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Lake Michigan’s Suitability for Bigheaded Carp: The Importance of Diet Flexibility and Subsurface Habitat

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28 Summary

- 29 1. As bighead [*Hypophthalmichthys nobilis*] and silver carp [*H. molitrix*] (collectively
30 bigheaded carp [BHC]) arrive at Lake Michigan's doorstep, questions remain as to whether
31 there is sufficient food to support these invasive filter-feeding fishes in the upper Laurentian
32 Great Lakes. Previous studies suggest that suitable BHC habitat is limited to a few
33 productive, nearshore areas. However, those studies did not consider the influence of BHC's
34 diet plasticity or the presence of spatially-discrete subsurface prey resources. This study
35 aimed to characterize Lake Michigan's suitability for BHC and evaluate the importance of
36 these considerations in habitat suitability assessments.
- 37 2. We used simulated outputs of prey biomass (phytoplankton, zooplankton, and detritus) and
38 water temperature from a three-dimensional biophysical model of Lake Michigan to evaluate
39 growth rate potential (GRP, quantitative index of habitat suitability) of adult BHC throughout
40 the entire volume of the lake. Our GRP model applied a foraging model and a bioenergetics
41 model to translate prey concentrations and water temperatures into habitat quality indexed by
42 individual fish growth rate. We defined suitable habitat as habitats that can support growth
43 rate potential $\geq 0 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$. We developed six feeding scenarios to evaluate the impact of diet
44 flexibility and subsurface prey resources on suitable habitat quantity. Scenarios were defined
45 by the number of prey types the fish could consume and the depths at which they could feed
46 (surface or whole water column).
- 47 3. Consistent with previous studies, we found that habitats with the highest quality were
48 concentrated near river mouths and in eutrophic areas of Green Bay. However, in contrast to
49 previous studies, we found suitable offshore habitat for bighead carp owing to our added
50 considerations of diet plasticity and subsurface prey resources. For silver carp, these
51 considerations extended suitable habitat within Green Bay and in some tributary-influenced
52 nearshore areas, but offshore areas remained predominantly unsuitable in all feeding
53 scenarios. Differences in simulated habitat suitability between these two species likely reflect
54 differences in energy density and mass of the specific fishes we used in our model. However,
55 reports of these two species in environments where they coexist indicate that bighead carp
56 grow at faster rates than silver carp as our model simulated.
- 57 4. Our vertical analysis at Muskegon, MI indicates that subsurface temperature and prey
58 biomass are not only sufficient to support bighead carp growth, but provide maximum habitat
59 quality during late summer stratification.
- 60 5. Overall, our study demonstrates that BHC are capable of surviving and growing in much
61 larger areas of Lake Michigan than predicted by previous studies, and thus suggests that the

62 risk of establishment is not sufficiently reduced by low plankton concentrations. Maps
63 generated by our model identified the potential for cross-lake migration corridors that may
64 facilitate and accelerate lake-wide movements. We believe these maps could be used to
65 prioritize surveillance protocols by identifying areas to which BHC might spread upon
66 entering the lake. More broadly, this research demonstrates how the physiology and trophic
67 ecology of BHC contributes to their high invasive capacity and can permit their survival in
68 novel environments.

69

70 Introduction

71

72 The ecological history of the Laurentian Great Lakes post-European settlement is arguably best
73 known for the intentional and unintentional introduction of aquatic non-indigenous species. However, of
74 the 180+ established non-native species in the Great Lakes, only a few have become invasive (as defined
75 by Executive Order 13112 in 1999). The undesirable, system-altering effects of the most notorious
76 invaders, i.e. the sea lamprey (*Petromyzon marinus*) and the dreissenid mussels (the quagga mussel
77 *Dreissena rostriformis bugensis* and zebra mussel *Dreissena polymorpha*), have contributed to the
78 decline of ecologically and recreationally important native species, altered trophic dynamics, influenced
79 patterns of productivity, and imposed significant socioeconomic burdens (Hecky *et al.*, 2004; Nalepa,
80 Fanslow & Lang, 2009; Vanderploeg *et al.*, 2010; Rosaen, Grover & Spencer, 2012; Madenjian *et al.*,
81 2013). As a result, stakeholders have become increasingly aware of the next major invader sitting on Lake
82 Michigan's doorstep: bighead carp *Hypophthalmichthys nobilis* and silver carp *Hypophthalmichthys*
83 *molitrix* (hereafter collectively referred to as bigheaded carp [BHC]) (International Joint Commission,
84 2018).

85 Bigheaded carp were imported to the US in the 1970s to control eutrophication in reservoirs and
86 sewage treatment lagoons (Kolar *et al.*, 2007). Following their escape, these species quickly spread
87 throughout the Mississippi River basin and have established dense populations in many of the reaches
88 they have invaded, including the Illinois River where they comprise 63% of the total fish biomass
89 (Garvey *et al.*, 2015). The impact of BHC in these invaded ecosystems and the proximity of the invasion
90 front to Lake Michigan have elevated concerns about a potential invasion into the Great Lakes via the
91 Chicago Area Waterway System; the man-made connection between the Illinois River and Lake
92 Michigan (ACRCC, 2016).

93 The effects of BHC on invaded ecosystems are often complex due to their capacity to directly and
94 indirectly affect multiple trophic levels. Intensive grazing of plankton by BHC can reduce phytoplankton
95 abundance in invaded habitats (Tumolo & Flinn, 2017; Deboer, Anderson & Casper, 2018) and alter
96 community composition by promoting the dominance of indigestible phytoplankton taxa (Görgényi *et al.*,
97 2016). In turn, BHC can exert significant pressure on zooplankton through predation and by reducing the
98 abundance of consumable food (Radke & Kahl, 2002; Cooke, Hill & Meyer, 2009; Sass *et al.*, 2014;
99 Deboer *et al.*, 2018). The decline in the body condition and populations of native planktivores in the
100 Illinois and Upper Mississippi rivers has been largely attributed to the competitive interaction with BHC
101 (Irons *et al.*, 2007; Sampson, Chick & Pegg, 2009; Pendleton *et al.*, 2017). Hypothetically, BHC not only
102 would compete with resident planktivores in the Great Lakes, but also with other fishes during their

103 plankton-dependent larval stage. Interestingly, evidence from Deboer *et al.* (2018) showed no signs of
104 silver carp having adverse effects on native larval fish biomass in the Illinois River. However, this
105 interaction might differ in a food-limited environment like Lake Michigan. If BHC invade Lake
106 Michigan, they could compete with an already-declining population of planktivorous prey fishes
107 (Madenjian *et al.*, 2012) for a limited prey supply (Vanderploeg *et al.*, 2010, 2012) and could effect a
108 trophic bottleneck that reduces the flow of energy to higher trophic levels (Irons *et al.*, 2007).

109 The magnitude of potential BHC effects in Lake Michigan is contingent upon their ability to
110 establish successfully. Establishment is a multi-faceted stage in the invasion process and a variety of
111 approaches have been used to address the probability of BHC establishment in the Great Lakes (Cooke &
112 Hill, 2010; Kocovsky, Chapman & McKenna, 2012; Cuddington, Currie & Koops, 2014; Anderson *et al.*,
113 2015). Previous modeling efforts have determined that BHC establishment would not be limited by
114 hydrologic and climatic conditions (Chen, Wiley & Mcnyset, 2007; Herborg *et al.*, 2007), and several
115 Great Lakes tributaries have viable spawning habitats (Kolar *et al.*, 2007; Kocovsky *et al.*, 2012; Murphy
116 & Jackson, 2013). However, the capacity of the oligotrophic offshore waters of Lake Michigan to support
117 invasive planktivores has generated skepticism around the likelihood of BHC establishment (Cooke &
118 Hill, 2010).

119 The oligotrophication of Lake Michigan that has occurred over the past 50 years has been linked
120 to several factors including climatic variation, reduced phosphorous loads, and, perhaps most notably, the
121 proliferation of the invasive quagga mussel (Warner & Lesht, 2015; Rowe *et al.*, 2017). The filtering
122 activity of the invasive dreissenid mussels has contributed to major changes in Lake Michigan's lower
123 trophic levels (Fahnenstiel *et al.*, 2010). Some of the strongest effects include the disappearance of the
124 spring phytoplankton bloom (Vanderploeg *et al.*, 2010), the redirection of nutrients and the flow of
125 energy to the nearshore (Hecky *et al.*, 2004), and changes in size structure and species composition in
126 zooplankton and phytoplankton communities (Vanderploeg *et al.*, 2012; De Stasio, Schrimpf & Cornwell,
127 2014). The dreissenid invasion also has altered energy dynamics in alewives (*Alosa pseudoharengus*) and
128 contributed to the declining biomass of planktivorous prey fishes in Lake Michigan (Madenjian *et al.*,
129 2006, 2012). The reductions in plankton and planktivorous fish biomass suggests that BHC would likely
130 be food-limited in most open water habitats of Lake Michigan. While the cold, less productive waters of
131 Lake Michigan are likely not as conducive for BHC growth and survival than the productive rivers in
132 their native and introduced ranges, the degree to which their establishment and spread are limited by these
133 factors has only recently been investigated.

134 Recent evaluations of BHC habitat suitability have used bioenergetics models to determine Lake
135 Michigan's capacity to support the growth of these invasive fishes (Cooke & Hill, 2010; Anderson *et al.*,
136 2017). Bioenergetics models are particularly useful in this application because they can translate prey

137 abundance and water temperatures into growth potential of BHC, thus highlighting where in Lake
138 Michigan there is sufficient food and thermal conditions for an individual fish to maintain weight or
139 grow. Cooke & Hill (2010) and Anderson *et al.* (2017) found that suitable habitat for BHC growth in
140 Lake Michigan is limited to a few productive, nearshore areas, but they did not account for the fishes'
141 flexible diet or evaluate habitat beneath the surface (>1 m). While BHC typically feed on phytoplankton
142 or zooplankton, they are also opportunistic feeders that are capable of surviving on diets dominated by
143 organic detritus and bacteria (Chen, 1982; Kolar *et al.*, 2007; Anderson, Chapman & Hayer, 2016).
144 Therefore, understanding how a BHC's diet plasticity influences their growth potential is an important
145 next step for advancing our understanding of establishment risk.

