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Ecosystem responses to aquatic invasive species management: A synthesis of two decades of bigheaded carp suppression in a large river

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ABSTRACT

The invasion of silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*) or "bigheaded carps" has caused extensive ecological and economic harm throughout the Mississippi River and its tributaries. To prevent their continued spread upstream toward the Great Lakes, intense commercial harvest was implemented on the Illinois River, a large tributary that connects the Mississippi River to Lake Michigan. Since implementation, harvest has reduced densities at the invasion front while also presenting an opportunity to generate a synthesis on ecosystem resilience in the face of accelerating invasion. Resilience, the ability of an ecosystem to recover after perturbation, was observed at local scales and within some taxa but has yet to manifest at a river-wide scale and often co-varied with abiotic environmental or seasonal factors. Thus, while intensive harvest has limited further spread of bigheaded carps, and evidence of additional secondary ecosystem benefits exists, opportunities remain to identify potential pathways that could spread such ecosystem benefits even farther.

1. Introduction

Understanding of the ecological response of native assemblages to the arrival and establishment of an aquatic invasive species has grown rapidly (Simberloff, 2014; Kopf et al., 2017). However, knowledge about the response of native assemblages to the suppression of aquatic invasive species efforts has lagged. Generally, when society and governments provide hundreds of millions of dollars in support of invasive species management, such as for barriers meant to protect the Laurentian Great Lakes, there is an implicit expectation of a measurable return on that investment. As one of the first extensively monitored ecosystems invaded by silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*), also referred to as "bigheaded carps (BHC)", the Illinois River (Fig. 1) has been a de facto testbed for a variety of management ideas including the application of targeted commercial harvest to suppress populations of the invaders. As BHC continue their rapid spread, the Illinois River is in a unique position to provide insight into both what has been learned and what remains uncertain about the benefits or limitations of BHC suppression through targeted harvest. A synthesis of this knowledge has far-reaching potential for natural resource planning, policy, and management of not only BHC, but also other invasive fishes across the continent (Altenritter and Casper, 2018).

The invasive BHC have established self-sustaining populations in three of the largest river basins in North America; the Mississippi, Missouri, and Ohio, since the late 1990's (Kammerer, 1990; Conover et al., 2007). Across the lower Illinois River (Fig. 1), the observed mean BHC density was as high as 1738 individuals per kilometer (Garvey et al., 2015) and their relative biomass is often greater than or equal to all other native fish species sampled (Fig. 2). Their rapid spread and potential to exploit the man-made connections among formerly separate ecosystems, for example the Illinois River and "Chicago Area Waterway System (CAWS)" that links the Mississippi River and Lake Michigan, supported the construction of three electric barriers to upstream fish passage in the CAWS (Moy et al., 2011). These barriers are meant to prevent BHC invasion into the Laurentian Great Lakes; a system that supports a fishery worth approximately seven billion dollars annually (Krantzberg and De Boer, 2008), but that new research suggests might be more suitable for BHC inhabitance than previously thought (Alsip et al., 2019). The ultimate magnitude of the socio-economic and ecological risk to the Great Lakes is so great that an additional

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multi-million-dollar expansion featuring a portfolio of advanced deterrent technologies (e.g., an electric barrier, acoustic fish deterrent, engineered channel, air bubble curtain, and flushing locks; USACE, 2018) is currently moving through the political process.

Intensive commercial harvest of BHC in a system with extensive, pre-invasion and pre-harvest records of ecological and environmental conditions provides an opportunity for evaluating harvest responses across multiple taxa. Indeed, the eradication or aggressive suppression of invasive species led to positive outcomes (e.g., an increase in the population of a native species) in 51% of 151 studies reviewed by Prior et al. (2018). Since 2000, the harvest of BHC in the lower Illinois River has occurred concomitantly with an established fishery for other important native commercial species like buffalo (*Ictiobus* spp.). BHC have accounted for the majority of landings by mass in the lower river since 2004 and by number of individuals in the upper river since 2011 (Fig. 3). BHC harvest was initiated in the upper Illinois River in 2010, an area that was previously closed to all commercial fishing. In the upper Illinois River, harvest reduced densities of BHC while limiting replenishment from adjacent habitats (MacNamara et al., 2016) and curbed the exponential growth of biomass as observed during the early years of invasion in the lower river (Fig. 2).

Although this invasion and its subsequent suppression are very recent, the impacts have been dramatic. Long-term surveys and empirical studies of zooplankton, fish, and water quality responses provide a large but unsynthesized body of information that we used to develop this conceptual framework of expected ecosystem responses (Fig. 4). Specifically, we examine the impact of BHC commercial harvest on; 1) the remaining population of BHC, 2) the planktonic foundations of the ecosystem, 3) competing native planktivores including both larval and adult fish, and 4) community diversity and food-web interactions. By linking documented impacts of BHC harvest with potential knowledge gaps and unintended consequences, we emphasize the broad scale over which such harvest does and could result in ecosystem alterations (Fig. 4).

2. The nature of contracted BHC harvest

The goal of targeted BHC harvest is to reduce the number of BHC waiting at the electric barrier's edge while also expanding the BHC-free area further downstream. As a secondary outcome, harvest may also benefit a previously invaded native assemblage (e.g., the 'rubber band' model, Lake et al., 2007) whereby stopping a "disturbance" allows a native assemblage to recover. Targeted BHC harvest is conducted by contracted commercial fishermen in the upper Illinois River (rkm 371 to 460) downstream of the existing electric barriers (i.e., the invasion front; ACRCC, 2017). The cumulative magnitude of BHC harvest in the upper Illinois River is substantial. For instance, the biomass of BHC harvested per river kilometer in the upper river exceeded that harvested in the lower river from 2014 to 2017 (Fig. 5) despite its shorter linear distance (approximately 24% of the lower river) and lower BHC density (approximately 5% of that in the lower river; Love et al., 2018). Although this level of harvest has not reversed increasing trends in BHC relative biomass in the upper river, it does correspond to a truncated increase compared to the exponential rise in BHC biomass that occurred in the lower river (Coulter et al., 2018, Fig. 2).

