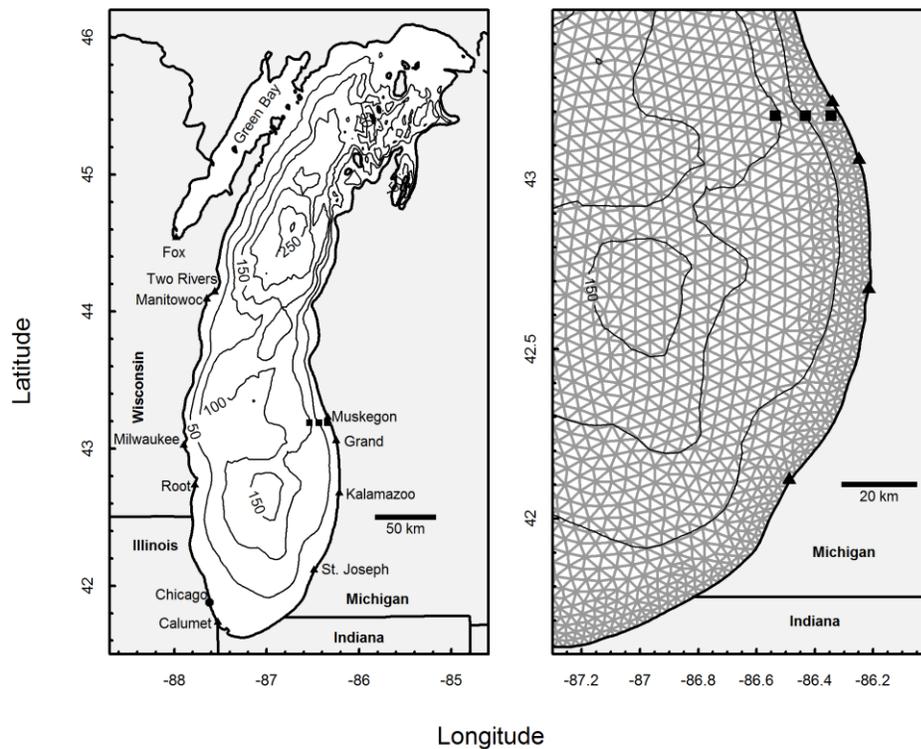


Figure 1. Left panel: Map of Lake Michigan, showing the spatial domain of FVCOM-GEM (white area), bathymetry (50-m contours), bordering states (bolded names), tributary phosphorus loads at 38 locations (filled triangles) labeled by name, and National Oceanic and Atmospheric Administration (NOAA) stations along a nearshore-offshore gradient near Muskegon, MI (filled squares). Right panel: Enlarged area of southeastern Lake Michigan, showing the hydrodynamic model grid, NOAA Muskegon stations (filled squares), and the location of four tributary mouths (filled triangles).

Model Development and Data Source

Growth Rate Potential Model

GRP models provide a quantitative metric for evaluating habitat quality by translating prey concentrations at a given water temperature into terms of fish biomass production as indexed by individual growth. GRP models have been developed for a variety of species in different systems (Brandt *et al.*, 1992; Mason, Goyke & Brandt, 1995; Luo *et al.*, 2001; Zhang *et al.*, 2014). Our GRP model integrates three main components: 1) a bioenergetics model to estimate growth; 2) a foraging model to estimate consumption inputs for the bioenergetics model; and 3) a spatially explicit 3-D environment. The GRP model is constrained by species-specific physiological parameters and is driven by habitat conditions (i.e., temperature and prey concentrations). Inputs to the foraging model and bioenergetics equations in the GRP model were output from a spatially explicit biophysical model. All simulations were coded and run in R (<https://CRAN.R-project.org>).

Bioenergetics Model

We used the Wisconsin Fish Bioenergetics 3.0 model (Hanson *et al.*, 1997), which uses a mass balance approach that estimates growth rate (G , $\text{g g}^{-1}\text{d}^{-1}$) of an individual by subtracting respiration (R), egestion (F), excretion (U), and specific dynamic action (S) from estimates of consumption (C):

$$1) \quad G = C - (R + F + U + S)$$

To better compare our results with those from previous studies (Cooke & Hill, 2010; Anderson *et al.*, 2015, 2017), we adopted their bioenergetics equations and parameter values for consumption, respiration, egestion and excretion, initial fish mass, and predator and prey energy density (Appendix 1, Tables A1.1 and A1.2). These studies used different parameter values for consumption (CA , CB), fish mass (W), and predator

energy density (ED_{Carp}). We used the values from Anderson *et al.* (2015) in our model for these parameters.

Foraging Model

We calculated C by taking the minimum value of two consumption estimates: maximum consumption based on mass and temperature (C_{max} , Appendix 1, Table A1.2) and foraging-based consumption (C_{FR}). C_{max} is determined by the bioenergetics equation for consumption whereas C_{FR} is a function of temperature ($f(T)$), prey concentration ($g L^{-1}$), and filtration rate (FR ; $L d^{-1}$), which itself is a function of fish mass W (g) and foraging hours (t) (from Smith, 1989):

$$1) \quad C_{FR} = (FR * \frac{(Phyto.conc.+ Zoopl.conc.+ Detritus conc.)}{W}) * f(T)$$

$$2) \quad FR = 1.54 * W^{.713} * t$$

We then multiplied the minimum value between C_{FR} and C_{max} by a prey-to-predator energy density (ED) ratio to calculate C ($g g^{-1}d^{-1}$):

$$3) \quad C = \min(C_{max}, C_{FR}) * \frac{ED_{Prey}}{ED_{Carp}}$$

BHC will feed opportunistically on a multiple prey types—often selecting for preferred prey when it is abundant and on less preferable prey when preferable prey is limited (Kolar *et al.*, 2007). To account for this foraging behavior, we assumed that the fish would aim to maximize its specific consumption rate, and only supplement their diet with detritus when favorable planktonic prey became limited (Appendix 2).

Spatially Explicit 3-D Environment

The three-dimensional, heterogeneous environment was defined by the prey concentrations (phytoplankton, zooplankton, and detritus) and water temperatures simulated by the Lake Michigan Finite Volume Community Ocean Model–General

Ecological Module (FVCOM-GEM, Figure 1) (Rowe *et al.*, 2015, 2017). FVCOM is a 3-dimensional, hydrodynamic numerical model that predicts currents, temperature, and water levels driven by external physical forcing including surface wind stress, and heat flux (Chen, Beardsley & Cowles, 2006). The unstructured grid and terrain-following sigma vertical coordinate of the model allows for accurate representation of complex coastline morphology. FVCOM includes a General Ecological Module (GEM), which allows for flexible representation of the lower food web (Ji *et al.*, 2008). FVCOM was applied to Lake Michigan using 20 sigma layers of uniform thickness, and an unstructured grid consisted of 5795 nodes and 10,678 model cells, with cell side lengths of 0.6 to 2.6 km near the coast and 4.5 to 6.8 km near the center of the lake (median 3.1 km) (Rowe *et al.*, 2015). Rowe *et al.* (2017) implemented GEM as a phosphorus-limited nutrient-phytoplankton-zooplankton-dreissenid (NPZD) model that simulates lower food web biomass and productivity, and included a dreissenid mussel (benthic filter feeder) compartment. Phosphorus loads from 38 tributaries were included. The geographic scope of our GRP model was confined by the boundary FVCOM's spatial grid, which included Lake Michigan and Green Bay, but not upstream tributaries or drowned river mouths (Figure 1) (Rowe *et al.*, 2015, 2017). Model development and skill assessment was reported by Rowe *et al.* (2015, 2017). We conducted an additional skill assessment of the biophysical model for Green Bay (Appendix 3) and Muskegon. Observational chlorophyll and zooplankton data came from De Stasio *et al.* (2014) and Reed (2017) for Green Bay, and from S. Pothoven (unpublished data) and Pothoven & Fahnenstiel (2013) at NOAA Great Lakes Environmental Research Laboratory (GLERL) and for Muskegon. POC data were obtained from the Lake Michigan Mass Balance Project (USEPA, 2006). We used Lake Michigan biophysical model output data from 2010 to develop our baseline model scenario for all simulations and analyses. This model scenario included dreissenid mussel biomass initialized from a 2010 benthic survey (Rowe *et al.*, 2015,

2017). For each simulation, we extracted biophysical model data from the day at the middle of each month unless otherwise noted.

Model Sensitivity

Phytoplankton Carbon Content and Foraging Duration

We evaluated the model's sensitivity to varying assumptions with respect to phytoplankton carbon content and foraging duration. We selected two wet phytoplankton biomass:carbon (C_{Phy}) ratios (20, 36) from the literature (Peters & Downing, 1984; Bowie *et al.*, 1985; Fahnenstiel *et al.*, 1989; Rowe *et al.*, 2017) and two foraging durations ($t = 12$ or $t = 24$ hours). Foraging duration values were based on recorded observations of carp feeding rhythms (Wang *et al.*, 1989; Dong & Li, 1994) and on previous BHC GRP models (Cooke & Hill, 2010; Anderson *et al.*, 2015, 2017). We considered scenarios for each combination of assumed carbon content and foraging duration. For each combination of assumptions, we determined the amount of prey required for BHC to maintain weight at temperatures typical of Lake Michigan (2 to 26 C°).

Feeding Scenarios

We ran the GRP model under six scenarios, characterized by the type(s) of prey and the volume of the water in which BHC can feed (surface layer or throughout the whole water column) to determine how these considerations affected the quality and quantity of suitable habitat. We defined suitable habitat as any cell that could support a non-negative growth ($GRP \geq 0 \text{ g g}^{-1} \text{ d}^{-1}$, i.e. at a minimum, the carp maintains its weight), whereas habitat quality refers to the GRP value estimated for a given grid cell (higher GRP = higher habitat quality). For both surface and whole water column scenarios, we ran simulations under three different diets: 1) Phytoplankton only; 2) Phytoplankton and Zooplankton; and 3) Phytoplankton, Zooplankton, and Detritus. We used prey energy density values of 2600 J g⁻¹ wet mass, 2512 J g⁻¹ wet mass, and 127.3 J g⁻¹ wet mass for phytoplankton, zooplankton, and detritus, respectively (Anderson *et al.*, 2015, 2016,

2017). We attributed the energy density of dreissenid mussel biodeposits to all Lake Michigan detritus—assuming that this is the most prevalent detrital food source in the lake (Madenjian, 1995). Anderson *et al.* (2016) reported the caloric quality of biodeposits (ED_{Det}) as 979 J g^{-1} . However, the poor nutritional and energetic quality of organic detritus often reduces the amount of energy a fish can assimilate, i.e. energy content of a food item that can be used for metabolism or growth (Bowen, Lutz & Ahlgren, 1995). We accounted for this by adjusting ED_{Det} by an assimilation efficiency coefficient of 0.13, which we derived by back-calculating the assimilated energy density from the growth of juvenile BHC at the given food rations reported by Anderson *et al.* (2016).

For each feeding scenario, we identified all cells containing suitable habitat and then calculated the volume-weighted GRP average within all of those cells to determine the overall quality of suitable habitat. We determined the total volume and extent of suitable habitat for each species and scenario. Total extent was calculated as the sum of the surface areas of water columns containing at least one non-negative GRP model cell (hereafter referred to as ‘GRP maxima’). These scenarios were run from April thru November.

Model Simulations and Analyses

Habitat suitability assessments

We evaluated habitat suitability throughout the lake for all 12 months of the year, while also investigating vertical distributions of habitat quality at three sites along a nearshore-offshore gradient at Muskegon, MI. These assessments were run assuming diets of phytoplankton, zooplankton, and detritus. For our lake-wide assessment, we determined the total extent, volume, and mean GRP of suitable habitat. Total extent was based on GRP maxima and as the sum of the surface areas of water columns with non-negative average GRP (WC Mean). To account for scale-related bias caused by averaging

GRP across variable depths (Mason & Brandt, 1996), we mapped seasonal averages of GRP at three discrete depth ranges: Near surface (NS; 0-10 m); Deep Chlorophyll Layer (DCL; 10-50 m); and the whole water column (WC Mean). NS is based on range of depths at which BHC typically occupy in the Illinois River (DeGrandchamp, Garvey & Colombo, 2008; Garvey *et al.*, 2012) and the DCL depths are defined by recent observations of DCLs in Lake Michigan (Bramburger & Reavie, 2016). For our vertical assessments, we focused on three sites along a nearshore to offshore transect near Muskegon, MI (nearshore (M15): 15 m depth; intermediate depth (M45): 45 m depth, offshore (M110): 110 m depth, Figure 1), that NOAA GLERL has sampled monthly since the mid-1990s (Pothoven & Fahnenstiel, 2013). Muskegon simulations were run on a daily time step and analyses focused on characterizing seasonal patterns, nearshore-offshore differences, and vertical distributions of habitat quality from April thru November.

Table 1. Habitat conditions and model-predicted GRP in environments where Bighead Carp (BC) and Silver Carp (SC) exist compared to those observed and simulated in Lake Michigan. GRP values are based on diets of phytoplankton and zooplankton at the reported temperatures. Observed zooplankton in lower Green Bay represents the average of the two southern most sites (Benderville and Shoemaker Point) reported by Reed (2017). Sites where a majority of the reported data came from one source have a footnote next to the location.