146 Consideration of the temporal and three-dimensional spatial complexities of Lake Michigan is
147 also essential for quantifying habitat suitability. For example, a thermally stratified limnetic environment
148 like Lake Michigan may offer opportunities for growth at depths that have yet to be assessed. Maximum
149 growth rate at lower temperatures is attained when feeding at reduced rations (Hanson *et al.*, 1997), and
150 the presence of a deep chlorophyll layer (DCL) during summer stratification suggests that BHC may find
151 sufficient food below Lake Michigan's surface (Pothoven & Fahnenstiel, 2013; Bramburger & Reavie,
152 2016). Given the potential energetic benefits of the DCL, it seems likely that BHC could reside there to
153 optimize their growth. Improving our understanding of establishment risk requires that all potential
154 habitats in the lake be investigated, and therefore, habitat suitability assessments need to evaluate spatially
155 explicit growth potential throughout the water column as well as across the entire extent of the lake.

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

170 Methods

171 Study Site

172 Lake Michigan is a temperate, meso-oligotrophic lake with a surface area of about 57,800 km², a
173 mean depth of 85 m, a maximum depth of 282 m, and average summer surface temperatures that reach
174 21-22 °C (NOAA Great Lakes CoastWatch Program, 2018) (Figure 1). Lake Michigan's biotic and
175 abiotic environment is spatially heterogeneous and dynamic (Rowe *et al.*, 2017). The lake is dimictic—
176 mixing in the spring and fall and thermally stratifying in the summer and winter. The formation of a
177 thermocline during summer stratification divides the water column into three ecologically distinct zones:
178 an epilimnion, metalimnion, and hypolimnion. Deep chlorophyll layers also occur during summer near
179 the base of the metalimnion at an average depth of 30 m (Bramburger & Reavie, 2016). The lake exhibits
180 a strong productivity gradient from nearshore to offshore, which has been amplified by the invasion of the
181 dreissenid mussels (Hecky *et al.*, 2004). Lake Michigan's large size, biophysical heterogeneity, and
182 seasonal dynamics highlight the need for models that can consider BHC invasion risk in a spatially and
183 temporally explicit context.

184 Model Development and Data Source

185 *Growth Rate Potential Model*

186 GRP models provide a quantitative metric for evaluating habitat quality by translating prey
187 concentrations and environmental conditions (e.g., water temperature) into terms of fish biomass
188 production as indexed by individual growth rate. GRP models have been developed for a variety of
189 species in different systems (Brandt *et al.*, 1992; Mason, Goyke & Brandt, 1995; Luo *et al.*, 2001; Zhang
190 *et al.*, 2014). Our GRP model integrates three main components: 1) a bioenergetics model to estimate
191 growth; 2) a foraging model to estimate consumption inputs for the bioenergetics model; and 3) a
192 spatially explicit 3-D environment. The GRP model is constrained by species-specific physiological
193 parameters and is driven by habitat conditions (i.e., temperature and prey concentrations) that were output
194 from a spatially explicit biophysical model. All simulations were coded and run in R version 3.5.1
195 (<https://CRAN.R-project.org>).

196 *Bioenergetics Model*

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

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

201 To better compare our results with those from previous studies (Cooke & Hill, 2010; Anderson *et al.*,
202 2015, 2017), we adopted their bioenergetics equations and parameter values for consumption, respiration,
203 egestion and excretion, initial fish mass, and predator and prey energy density (Supplementary
204 information, Tables S1.1 and S1.2). When these studies used different parameter values (e.g.,
205 consumption CA , CB ; fish mass W ; and predator energy density ED_{Carp}), we used the values from
206 Anderson *et al.* (2015).

207 *Foraging Model*

208 We calculated C by taking the minimum value of two consumption estimates: maximum
209 consumption based on mass and temperature (C_{max} , Supplementary information, Table S1.2) and
210 foraging-based consumption (C_{FR}). C_{max} is determined by the bioenergetics equation for consumption
211 whereas C_{FR} is a function of temperature ($f(T)$), prey concentration ($g L^{-1}$), and filtration rate (FR ; $L d^{-1}$),
212 which itself is a function of fish mass W (g) and foraging hours (t) (from Smith, 1989):

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

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

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

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

218 Bigheaded Carp will feed opportunistically on a multiple prey types—often selecting for
219 preferred prey when it is abundant and on less preferable prey when preferred prey is limited (Kolar *et al.*,
220 2007). To account for this foraging behavior, we assumed that the fish would aim to maximize its specific
221 consumption rate, and only supplement their diet with detritus when favorable planktonic prey became
222 limited (Supplementary information, S2).

223 *Spatially Explicit 3-D Environment*

224 The three-dimensional, heterogeneous environment was defined by prey concentrations
225 (phytoplankton, zooplankton, and detritus) and water temperatures simulated by the Lake Michigan Finite
226 Volume Community Ocean Model–General Ecological Module (FVCOM-GEM, Figure 1) (Rowe *et al.*,
227 2015, 2017). FVCOM is a 3-dimensional, hydrodynamic numerical model that predicts currents,
228 temperature, and water levels driven by external physical forcings including surface wind stress and heat
229 flux (Chen, Beardsley & Cowles, 2006). The unstructured grid and terrain-following sigma vertical

230 coordinate of the model allows for accurate representation of coastline morphology. FVCOM includes a
231 General Ecological Module (GEM), which allows for flexible representation of the lower food web (Ji *et*
232 *al.*, 2008). FVCOM was applied to Lake Michigan using 20 sigma layers of uniform thickness, and an
233 unstructured grid consisted of 5795 nodes and 10,678 model cells, with cell side lengths of 0.6 to 2.6 km
234 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*
235 *al.* (2017) implemented GEM as a phosphorus-limited, nutrient-phytoplankton-zooplankton-detritus
236 (NPZD) model that simulates lower food web biomass and productivity, and included a dreissenid mussel
237 (benthic filter feeder) compartment. Phosphorus loads from 38 tributaries were included in FVCOM-
238 GEM. The geographic scope of our GRP model was confined by the boundary of FVCOM's spatial grid,
239 which included Lake Michigan and Green Bay, but not upstream tributaries or drowned river mouths
240 (Figure 1) (Rowe *et al.*, 2015, 2017). Model development and skill assessment was reported by Rowe *et*
241 *al.* (2015, 2017). We conducted additional skill assessment of the biophysical model for Green Bay
242 (Supplementary Information, S3) and a nearshore-offshore transect near Muskegon, MI. Observed
243 chlorophyll-a and zooplankton data came from De Stasio *et al.* (2014) and Reed (2017) for Green Bay. S.
244 Pothoven (unpublished data) at NOAA Great Lakes Environmental Research Laboratory (GLERL) and
245 Pothoven & Fahnenstiel (2013) provided data for Muskegon. Particulate organic carbon (POC) data were
246 obtained from the Lake Michigan Mass Balance Project (USEPA, 2006). We used output data from 2010
247 from the Lake Michigan biophysical model to develop our baseline model scenario for all simulations and
248 analyses (Rowe *et al.*, 2015, 2017). For each simulation, we extracted biophysical model data from the
249 day at the middle of each month unless otherwise noted.

250 Model Sensitivity

251 *Phytoplankton Carbon Content and Foraging Duration*

252 We evaluated the model's sensitivity to varying assumptions with respect to phytoplankton
253 carbon content and foraging duration. We selected two wet phytoplankton biomass:carbon (C_{phy}) ratios
254 (20, 36) from the literature (Peters & Downing, 1984; Bowie *et al.*, 1985; Fahnenstiel *et al.*, 1989; Rowe
255 *et al.*, 2017) and two foraging durations ($t = 12$ or $t = 24$ hours). Foraging duration values were based on
256 recorded observations of carp feeding rhythms (Wang *et al.*, 1989; Dong & Li, 1994) and on previous
257 BHC GRP models (Cooke & Hill, 2010; Anderson *et al.*, 2015, 2017). We considered scenarios for each
258 combination of assumed carbon content and foraging duration. For each combination of assumptions, we
259 determined the amount of prey required for BHC to maintain weight at temperatures typical of Lake
260 Michigan (2 to 26 C°).

261 *Feeding Scenarios*

262 We ran the GRP model under six scenarios, characterized by the type(s) of prey and the volume
263 of the water in which BHC can feed (surface layer or throughout the whole water column) to determine
264 how these considerations affected the quality and quantity of suitable habitat. We defined suitable habitat
265 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
266 maintains its weight), whereas habitat quality refers to the GRP value estimated for a given grid cell
267 (higher GRP = higher habitat quality). For both surface and whole water column scenarios, we ran
268 simulations under three different diets: 1) Phytoplankton only; 2) Phytoplankton and Zooplankton; and 3)
269 Phytoplankton, Zooplankton, and Detritus. We used prey energy density values of 2600 J g^{-1} wet mass,
270 2512 J g^{-1} wet mass, and 127.3 J g^{-1} wet mass for phytoplankton, zooplankton, and detritus, respectively
271 (Anderson *et al.*, 2015, 2016, 2017). We attributed the energy density of dreissenid mussel biodeposits to
272 all Lake Michigan detritus—assuming that this is the most prevalent detrital food source in the lake
273 (Madenjian, 1995). Anderson *et al.* (2016) reported the caloric quality of biodeposits (ED_{Det}) as 979 J g^{-1} .
274 However, the poor nutritional and energetic quality of organic detritus often reduces the amount of energy
275 a fish can assimilate, i.e. energy content of a food item that can be used for metabolism or growth
276 (Bowen, Lutz & Ahlgren, 1995). We accounted for this by adjusting ED_{Det} by an assimilation efficiency
277 coefficient of 0.13, which we derived by back-calculating the assimilated energy density from the growth
278 of juvenile BHC at the given food rations reported by Anderson *et al.* (2016). For each feeding scenario,
279 we identified all cells containing suitable habitat and then calculated the volume-weighted GRP average
280 within all of those cells to determine the overall quality of suitable habitat. We determined the total
281 volume and extent of suitable habitat for each species and scenario. Total extent was calculated as the
282 sum of the surface areas of water columns containing at least one non-negative GRP model cell (hereafter
283 referred to as ‘GRP maxima’). These scenarios were run from April thru November.

