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PERSPECTIVES AND PARADIGMS

Anticipating the spread and ecological effects of invasive bigheaded carps (*Hypophthalmichthys* spp.) in North America: a review of modeling and other predictive studies

Sandra L. Cooke

Abstract Bighead carp (*Hypophthalmichthys nobilis* Valenciennes 1844) and silver carp (*H. molitrix* Richardson 1845), collectively called bigheaded carps, have invaded the Mississippi River Basin and may have already entered the Laurentian Great Lakes where they could affect fishing and other industries. Developing models to predict potential spread and effects is difficult because local adaptation may have occurred among populations, parameter values for biological characteristics vary widely for these opportunistic generalists, and methodological differences complicate comparison and synthesis of studies. I review bigheaded carp biological parameters across a wide range of literature, including studies of native and introduced populations. I then evaluate how predictive models are parameterized, noting inconsistencies and highlighting data gaps. My analysis finds that although parameter values tend to vary substantially among and within systems, models are generally parameterized using the best information available, although bioenergetics and trophic models particularly need improvement. Some predictive tools can be updated using existing data (e.g., velocity requirements for spawning), but in other cases further research is needed. Research priorities include (1) better understanding bigheaded carp phenotypic plasticity among and within systems, (2) determining key biological traits of bigheaded carp populations at risk of seeding further invasions (e.g., Illinois River populations that may spread to Lake Michigan), and (3) monitoring bigheaded carp ecological effects on native fishes and plankton communities. A more complete awareness of strengths and limitations of predictive tools will lead to their improvement, thereby aiding managers in anticipating and counteracting bigheaded carp spread and effects.

Keywords Silver carp · Bighead carp · Asian carp · Mississippi River

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Introduction

Asian carps of the genus *Hypophthalmichthys* spp. are a valued food resource not only in their native range of eastern and southern Asia, but also in regions throughout the globe. Silver carp (*H. molitrix* Richardson 1845) and bighead carp (*H. nobilis* Valenciennes 1844), collectively referred to as bigheaded carps, are common aquaculture species, ranked second and fourth, respectively, in global aquaculture production in 2009 (FAO 2011). Capture fisheries for bighead and silver carps are also economically important in Asia. Precipitous declines in commercial catches of these two species in the middle and lower Yangtze River—part of the carps'

native range—following the construction of the Three Gorges Dam are thus concerning (Zhang et al. 2012).

Conversely, bigheaded carps are considered invasive species in many of the countries where they have been introduced (Kolar et al. 2007). The biological characteristics that make these freshwater, planktivorous fishes both desirable aquaculture species and successful invaders include rapid growth and reproductive rates, broad-ranging environmental tolerances (e.g., temperature, oxygen, salinity, stream velocity), and generalist feeding habits (Kolar et al. 2007). Both species are high volume filter-feeders that consume phytoplankton and zooplankton, which makes them effective biological control agents in sewage treatment and aquaculture ponds, but may also enable them to compete with native planktivores.

In the United States and Canada, the potential threat of bigheaded carps has escalated in recent years as they have spread throughout the Mississippi River Basin (MRB; Figs. 1, 2) and increased in population size and biomass. For example, in the La Grange Reach of the

Illinois River, silver carp biomass increased exponentially between 1990 and 2005 (Irons et al. 2007), and mark-recapture sampling in 2008 conservatively estimated that silver carp comprised 51 % of total fish collections (Sass et al. 2010). Furthermore, environmental DNA (eDNA) surveillance and live specimen captures indicate that the bigheaded carp invasion front may have reached the Calumet Harbor region of Lake Michigan (Jerde et al. 2013). Concern over bigheaded carps has reached beyond the scientific and natural resource management communities to larger political and societal sectors. For example, in 2012 politicians from states bordering the Laurentian Great Lakes succeeded in ushering into law the "Stop Invasive Species Act" (S. 2317-112), which requires the U.S. Army Corps of Engineers to prevent bigheaded carps from entering the Great Lakes.