Location	Carp biomass (metric tons km ⁻¹)	BC GRP (g g ⁻¹ d ⁻¹)	SC GRP (g g ⁻¹ d ⁻¹)	Mean Summer Temp (C ^o)	Chl (ug L ⁻¹)	Zooplankton (mg L ⁻¹ w.w.)	POC (mgC L ⁻¹)	Data source & Notes
Illinois River	3.3 [†]	0.003 - 0.022	0.0002 - 0.013	26 [‡]	2.8 - 21 [‡]	0.237 - 0.650 [§]		Garvey <i>et al.</i> (2012) [†] ; USGS National Water Information System (waterdata.usgs.gov/nwis) [‡]
Middle Mississippi River		0.022	0.013	27 [†]	23.8 - 49 [†]	0.005 - 0.05 [‡]		Long Term Resource Monitoring Program (umesc.usgs.gov/data_library/) [†] ; Sass <i>et al.</i> (2014) [§] ; Williamson & Garvey (2005) [‡]
Ohio River		0.008	0.004	27.9	6.8 ± 0.5	0.13 - 0.2	0 - 1	Bukaveckas <i>et al.</i> (2011); Zooplankton converted to wet weight using length-weight parameters from Bottrell <i>et al.</i> (1976)
Missouri River		0.022	0.012	23.8	19.7 ± 1.1	0.86 - 0.9	2.5 - 4	
Lake Balaton, Hungary	4.2 [†]	0.002 - 0.015	-9.2 × 10 ⁻⁵ - 0.007	20.4 [‡]	1.5 - 7.3 [‡]	1.07 - 6.59 [‡]	1 - 4.6 [§]	Weiperth <i>et al.</i> (2014) [†] ; Mozsár <i>et al.</i> (2017) [‡] ; Zánkai & Ponyi (1986) [§]
Lower Green Bay, Lake Michigan (LM)		0.022	0.012 - 0.013	24.1 - 26 [†]	17 - 197 [‡]	2.07 [§]	0.31 [¶]	Great Lakes Aquatic Habitat Framework (https://www.glahf.org/explorer/) [†] ; De Stasio <i>et al.</i> (2014) [‡] ; Reed (2017) [§] ; USEPA (2006) [¶]
Muskegon Nearshore, LM [†]		0.0001 - 0.004	-0.001 - 0.0012	18.9	0.98 - 4.47	0.06 - 0.38	0.11 - 0.18 [‡]	Pothoven (unpubl.) [†] ; USEPA (2006) [‡]
Muskegon Nearshore, LM (simulated)		-0.0002 - 0.0014	-0.0006 - 5.5 × 10 ⁻⁵	20.8	0.48 - 3.6	0.05 - 0.76	0.12 - 0.36	Prey concentrations represent range of monthly means from March - December
DCM at Muskegon Offshore, LM		6.8 × 10 ⁻⁵	-0.0003	5 [†]	2.52 ± 0.21 [‡]	0.3 [§]	0.15 - 0.18 [¶]	Bramburger & Reavie (2016) [†] ; Pothoven & Fahnenstiel (2013) [‡] ; Pothoven (unpubl.) [§] ; USEPA (2006) [¶] ; Zooplankton represents water column average.
DCM at Muskegon Offshore, LM (simulated)		0.0002	-0.0004	9.5	1.45	0.61	0.2	All values averaged from DCM in August and September

Results

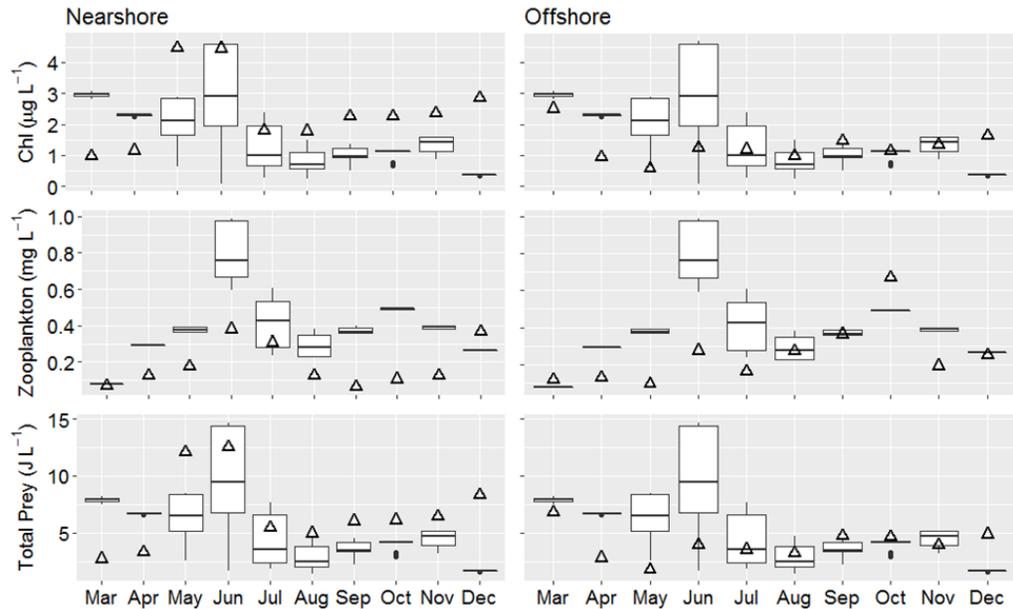


Figure 2. Simulated (box plots) and observed (triangles; Pothoven, unpublished) mean prey biomass in the water column at nearshore and offshore Muskegon in 2010 from March – December.

Comparison of FVCOM-GEM outputs to observations in Green Bay and Muskegon

Biophysical outputs reflected the spatial and temporal patterns of temperature and prey in Green Bay and Muskegon. FVCOM-GEM simulated higher prey concentrations in Green Bay in comparison to the main lake as well as the characteristic trophic gradient within the lower bay that stems from the mouth of the Fox River (De Stasio *et al.*, 2014) (Figures A3.2-A3.4). The distribution of simulated prey concentrations at Muskegon reflected the nearshore-offshore gradient and plankton phenology with high prey concentrations in May and June in the nearshore and the formation of the deep chlorophyll maxima (DCM) in the offshore during late stratification (Figure 2; Table 1).

The range of prey values simulated by the model tended to underestimate chlorophyll and overestimate zooplankton in Green Bay (Table A3.1) and nearshore Muskegon (Figure 2; Table 1). At Muskegon, simulated planktonic prey biomass (Phytoplankton + Zooplankton; J L^{-1}) typically showed better agreement with observed data than when compared to each prey type individually (range of monthly means [March – December] at nearshore Muskegon: simulated = 2.0 – 10.02 J L^{-1} , observed = 2.7 - 12.5 J L^{-1} ; Figure 2). In offshore Muskegon during June-October, the model reasonably simulated the range of planktonic prey biomass throughout the water column. The simulated DCM in late stratification (August-September) underestimated values reported by Pothoven & Fahnenstiel (2013) by about 1 $\mu\text{g L}^{-1}$ and simulated temperature at the Muskegon DCM was approximately 2 \times greater than average temperature of Lake Michigan's DCLs (Table 1). Running our GRP model with observed total plankton biomass and temperatures at the offshore DCM near Muskegon indicated that Bighead Carp could still maintain minimal growth, but GRP was 34% of what was predicted by the model when it was ran with simulated data. In Green Bay, reported prey biomass far exceeds the energetic inputs required by each species to maintain weight (Figures A3.4 & A3.5; Table 2). Thus, biases in the biophysical model outputs had a minor effect on the GRP model's determination of habitat suitability in Green Bay or Muskegon.

Table 2. Prey concentrations and energy density required for a Bighead Carp and Silver Carp to maintain weight in Lake Michigan's thermal regime for different combinations of filtration hours (t) and Wet Phytoplankton Biomass:Carbon ratios (C_{Phy}).

Filtration Hours	Energetic Requirement ($J L^{-1}$)	Chl ($\mu g L^{-1}$)		Zooplankton ($mg L^{-1}$)
Bighead Carp		$C_{Phy} = 20$	$C_{Phy} = 36$	
12	4.62 - 17.8	3.2 - 12.3	1.8 - 6.8	1.84 - 7.08
24	2.31 - 8.9	1.6 - 6.2	0.9 - 3.4	0.92 - 3.54
Silver Carp				
12	13.69 - 43.24	9.5 - 29.9	5.3 - 16.6	5.45 - 17.21
24	6.85 - 21.62	4.7 - 15.0	2.6 - 8.3	2.72 - 8.61

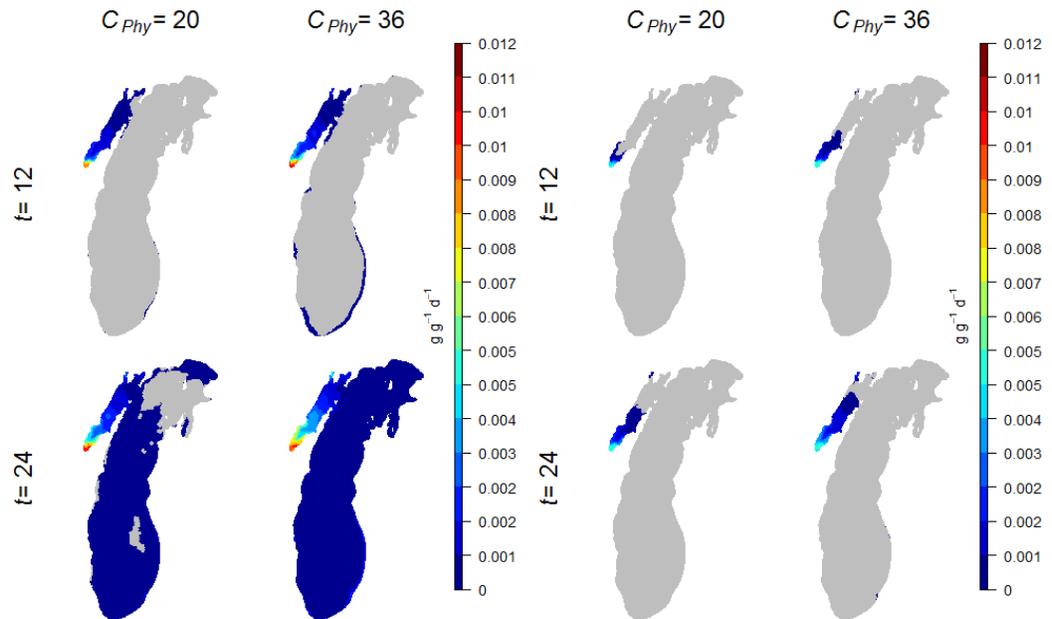


Figure 3. Average Bighead Carp GRP ($g g^{-1} d^{-1}$) from March - December for different combinations of filtration hours (t) and Wet Phytoplankton Biomass:Carbon ratios (C_{Phy}). Suitable habitats were defined by GRP maxima $\geq 0 g g^{-1} d^{-1}$ for each water column. Gray areas indicate unsuitable habitat ($g g^{-1} d^{-1}$).

Figure 4. Average Silver Carp GRP ($g g^{-1} d^{-1}$) from March - December for different combinations of filtration hours (t) and Wet Phytoplankton Biomass:Carbon ratios (C_{Phy}). Suitable and unsuitable habitats follow the criteria for figure 3.

Model sensitivity to phytoplankton carbon content and foraging hours

The assumptions we used for our model indicated that Bighead Carp require $0.9 - 3.4 \mu\text{g L}^{-1}$ of chlorophyll and Silver Carp require $3.3 - 8.3 \mu\text{g L}^{-1}$ of chlorophyll to maintain weight at Lake Michigan temperatures (Table 2). Increases in temperature resulted in higher respiration rates, which increased the total amount of prey (g d^{-1}) required for weight maintenance. However, consumption rates were also positively influenced by temperature, which decreased the concentration of prey (g L^{-1}) required to maintain weight. The difference between 12 and 24-hour filtration had a greater effect on the extent and volume of suitable habitat for both species than did differences in phytoplankton carbon content. However, Bighead Carp was more sensitive to changes to either parameter than was Silver Carp (Figures 3 & 4). Additionally, adjusting both parameters resulted in offshore habitat becoming available for Bighead Carp, but Silver Carp habitat largely remained in Green Bay.

Feeding Scenarios

The average extent and volume of suitable Bighead and Silver carp habitat from April – November increased with the number of diet items for both surface and water column scenarios (Table 3, Figures 5 & 6). The extent of suitable habitat for fish feeding throughout the water column was 1.0-1.9× greater than when the same fish fed on the same diet items at the surface. The difference in suitable habitat extent between water column and surface scenarios decreased as diet items increased. When feeding throughout the water column, the broadest diet (phytoplankton, zooplankton, and detritus [PP_ZP_Det]) produced suitable habitat volumes 4.6× and 2.3× greater than the narrowest diet (phytoplankton only [PP]) for Bighead and Silver carp, respectively. The least restrictive scenario, which was when the fish fed on all three prey types throughout the water column, increased the extent of suitable habitat by 3× for Bighead Carp and by 1.1× for Silver Carp compared to the most restrictive scenario where the fish fed only on phytoplankton at the surface.

Table 3. Area, volume, and mean GRP of suitable habitat for BHC under different feeding scenarios averaged from April-November. Diets: Phytoplankton only[†]; Phytoplankton and Zooplankton[‡]; Phytoplankton, Zooplankton, and Detritus[§].