284 Model Simulations and Analyses

285 *Habitat suitability assessments*

286 We evaluated habitat suitability throughout the lake for all 12 months of the year, while also
287 investigating vertical distributions of habitat quality at three sites along a nearshore-offshore gradient at
288 Muskegon, MI. These assessments were run assuming diets of phytoplankton, zooplankton, and detritus.
289 For our lake-wide assessment, we determined the total extent, volume, and mean GRP of suitable habitat.
290 Total extent was based on GRP maxima. To account for scale-related bias caused by averaging GRP
291 across variable depths (Mason & Brandt, 1996), we mapped seasonal averages of GRP at three discrete
292 depth ranges: Near surface (NS; 0-10 m); Deep Chlorophyll Layer (DCL; 10-50 m); and the whole water
293 column (WC Mean). NS is based on range of depths at which BHC typically occupy in the Illinois River

294 (DeGrandchamp, Garvey & Colombo, 2008; Garvey *et al.*, 2012) and the DCL depths are defined by the
295 range of recent observations of DCLs in Lake Michigan (Bramburger & Reavie, 2016). For our vertical
296 assessments, we focused on three sites along a nearshore to offshore transect near Muskegon, MI
297 (nearshore (M15): 15 m depth; intermediate depth (M45): 45 m depth, offshore (M110): 110 m depth,
298 Figure 1), that NOAA GLERL has sampled monthly since the mid-1990s (Pothoven & Fahnenstiel,
299 2013). Muskegon simulations were run on a daily time step and analyses focused on characterizing
300 seasonal patterns, nearshore-offshore differences, and vertical distributions of habitat quality from April
301 thru November.

302 Results

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

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

311 The range of prey values simulated by the model tended to underestimate chlorophyll and
312 overestimate zooplankton in Green Bay (Table S3.1) and nearshore Muskegon (Figure 2; Table 1). At
313 Muskegon, simulated planktonic prey biomass (Phytoplankton + Zooplankton; $J L^{-1}$) typically showed
314 better agreement with observed data than when compared to each prey type individually (range of
315 monthly means [March – December] at nearshore Muskegon: simulated = 2.0 – 10.02 $J L^{-1}$, observed =
316 2.7 - 12.5 $J L^{-1}$; Figure 2). In offshore Muskegon during June-October, the model reasonably simulated
317 the range of planktonic prey biomass throughout the water column. The simulated DCM in late
318 stratification (August-September) underestimated values reported by Pothoven & Fahnenstiel (2013) by
319 about 1 $\mu g L^{-1}$ and simulated temperature at the Muskegon DCM was approximately 2 \times greater than
320 average temperature of Lake Michigan's DCLs (Table 1). Running our GRP model with observed total
321 plankton biomass and temperatures at the offshore DCM near Muskegon indicated that bighead carp
322 could still maintain minimal growth, but GRP was 34% of what was predicted by the model when it was
323 run with simulated data. In Green Bay, reported prey biomass far exceeds the energetic inputs required by
324 each species to maintain weight (Figures A3.4 & A3.5; Table 2). Thus, biases in the biophysical model

325 outputs had a minor effect on the GRP model's determination of habitat suitability in Green Bay or
326 Muskegon.

327 Model sensitivity to phytoplankton carbon content and foraging hours

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

338 Feeding Scenarios

339 The average extent and volume of suitable bighead and silver carp habitat from April –
340 November increased with the number of diet items for both surface and water column scenarios (Table 3,
341 Figure 4). The extent of suitable habitat for fish feeding throughout the water column was 1.0-1.9 \times
342 greater than when the same fish fed on the same diet items at the surface. The difference in suitable
343 habitat extent between water column and surface scenarios decreased as diet items increased. When
344 feeding throughout the water column, the broadest diet (phytoplankton, zooplankton, and detritus
345 [PP_ZP_Det]) produced suitable habitat volumes 4.6 \times and 2.3 \times greater than the narrowest diet
346 (phytoplankton only [PP]) for bighead and silver carp, respectively. The least restrictive scenario, which
347 was when the fish fed on all three prey types throughout the water column, increased the extent of
348 suitable habitat by 4 \times for bighead carp and 2.1 \times for silver carp compared to the most restrictive scenario
349 where the fish fed only on phytoplankton at the surface.

350 Habitat Suitability Assessments

351 The extent (as indicated by total surface area), total volume, and quality of suitable habitat for
352 BHC varied throughout the year (Figure 5). Bighead carp habitat was available from March through
353 December, with the greatest volume attained in November (1734 km^3 , 35% of the total volume) and the
354 greatest extent in September and October (57630 km^2 , 100% of the biophysical model's total surface

355 area). Silver carp habitat was available from March through November, with the total volume and extent
356 of suitable habitat peaking in August (51 km³ and 1% of the total volume, 6193 km² and 11% of total
357 surface area). The highest average quality of suitable habitat was in September for bighead carp (0.0008 g
358 g⁻¹ d⁻¹) and in August for silver carp (0.00164 g g⁻¹ d⁻¹).

359 The spatial distribution of suitable habitat differed between species and varied throughout the
360 year. During the spring, silver carp habitat was predominantly concentrated in southern Green Bay and
361 supported average growth rates of 0.0003 - 0.0006 g g⁻¹ d⁻¹ (Figures 5, 6, & A4.1). Suitable habitat
362 became available near Chicago, Milwaukee, and several river mouths along the southeastern lakeshore
363 (e.g. St. Joseph, Kalamazoo, and Muskegon Rivers) in May and the subsequent summer months (June –
364 August; Figure S4.1). During the summer, silver carp habitat covered a majority of Green Bay and
365 expanded along the Indiana, Illinois, and Michigan shorelines. Several areas along the western shore
366 influenced by tributary loads (e.g. Milwaukee, mouth of Root River, and Two Rivers, WI) also provided
367 suitable habitat. Silver carp habitat receded back into the southern portion of Green Bay as fall
368 (September-November) progressed. By December, all suitable silver carp habitat had disappeared.
369 Averaging across the different depth ranges did not significantly affect extent of silver carp habitat for
370 any season with exception to the DCL depth range since most of the suitable habitat was in shallow Green
371 Bay and nearshore areas less than 10 m deep (Figure 6; NS, DCL, WC Mean).

372 Bighead carp habitat was more extensive than silver carp habitat throughout the year. Habitat
373 along most of the southern shoreline and in Green Bay was capable of supporting bighead carp growth
374 (0.0002 - 0.0004 g g⁻¹ d⁻¹) in the spring (Figures 5, 7, & A4.2). From June – November, most of the lake
375 contained at least some suitable habitat in the water column (Figure S4.2). The southern portion of Green
376 Bay, near the mouth of the Fox River, contained the best habitat quality throughout the year and was the
377 only location capable of supporting growth in December (mean GRP = 8.0×10⁻⁵ g g⁻¹ d⁻¹). Suitable habitat
378 deepened from spring to fall (Figure 7). There were no obvious differences among the extent of suitable
379 habitat for each depth range in the spring. In summer, however, average GRP in the NS produced a
380 greater extent of suitable habitat than when GRP was averaged across the DCL depth range or the whole
381 water column. The amount of suitable habitat across the DCL depth range increased substantially in the
382 summer and fall relative to the spring, but the quality of suitable habitat at these depths was relatively
383 poor throughout the year.

384 *Vertical Distribution of Habitat Quality near Muskegon*

385 Average prey concentrations and temperatures exhibited vertical, nearshore-offshore, and
386 seasonal patterns at Muskegon. Mean prey concentrations and water temperatures were greater in the

387 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
388 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: $3.7 \pm 0.3 \text{ J L}^{-1}$;
389 $7.5 \pm 2.4 \text{ }^\circ\text{C}$) locations throughout the model run. Nearshore-offshore gradients in average prey
390 concentration and temperature were more apparent in spring than in summer or fall. June yielded the
391 highest average prey concentrations in the nearshore and intermediate depth locations. Average prey
392 concentrations in the offshore were greatest in November but overall exhibited little seasonal variability
393 (April – November mean and standard deviation: $3.7 \pm 0.3 \text{ J L}^{-1}$). Summer months (June – August)
394 exhibited the most variability in the vertical distribution of prey and temperature for all depth locations.
395 Vertical distributions of prey and temperature were evenly distributed throughout the water column
396 during periods of mixing and unevenly distributed during periods of stratification (Figure 8). Prey
397 concentrations were highest in the epilimnion in June for all locations but the offshore, which saw
398 maximum prey concentrations around 25 m. Prey concentration maxima were located beneath the surface
399 from July through October.

400 Variations in prey concentrations and water temperature resulted in varied vertical, nearshore-
401 offshore, and temporal distributions of habitat quality for BHC (Figures 8 & 9). Vertical distribution of
402 habitat quality exhibited similar seasonal patterns at all depth locations. In April, GRP was ubiquitously
403 distributed throughout the water column, but suitable habitat only existed for bighead carp in the
404 nearshore (Figure 9). In June, GRP maxima were observed in the epilimnion across all locations; the
405 nearshore epilimnion in June produced the greatest GRP at Muskegon for both species throughout the
406 model run. Suitable silver carp habitat was present from late May to late September in the nearshore, only
407 in June at the intermediate depth location, and never present in the offshore. In late summer, the highest
408 quality habitat for both species within each transect was between 10-20 m, although, at this time, suitable
409 silver carp habitat was only present in the nearshore whereas the model simulated suitable bighead carp
410 habitat in all three transects. For both species, there was a clear nearshore-offshore gradient as the
411 nearshore retained the highest habitat quality throughout most of the year and dwarfed offshore GRP
412 maxima by an order of magnitude (Figure 9).