Movement of BHC from the densely populated lower river to the intensely harvested upper river likely undermines efforts to suppress BHC abundance in the upper river (MacNamara et al., 2016). This

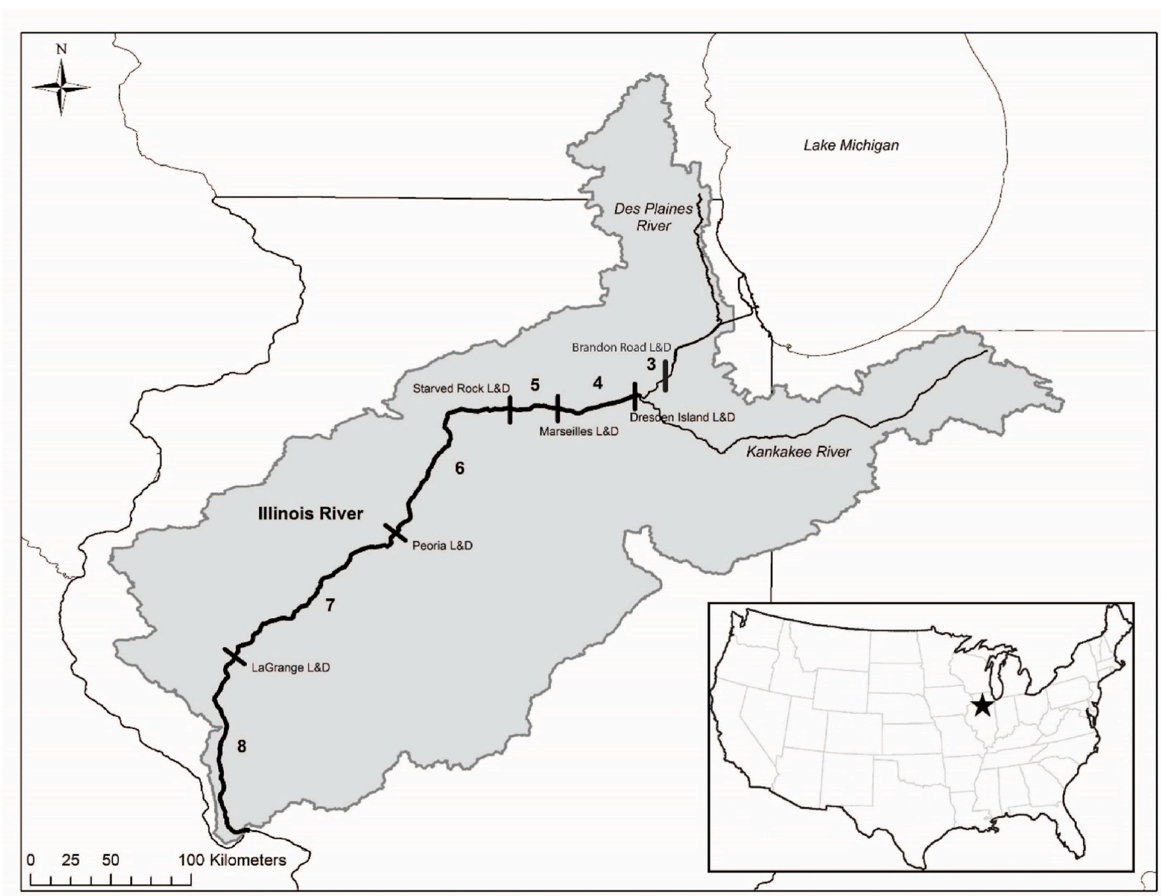

Fig. 1. Map of the Illinois River Waterway indicating pool delineations separated by lock and dam structures (black lines perpendicular to river). The lower Illinois River includes reaches 6–8 (river kilometers 0–372), and the upper Illinois River includes reaches 3–4 (river kilometers 372–460).

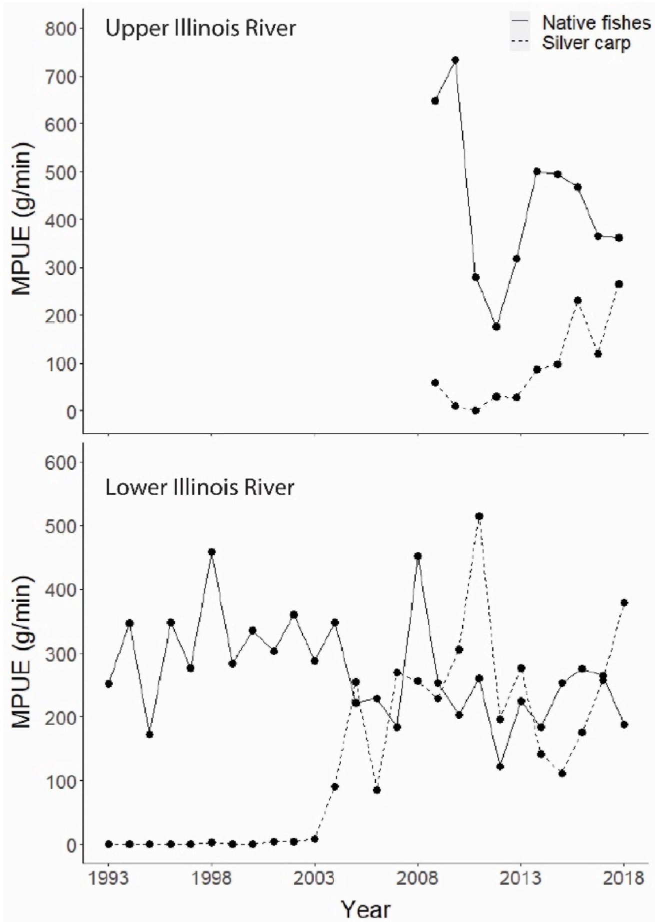

Fig. 2. The total relative biomass or mass per unit effort (MPUE) over time of native fishes (closed circle solid line) and silver carp (open circle, dashed line) sampled in the upper and lower Illinois River. Estimates are based on standardized boat electrofishing in main channel border habitats during sampling for the Long-Term Survey and Assessment of Large-River Fishes in Illinois (upper river) program and Upper Mississippi River Restoration Program Long Term Resource Monitoring program (lower river). Landings of silver carp in the upper river correspond with a truncated MPUE increase relative to the lower river that experienced exponential growth in the early years of invasion.