Species	Diet	Suitable area (km ²)		Suitable Volume (km ³)		Mean GRP (g g ⁻¹ d ⁻¹)	
		Surface	Water Column	Surface	Water Column	Surface	Water Column
Bighead	PP [†]	11,143.50	21,205.88	11.14	248.87	0.0009	0.0004
	PP_ZP [‡]	31,224.03	37,373.66	31.22	769.37	0.0008	0.0004
	PP_ZP_Det [§]	43,308.28	44,548.71	43.31	1,144.91	0.0008	0.0005
Silver	PP	1,435.93	1,584.67	1.44	12.41	0.0016	0.0011
	PP_ZP	2,125.73	2,284.13	2.13	20.84	0.0017	0.0012
	PP_ZP_Det	2,757.90	3,043.10	2.76	28.82	0.0014	0.0010

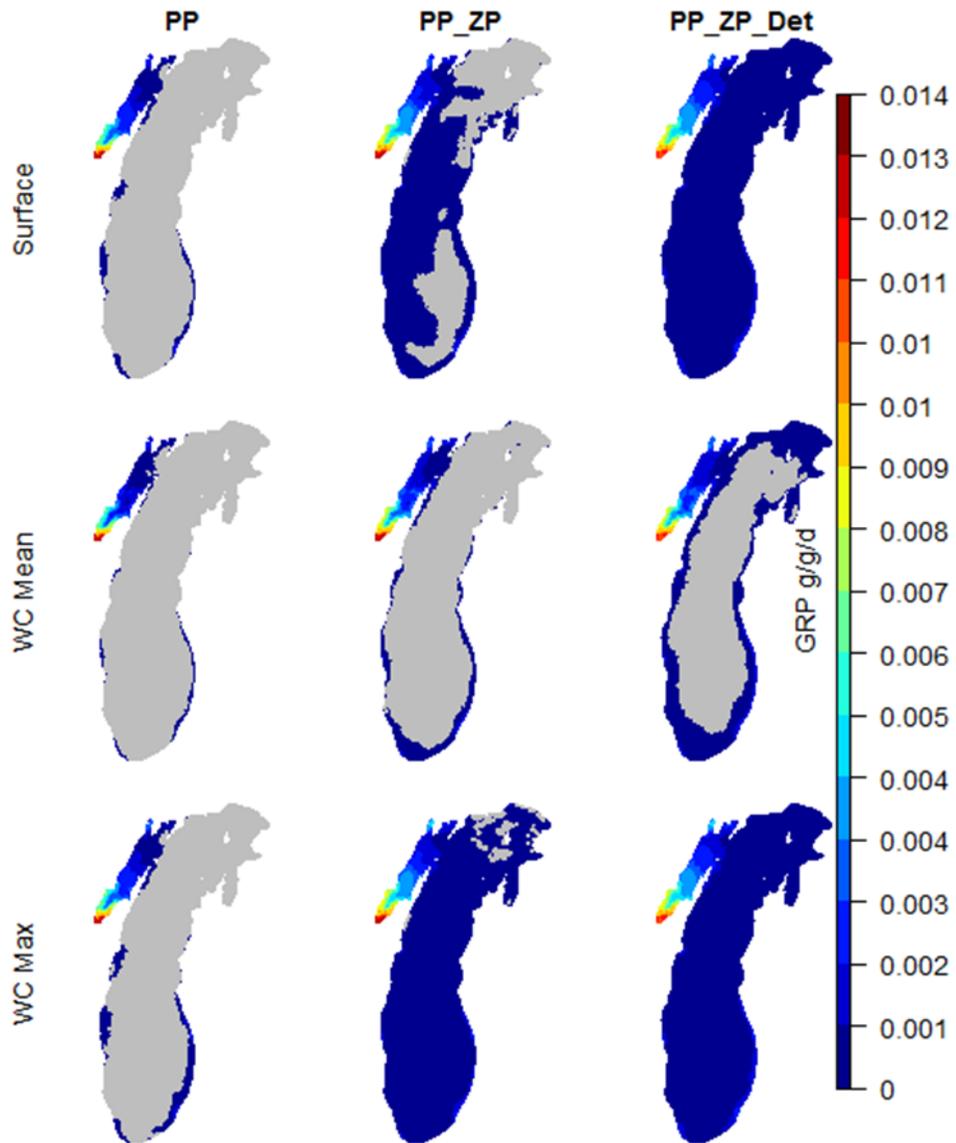


Figure 5. Average Bighead Carp habitat suitability from April – November under different feeding scenarios and water column (WC) generalizations of GRP (Mean or Max). PP = Phytoplankton only; PP_ZP = Phytoplankton and Zooplankton; PP_ZP_Det = Phytoplankton, Zooplankton, and Detritus.

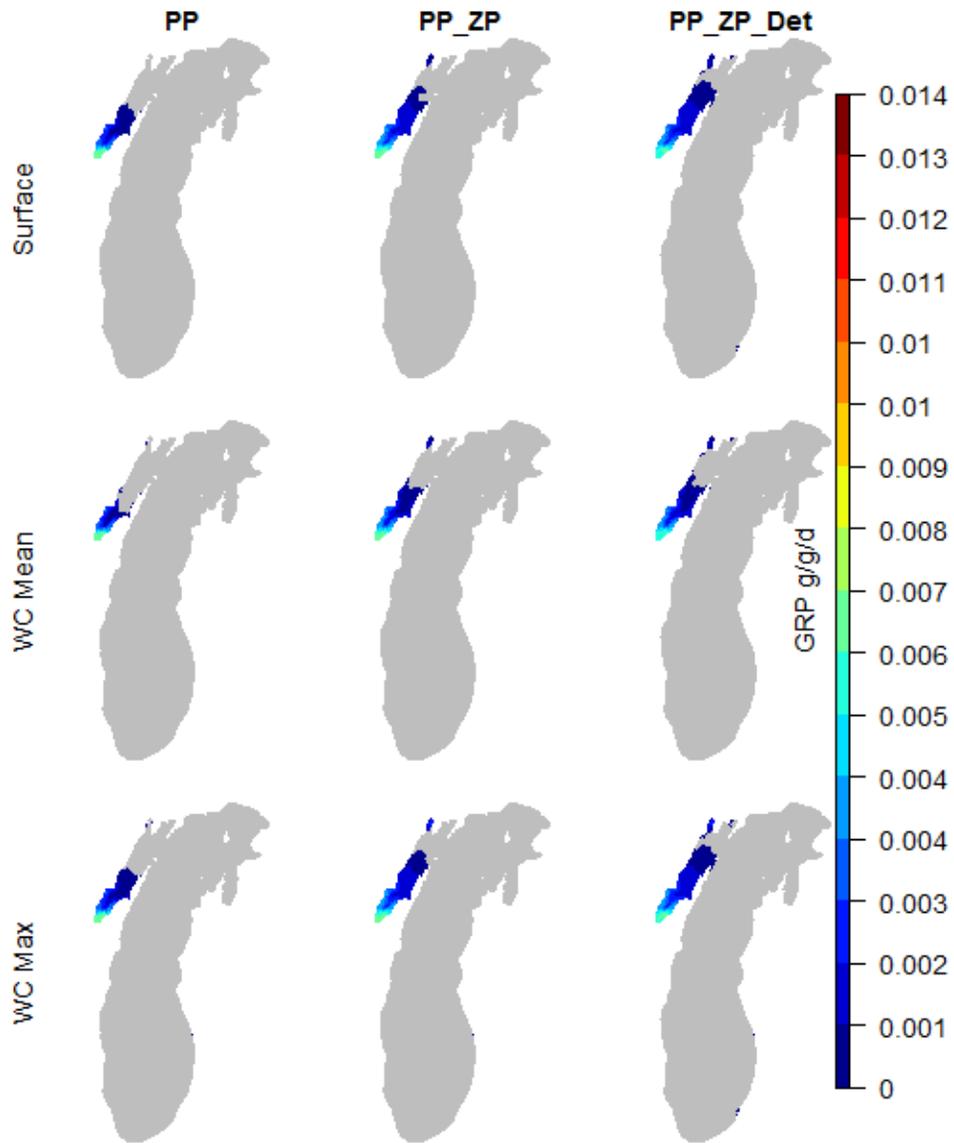


Figure 6. Silver Carp habitat suitability from April – November under different feeding scenarios and water column (WC) generalizations of GRP (Mean or Max). PP = Phytoplankton only; PP_ZP = Phytoplankton and Zooplankton; PP_ZP_Det = Phytoplankton, Zooplankton, and Detritus.

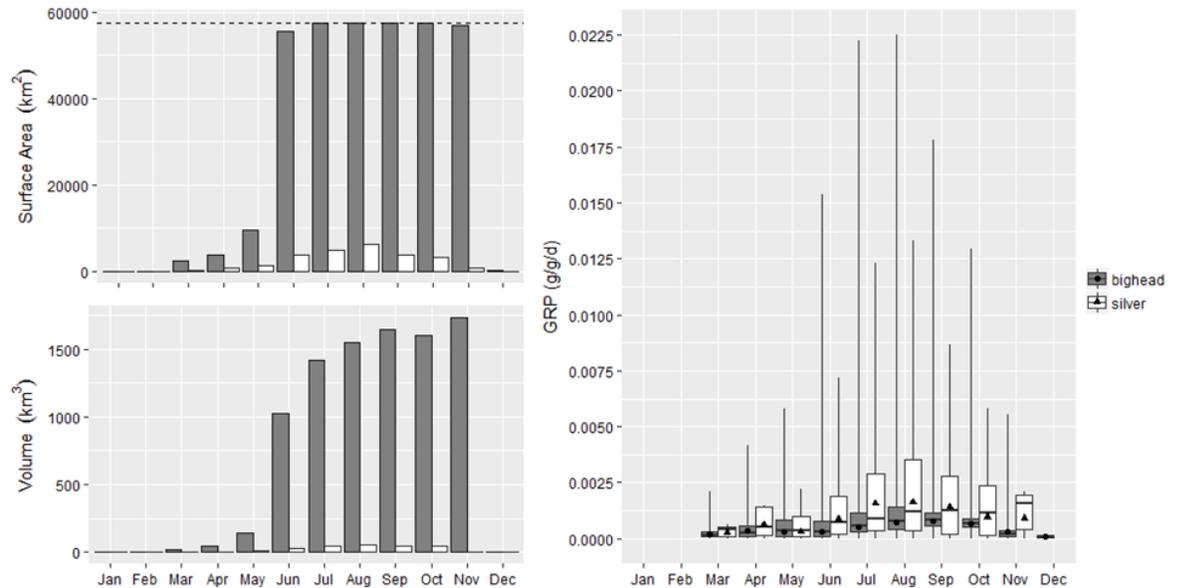


Figure 7. Total surface area (top left), volume (bottom left), and monthly GRP of suitable habitat for BHC ($\text{GRP} \geq 0.0 \text{ g g}^{-1} \text{ d}^{-1}$) from January through December. Dotted line in top left plot is the maximum surface area of the biophysical model's grid. Mean GRP is indicated by the filled circles (Bighead) and triangles (Silver) in each month's box plot.

Habitat suitability assessments

The extent (as indicated by total surface area), total volume, and quality of suitable habitat for BHC varied throughout the year (Figure 7). Bighead Carp habitat was available from March through December, with the greatest volume attained in November (1734 km^3 , 35% of the total volume) and the greatest extent in September and October (57630 km^2 , 100% of the biophysical model's total surface area). Silver Carp habitat was available from March through November, with the total volume and extent of suitable habitat peaking in August (51 km^3 and 1% of the total volume, 6193 km^2 and 11% of total surface area). The highest average quality of suitable habitat was in September for Bighead Carp ($0.0008 \text{ g g}^{-1} \text{ d}^{-1}$) and in August for Silver Carp ($0.00164 \text{ g g}^{-1} \text{ d}^{-1}$).

The spatial distribution of suitable habitat differed between species and varied throughout the year. During the spring, Silver Carp habitat was predominantly concentrated in southern Green Bay and supported average growth rates of $0.0003 - 0.0006 \text{ g g}^{-1} \text{ d}^{-1}$ (Figures 7 - 9). Suitable habitat became available near Chicago, Milwaukee, and several river

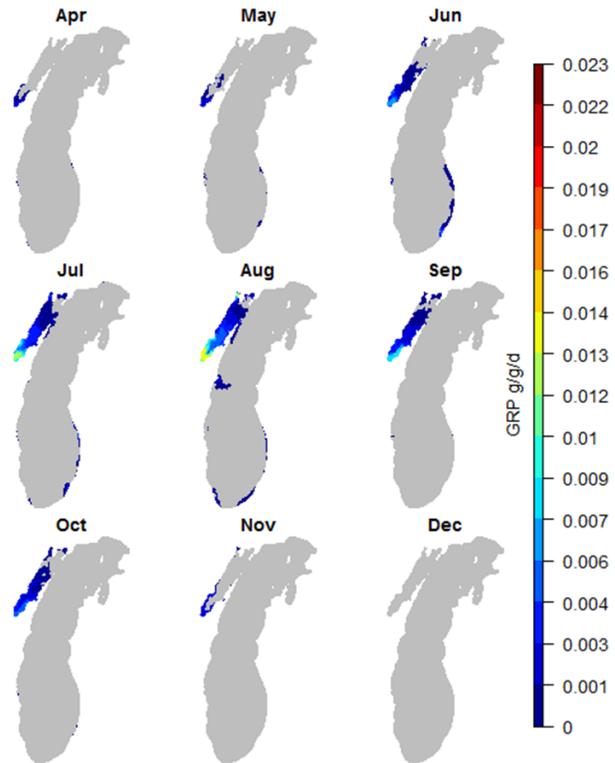


Figure 8. Suitable Silver Carp habitat from April through November. Suitable habitats were defined by $\text{GRP maxima} \geq 0 \text{ g g}^{-1} \text{ d}^{-1}$ for each water column.

mouths along the southeastern lakeshore (e.g. St. Joseph, Kalamazoo, and Muskegon Rivers) in May and the subsequent summer months (June – August; Figure 8). During the summer, Silver Carp habitat covered a majority of Green Bay and expanded along the Indiana, Illinois, and Michigan shorelines. Several areas along the western shore influenced by tributary loads (e.g. Milwaukee, mouth of Root River, and Two Rivers, WI) also provided suitable habitat. Silver Carp habitat receded back into the southern portion of Green Bay as fall (September-November) progressed. By December, all suitable Silver Carp habitat had disappeared. Averaging across the different depth ranges did not significantly affect extent of Silver Carp habitat for any season with exception to the DCL depth range since most of the suitable habitat was in shallow Green Bay and nearshore areas less than 10 m deep (Figure 9; NS, DCL, WC Mean).