413 Discussion

414 Diet flexibility improves establishment potential

415 In support of our hypothesis, the addition of zooplankton and detritus to model diets increased the
416 amount of suitable habitat for both species and extended it into the offshore for bighead carp. Diet
417 plasticity is a trait common to highly invasive fishes (Pettitt-Wade *et al.*, 2015) including BHC, which
418 feed opportunistically based on the relative abundance of different prey types in their immediate

419 environment (Chen, 1982; Kolar *et al.*, 2007; Cooke *et al.*, 2009; Mozsár *et al.*, 2017). Bigheaded carp
420 feed heavily on zooplankton, detritus, bacteria, and algae in Lake Donghu, China (Chen, 1982), and they
421 are thriving on diets dominated by inorganic matter and zooplankton in Lake Balaton, Hungary (Boros *et*
422 *al.*, 2014; Mozsár *et al.*, 2017). However, BHC do not exist in any ecosystems that are exactly
423 comparable to Lake Michigan and there is a lack of information on how BHC have adapted to the cool,
424 less productive lakes they do inhabit. In light of this, Lake Balaton may be the best available reference for
425 predicting how BHC might adapt to Lake Michigan, as Lake Balaton is a dreissenid-invaded, meso-
426 oligotrophic lake in a temperate climate with accessible information on the ecology of its established
427 hybrid BHC (bighead × silver) population. While Lake Michigan is deeper, larger, and generally colder
428 than Lake Balaton, our model suggests that the ability of BHC to flexibly feed on phytoplankton,
429 zooplankton, and detritus mitigates their risk of starvation—even in offshore waters—and, therefore,
430 increases their probability of establishment. Furthermore, Anderson *et al.* (2016) demonstrated that BHC
431 mitigated their weight loss and, in some cases, even gained weight when feeding only on dreissenid
432 biodeposits. This suggests that the beneficial effect of supplementing model diets with detritus simulated
433 by our model was reasonable given that BHC would have access to additional prey resources and a
434 greater abundance of biodeposits in Lake Michigan than the rations fed to them by Anderson *et al.*
435 (2016).

436 Broadening the model diets of BHC increased the connectivity of suitable habitat, which has
437 implications for their ability to spread throughout the lake. Bigheaded carp would have to travel through
438 long stretches of plankton-depleted, open waters to reach productive areas in Lake Michigan. However,
439 BHC are capable of swimming long distances and fasting for extended periods (DeGrandchamp *et al.*,
440 2008; Sheng & Ma, 2008). These traits, paired with our results, suggest that Lake Michigan's poor food
441 conditions would not deter bighead carp from reaching more eutrophic areas if they feed opportunistically
442 on detritus and plankton during their migration through less productive corridors. Using an area-restricted
443 individual-based model, Currie *et al.* (2012) determined that BHC could reach Green Bay and other
444 productive areas within the first year of escape from the Chicago Sanitary Shipping Canal and could find
445 favorable habitat within a month. Therefore, it seems likely BHC could survive, establish, and spread to
446 favorable habitat in Lake Michigan and its tributaries despite having to travel across expansive areas with
447 minimal plankton biomass.

448 Refuge beneath the surface

449 Our findings indicate that subsurface temperatures and prey biomass are sufficient to support
450 bighead carp growth and provide favorable habitat quality during late summer stratification. However,

451 average chlorophyll concentrations ($2.52 \mu\text{g L}^{-1}$) at the offshore DCM during late stratification (August -
452 September) are near the lower limit required for bighead carp to maintain weight at average DCL
453 temperature (5°C). This indicates that the suitability of this habitat is likely highly sensitive to variability
454 in prey and temperature, which could affect how BHC would utilize the DCL.

455 It is uncertain how these fishes would use subsurface habitat and distribute themselves throughout
456 Lake Michigan's water column. In the Illinois River, BHC typically occupy depths between 4-5 m and
457 demonstrate seasonal habitat preferences (DeGrandchamp *et al.*, 2008; Garvey *et al.*, 2012). In Lake
458 Michigan, however, peak prey biomass at the DCL and preferred temperatures are vertically separated
459 when the lake is stratified causing GRP to be differentially regulated by these two variables based on the
460 fishes' position in the water column. While BHC exist in dimictic lakes (e.g. Lakes Dgal Wielki and Dgal
461 Maly in Poland; see Napiórkowska-Krzebietke *et al.* (2012)), there is a lack of accessible information on
462 how they behave in these systems. We assume BHC would migrate to warm and productive tributaries
463 rather than reside in the main lake. However, if they were to reside in the lake, our results suggest that
464 BHC might inhabit depths outside of their preferred thermal range to optimize growth during summer
465 stratification. Furthermore, BHC might optimize their growth through behaviors that our model could not
466 simulate. For instance, it is possible that BHC would feed at the cooler DCL but reside in warmer surface
467 waters when they were not feeding. Bioenergetic optimization has been used to explain depth
468 distributions of fishes in thermally stratified lakes (e.g. Plumb, Blanchfield & Abrahams (2014)), so it
469 seems plausible that BHC would change their position in the water column to enhance their growth.
470 However, our model did not account for energetic costs of movement, which could be an important
471 consideration for evaluating the energetic tradeoffs of foraging at the DCL. Identifying and translating
472 literature published in non-English languages on BHC behavior in dimictic lakes, as well as developing
473 individual-based models that can simulate potential behaviors and movements (e.g. Currie *et al.* (2012)),
474 would be worthy research endeavors for understanding how BHC might adapt to the Great Lakes.

475 Interspecific differences

476 The difference in habitat suitability between bighead carp and silver carp was one of the more
477 counterintuitive findings from our research considering that these species share many ecological traits.
478 Our model suggests that silver carp have greater prey requirements for growth than bighead carp and,
479 therefore, the amount of suitable silver carp habitat is limited to the most productive areas of Lake
480 Michigan. Our simulations agree with observed individual growth rates of bighead and silver carp
481 existing in the same environments. Ke, Xie & Guo (2008) observed that bighead carp grew more quickly
482 than silver carp in the hypereutrophic Lake Taihu in China, although the difference between the two

483 species' growth rates was greatly reduced in years of high competition compared to years of low
484 competition. Additionally, length-at-age data from the Middle Mississippi River (MMR) suggests that
485 bighead carp grow more quickly than silver carp, but silver carp maintain higher growth conditions
486 (Weight/Length) in this system (Nuevo, Sheehan & Willis, 2004; Williamson & Garvey, 2005). Thus, the
487 interspecific differences we simulated are partially corroborated by reported growth rates, but further
488 consideration is warranted of how certain model parameters could be affecting this.

489 The specific bighead and silver carp we used in our model had notably different energy densities,
490 which might explain the difference in the amount of suitable habitat our model predicted for the two
491 species. We used species-specific parameters for fish mass and energy density, which were averaged from
492 10 fish from the Mississippi and Missouri River drainages derived by Anderson *et al.* (2015). The silver
493 carp used in that study were in excellent condition and the females had highly developed ovaries, whereas
494 the bighead carp exhibited moderate to low condition, as is common for this species in parts of North
495 America where they coexist with a dense population of silver carp (D.C. Chapman, US Geological
496 Survey, Columbia Environmental Research Center – Personal Comm.). Coulter *et al.* (2018) documented
497 this negative relationship of BHC body condition and population density in the Illinois River, which
498 demonstrates that fish at the invasion front are in higher condition due to less intraspecific and
499 interspecific competition. Our model does not account for the effects of competition between the species
500 on GRP, but realized growth rates would be affected by this and could have implications on which species
501 is most likely to establish in Lake Michigan and whether coexistence is possible. Therefore, the
502 interspecific differences our model simulated agree with observations from other ecosystems, but likely
503 only represent a potential scenario of Lake Michigan's suitability for BHC given the condition of the
504 fishes we assumed in our model and the absence of competition. We hypothesize that the amount of
505 suitable habitat for silver carp would be similar to that predicted for bighead carp if we had assumed a
506 similarly low energy density for both species. Furthermore, energy density was static in our simulations
507 but in fishes this can fluctuate seasonally, ontogenetically, and in response to starvation (Hartman &
508 Brandt, 1995; Madenjian *et al.*, 2006; Breck, 2008). Thus, the energy density of BHC could decrease in
509 response to low food availability in certain areas of Lake Michigan, which in turn could affect their
510 growth potential or habitat suitability in ways that our model could not capture.

511 Oases in the desert: Tributary-affected nearshore areas & river mouths

512 While our results show that the overall extent of high quality habitat for BHC remains relatively
513 small, we maintain that the risk of localized establishment events is still high near river mouths and other
514 areas affected by tributary nutrient loads. Our model simulated suitable habitat near the mouths of several

515 tributaries throughout the year, including the Milwaukee and St. Joseph Rivers, which both possess
516 sufficient water quality characteristics, temperatures, and hydraulics to support BHC spawning and egg
517 development (Murphy & Jackson, 2013). The availability of productive feeding grounds and viable
518 spawning habitat upstream suggests that carp may concentrate near river mouths, and thus improve their
519 probability of establishing sustainable populations in light of low propagule pressure and population
520 density (Jerde, Bampfylde & Lewis, 2009; Cuddington *et al.*, 2014). Cuddington *et al.* (2014) found that a
521 greater number of suitable spawning rivers reduced the chance of BHC finding mates given a small
522 introduction event (i.e. 20 males, 20 females). This suggests that the limited availability of viable
523 spawning rivers may actually facilitate BHC establishment rather than deter it. Similarly, it seems that the
524 limited amount of productive habitats could further increase the probability of finding a mate. Bigheaded
525 carp locate and selectively feed in areas of higher prey concentrations (Dong & Li, 1994; Calkins, Tripp
526 & Garvey, 2012; Currie *et al.*, 2012), which for spawning females, can lead to higher fecundities and
527 potentially higher recruitment rates due to improved maternal condition (Degrandchamp, Garvey &
528 Csoboth, 2007). Food requirements for BHC in their early life stages are likely less—due to their smaller
529 size and energy densities—than that for the adult BHC we used in our study, which suggests productive
530 river mouths that can support adult BHC growth would also provide sufficient food for the completion of
531 larval and juvenile stages. Therefore, the benefits river mouths provide make these areas—and the variety
532 of resident fish species that depend on them in their early life stages (Janetski *et al.*, 2013; Harris *et al.*,
533 2017)—particularly vulnerable to a BHC invasion.