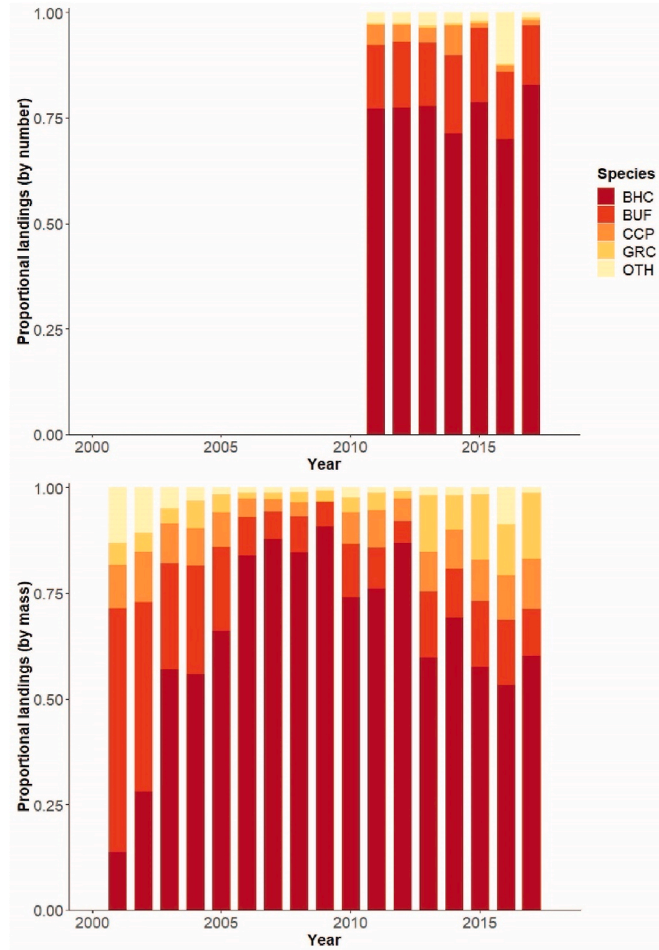

Fig. 3. Proportional landings of bigheaded carps (BHC), native buffalo species (BUF), common carp (CCP), and grass carp (GRC), and other fishes (OTH) caught using gill and trammel nets fished in the upper (top panel) and lower (bottom panel) Illinois River. Proportional landings are by number in the upper river where the aim of contracted commercial harvest is to remove as many BHC as possible to defend the electric dispersal barrier at Joliet, Illinois. Lower river data provided by R. Maher. Upper river data available in ACRCC (2017).

problem is compounded by sporadic but successful BHC reproduction in the lower river (Gibson-Reinemer et al., 2017a) and relatively open river conditions during high water periods (MacNamara et al., 2016). Nonetheless, we suggest that the upper river is indeed benefiting from the suppression of BHC, because a greater proportion of the population is being harvested, and this harvest was initiated prior to the population of BHC reaching an exponential growth phase as occurred in the lower river. Reproduction of BHC in the upper river is also extremely limited, with larvae and early life stage BHC last observed in 2015, but not since (ACRCC, 2020). Additionally, long-term fisheries independent monitoring has provided evidence of improvement in the condition of selected native competitors in the upper river (Love et al., 2018). A less-common question worth asking is whether the benefits of suppression through harvest cascade broadly through invaded systems.

3. Planktonic community

3.1. Response to invasion

Zooplankton play a variety of important roles in large river ecosystems including nutrient cycling, as a conduit for primary production to reach secondary consumers, and as a foundation for fish diversity and productivity (Welker et al., 1994; Thorp and Casper, 2003; Lair, 2006; Strayer et al., 2008). Thus, any major changes in either the type or strength of their drivers and stressors, such as the arrival of large numbers of a dominant new planktivore, would have both direct and indirect impacts throughout the ecosystem and food web.

BHC feed on a wider range of particle sizes than native vertebrate planktivores (Sampson et al., 2009) and as a result, their proliferation in the lower Illinois River over the last 20-years is associated with a 90% reduction in the density, biomass, and species richness of macro-zooplankton (Sass et al., 2014; DeBoer et al., 2018; Chará-Serna and Casper, 2021). In contrast, the response of microplankton like rotifers has been more mixed. Mesocosm experiments show BHC planktivory selectively favors some taxa of smaller bodied rotifers while concurrent field studies find the density of rotifers is either unaffected by or even elevated where BHC abundance is highest (Sass et al., 2014; Collins and Wahl, 2018; Chará-Serna and Casper, 2021). The characteristic of rotifers that appears responsible for this response is reproduction; rotifers have shorter generation times than the majority of macroplankton (Lu et al., 2002; Lair, 2006). Combined with their larger initial abundance (up to 98% of the total zooplankton density in the lower Illinois River and 88% in the upper Illinois River, Sass et al., 2014, DeBoer et al., 2018; Chará-Serna and Casper, 2021), this allows their populations to expand rapidly as BHC pressure on macroplankton

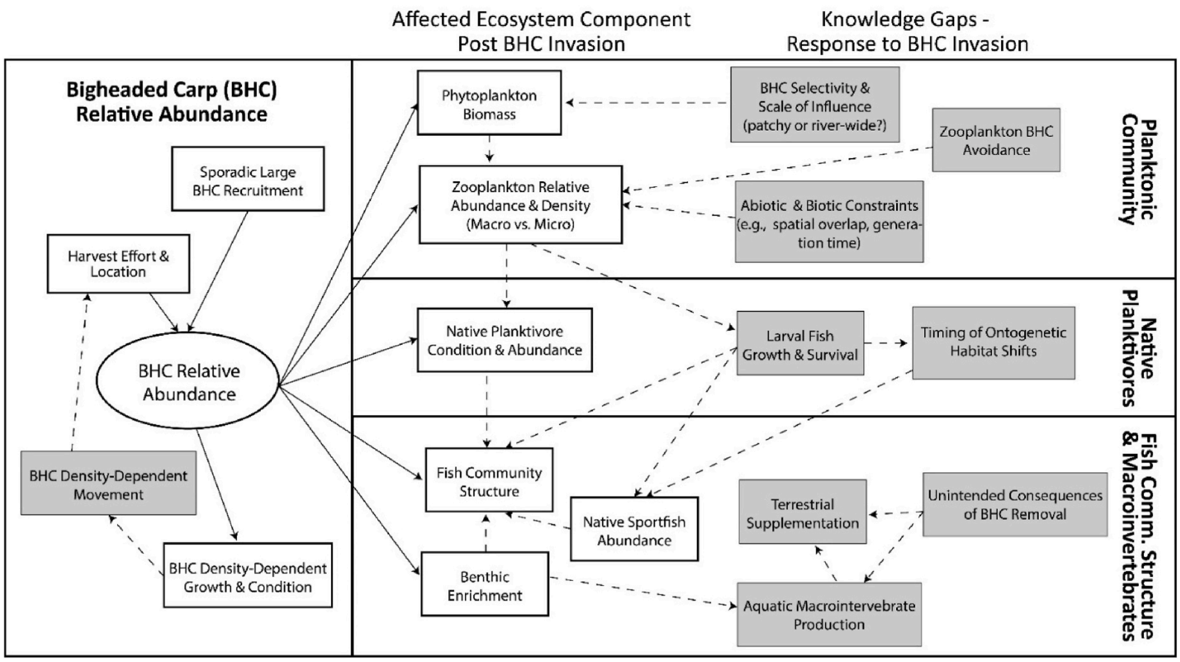

Fig. 4. Conceptual model linking BHC relative abundance to documented effects on ecosystem components in the Illinois River (open boxes, solid lines). Gray boxes indicate knowledge gaps related to each component. Dashed lines represent hypothesized pathways of influence that demonstrate potential for cascading effects as more information is acquired.