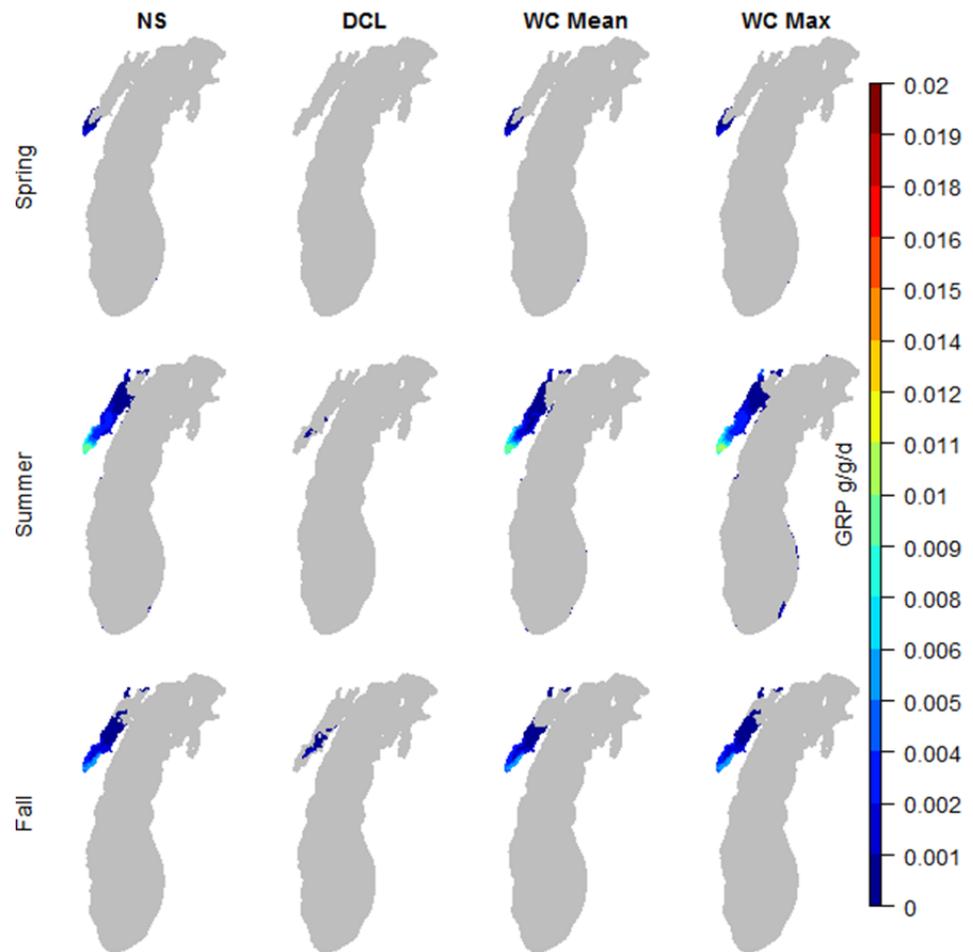


Figure 9. Seasonal distribution of suitable Silver Carp habitat as represented by average GRP in the near surface waters (NS: 0 – 10 m), Deep Chlorophyll Layer (DCL; 10 – 50 m), whole water column (WC Mean), and GRP maxima observed throughout the water column (WC Max). Spring: March – May; Summer: June – August; Fall: September – November.

Bighead Carp habitat was more extensive than Silver Carp habitat throughout the year. Habitat along most of the southern shoreline and in Green Bay was capable of supporting Bighead Carp growth ($0.0002 - 0.0004 \text{ g g}^{-1} \text{ d}^{-1}$) in the spring (Figures 7, 10, & 11). From June – November, most of the lake contained at least some suitable habitat in the water column

(Figure 10). The southern portion of Green Bay, near the

mouth of the Fox River, contained the best habitat quality throughout the year and was the only location capable of supporting growth in December (mean GRP = $8.0 \times 10^{-5} \text{ g g}^{-1} \text{ d}^{-1}$). Suitable habitat deepened from spring to fall (Figure 11). There were no obvious differences among the extent of suitable habitat for each depth range in the spring. In summer, however, average GRP in the NS produced a greater extent of suitable habitat than when GRP was averaged across the DCL depth range or the whole water column. The amount of suitable habitat across the DCL depth range increased substantially in the summer and fall relative to the spring, but the quality of suitable habitat at these depths was relatively poor throughout the year.

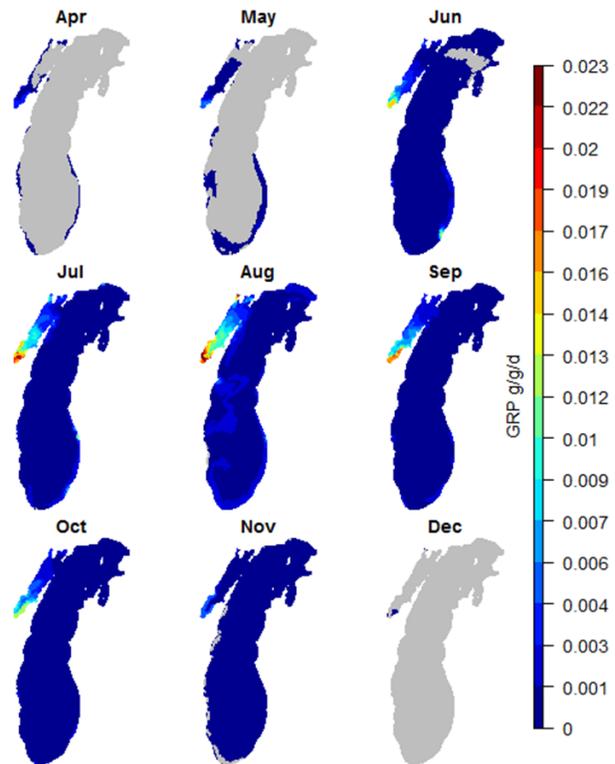


Figure 10. Suitable Bighead Carp habitat from April through November. Suitable habitats were defined by GRP maxima $\geq 0 \text{ g g}^{-1} \text{ d}^{-1}$ for each water column.

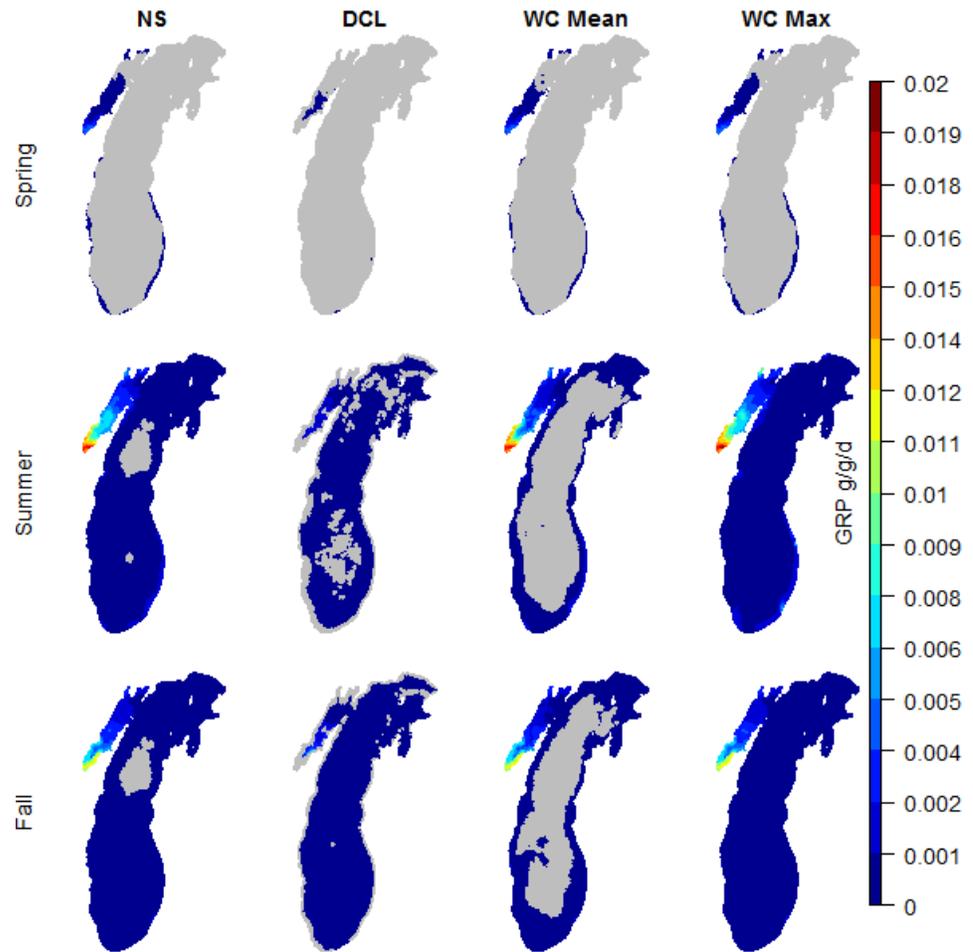


Figure 11. Seasonal distribution of suitable Bighead Carp habitat as represented by average GRP in the near surface waters (NS: 0 – 10 m), Deep Chlorophyll Layer (DCL; 10 – 50 m), whole water column (WC Mean), and GRP maxima observed throughout the water column (WC Max). Spring: March – May; Summer: June – August; Fall: September – November.

Vertical Distribution of Habitat Quality near Muskegon

Average prey concentrations and temperatures exhibited vertical, nearshore-offshore, and seasonal patterns at Muskegon. Mean prey concentrations and water temperatures were greater in the nearshore (M15) and expressed more seasonal variability ($8.5 \pm 3.5 \text{ J L}^{-1}$; $13.6 \pm 5.1 \text{ }^\circ\text{C}$) than did prey and temperatures in the intermediate (M45: $5.9 \pm 1.2 \text{ J L}^{-1}$; $11.5 \pm 4.0 \text{ }^\circ\text{C}$) and offshore (M110: $3.7 \pm 0.3 \text{ J L}^{-1}$; $7.5 \pm 2.4 \text{ }^\circ\text{C}$) locations throughout the model run. Nearshore-offshore gradients in average prey concentration and temperature were more apparent in spring than in summer or fall. June yielded the highest average prey concentrations in the nearshore and intermediate depth locations. Average prey concentrations in the offshore were greatest in November but overall exhibited little seasonal variability (April – November mean and standard deviation: $3.7 \pm 0.3 \text{ J L}^{-1}$). Summer months (June – August) exhibited the most variability in the vertical distribution of prey and temperature for all depth locations. Vertical distributions of prey and temperature were evenly distributed throughout the water column during periods of mixing and unevenly distributed during periods of stratification (Figure 12). Prey concentrations were highest in the epilimnion in June for all locations but the offshore, which saw maximum prey concentrations around 25 m. Prey concentration maxima were located beneath the surface from July through October.

Variations in prey concentrations and water temperature resulted in varied vertical, nearshore-offshore, and temporal distributions of BHC habitat quality (Figures 12 & 13). Vertical distribution of habitat quality exhibited similar seasonal patterns at all depth locations. In April, GRP was ubiquitously distributed throughout the water column, but suitable habitat only existed for Bighead Carp in the nearshore. In June, GRP maxima

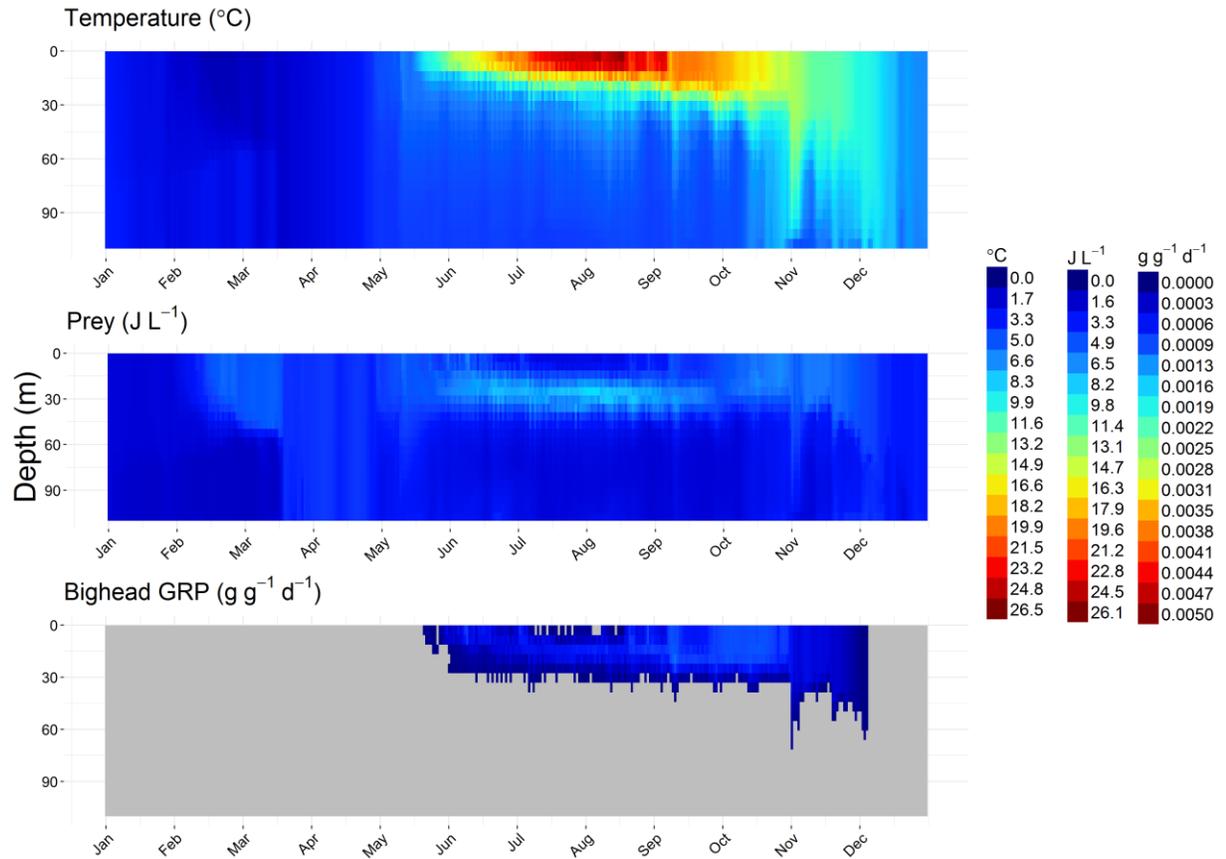


Figure 12. Vertical distribution of temperature (top), prey (middle), and Bighead Carp habitat quality (bottom) at the offshore depth location along the Muskegon transect (Figure 1; filled squares) throughout the year. Gray areas in the bottom panel indicate unsuitable habitat ($\text{GRP} < 0.0 \text{ g g}^{-1} \text{ d}^{-1}$).

were simulated in the epilimnion across all locations; the nearshore epilimnion in June produced the greatest GRP for both species throughout the model run. Suitable Silver Carp habitat was present from late May to late September in the nearshore, only in June at the intermediate depth location, and never in the offshore. In late summer, the highest quality habitat for both species within each transect was between 10-20 m, although, at this time, suitable Silver Carp habitat was only present in the nearshore at this time whereas the model simulated suitable Bighead Carp habitat at all three stations. For both species, there was a clear nearshore-offshore gradient as the nearshore retained the

highest habitat quality throughout most of the year and dwarfed offshore GRP maxima by an order of magnitude (Figure 13).