534 Model limitations and uncertainty

535 We designed our feeding scenarios to assess the importance of diet flexibility in a way that would
536 reflect realistic foraging behavior and make our results comparable to Anderson *et al.* (2017) and (Cooke
537 & Hill, 2010). Thus, the design of this analysis was to evaluate realistic conditions and scenarios
538 comparable to previous work instead of using a factorial design that would evaluate the individual
539 importance of each food type to habitat suitability.

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

548 than our model could effectively assess (range of grid cell surface areas = 0.2 km² – 29.5 km², median =
549 7.2 km²). GRP model predictions are influenced by the spatial resolution of environmental data and the
550 scale at which it is analyzed (Mason & Brandt, 1996), which indicates that higher resolution data would
551 allow our model to better capture the patchiness in prey and the resulting extremes in GRP within a scale
552 more similar to the foraging radius of BHC.

553 Developing consumption parameters and a filtration equation for an adult BHC would improve
554 the model's reliability. We used the same values for *CA* and *CB* as Anderson *et al.* (2015, 2017), which
555 were derived from Wang *et al.* (1989). Anderson *et al.* (2015) states that these values produced more
556 realistic simulations than the values Cooke & Hill (2010) derived from Smith (1989), however, both
557 Wang *et al.* (1989) and Smith (1989) focused on analyzing consumption patterns in juvenile bigheaded
558 carp much smaller than those used in our simulations. Extrapolating relationships for filtration rate and
559 consumption from juvenile fish to adult fish likely biases consumption and GRP. Thus, future research
560 could improve on our model by researching, integrating, and validating the consumption parameters and
561 filtration rate equation for larger BHC.

562 Our model assumed 100% filtration and retention efficiency for both species and, therefore, did
563 not account for the effect of prey size on BHC consumption and GRP. Differences in gill morphology
564 dictate the particle size that these fishes can efficiently filter, with bighead carp more efficient at
565 removing larger particles and silver carp are more adept at filtering finer particulates (Dong & Li, 1994).
566 However, both species see significantly reduced efficiencies for particles near 8-10 μm (Cremer &
567 Smitherman, 1980; Smith, 1989). This is relevant considering >50% of Lake Michigan chlorophyll is
568 comprised of pico- (<2 μm) and nanoplankton (2 - 20 μm) communities (Cuhel & Aguilar, 2013; Carrick
569 *et al.*, 2015), which historically have included more single-celled organisms than the colonial organisms
570 (Fahnenstiel & Carrick, 1992) that would be more susceptible to BHC filtration. An exception to this
571 might be in eutrophic areas like Green Bay (see De Stasio *et al.* (2014)) where the size-selective grazing
572 pressure of dreissenid mussels has promoted the dominance of colonial species (e.g. *Microcystis*), that are
573 not effectively filtered by dreissenids but could be easily consumed by BHC. Additionally, FVCOM-
574 GEM's zooplankton variable was calibrated to data reported by Vanderploeg *et al.* (2012) who used 153-
575 μm vertical net tows, which cannot effectively capture microzooplankton such as rotifers that are
576 common in the diets of BHC (Williamson & Garvey, 2005; Sampson *et al.*, 2009). Thomas, Chick &
577 Czesny (2017) found that microzooplankton made up 74% of mean total zooplankton biomass with
578 rotifers comprising 51% alone, and that sampling with 64-μm mesh nets underestimates total zooplankton
579 biomass by nearly three-fold compared to methods that utilize finer mesh screens (i.e. 20-μm). Therefore,
580 incorporating microzooplankton biomass and particle size-based filtration and retention efficiencies into

581 future GRP models should be a priority given the potential implications it could have on the
582 establishment of BHC.

583 Conclusion

584 Our model predicted a greater extent of suitable habitat for BHC than did previous models;
585 however, the best habitat was concentrated in nearshore areas and Green Bay, which is in agreement with
586 the findings of Anderson *et al.* (2017) and Cooke & Hill (2010). Moreover, our results suggest that there
587 may be cross-lake migration corridors that could facilitate establishment and spread. We were able to
588 build on previous research and advance current understanding of establishment risk by running our
589 bioenergetics model with simulated water quality variables from a Lake Michigan biophysical model
590 (Rowe *et al.*, 2017), which allowed us to demonstrate how diet plasticity and the availability of
591 subsurface prey increases Lake Michigan's vulnerability to BHC establishment. Our findings provide
592 further evidence of the invasion risk these species pose to the Great Lakes and can help managers
593 prioritize surveillance efforts by identifying where in the lake BHC might spread upon introduction.

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Data Availability Statement

The data that support the findings of this study are openly available in University of Michigan's Deep Blue data repository at <http://doi.org/doi:10.7302/Z2T151WJ>.

Conflict of Interests

The authors have no conflicts of interests to declare.

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840 Supplementary Information

841 S1: Growth Rate Potential Model Equations and Parameters

842 S2: Foraging Behavior Assumptions

843 S3: Simulated Water Quality Outputs compared to Observed Values in Green Bay

844 S4: Monthly Habitat Suitability Maps

845

846 Tables

847 Table 1. Habitat conditions and model-predicted growth rate potential (GRP) in environments where
848 bighead carp *Hypophthalmichthys nobilis* (BC) and silver carp *H. molitrix* (SC) exist compared to those
849 observed and simulated in Lake Michigan. GRP values are based on diets of phytoplankton and
850 zooplankton at the reported temperatures. Observed zooplankton in lower Green Bay represents the
851 average of the two southern most sites (Benderville and Shoemaker Point) reported by Reed (2017).
852 Footnotes next to the location indicate sources that provide data on three or more variables for that
853 location. (POC = Particulate Organic Carbon; Chl = Chlorophyll-a).

| Location | BHC biomass (metric tons km ⁻¹) | BC GRP (g g ⁻¹ d ⁻¹) | SC GRP (g g ⁻¹ d ⁻¹) | Mean Summer Temp (C°) | Chl (ug L ⁻¹) | Zooplankton (mg L ⁻¹ w.w.) | POC (mgC L ⁻¹) | Data source & Notes |
|---|--|--|--|--------------------------------|--------------------------------------|---|-------------------------------|---|
| Illinois River | 3.3 [†] | 0.0008 - 0.022 | 6.0 × 10 ⁻⁶ - 0.013 | 26.3 [‡] | 2.8 - 21 [‡] | 0.237 – 0.650 [§] | | Garvey <i>et al.</i> (2012) [†] ; USGS National Water Information System (waterdata.usgs.gov/nwis) [‡] ; Sass <i>et al.</i> (2014) [§] |
| Middle Mississippi River | | 0.002 - 0.022 | 0.0006 - 0.013 | 26.6 [†] | 18.5 - 49 [†] | 0.015 – 0.05 [‡] | | Long Term Resource Monitoring Program (umesc.usgs.gov/data_library/) [†] ; 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 |
| Missouri River | | 0.022 | 0.012 | 23.8 | 19.7 ± 1.1 | 0.86 – 0.9 | 2.5 - 4 | converted to wet weight using length-weight |
| Lake Balaton, Hungary | 4.2 [†] | 0.002 - 0.015 | 0.0005 - 0.008 | 20.4 [‡] | 1.5 - 7.3 [‡] | 1.07 – 6.59 [‡] | 1 - 4.6 [§] | parameters from Bottrell <i>et al.</i> (1976) Weiperth <i>et al.</i> (2014) [†] ; Mozsár <i>et al.</i> (2017) [‡] ; Zánkai & Ponyi (1986) [§] |
| Lower Green Bay, Lake Michigan (LM) | | 0.004 - 0.022 | 0.001 - 0.013 | 24.1 - 26 [†] | 2.44 [‡] - 197 [§] | 2.07 [‡] | 0.31 [¶] | Great Lakes Aquatic Habitat Framework (https://www.glahf.org/explorer/) [†] ; Reed (2017) [‡] ; De Stasio <i>et al.</i> (2014) [§] ; 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 [†] | | -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 |

| | | | | | | | |
|--|----------------------|---------|----------------|----------------------------|------------------|-----------------------------|--|
| Offshore DCM, Southeast LM | 6.8×10^{-5} | -0.0003 | 5 [†] | $2.52 \pm 0.21^{\ddagger}$ | 0.3 [§] | 0.15 - 0.18 [¶] | Bramburger & Reavie (2016) [†] ; Pothoven & Fahnenstiel (2013) [‡] ; Pothoven (unpubl) [§] ; USEPA (2006) [¶] ; Zooplankton represents water All values averaged from DCM in August and September |
| Offshore DCM, Southeast LM (simulated) | 0.0002 | -0.0004 | 9.5 | 1.45 | 0.61 | 0.2 | |

Table 2. Prey concentrations and energy density required for a 5480 g bighead carp *Hypophthalmichthys nobilis* and a 4350 g silver carp *Hypophthalmichthys molitrix* 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 (µg 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 |

| 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 |

Table 3. Area, volume, and mean growth rate potential (GRP) of suitable habitat for bighead carp *Hypophthalmichthys nobilis* and silver carp *H. molitrix* under different feeding scenarios averaged from April-November. PP = Phytoplankton only; PP_ZP = Phytoplankton and Zooplankton; PP_ZP_Det = Phytoplankton, Zooplankton, and Detritus.

| | | | | | | | |
|--------|-----------|-----------|-----------|-------|----------|--------|--------|
| | PP_ZP_Det | 43,308.28 | 44,548.71 | 43.31 | 1,144.91 | 0.0008 | 0.0005 |
| | PP | 1,435.93 | 1,584.67 | 1.44 | 12.41 | 0.0016 | 0.0011 |
| Silver | 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 |

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Figure Captions

Figure 1. Map of Lake Michigan (a), showing the spatial domain of Finite Volume Community Ocean Model – General Ecosystem Module (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). Enlarged area of southeastern Lake Michigan (b), showing the hydrodynamic model grid, NOAA Muskegon stations (filled squares), and the location of four tributary mouths (filled triangles).