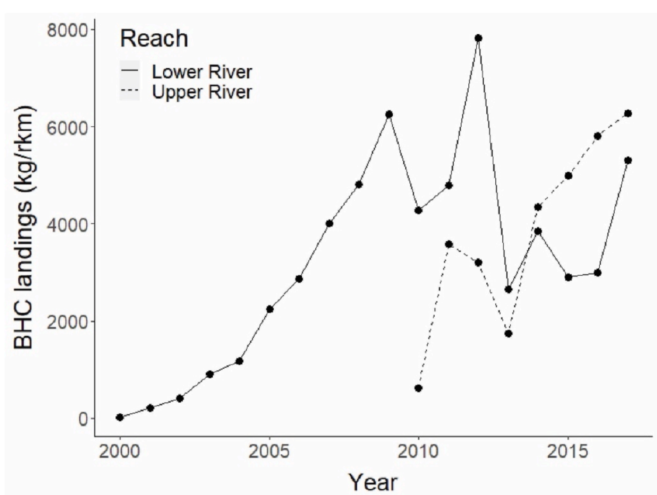

Fig. 5. BHC commercial landings in the lower (solid line) and upper (dashed line) Illinois River standardized by the number of river kilometers in each reach. Landings per river kilometer in the upper river exceeded those in the lower river by 2014 indicating high commercial fishing pressure relative to BHC ambient abundance which is much greater in the lower Illinois River.

increases. However, rotifer populations are also influenced by a variety of abiotic factors other than BHC planktivory like hydrology, food resources, and predatory or competitive interactions with other common riverine plankters (Chará-Serna and Casper, 2021). Thus, even if increasing BHC abundance is having little direct negative impact on rotifers, the invasion could still have a strong indirect effect, such as the release of microplankton from competition with macroplankton.

Zooplankton, and most large river food webs, are ultimately supported by primary production, particularly pelagic phytoplankton (Delong and Thorp, 2006; Brett et al., 2017). This means that to understand the ecological impact of BHC suppression, we should understand its influence on other trophic levels, especially phytoplankton. Unlike most of the common native planktivores of the Mississippi River system, BHC are generalist filter-feeders that can reduce phytoplankton abundance while simultaneously shifting the species assemblage toward smaller sized taxa (Burke et al., 1986; Lieberman, 1996; Vörös et al., 1997; Domaizon and Devaux, 1999; Radke and Kahl, 2002; Calkins et al., 2012). Even in the productive Illinois River, phytoplankton biomass indexed by chlorophyll-a was negatively related to silver carp biomass between 2002 and 2015 (DeBoer et al., 2018; Chará-Serna and Casper, 2021). Given the potential for both direct and indirect influences, it is not surprising that BHC planktivory can initiate a trophic cascade in a planktonic food web where BHC both directly predate on zooplankton and compete for phytoplanktonic resources (Lu et al., 2002). This might lead to an extrapolation that this invader affects all phytoplankton similarly, however diet analysis tells us that their feeding is actually selective (Ochs et al., 2019). Combined with BHC reduction of herbivorous cladocerans, this would result in an increase in small algae taxa favored by rotifers and other microplankton (Miura, 1990; Domaizon and Devaux, 1999). Thus, rather than the BHC reducing primary production, it is more likely that the invasion will favor smaller taxa of phytoplankton that are not constrained by this new planktivory regime and are still adapted to large river hydrogeomorphology (Thorp et al., 2006). What remains uncertain is whether other indirect factors such as reduced phosphorous recycling by zooplankton (Shostell and Bukaveckas, 2004) or the shunting of nutrients away from the pelagic zone (Yallaly et al., 2015; Collins and Wahl, 2017) will also play compensatory, antagonistic or synergistic roles in this new dynamic.

3.2. *Response to harvest*

The basic 'rubber band' model of resilience to perturbation (Lake et al., 2007) suggests that at some level of BHC harvest intensity plankton should rebound to an initial, pre-invasion state. We categorized BHC harvest into two regimes in the Illinois River to explore plankton responses, year-round lower-intensity harvests spread over larger areas and single high-intensity harvest events focused on a single location. The results of the low-intensity harvest demonstrate that there is both a required harvest intensity threshold plus complex taxa-specific response (Zalay and Casper, 2018). Harvest at multiple intensities from nine different off-channel habitats between August and October of 2015 revealed that rotifer and microplankton abundance at harvested sites were 52%–66% higher than controls within as little as 30 days (harvest ranged from 951 to 8229 kg of BHC/km^2/month). In contrast, Cladocera were unresponsive to any harvest level while Copepoda abundance (5.8 individuals/L) in only the most intensively harvested areas (8229 kg of BHC/km^2/month) was greater than the no harvest control sites (0.3 individuals/L). However, this positive response took more than 60 days to manifest. The authors concluded that, while a harvest intensity of 8229 kg of BHC/km^2/month elicited an immediate positive response in rotifers, greater intensity will be needed to benefit the entire zooplankton assemblage.

In contrast, intensive harvest efforts during 12-day periods in spring 2016 and 2017 yielded approximately 43 and 34 thousand kilograms of BHC, respectively (MRWG, 2016a; 2017a). Although these harvests benefited plankton, macro- and microzooplankton response differed and was not consistent between years. Specifically, while adult copepod abundance increased in harvested areas in both years, naupliar copepod abundance increased post-harvest in 2016, but in 2017 an initial increase was followed by a decline to pre-harvest levels 145 days post-harvest (Maxson et al., 2018). This was best explained by the interaction of harvest and month in both years, leading to speculation that untested interannual differences in abiotic conditions may be mitigating the recovery from BHC planktivory (Maxson et al., 2018). Additionally, because the two harvest events were in consecutive years, responses may reflect cumulative pressure rather than discrete events.