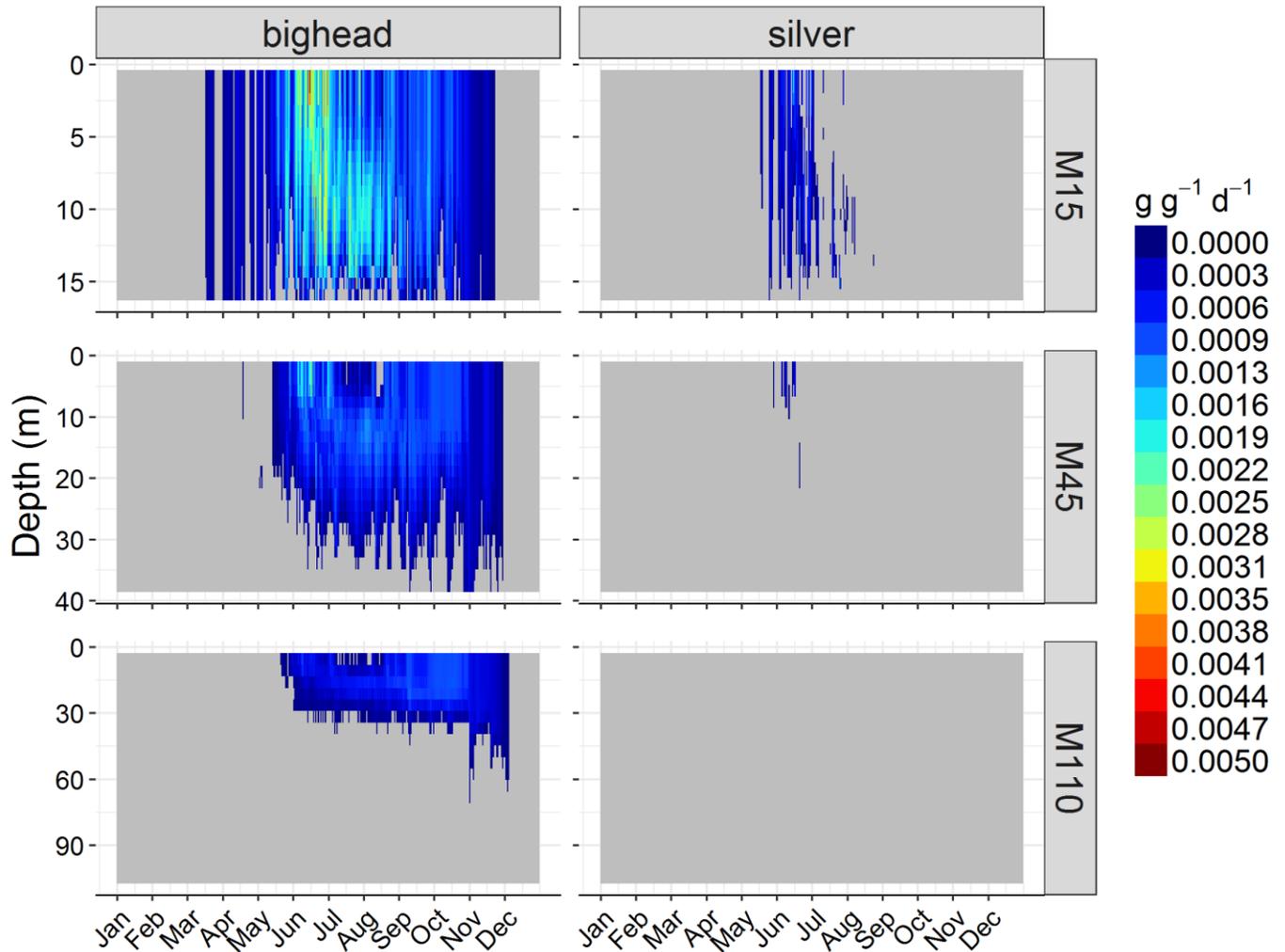


Figure 13. Vertical distribution of Bighead and Silver carp habitat quality at three depth locations along the Muskegon transect (Figure 1; filled squares) throughout the year. Gray areas indicate unsuitable habitat (GRP < 0.0 g g⁻¹ d⁻¹). M15 = Nearshore depth location; M45: Intermediate depth location; M110: Offshore depth location.

Discussion

Our model suggests that suitable habitat for BHC in Lake Michigan is more extensive than predicted by previous assessments (Cooke & Hill, 2010; Anderson *et al.*, 2017). Anderson *et al.* (2017) determined nearshore areas of Lake Michigan were suitable for BHC growth based on remote sensing data of *Microcystis* and green algae concentrations. However, the satellite used in their study was limited to evaluating surface waters where chlorophyll concentrations are at least $4 \mu\text{g L}^{-1}$ (Anderson *et al.*, 2017), which is about 4 - 5 times greater than concentrations throughout much of the lake (Fahnenstiel *et al.*, 2016) and 1.5 - 4 times greater than what BHC require to maintain weight at summer surface temperature (Table 2). Our findings indicate that these limitations notably underestimate the extent of suitable habitat for Bighead Carp but not for Silver Carp. Our model determined that 15,392 km² of Lake Michigan could support Bighead Carp growth during June-October when feeding only on surface phytoplankton, which is 6 - 33× greater than the extent of suitable habitat predicted by Anderson *et al.* (2017) for that time period. Suitable habitat estimates between these two studies became even more divergent when we broadened the scope of our evaluation to include three prey items throughout the water column.

Diet flexibility improves establishment potential

In support of our hypothesis, the addition of zooplankton and detritus to model diets increased the amount of suitable habitat for both species and extended it into the offshore for Bighead Carp. Diet plasticity is a trait common to highly invasive fishes (Pettitt-Wade *et al.*, 2015) including BHC, which feed opportunistically based on the relative abundance of different prey types in their immediate environment (Kolar *et al.*, 2007). BHC feed heavily on zooplankton, detritus, bacteria, and algae in Lake Donghu, China (Chen, 1982), and they are thriving on diets dominated by inorganic matter and

zooplankton in Lake Balaton, Hungary (Boros *et al.*, 2014; Mozsár *et al.*, 2017). There are no ecosystems where BHC exist that are exactly comparable to Lake Michigan and there is a lack of information on how these species have adapted to the cool, less productive lakes they do inhabit. In light of this, Lake Balaton may be the best available reference for predicting how BHC might adapt to Lake Michigan due to it being a dreissenid-invaded, meso-oligotrophic lake in a temperate climate with accessible information on the ecology of its established hybrid BHC (Bighead × Silver) population (Table 1). While Lake Michigan is deeper, larger, and generally colder than Lake Balaton, our model suggests that ability of BHC to flexibly feed on phytoplankton, zooplankton, and detritus mitigates their risk of starvation—even in offshore waters for Bighead Carp—and, therefore, increases their probability of establishment.

Broadening the model diets of BHC increased the connectivity of suitable habitat, which has implications for their ability to spread throughout the lake. BHC would have to travel through long stretches of plankton-depleted, open waters to reach productive areas in Lake Michigan. However, BHC are capable of swimming long distances and fasting for extended periods (DeGrandchamp *et al.*, 2008; Sheng & Ma, 2008). These traits, paired with our results, suggest that Lake Michigan's poor food conditions would not deter Bighead Carp from reaching more eutrophic areas if they feed opportunistically on detritus and plankton during their migration through less productive corridors. Using an area-restricted individual-based model, Currie *et al.* (2012) determined that BHC could reach Green Bay and other productive areas within the first year of escape from the Chicago Sanitary Shipping Canal and could find favorable habitat within a month. Therefore, it seems likely BHC could survive, establish, and spread to favorable habitat in Lake Michigan and its tributaries despite having to travel across expansive areas with minimal plankton biomass.

Refuge beneath the surface

Our findings indicate that subsurface temperatures and prey biomass are sufficient to support Bighead Carp growth and provides favorable habitat quality during late summer stratification. However, average chlorophyll concentration at the offshore DCM ($2.52 \pm 0.13 \mu\text{g L}^{-1}$, Pothoven & Fahnenstiel (2013)) during late stratification (August - September) are near the lower limit required for Bighead Carp to maintain weight at average DCL temperatures ($2.47 \mu\text{g L}^{-1}$) (Tables 1 & 2), which indicates that the suitability of this habitat is likely highly sensitive to variability in prey and temperature. Furthermore, it is uncertain how these fishes would use subsurface habitat and distribute themselves throughout Lake Michigan's water column. In the Illinois River, BHC typically occupy depths between 4-5 m and demonstrate seasonal habitat preferences (DeGrandchamp *et al.*, 2008; Garvey *et al.*, 2012). In Lake Michigan, however, peak prey biomass at the DCL and preferred temperatures are vertically separated when the lake is stratified causing GRP to be differentially regulated by these two variables based on the fishes' position in the water column. While BHC exist in dimictic lakes (e.g. Lakes Dgal Wielki and Dgal Maly in Poland; see Napiórkowska-Krzebietke *et al.* (2012)), there is a lack of accessible information on how they behave in these systems. We assume BHC would migrate to warm and productive tributaries rather than reside in the main lake. However, if they were to reside in the lake, our results suggest that BHC might inhabit depths outside of their preferred thermal range to optimize growth during summer stratification. Furthermore, BHC might optimize their growth through behaviors that our model could not simulate. For instance, it is possible that BHC would feed at depths outside of their thermal range but reside in warmer surface waters when they were not feeding. Bioenergetic optimization has been used to explain depth distributions of fishes in thermally stratified lakes (e.g. Plumb, Blanchfield

& Abrahams (2014)), so it seems plausible that BHC would change their position in the water column to enhance their growth. Identifying and translating foreign literature on BHC behavior in dimictic lakes, as well as developing individual-based models that can simulate potential behaviors and movements (e.g. Currie *et al.* (2012)), would be worthy research endeavors for understanding how BHC might adapt to the Great Lakes.

Interspecific differences

The difference in habitat suitability between Bighead Carp and Silver Carp was one of the more conspicuous findings from our research. Our model suggests that Silver Carp have greater prey requirements for growth than Bighead Carp and, therefore, the amount of suitable Silver Carp habitat is limited to the most productive areas of Lake Michigan. Our simulations agree with observed individual growth rates of Bighead and Silver carp existing in the same environments. Ke, Xie & Guo (2008) observed that Bighead Carp grew more quickly than Silver Carp in the hypereutrophic Lake Taihu in China, although the difference between the two species' growth rates was greatly reduced in years of high competition compared to years of low competition. Additionally, length-at-age data from the Middle Mississippi River (MMR) suggests that Bighead Carp grow more quickly than Silver Carp, but Silver Carp maintain higher growth conditions (Weight/Length) in this system (Nuevo, Sheehan & Willis, 2004; Williamson & Garvey, 2005).

While the interspecific differences we simulated seem reasonable based on reported growth rates, the influence of energy density on bioenergetics models (Hartman & Brandt, 1995) and the dissimilarity between the two species' values for this parameter suggest that these differences are in part due to the condition of the specific fish we used in our model. We used species-specific parameters for fish mass and energy density,

which were averaged from 10 fish from the Mississippi and Missouri River drainages derived by Anderson *et al.* (2015). The Silver Carp used in that study were in excellent condition and the females had highly developed ovaries, whereas the Bighead Carp exhibited moderate to low condition, as is common for this species in parts of North America where they coexist with a dense population of Silver Carp (D.C. Chapman, US Geological Survey, Columbia Environmental Research Center – Personal Comm.). Therefore, the interspecific differences our model simulated agree with observations from other ecosystems, but likely only represent a potential scenario of Lake Michigan's suitability given the condition of the fishes we assumed in our model. We hypothesize that the amount of suitable habitat for Silver Carp would be similar to that predicted for Bighead Carp if we had assumed a similarly low energy density for both species. Furthermore, energy density was static in our simulations but in fishes this can fluctuate seasonally, ontogenetically, and in response to starvation (Hartman & Brandt, 1995; Madenjian *et al.*, 2006; Breck, 2008). Thus, the energy density of BHC could decrease in response to low food availability in certain areas of Lake Michigan, which in turn could affect their growth potential in ways that our model could not capture.