Figure 2. Simulated (box plots) and observed (triangles; Pothoven, unpubl.) mean chlorophyll concentration, zooplankton biomass, and total planktonic prey (phytoplankton & zooplankton) biomass in the water column at nearshore and offshore Muskegon in 2010 from March – December. Boxplot whiskers are $1.5 \times$ interquartile range.

Figure 3. Average of bighead carp *Hypophthalmichthys nobilis* (a,b,e,f) and silver carp *H. molitrix* (c,d,g,h) growth rate potential (GRP, $\text{g g}^{-1} \text{d}^{-1}$) in Lake Michigan 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 $\geq 0 \text{ g g}^{-1} \text{d}^{-1}$ for each water column. Gray areas indicate unsuitable habitat (GRP $< 0 \text{ g g}^{-1} \text{d}^{-1}$).

Figure 4. Average of bighead carp *Hypophthalmichthys nobilis* (a-c, g-i) and silver carp *H. molitrix* (d-f, j-l) growth rate potential (GRP) from April – November in Lake Michigan under different feeding scenarios. Suitable habitats were defined by GRP maxima $\geq 0 \text{ g g}^{-1} \text{d}^{-1}$ for each water column. Gray areas indicate unsuitable habitat (GRP $< 0 \text{ g g}^{-1} \text{d}^{-1}$). PP = Phytoplankton only; PP_ZP = Phytoplankton and Zooplankton; PP_ZP_Det = Phytoplankton, Zooplankton, and Detritus.

Figure 5. Total surface area (top left), volume (bottom left), and monthly growth rate potential (GRP) of suitable habitat for bighead carp *Hypophthalmichthys nobilis* and silver carp *H. molitrix* (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 boxplot. Boxplot whiskers represent the minimum and maximum GRP values for each species and month.

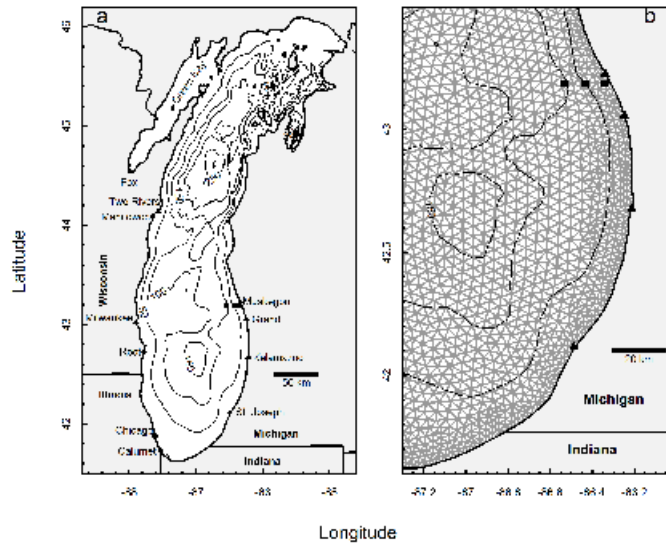
Figure 6. Seasonal distribution of suitable silver carp *Hypophthalmichthys molitrix* habitat as represented by average growth rate potential (GRP) in the near surface waters (NS: 0 – 10 m), Deep Chlorophyll Layer (DCL; 10 – 50 m), whole water column (WC Mean), and GRP maxima observed throughout the water column (WC Max). Spring: March – May; Summer: June – August; Fall: September – November.

Figure 7. Seasonal distribution of suitable bighead carp *Hypophthalmichthys nobilis* habitat as represented by average growth rate potential (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.

Figure 8. Vertical distribution of temperature (top), prey (middle), and bighead carp *Hypophthalmichthys nobilis* habitat quality (bottom) at the offshore depth location along a nearshore-offshore transect at Muskegon, MI (Figure 1; filled squares) throughout the year. Gray areas in the bottom panel indicate unsuitable habitat (growth rate potential [GRP] < 0.0 g g⁻¹ d⁻¹).

Figure 9. Vertical distribution of bighead *Hypophthalmichthys nobilis* and silver carp *H. molitrix* habitat quality at three depth locations along a nearshore-offshore transect at Muskegon, MI (Figure 1; filled squares) throughout the year. Gray areas indicate unsuitable habitat (growth rate potential [GRP] < 0.0 g g⁻¹ d⁻¹). M15: Nearshore depth location; M45: Intermediate depth location; M110: Offshore depth location.

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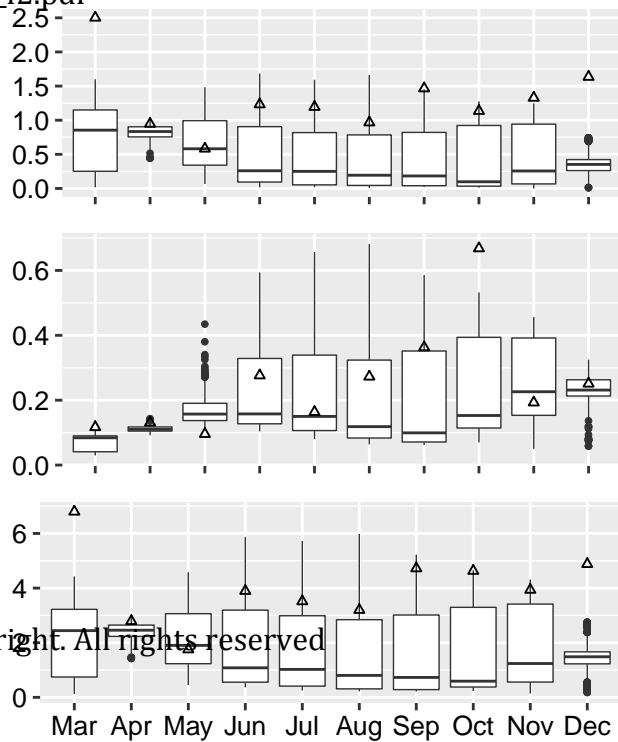
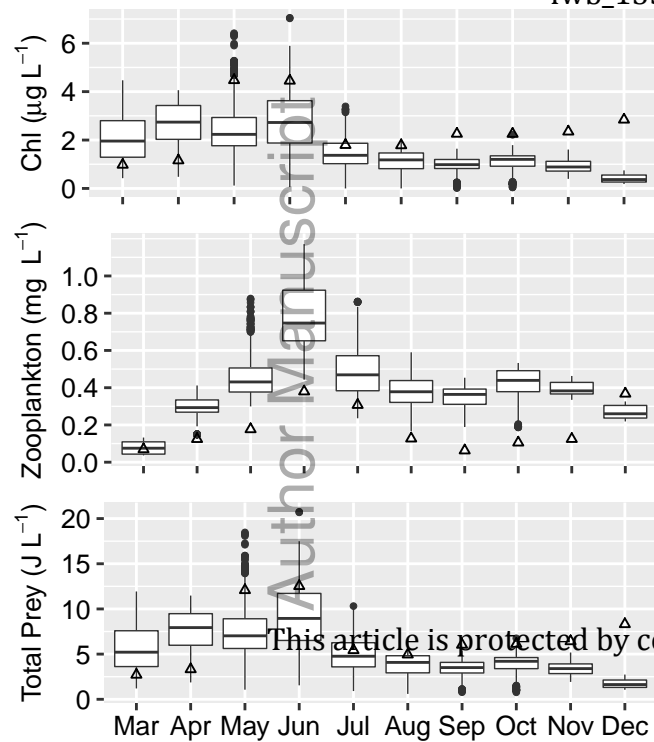