Taken together, the natural experiments confirm that zooplankton can respond directly to suppression of BHC *in situ* and in the same year as the effort is conducted. However, a parallel but independent survey of main channel zooplankton suggests that, despite cumulative BHC harvest that exceeded 2.7 million kilograms in the upper river from 2010 to 2017, and 21.3 million kilograms in the lower river from 2000 to 2017 (Table 1), zooplankton in the main channel did not follow the results of the natural experiments (Chará-Serna and Casper, 2021). Instead, the authors found no rebound in taxonomic richness across the basin, and that fluctuating total density and biomass of zooplankton in the upper river had no direct connection to planktivore biomass while in the lower river planktivore biomass was consistently important (Chará-Serna and Casper, 2021). The authors interpret this as evidence of significant spatial/geographic variability in the ecological response to harvest.

Table 1
Annual cumulative commercial landings of BHC from the lower and upper Illinois River (ILR). Harvest in the upper river was not permitted prior to 2010. Data was provided by R. Maher of the IDNR (Lower ILR) and accessed in ACRCC 2017 (Upper ILR).

Year	BHC commercial landings (millions of kg)	
	Lower ILR	Upper ILR
2000	0.003	–
2001	0.078	–
2002	0.151	–
2003	0.338	–
2004	0.435	–
2005	0.829	–
2006	1.063	–
2007	1.486	–
2008	1.782	–
2009	2.321	–
2010	1.584	0.056
2011	1.779	0.318
2012	2.902	0.285
2013	0.985	0.155
2014	1.429	0.386
2015	1.077	0.443
2016	1.109	0.517
2017	1.971	0.558
Total	**21.323**	**2.717**

They also found that abiotic factors like water temperature, turbidity, and total phosphorous accounted for as much of variation in zooplankton density and biomass as the BHC and native planktivore biomass. This emphasizes the importance of considering the mosaic of hydrogeomorphic functional process zones when evaluating driver-response patterns of the zooplankton community (Chará-Serna and Casper, 2021; DeBoer et al., 2020). Thus, while the establishment of large numbers of BHC is certainly influencing zooplankton dynamics, zooplankton can be resilient to this pressure. The caveat would be that ecosystem response to suppression of the invader does not conform to the simple 'rubber band' response model as so often assumed.

4. Native planktivores (early stages and adult fish)

4.1. Response to invasion

Field studies of the response of adult native planktivores showed functional overlap between BHC and gizzard shad (*Dorosoma cepedianum*), a facultative planktivore, and bigmouth buffalo (*Ictiobus cyprinellus*), an obligate planktivore (Sampson et al., 2009). Not surprisingly, the relative weight (an index of body condition) of gizzard shad fell by 5% and bigmouth buffalo by 7% between the initial invasion of BHC (1983–2000) and establishment (2007–2013) in the Illinois River (Irons et al., 2007; Pendleton et al., 2017; Love et al., 2018), which led to declines in relative abundance of both species (Irons et al., 2007; Pendleton et al., 2017).

The competitive effects of BHC are not limited to adults. Despite apparent differences in foraging habitat and behavior, both experiments and empirical evidence show that early life stage fish development is also affected. For example, when larval bluegill (*Lepomis macrochirus*) were reared in mesocosms with juvenile bighead carp, bluegill growth was reduced by 58%–87% relative to a control with no competitor (Fletcher et al., 2019). This was estimated to result in a 9- to 24-day delay in the bluegill's ontogenetic shift from open waters to littoral habitat. However, this effect is variable across species; the same experiment also found this delay was only one to three days for bluegill in the presence of native golden shiner (*Notemigonus crysoleucas*) (Fletcher et al., 2019). Growth is a rate function that in addition to recruitment and mortality regulate trends in fish abundance (Brown and Guy, 2007). If competition with BHC results in less food available to support growth, then young fish may experience elevated size-dependent predation that could contribute to declines in recruitment (Houde, 2002). Indeed, long-term studies on the Illinois and Mississippi Rivers show declines in relative abundance of popular sportfish like bluegill and largemouth bass in BHC-invaded areas when compared to BHC-free areas (Solomon et al., 2019; Chick et al., 2020). While many environmental factors are also suspected of contributing to these declines (Solomon et al., 2019), a separate study documented declines in larval bluegill growth with declining zooplankton biomass in both mesocosm and natural experiments (Welker et al., 1994). Thus, it is possible that the growth and subsequent recruitment of juvenile sportfish is less constrained in areas that are BHC-free due to a lack of competition for zooplankton with BHC (Chick et al., 2020).

While the population effects of resource depletion and competitive exclusion on recruitment, condition, and population abundance conform to the general expectations, there is also evidence of both population-level resiliency in gizzard shad and individual-level condition of bigmouth buffalo. Gizzard shad populations, despite post-BHC declines in their size structure (Table 2; Gabelhouse, 1984) and abundance, continue to periodically produce cohorts large enough to maintain a population through time in the Illinois River (Pendleton et al., 2017). In contrast, the resiliency of bigmouth buffalo is seen in increasing size structure (Table 2; Gabelhouse, 1984) and individual body condition which has increased in a density-dependent manner since their numbers have declined markedly (Pendleton et al., 2017). This suggests diverging amounts of influence of the BHC: the

Table 2
Average proportional size distributions (PSD) of gizzard shad and bigmouth buffalo collected during the "Long Term Survey and Assessment of Large-River Fishes in Illinois (LTEF)" AC boat-electrofishing surveys in main-channel border habitats of the Illinois River between 1957 and 2015. The pre-bigheaded carp period includes years from 1957 to 1999 and post-bigheaded carp period includes years from 2000 to 2015. PSD categories (stock, quality, and preferred) are based on measured total lengths (mm) proportional to the world record length for that species. No size delineations exist for gizzard shad above quality (gizzard shad are not typically targeted by sportfish anglers) and there were no bigmouth buffalo captured that fell in the next largest size categories of memorable and trophy. Numbers in parentheses indicate 95% confidence intervals.

Species	Time period	Stock (<180 mm)	Quality (≥180 mm, < 280 mm)	Preferred
Gizzard shad	Pre-BHC	80.6 (76.6–84.6)	19.4 (15.4–23.4)	NA
	Post-BHC	90.8 (85.6–96.1)	9.2 (3.9–14.4)	NA
Species	**Time period**	**Stock (< 280 mm)**	**Quality (≥ 280 mm, < 460 mm)**	**Preferred (≥ 460 mm, < 610 mm)**
Bigmouth buffalo	Pre-BHC	80.7 (75.8–85.6)	17.9 (13.1–22.7)	0.26 (0.10–0.40)
	Post-BHC	75.5 (70.7–80.3)	23.2 (18.7–27.8)	0.31 (0.00–0.60)

relationship to BHC is much more direct for the buffalo. Despite overall declines in the relative abundance of these native species, these species-specific differences in the response to competition allow both to persist, albeit at levels below historical expectations. Ultimately, while the native assemblage may be considered diminished, if non-native competitors are suppressed below a certain abundance threshold, then native species can persist when abiotic conditions are favorable (Pendleton et al., 2017).