Oases in the desert: River mouths & tributary-influenced nearshore areas

While our results show that the overall extent of high quality suitable habitat for BHC, especially for Silver Carp, remains relatively small, we maintain that the risk of localized establishment events are still high—particularly in river mouths and the surrounding nearshore areas affected by tributary nutrient loads. Our model simulated suitable habitat near the mouths of several tributaries throughout the year, including the Milwaukee and St. Joseph Rivers, which both possess sufficient water quality characteristics, temperatures, and hydraulics to support BHC spawning and egg development (Murphy & Jackson, 2013). The availability of productive feeding grounds

and viable spawning habitat upstream suggests that carp may concentrate near river mouths, and thus improve their probability of establishing sustainable populations in light of low propagule pressure and population density (Jerde, Bampfylde & Lewis, 2009; Cuddington *et al.*, 2014). Cuddington *et al.* (2014) found that a greater number of suitable spawning rivers available to carp reduced the chance of carp finding mates given a small introduction event (i.e. 20 males, 20 females). This suggests that the limited availability of viable spawning rivers may actually facilitate BHC establishment rather than constrain it. Similarly, it seems that the limited amount of productive habitats could further increase the probability of finding a mate. BHC locate and selectively feed in areas of higher prey concentrations (Dong & Li, 1994; Calkins, Tripp & Garvey, 2012; Currie *et al.*, 2012), which for spawning females, can lead to higher fecundities and potentially higher recruitment rates due to improved maternal condition (Degrandchamp, Garvey & Csoboth, 2007). Therefore, the benefits river mouths provide make these areas—and the variety of resident fish species that depend on them in their early life stages (Janetski *et al.*, 2013; Harris *et al.*, 2017)—particularly vulnerable to a BHC invasion.

Model limitations and uncertainty

The sensitivity of BHC GRP to assumed phytoplankton carbon content and foraging duration in the model reinforce the importance of estimated prey consumption to overall model accuracy (Bartell *et al.*, 1986; Mason *et al.*, 1995). Carbon composition of phytoplankton varies by species, cell size, physiological conditions, and environmental conditions (Bowie *et al.*, 1985), and foraging duration can vary in accordance with day light hours, food availability, and water temperature (Li, Yang & Lu, 1980; Wang *et al.*, 1989; Dong & Li, 1994). Adjusting carbon content of prey and foraging duration significantly influenced estimated consumption rates and GRP in our model, which translated into substantially different estimates of suitable habitat (Figures 3 & 4).

Our model assumed 100% filtration and retention efficiency for both species and, therefore, did not account for the effect of prey size on BHC consumption and GRP. Differences in gill morphology dictate the particle size that these fishes can efficiently filter, with Bighead Carp more efficient at removing larger particles and Silver Carp are more adept at filtering finer particulates (Dong & Li, 1994). However, both species see significantly reduced efficiencies for particles near 8-10 μm (Cremer & Smitherman, 1980; Smith, 1989), which is relevant considering pico- (<2 μm) and nanoplankton (2 - 20 μm) account for >50% of chlorophyll in parts of Lake Michigan (Cuhel & Aguilar, 2013; Carrick *et al.*, 2015). Additionally, FVCOM-GEM's zooplankton variable was calibrated to data reported by Vanderploeg *et al.* (2012) who used 153- μm vertical net tows, which cannot effectively capture microzooplankton such as rotifers that are common in the diets of BHC (Williamson & Garvey, 2005; Sampson *et al.*, 2009). Thomas, Chick & Czesny (2017) found that microzooplankton made up 74% of mean total zooplankton biomass with rotifers comprising 51% alone, and that sampling with 64- μm mesh nets underestimates total zooplankton biomass by nearly three-fold compared to methods that utilize finer mesh screens (i.e. 20- μm). Incorporating microzooplankton biomass and particle size-based filtration and retention efficiencies into future GRP models should be a priority given the potential implications it could have on the establishment of BHC.

Conclusion

While our model predicts a greater extent of suitable habitat for BHC than previous models, the best habitat was concentrated in nearshore areas and Green Bay, which confirms the findings of Anderson *et al.* (2017) and Cooke & Hill (2010). Moreover, evidence suggests that there may be cross-lake migration corridors that could facilitate establishment and spread. Running our bioenergetics model with simulated water quality variables from a Lake Michigan biophysical model (Rowe *et al.*, 2017) allowed us to build on previous research and advance current understanding of establishment risk by demonstrating how diet plasticity and the availability of subsurface prey increases Lake Michigan's vulnerability to BHC establishment. Our findings provide further evidence of the invasion risk these species pose to the Great Lakes and can help managers prioritize surveillance efforts by identifying where in the lake BHC might spread upon introduction.

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Appendix 1: Growth Rate Potential Model Equations and Parameters

Table A1. 1 Bioenergetic model parameters for bigheaded carp. All parameters were borrowed from Anderson *et al.* (2015) and Cooke & Hill (2010) unless otherwise noted. All prey and predator energy density values are in J g^{-1} wet weight.

Parameters	Parameter description	Bighead	Silver
Consumption (C)			
CA	Intercept for maximum consumption	0.369	
CB	Mass dependence coefficient	-0.225	
CQ	Temperature dependence coefficient	2.5	
CTO	Optimum Temperature ($^{\circ}\text{C}$)	26	29
CTM	Maximum Lethal Temperature ($^{\circ}\text{C}$)	38	43
ED_{PP}	Energy density of phytoplankton (J g^{-1})	2600	
ED_{ZP}	Energy density of zooplankton (J g^{-1})	2512	
ED_{Det}	Adjusted energy density of detritus (J g^{-1})	127.3 [†]	
ED_{Carp}	Energy density of bigheaded carp (J g^{-1})	3500	5200
W	Fish mass (g)	5480	4350
Respiration (R)			
RA	Intercept of mass dependence function	0.00528	0.00279
RB	Slope of mass dependence function	-0.299	-0.239
RQ	Approximates Q_{10} over low temperatures	0.048	0.076
ACT	Activity multiplier	1	
SDA	Specific dynamic action	0.1	
Egestion (F) and excretion (U)			
FA	Intercept of the proportion of consumed energy egested	0.212	
FB	Temperature dependence coefficient for egestion	-0.222	
FG	Ration dependence coefficient for egestion	0.631	
UA	Intercept of the proportion of consumed energy excreted	0.031	
UB	Temperature dependence coefficient for excretion	0.58	
UG	Ration dependence coefficient for excretion	-0.299	

[†]Anderson, Chapman & Hayer (2016)

Table A1. 2. Bioenergetic equations for bigheaded carp from Cooke & Hill (2010), Anderson *et al.* (2015, 2017), and Hanson *et al.* (1997).

Equations	Equation description
Growth Rate Potential	
$GRP = C - (R + S + F + U)$	Specific growth rate potential (g g ⁻¹ d ⁻¹)
Consumption	
$V = \frac{CTM - T}{CTM - CTO}$	
$X = (Z^2 * \frac{\left(1 + \left(1 + \frac{40}{Y}\right)^5\right)^2}{400})$	
$Z = LN(CQ) * (CTM - CTO)$	
$Y = LN(CQ) * (CTM - CTO + 2)$	
$f(T) = V^X * e^{X*(1-V)}$	Temperature function
$FR = 1.54 * W^{.713} * 24$	Filtration rate (liters d ⁻¹ fish ⁻¹)
$Cmax = CA * W^{CB} * f(T)$	Temperature dependent maximum consumption (gPrey gCarp ⁻¹ d ⁻¹)
$C_{FR} = \left(FR * \frac{(PP+ZP+Det)}{W}\right) * f(T)$	Foraging-based consumption (gPrey gCarp ⁻¹ d ⁻¹)
$C = pmin(Cmax, C_{FR}) * \frac{ED_{Prey}}{ED_{Carp}}$	Specific consumption rate (g g ⁻¹ d ⁻¹)
$p = \frac{pmin(Cmax, C_{FR})}{Cmax}$	Proportion of maximum consumption
Respiration (R) and Specific Dynamic Action (S)	
$f(T_{resp}) = e^{RQ*T}$	Respiration temperature function
$R = RA * W^{RB} * f(T_{resp}) * ACT$	Specific respiration rate (g g ⁻¹ d ⁻¹)
$S = SDA * (C - F)$	Specific dynamic action (g g ⁻¹ d ⁻¹)
Egestion (F) and excretion (U)	
$F = FA * T^{FB} * e^{FG*p} * C$	Specific egestion rate (g g ⁻¹ d ⁻¹)
$U = UA * T^{UB} * e^{UG*p} * (C - F)$	Specific excretion rate (g g ⁻¹ d ⁻¹)

Table A1. 3. Conversions (C) and adjustments (A) from Anderson *et al.* (2015) unless noted otherwise.

Parameters	C/A	Values
Chla: Carbon ^a	C	0.036
Chla: Dry Phytoplankton Biomass	C	0.01
Dry: Wet Phytoplankton Biomass	C	0.1
Wet Phytoplankton Biomass: Carbon	C	36
Carbon: Dry ^b Zooplankton Biomass	C	0.4
Dry: Wet Zooplankton Biomass	C	0.1
Carbon: Dry Detritus ^c	C	0.044
Dry: Wet Detritus ^d	C	0.16
Detritus Assimilation coefficient ^d	A	0.13
Weighted prey energy density	A	$ED_{Prey} = \frac{(ED_{PP} * PP) + (ED_{ZP} * ZP) + (ED_{Det} * Det)}{(PP + ZP + Det)}$

[†]Rowe *et al.* (2017); [‡]Peters & Downing (1984); [§]Ozersky, Evans & Ginn (2015);

[¶]Anderson *et al.* (2016)

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Appendix 2: Foraging Behavior Assumptions

Food saturation constrains suitable habitat

Adding detritus to our model affected bigheaded carp habitat differently based on the amount of zooplankton and phytoplankton in a given location. In some areas where planktonic prey concentrations were too low to support growth, feeding on detrital supplements effectively increased the habitat quality and made those habitats suitable (e.g. much of the nearshore of southern Lake Michigan for Bighead Carp, Figure A2.1). However, in locations where planktonic prey concentrations were already capable of supporting growth without detrital supplements, adding detritus into the prey pool effectively diluted the average food energy density ($J g^{-1}L^{-1}$). Thus, if bigheaded carp indiscriminately fed on plankton and detritus it would reach its maximum consumption with lower quality food compared to if it fed only on plankton. This resulted in reduced habitat quality and even rendered habitat unsuitable in some locations. A notable example of this occurred in Green Bay and near Manitowoc, WI for both species (Figures A2.1 and A2.2). The large quantity and poor quality of detritus in these productive areas. We addressed this issue in our models below.

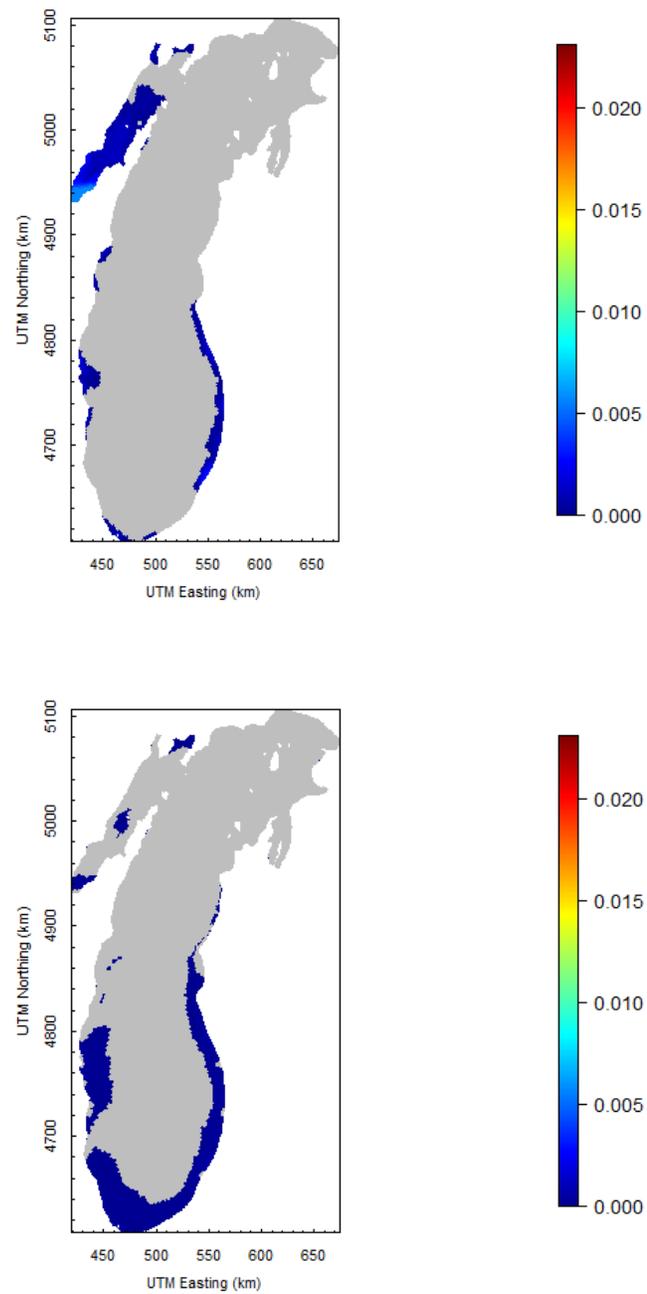


Figure A2. 1. Bighead Carp suitable habitat (pixels defined by water column GRP maxima) in May when feeding on phytoplankton and zooplankton (top) and phytoplankton, zooplankton, and detritus (bottom). Notice the reduction of suitable habitat in Green Bay and addition of suitable habitat in Southern Lake Michigan. Color bar is in $\text{g g}^{-1} \text{day}^{-1}$.