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Nearshore

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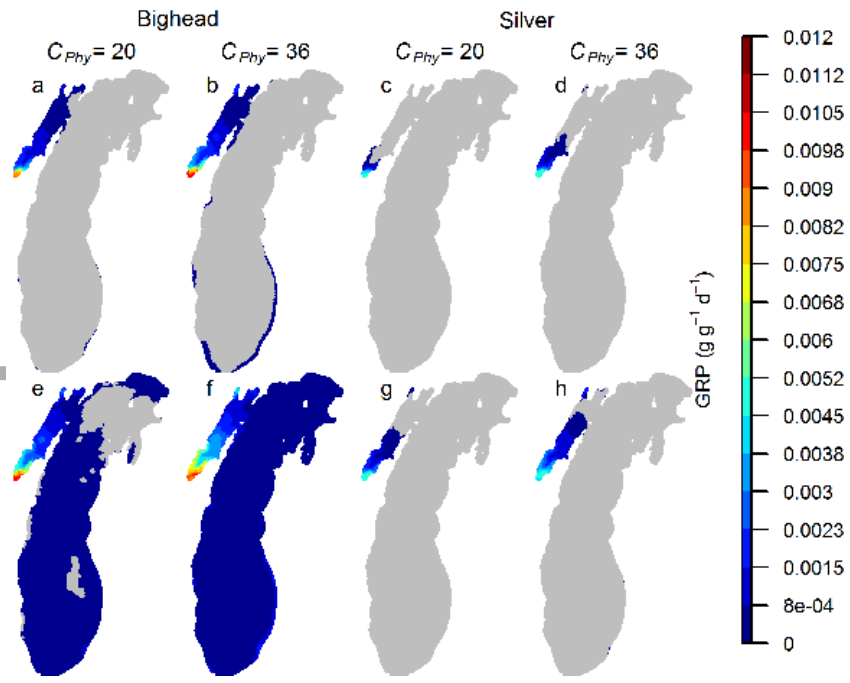
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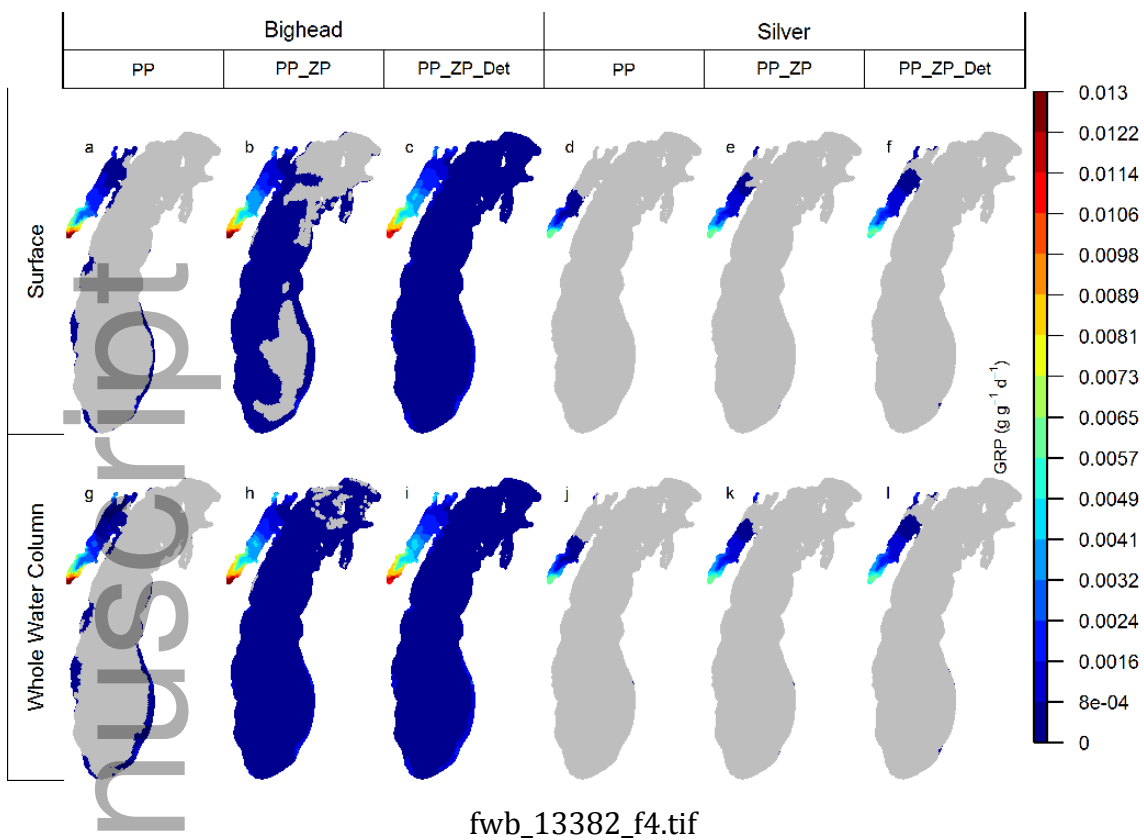
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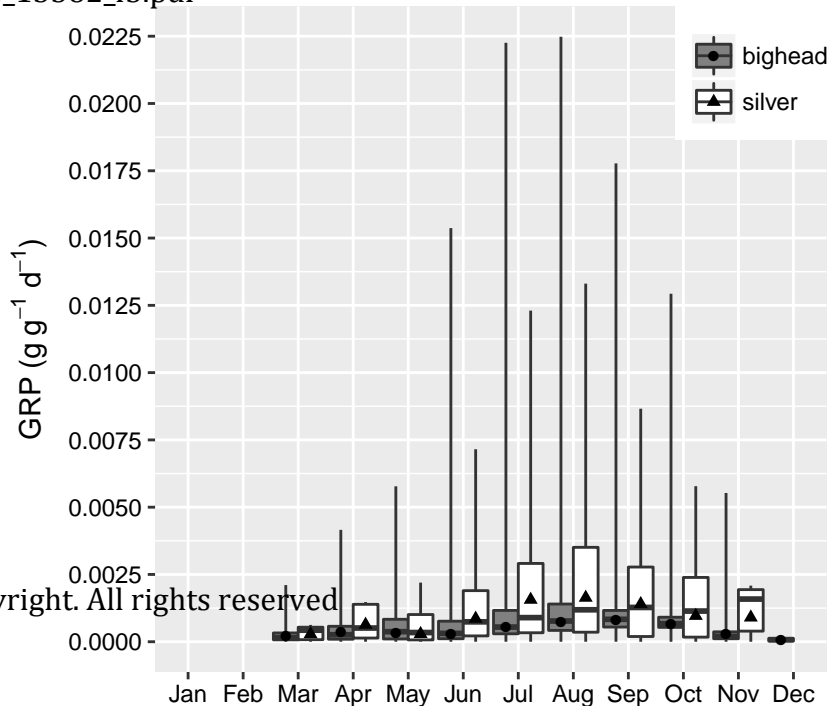
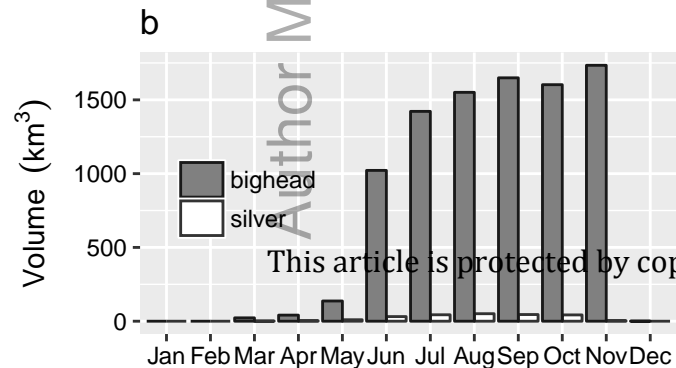
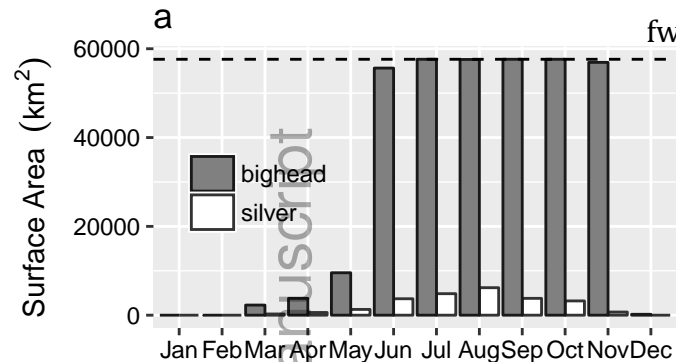
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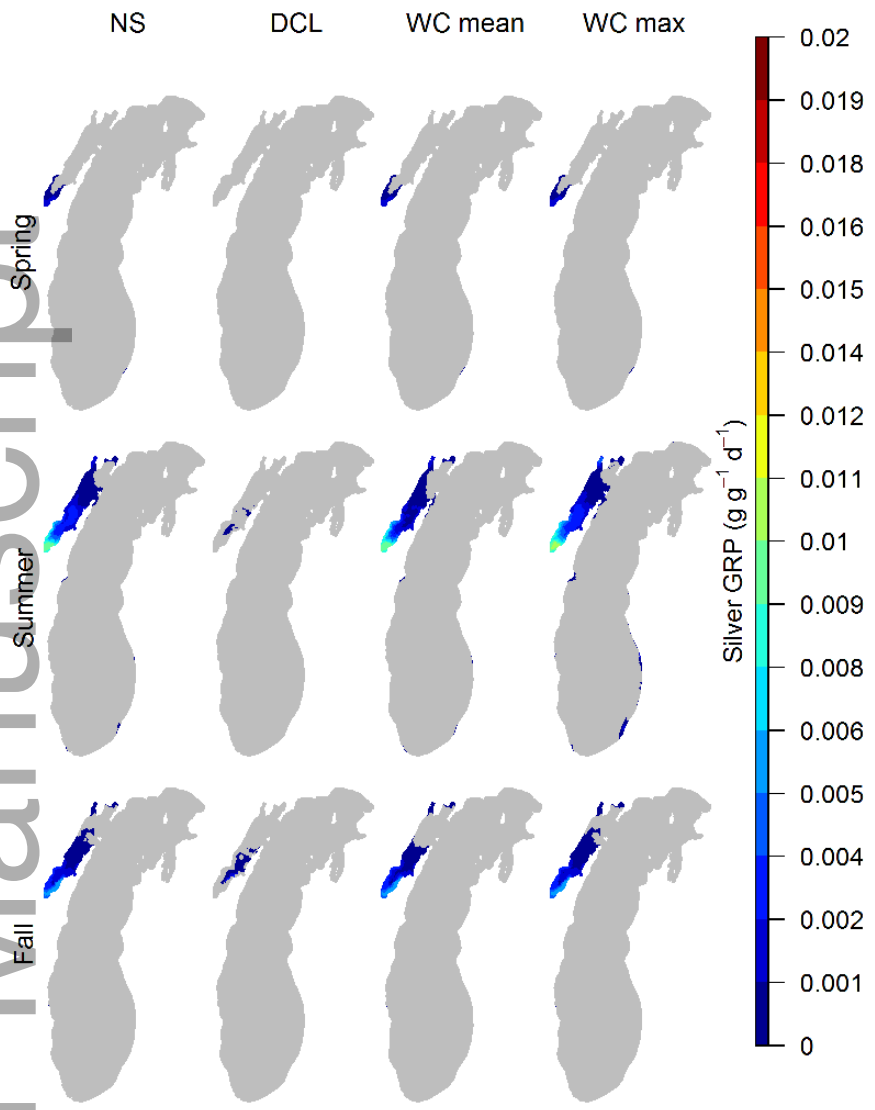
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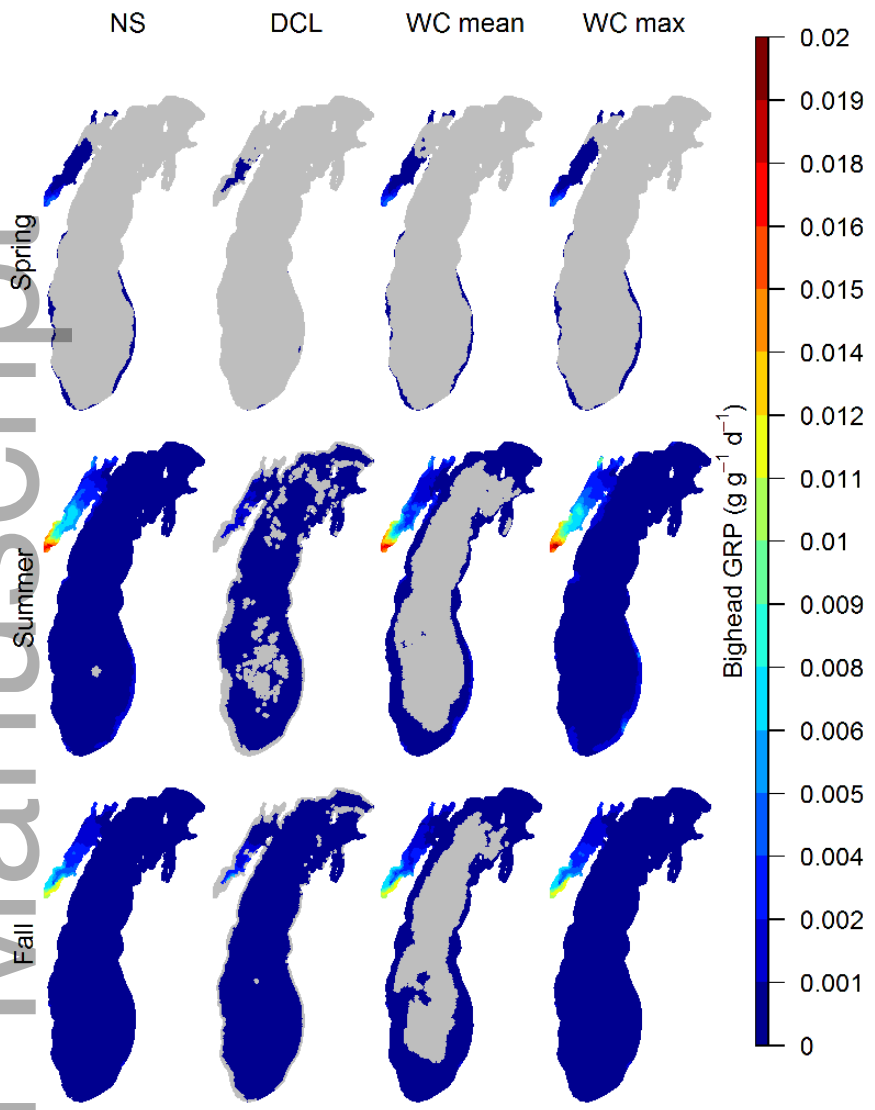
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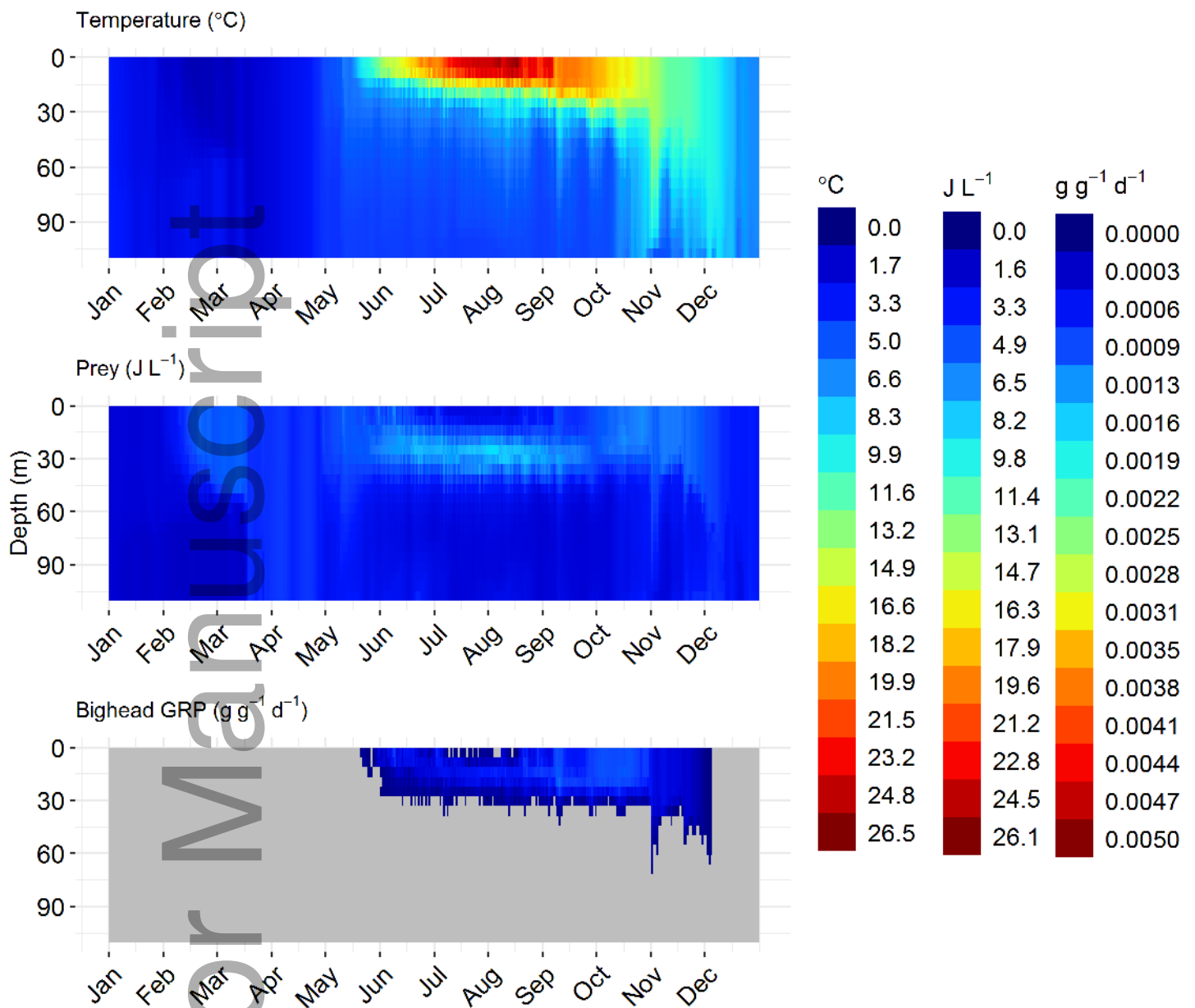