4.2. Response to harvest

Experimental and empirical studies clearly show the cascading influence of two decades of expanding BHC competition on growth and ontogeny of native fishes. Because so few attempts at suppression have been tried in large open systems like rivers there is still much uncertainty about how native fish assemblages respond to suppression of BHC. If the harvest of BHC reduces competition, then declines in larval fish growth and the potential for delayed ontogenetic habitat shifts (as seen with bluegill) might be ameliorated. However, the details of this process remain uncertain; while larval bluegill growth was depressed in the presence of BHC, a doubling of BHC number did not further reduce their growth (Fletcher et al., 2019). This indicates that questions remain open about how BHC density and other mitigating factors might be important to native planktivores.

Responses in native planktivore body condition and abundance to BHC harvest are complex and are influenced by both river reach and the body size of the native species. Neither relative weight nor CPUE of gizzard shad from the lower river improved between 2010 and 2014 despite continuous BHC harvest in this region since 2000 (Love et al., 2018). In contrast, the relative weight of gizzard shad from the upper river, where the harvest relative to BHC abundance is higher, rebounded to pre-invasion levels within five years of targeted commercial harvest that began in 2010 (Love et al., 2018). The connection between individual condition and population dynamics for gizzard shad in the upper river was more mixed; there were no changes in CPUE of small (<180 mm) gizzard shad five years post-harvest, but the CPUE for large (>180 mm) gizzard shad has exceeded both the pre- and post-invasion values from across the basin (Love et al., 2018). This may be evidence of less resilience to invasion by small gizzard shad that are potentially gape limited and mainly planktivorous compared to larger individuals that are flexible and can feed omnivorously in the benthos (Love et al., 2018). Indeed, small gizzard shad (mean total length of 35 mm) from the lower Missouri River showed high (>90%) trophic niche overlap with BHC suggesting a high degree of resource competition (Wang et al., 2018).

5. Community and trophic implications

5.1. Response to invasion

To date there is little evidence that BHC have eliminated native fish species or dramatically reduced overall diversity in the two decades they have been present in the Upper Mississippi River system (McClelland et al., 2012; Gibson-Reinemer et al., 2017a). However, there have been shifts in native fish community composition since the invasion started (Solomon et al., 2016; Chick et al., 2020) and the responses are not uniform across all species. For example, while ontogenetic shifts and growth of some species are reduced (e.g., bluegill by up to 24 days; Collins et al., 2017; Fletcher et al., 2019) others, that undergo earlier ontogenetic habitat shifts (e.g., gars) may experience reduced direct competition with BHC thereby limiting the negative effects on abundance (Solomon et al., 2016). Notably, since the invasion of BHC, the relative abundance of shortnose gar (*Lepisosteus platostomus*) and longnose gar (*Lepisosteus osseus*) has increased in the lower Illinois River while juvenile recruitment for 19 native species including bluegill declined during a decade when silver carp populations were growing exponentially (Solomon et al., 2016; Chick et al., 2020). Rather than solely a result of species-to-species resource competition, the resulting restructured assemblage will also be influenced by a suite of more indirect interactions including species-specific timing of ontogenetic habitat shifts and recruitment dynamics.

There is also ample evidence that BHC are impacting pre-cursors thought to facilitate trophic cascades. For example, BHC have altered food web dynamics by shunting organic material to the benthos through egestion, facilitated trophic cascades, and mediated native predator-prey interactions. Egested organic material as a benthic subsidy promoted both positive growth in age-0 channel catfish (*Ictalurus punctatus*) and blue catfish (*Ictalurus furcatus*) through direct consumption of fecal pellets (Yallaly et al., 2015) and corresponded with elevated biomass of Chironomidae larvae in experimental ponds (Collins and Wahl, 2017). In the latter study, bighead carp predation also reduced zooplankton production, which had a cascading effect leading to elevated chlorophyll-a concentration. Ultimately, this trophic restructuring led to declines in the native golden shiner, an obligate planktivore (Collins and Wahl, 2017). Similarly, the influence of BHC extends beyond fish competitors to reach imperiled freshwater unionid mussels. Unionid mussels represent a trophic component with links to the planktonic assemblage through feeding and dispersal. Experiments by Tristano et al. (2019) found that in the presence of silver carp the growth of individual fatmucket (*Lampsilis siliquoidea*) in mesocosms declined as energetically demanding foraging movements increased. In a case of possible facilitation, juvenile bluegill reared in experimental ponds experienced greater growth in the presence of bighead carp than without, even when treatments contained fewer fish overall (Collins et al., 2017). Those authors postulated that as cladoceran prey shifted towards littoral habitats to avoid bighead carp they became more vulnerable to predation by juvenile bluegill (Collins et al., 2017). While it remains to be seen if such dynamics manifest in the wild, these experiments provide evidence of the adaptability of the river food web including phytoplankton, zooplankton, benthos, and the broader fish community and suggests that classic trophic cascades are likely.

Bigheaded carps are also prolific spawners capable of large-scale production of offspring when hydrologic conditions are favorable

(Gibson-Reinemer et al., 2017b), which could create a hyper-abundant, new forage base that benefits native piscivores. While some evidence supports this assertion, caveats exist. Native predatory fishes consume BHC; silver carp were the most frequently encountered prey item in stomachs of blue catfish (*Ictalurus furcatus*) caught in the Mississippi River (Locher, 2018) and largemouth bass reared in mesocosms readily attacked and consumed juvenile BHC even in the presence of native prey (Sanft et al., 2018). Other studies demonstrate that BHC were not selected for, or against by native fishes under natural and laboratory conditions (Wolf and Phelps, 2017), and the fast growth of silver carp may allow them to quickly exceed the gape of some native predators (Lampo et al. personal communication). Therefore, whether native predatory fish benefit from this seemingly abundant source of novel prey remains equivocal. Long-term monitoring on the lower Illinois River hints at this conundrum given overall declines in the relative abundance of largemouth bass (Solomon et al., 2019) but increases in other piscivores like flathead catfish (*Ictalurus punctatus*) and gars (Solomon et al., 2016) during the BHC invasion period. However, disentangling the relative contribution of diet from a multitude of other factors (e.g., competition for zooplankton, growth, and recruitment) influencing population trends in predatory fishes requires more targeted analysis of diet across multiple piscivores.