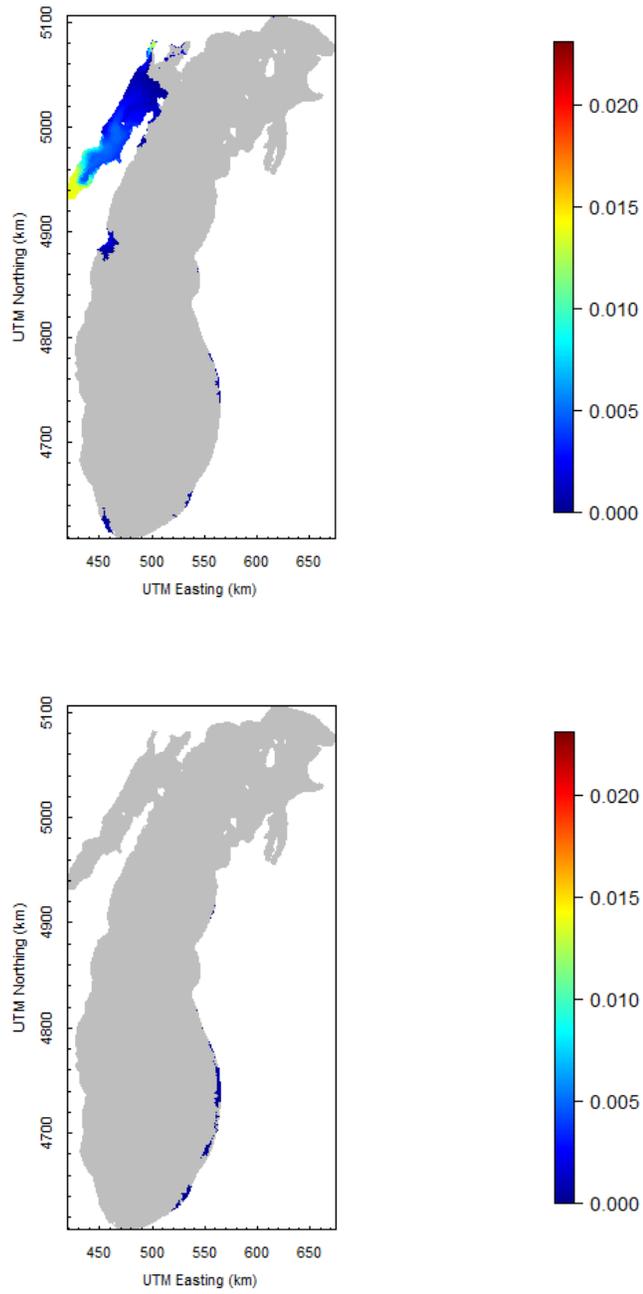


Figure A2. 2. Silver Carp suitable habitat (pixels defined by water column GRP maxima) in August when feeding on phytoplankton and zooplankton (top) and phytoplankton, zooplankton, and detritus (bottom). Notice the reduction of suitable habitat in areas like Green Bay and Manitowoc, and the addition of suitable habitat near river mouths in southeastern Lake Michigan. Color bar is in $\text{g g}^{-1} \text{day}^{-1}$.

Foraging Behavior

Bigheaded carp have been known to exhibit adaptive foraging behavior by selecting for preferred prey when it is abundant (hereafter referred to as discriminatory foraging) and for less preferable prey when it is abundant and preferable prey is limited (hereafter referred to as opportunistic foraging) (Kolar *et al.*, 2007). To account for adaptive foraging behavior, we assumed that the fish would aim to maximize its specific consumption rate in all habitat cells throughout the Lake Michigan grid. The fundamental underpinning of this assumption is that bigheaded carp would only supplement their diet with detritus when favorable planktonic prey became scarce. We coded this assumption into our model by calculating consumption under two diet scenarios:

- 1) Phytoplankton and Zooplankton;
- 2) Phytoplankton, Zooplankton, and Detritus.

First, we calculated the foraging-based consumption (C_{FR} , see section “Foraging Model” in the main manuscript for details) assuming either discriminate (Diet 1) or opportunistic foraging (Diet 2). We then took a pairwise maximum of the C_{FR} values for each cell in the grid between the two diets and created a composite matrix. Cells where diet 2 produced greater consumption rates are indicative of habitats where detritus is a primary resource for bigheaded carp because zooplankton and phytoplankton concentrations are too low to support primarily planktivorous feeding. Therefore, cells where diet 1 resulted in a higher consumption rate are indicative of habitats containing zooplankton and phytoplankton in concentrations sufficient to allow the carp to forage discriminately between plankton and detritus (Figure A2.3). This effectively prevented the carp from becoming saturated with detritus when higher quality food was abundant. Furthermore, if maximum consumption was not reached from feeding on zooplankton

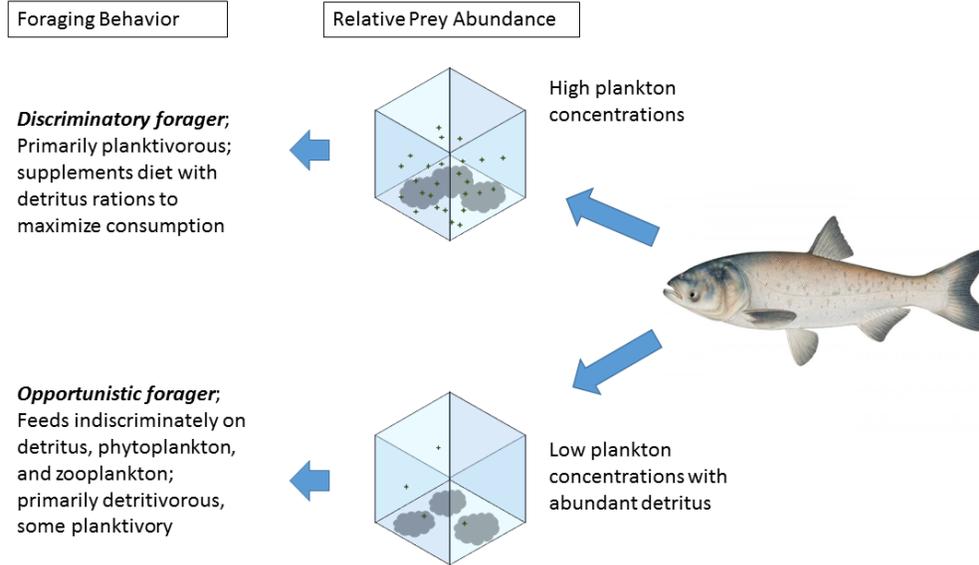


Figure A2. 3. Visualization of foraging assumption. Relative prey abundance dictates whether the carp fed opportunistically (indicating low plankton concentrations) or discriminately (indicating high plankton concentrations).

and phytoplankton in habitats characterized by diet 1, we allowed the carp to supplement its diet with detritus rations to maximize its consumption rate. In habitats where this was the case, we subtracted diet 1's consumption rate from the maximum consumption to determine the proportion of additional prey ($\text{gPrey gCarp}^{-1} \text{d}^{-1}$) the carp would require to reach maximum consumption (Det_{ration}). Using the foraging model, we then calculated the amount of detritus the carp could consume ($\text{gDet gCarp}^{-1} \text{d}^{-1}$) based on the amount available in a given habitat cell (C_{Det}). The minimum of those two values was multiplied by ratio of detritus: carp energy density and the product defined the consumption rate ($\text{gCarp gCarp}^{-1} \text{d}^{-1}$) when the carp fed on detritus rations (C_{newDet}). C_{newDet} was added to the consumption rate from diet 1 ($C_{newPP,ZP}$) to determine the overall consumption rate for a given cell.

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Appendix 3: Green Bay Skill Assessment

Our GRP model outputs are dependent on the accuracy of FVCOM-GEM. However, it did not have its skill assessed for Green Bay (Rowe *et al.*, 2017). Thus, we conduct a skill assessment here with available observations from Green Bay.

Data sources and processing:

Reported values of chlorophyll concentrations were taken from De Stasio, Schrimpf & Cornwell (2014), who sampled 5 sites along a trophic gradient in lower Green Bay from June through August in 2006-2007 (Figure A3.1). We approximated the coordinates for each site and used that to identify five FVCOM nodes with similar locations. We replicated De Stasio *et al.*'s (2014) sampling procedure by extracting simulated water quality outputs from the top 4 m in the water column at these nodes on a biweekly time step for June, July, and August. We then compared the simulated chlorophyll values to the observed summer mean values for 2006 and 2007 for each sampling location.

Reed (2017) reported average zooplankton biomass across four sites in Green Bay (Fish Creek, Sturgeon Bay, Benderville, Shoemaker's Point, Figure A3.1) from June through September in 2013-2014. They measured zooplankton biomass with two different sampling methods: one method utilized two different size meshes (20 and 63 μm to capture micro- and macrozooplankton, respectively; hereafter referred to as the dual method) and another used only 63 μm mesh nets (to capture most macrozooplankton; hereafter referred to as the net only method). We compared FVCOM-GEM's zooplankton outputs, which were initialized and calibrated to samples collected with 153 μm mesh nets (Vanderploeg *et al.*, 2012), to reported values from the dual method and, when available, the net only method.

We also compared FVCOM-GEM simulated values to observed values of total prey biomass (J L^{-1}). Chlorophyll data from De Stasio *et al.* (2014) were averaged across years for each site and then converted into phytoplankton biomass. We converted phytoplankton and zooplankton biomass reported by Reed (2017) to joules per liter (J L^{-1}).

Table A3. 1. Comparison between FVCOM-GEM simulated and observed summer means (\pm one standard error) of chlorophyll concentration, wet zooplankton biomass, and prey biomass (J L^{-1}) in Green Bay. Observed zooplankton values were reported for two different methods: Net only (Macrozooplankton) and dual method (Total Zooplankton [Micro + and Macrozooplankton]). Simulated prey biomass refers to the energetic sum of zooplankton and phytoplankton (J L^{-1}). Observed prey biomass only refers to chlorophyll concentrations converted to phytoplankton (J L^{-1}) from De Stasio *et al.* (2014).

	Simulated	Observed
Chla ($\mu\text{g L}^{-1}$)	35 ± 1.3	58 ± 17.9
Macrozooplankton (mg L^{-1} w.w.)	2.75 ± 0.08	1.15 ± 0.21
Total Zooplankton (mg L^{-1} w.w.)	2.75 ± 0.08	1.52 ± 0.18
Prey biomass (J L^{-1})	101.25 ± 3.37	150.88 ± 46.6

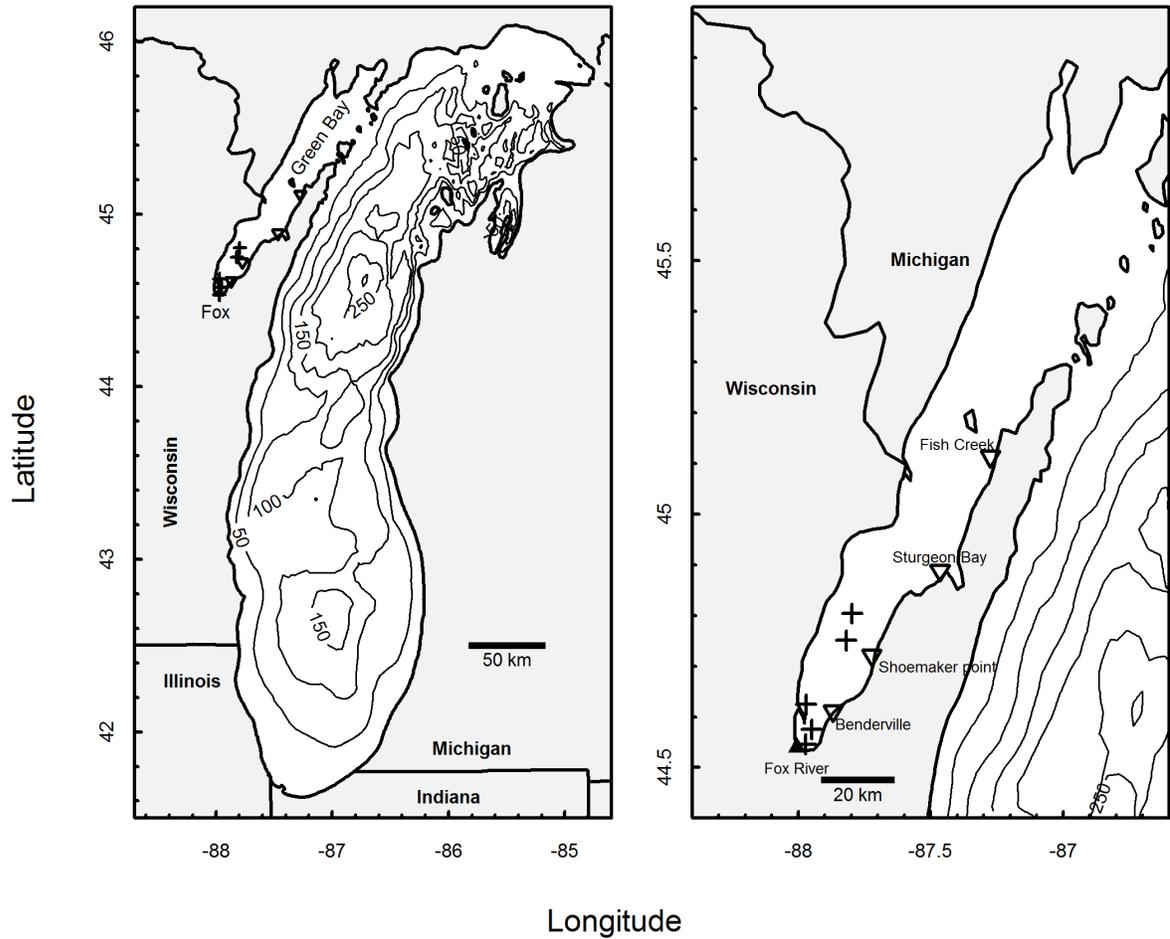


Figure A3. 1. Map denoting sites in lower Green bay, Lake Michigan sampled by De Stasio *et al.* (2014) (crosses) and Reed (2017) (unfilled triangles). FVCOM-GEM's chlorophyll outputs used for this comparison were from all nodes south of Sturgeon Bay's latitude following a trophic gradient starting at the mouth of the Fox River. Simulated zooplankton outputs were taken from two sites in lower Green Bay (Benderville, WI & Shoemaker Point, WI), and two sites in mid- to upper Green Bay (Fish Creek, WI and Sturgeon Bay).