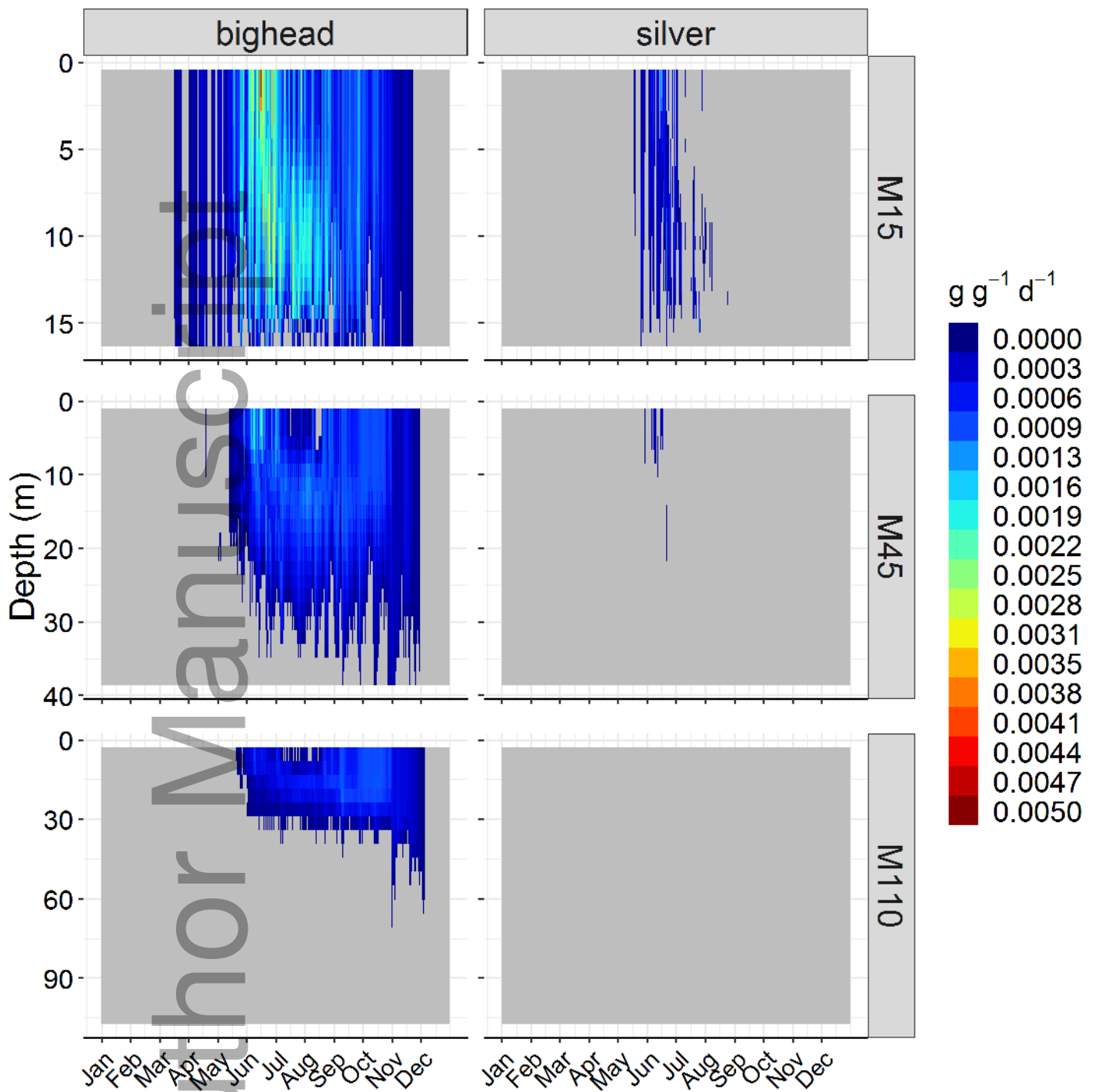
fwb_13382_f6.tif



fwb_13382_f7.tif



fwb_13382_f8.tif



fwb_13382_f9.tif