5.2. Response to harvest

The targeted harvest of BHC is occurring concomitantly with dramatic changes to water quality, hydrogeomorphology, and diversity in the Illinois River (Parker et al., 2014; Gibson-Reinemer et al., 2017a; DeBoer et al., 2019; Solomon et al., 2019) making it difficult to isolate the effect of primary drivers of interest (e.g., harvest) from an ensemble of potential co-factors (Diamond, 1983). For instance, major water quality improvements are clearly associated with fish and zooplankton assemblage changes, which spatially and temporally overlap with the BHC invasion and subsequent harvest efforts (Gibson-Reinemer et al., 2017a; Whitten and Gibson-Reinemer, 2018; Chará-Serna and Casper, 2021). Complexity of interacting drivers makes the role of each difficult but not impossible to untangle if long-term monitoring is available (e.g., Chick et al., 2020; Chará-Serna and Casper, 2021). Thus, it should not be surprising that community-scale responses are not yet clearly attributable to BHC harvest, especially given the numerous unpredictable and often indirect ecological responses we have identified.

While we currently lack understanding of community-scale responses to BHC harvest, we have detailed clear connections between the planktivore component of the food web and both higher and lower trophic levels. For example, targeted removal of BHC led to rapid shifts in its competitors as seen in the rebound of native gizzard shad abundance following sustained harvest (Love et al., 2018). Such rebounds could affect bottom-up processes in the food web with implications for native predators at higher trophic levels. However, while theory helps us identify potential mechanisms, we still lack the empirical evidence of the associated ecological responses. At this stage of the North American invasion, potential indirect effects are only now beginning to be assessed and many questions remain concerning how suppression might mediate those effects.

6. Knowledge gaps and research needs

Once an invader has a foothold in a new ecosystem, a primary goal of managers, policymakers, and society becomes limiting further spread while supporting the resiliency of native biota. Since their arrival in the Illinois River in the late 1990's, inter-agency and inter-state cooperation via the Invasive Carp Regional Coordinating Committee (ICRCC) has prevented BHC from establishing in Lake Michigan. Going forward the ICRCC now also includes an additional goal of reducing the density of BHC pressuring the current electric barriers while simultaneously moving the invasion front further downstream. An unintended benefit of the harvest-suppression effort has been relieving direct competition with native planktivorous fishes in reaches where the invader has been long established (Love et al., 2018). However, much remains uncertain regarding the potential for cascading responses to harvest. Despite some uncertainty, we are hopeful that insights gained from the Illinois River experience can inform similar efforts at aquatic invasive species management elsewhere, and that the information will spread as quickly as the fish themselves.

6.1. Optimizing the efficiency of harvest methods

Removing large numbers of BHC may reduce predatory and competitive pressures on native biota, but simultaneously reduces resource competition for conspecifics. Individual BHC experiencing density-dependent limitations on growth and fitness may seek out alternate habitats when confronted with large numbers of competitors (Olsson et al., 2006). This seems a likely scenario given evidence of density-dependent declines in average relative weight of silver carp with increasing biomass in the lower Illinois River (DeBoer et al., 2018) and the long-distance movement capabilities of BHC (409 km in a single season and up to 95 km in one day; Norman and Whitledge, 2015; Coulter et al., 2016; Prechtel et al., 2018). Therefore, it will be important to both monitor immigration into harvested areas and identify where the individuals are originating (Fig. 4 – *Bigheaded Carp Relative Abundance*). A better understanding of the drivers of movement ecology will help to optimize the location and timing of harvest.

One approach to limit the replenishment of BHC in harvested regions is to expand harvest farther downstream. Such an expansion began in September 2019 with enhanced contract fishing occurring in the Peoria reach of the Illinois River and resulted in approximately 907 thousand kilograms (2 million pounds) of BHC harvested in the first year (ACRCC, 2020). This harvest is anticipated to aid in achieving a goal of between 9.1 and 22.6 million kilograms (20 and 50 million pounds) of BHC from the Illinois River below Starved Rock Lock and Dam (ACRCC, 2020). However, successful reproduction and recruitment of BHC occurs throughout the lower Illinois River and although sporadic, appears to sustain the population (Gibson-Reinemer et al., 2017b; Sullivan et al., 2018). This is unlike the upper river where evidence of recruitment is limited, and where commercial harvest has successfully reduced densities of BHC by up to 93% near the invasion front (MacNamara et al., 2016; ACRCC, 2017). Understanding whether BHC populations respond to harvest like they have in the upper river when the harvest expands to high-density areas with successful reproduction will be critical to adapting the harvest strategy developed in the Illinois River to more densely populated river systems (Fig. 4 – *Bigheaded Carp Relative Abundance*).

6.2. Planktonic community

The basin-wide increase in BHC planktivory since the 2000's has had a clear negative effect on zooplankton diversity while a simultaneously mixed and taxa-specific influence on zooplankton abundance and biomass (Sass et al., 2014; Chará-Serna and Casper, 2021). The responses to the range of harvest intensities used since the 2000's have been more complex and varied (Zalay and Casper, 2018; Maxson et al., 2018; Chará-Serna and Casper, 2021). Because of the knowledge gap surrounding both zooplankton habitat and seasonal patterns as well as specifics about which type of zooplankton are important in the food web, we are uncertain if consumers can compensate for the large declines in macroplankton or whether increasing microplankton fill the same roll in nutrient cycling as macroplankton. In addition, strong but sporadic BHC recruitment and habitat-specific distribution of both plankton and their consumers mean that actual planktivory itself can vary significantly in space and time (Gibson-Reinemer et al., 2017b; Abeln, 2018; Chará-Serna and Casper, 2021). Therefore, a primary knowledge gap becomes understanding how the zooplankton structure and function is distributed in heterogenous large rivers, especially where and when they overlap with native and invasive consumers. A second knowledge gap would be understanding what resiliency in space and time looks like for the plankton component of the assemblage. For example, how might thresholds or time lags as well as oscillations in magnitude, duration, and frequency of both abiotic conditions and biotic dynamics manifest in plankton population dynamics (Fig. 4 – *Planktonic Community*)?

Autochthonous productivity is a principal driver of productivity for freshwater systems in general, and for large rivers in particular. While BHC may prefer the more bioenergetically advantageous zooplankton, they can certainly feed and survive on an algal diet. However, there are several aspects of the direct and indirect links between BHC and primary productivity that are unknown. For instance, how selective is grazing by BHC, which taxa are favored, and how does this affect algal community structure and function? What is the nature of the influence of BHC on rates of primary productivity, and are these patchy and habitat specific or is the entire river system affected? Primary productivity is a driver of many aspects of community and population dynamics, but how it enhances or constrains BHC population dynamics and, ultimately, the efficacy of creating a commercial fishery to suppress them remains uncertain. These open questions that are all linked to a better understanding of the connection between the BHC and phytoplankton dynamics.