Results and Discussion:

FVCOM-GEM accurately simulated spatial patterns characteristic of Green Bay. Simulated prey concentrations in Green Bay were greater than those simulated in the main lake, and the spatial distribution of prey concentrations in the lower bay reflected the trophic gradient that stems from the mouth of the Fox River (De Stasio *et al.*, 2014) (Figures A3.2-A3.4). Comparisons between simulated prey concentrations and those observed by De Stasio *et al.* (2014) and Reed (2017) indicate that FVCOM-GEM was biased low relative to the available observations of total prey density in Green Bay (Table A3.1; Figure A3.4). Simulated chlorophyll concentrations were lower than reported averages at each site, while simulated zooplankton biomass was typically greater than reported values, regardless of sampling method. Despite these biases, we found that our GRP model outputs agreed with the current consensus that Green Bay provides the best habitat for bigheaded carp growth in Lake Michigan (Cooke & Hill, 2010; Anderson *et al.*, 2017). The higher observed prey biomass in Green Bay exceed the energetic inputs required by each species to maintain weight (Figures A3.4 & A3.5; Table 2 in main manuscript), and thus, our assessment of suitable habitat in Green Bay is not significantly affected by biased simulated prey concentrations. Nevertheless, finer-scale and more accurate estimates of GRP within Green Bay are warranted, which would require further calibration of FVCOM-GEM outputs, particularly near the mouth of the Fox River and the northern portion of the bay that is exposed to the main lake.

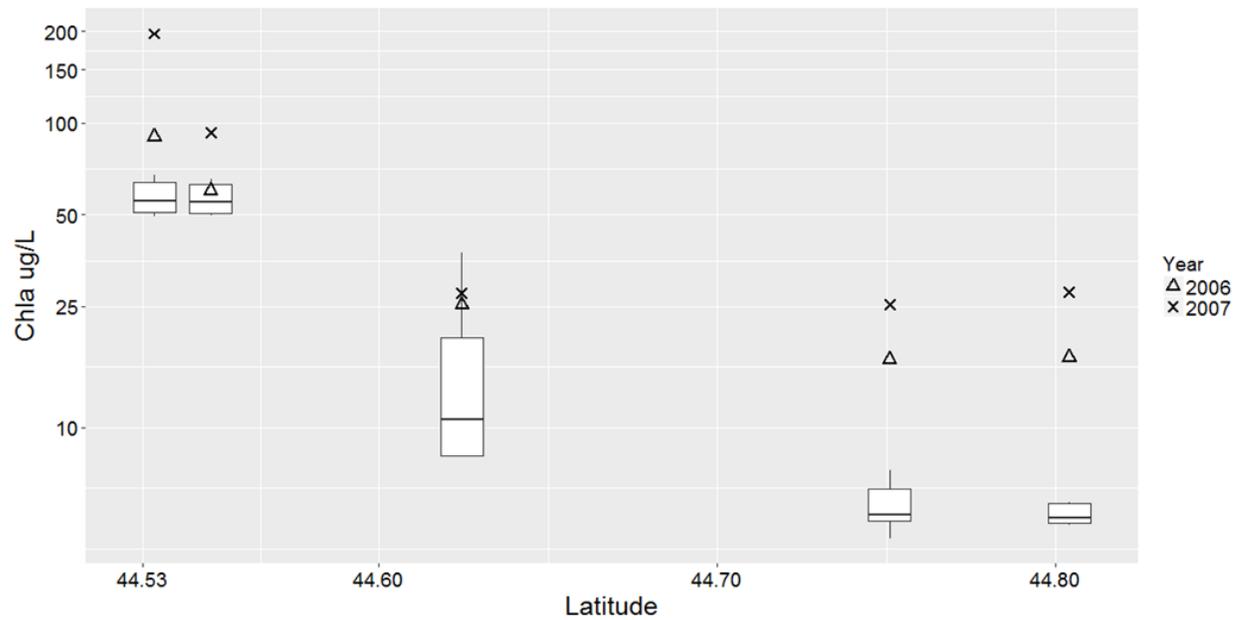


Figure A3. 2. Distribution of simulated summer chlorophyll concentrations (box plots) in lower Green Bay along a latitudinal gradient compared to reported summer means from De Stasio *et al.* (2014) (Triangles and \times 's). Greater latitudes are farther from the mouth of the Fox River. Scale on y-axis is \log_{10} transformed.

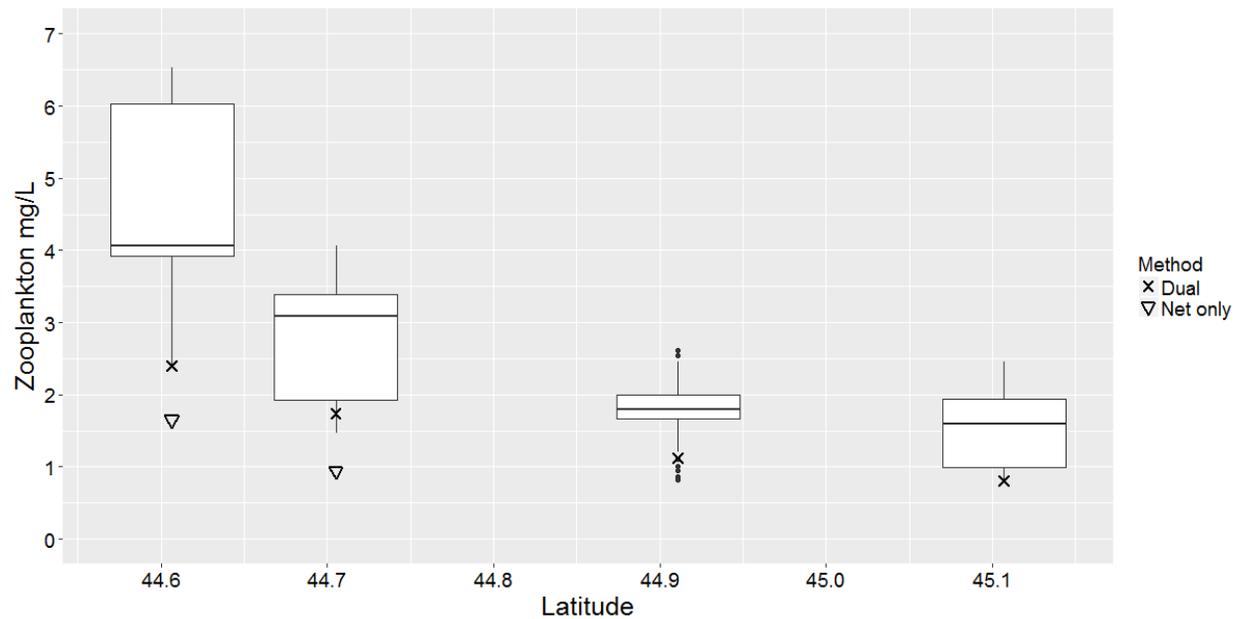


Figure A3. 3. Distribution of simulated summer zooplankton biomass (wet weight) (box plots) in Green Bay along a latitudinal gradient compared to reported summer (June through September) means from Reed (2017) using two different sampling methods (Dual (Triangles): 20 μm and 63 μm mesh nets; Net only (\times): 63 μm mesh nets). The northernmost latitude was near Fish Creek, WI and the southernmost was near Benderville, WI.

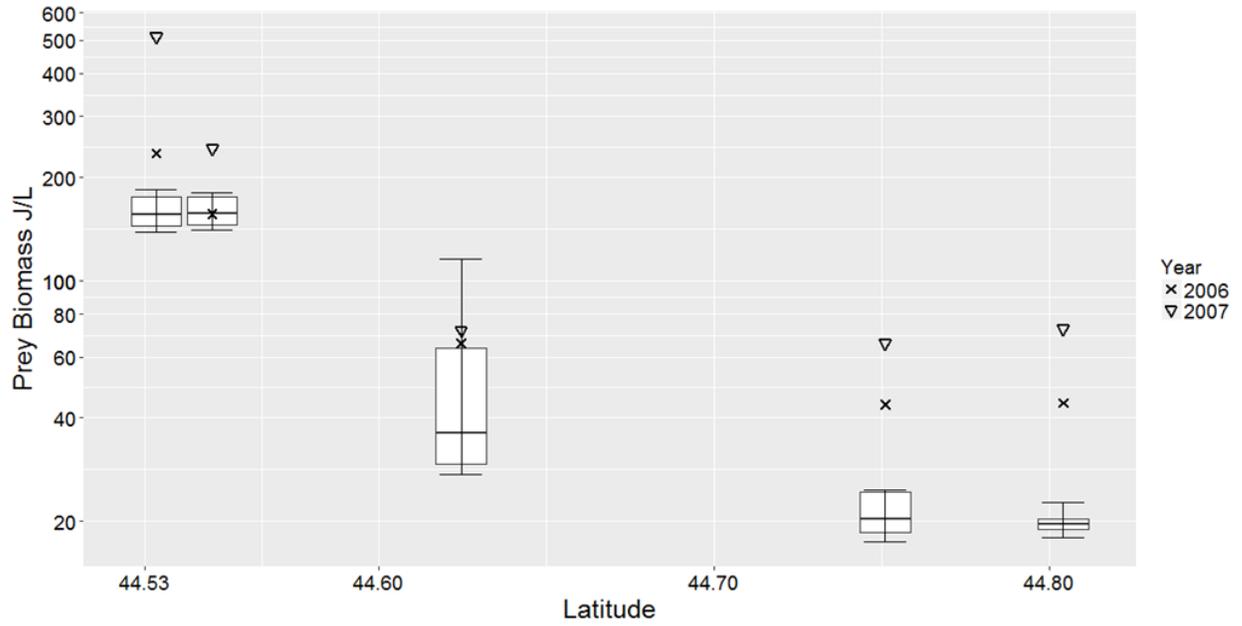


Figure A3. 4. Distribution of simulated phytoplankton and zooplankton prey biomass (boxplots) along a latitudinal gradient compared to observed phytoplankton biomass (× and triangles) reported by De Stasio *et al.* (2014). Scale on y-axis is log₁₀ transformed.

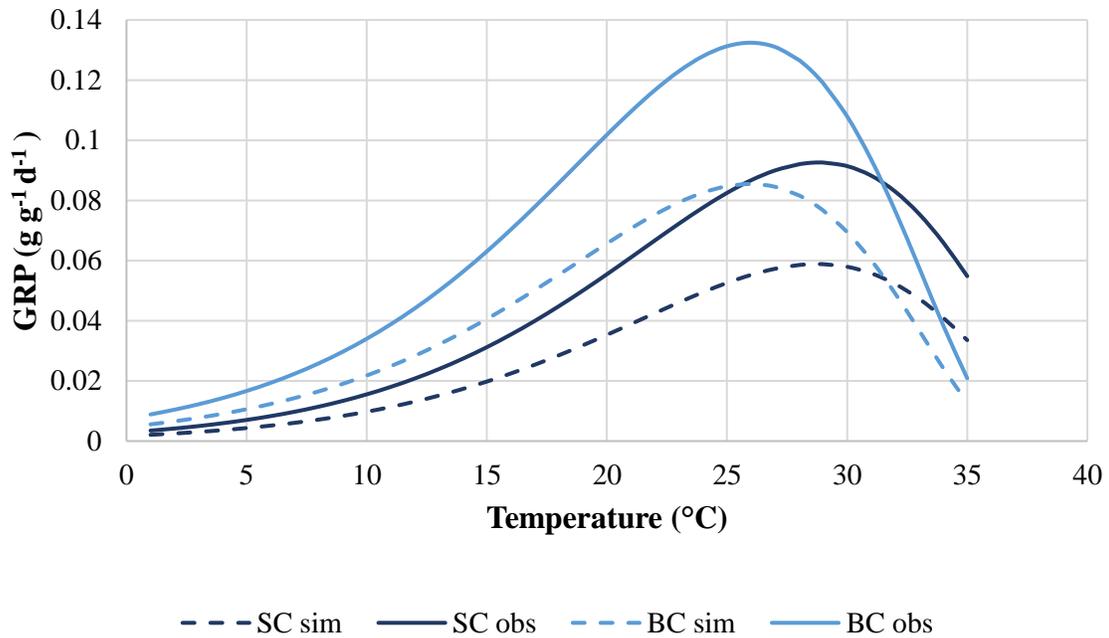


Figure A3. 5. Bighead (BC) and Silver carp (SC) growth rate potential (GRP) modeled as a function of temperature with fixed inputs of simulated (sim) and observed (obs) averages of prey concentrations in Green Bay.

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