6.3. *Native planktivores (early stages and adult fish)*

Mesocosm experiments show larval native fishes are in direct competition with BHC (Collins and Wahl, 2018; Fletcher et al., 2019) while field studies show declines in these same native species as BHC populations expand (Chick et al., 2020). Addressing knowledge gaps among BHC recruitment, commercial harvest intensity, and responses by native planktivores would be a major improvement. For example, establishing relative recruitment metrics such as year-class strength (YCS) by indexing the abundance of juvenile BHC before they recruit to commercial gears could inform decisions about harvest intensities across years (Fig. 4 – *Native Planktivores*). Additionally, assessing under what conditions BHC competition is strongest would be an advantage; should harvest be accelerated or otherwise modified in years where plankton resources are low due to hydrology or in habitats where they are abundant?

The responses of native planktivores other than gizzard shad to BHC invasion and harvest remain relatively unknown. However, some native planktivores like bigmouth buffalo and paddlefish (*Polyodon spathula*) are important commercial species throughout the Illinois and Mississippi Rivers. While declines in bigmouth buffalo abundance correspond with increases in BHC abundance (Irons et al., 2007), trends in other important demographic responses (e.g., age-size structure, and recruitment) remain unknown. Moreover, whether competition with BHC is more or less important than hydrology or water quality in determining population demographics of bigmouth buffalo is unknown. Even less is known about responses by paddlefish to BHC invasion. What is known is that both species are relatively long-lived and highly fecund (bigmouth buffalo up to 112 years, Lackmann et al., 2019, paddlefish up to 30 years, Jennings and Zigler, 2009) where the retention of large, old females supports a bet-hedging mechanism acting to insure the population against unfavorable environmental conditions (Hixon et al., 2014). Therefore, monitoring trends in population productivity of both species along with varying BHC harvest intensities and approaches will help inform the relative importance of competition with BHC with both short-term (e.g., fishery landings) and longer-term (e.g., population resilience) implications (Fig. 4 – *Native Planktivores*).

6.4. *Fish community structure and macroinvertebrates*

Research shows that the arrival of BHC can fundamentally affect basin-wide fish community structure (Solomon et al., 2016; Gibson--Reinemer et al., 2017a; Whitten and Gibson-Reinemer, 2018). However, in cases where invaded fish communities have shown little temporal difference in diversity, such as in the upper reaches of the Illinois River (Whitten and Gibson-Reinemer, 2018), we do not know what accounts for this discrepancy. Potential external influences that are unrelated to invaders but are known to influence fish community structure in the Illinois River include a mixture of legacy anthropogenic effects from diversion of Lake Michigan water, navigation infrastructure, and extensive urbanization layered onto natural landscape or climate features like the underlying glacial geology or precipitation patterns of the region (McClelland et al., 2012; Parker et al., 2014; Gibson-Reinemer et al., 2017a; DeBoer et al., 2020). Similarly, there are internal processes that are largely unexplored. For instance, significant change in the lower Illinois River fish community became evident in 2005, five years after the apparent invasion (Solomon et al., 2016). We do not know if this is due to an ecological time lag associated with recruitment let alone whether these are density dependent, competition based, or stochastic mechanisms. The fact that many drivers are shaping divergent community dynamics emphasizes the importance of considering not just the temporal scope of invasion, but interactions among the invader's traits, the ecosystem, and response variable(s) of interest (Strayer et al., 2019).

In addition to direct competition with native planktivores, BHC have been shown to have less obvious indirect effects on other trophic levels and functional groups. One example is the shunting of planktonically sourced nutrients to the benthos through egestion (Yallaly et al., 2015; Collins and Wahl, 2017). More specifically, it is unknown whether benthic macroinvertebrates in the Illinois River, some of which have a terrestrial adult life stage, benefit from transfers of egested nutrients to the benthos (*sensu* Yallaly et al., 2015). A second similar example is the movement of those nutrients and carbon into terrestrial biota (Feltrop et al., 2016; Guilfoyle and Schultz, 2017). The variety and importance of these types of transfers across the aquatic-terrestrial transition zone remain understudied in freshwater systems. Thus, important knowledge gaps remain; have BHC stimulated the productivity of benthic macroinvertebrates that ultimately subsidize the riparian zone along the Illinois River through their terrestrial stages? If so, then could BHC suppression have unintended consequences on organisms that have benefitted from the increased flow of energy and nutrients? Exploring the potential links among BHC abundance and benthic production of invertebrates could help elucidate cross-taxonomic responses to BHC harvest (Fig. 4 – *Fish Community Structure and Macroinvertebrates*).

7. Conclusions

Preventing the spread of BHC via suppression is the primary harvest management objective on the Illinois River. However, unexpected outcomes from invasive species manipulations are common (Zavaleta et al., 2001; Ruscoe et al., 2011). One example of this evidence is a density-dependent shift in the population growth and size structure of the invader itself. Long-term monitoring shows that the size distribution of both juvenile and adult cohorts have consistently fallen as population densities increased in the lower river, by 67%, and 25% respectively, strongly implying density-dependence (Gibson-Reinemer et al. *In Press*). Meanwhile, population modelling in the upper river finds that the body condition of the remaining BHC is a density-dependent function of harvest pressure (Coulter et al., 2018). Those authors also note that this density-dependent condition relationship may be unintentionally encouraging BHC from the lower river to move to less densely populated upstream habitats, a product of intense harvest. However, there is evidence of important secondary benefits of harvest such as the maintenance and support of the competing native species in areas where the invader was already well-established.

In terms of insights into large river ecology, the arrival of BHC has had major impacts. Nonetheless, it is inaccurate to think of these as simply the decimation of a freshwater ecosystem. It would be much closer to the truth to see this as a reordering of the community and trophic structure and function of large rivers. Adopting that perspective may inform how various management and restoration tools could help to maintain some aspects of the previous species assemblages alongside the new non-indigenous community members. In terms of aquatic invasive species management, these initial insights suggest that unexpected outcomes, like the inadvertent promotion of upstream BHC movement, counters the expectation that these invaders could ultimately be 'fished out'. Instead, continual replenishment of BHC into harvested areas regardless of harvest pressure likely means suppression efforts will be necessary for the foreseeable future. The Illinois River experience to date suggests an alternative management goal, the development of a harvest control strategy that can suppress BHC populations over extended periods (Tsehaye et al., 2013) while simultaneously limiting the impacts on native biodiversity and productivity.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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