Addressing such a critical, time-sensitive issue requires science that can readily be translated to effective management plans, especially in regard to the Great Lakes, which support an annual $7 billion
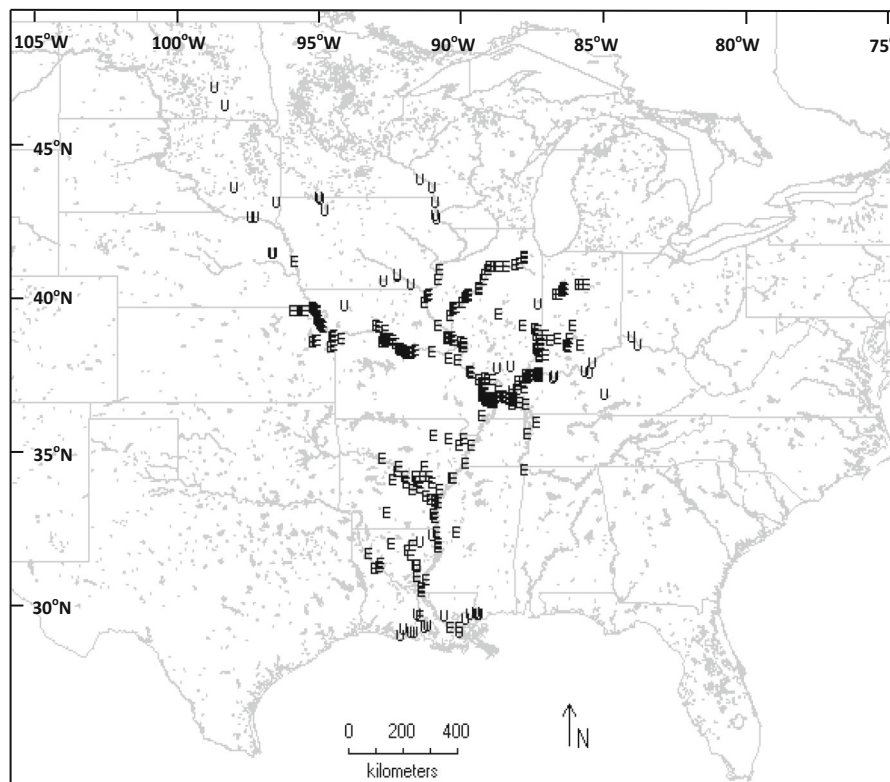
Fig. 1 Distribution of silver carp in the United States including habitats where the species is established (*E*) and sites where a specimen was once collected but the species' current status is unknown (*U*). Data obtained from the United States Geological Survey Nonindigenous Aquatic Species database and used with permission
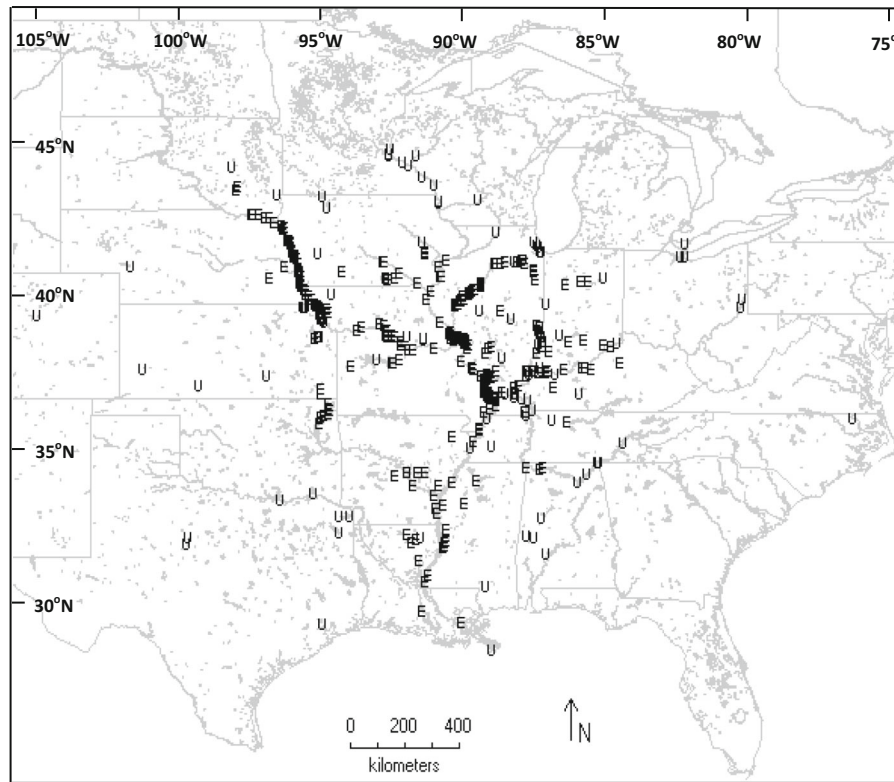
Fig. 2 Distribution of bighead carp in the United States including habitats where the species is established (*E*) and sites where a specimen was once collected but the species' current status is unknown (*U*). Data obtained from the United States Geological Survey Nonindigenous Aquatic Species database and used with permission

fishing industry in the U.S. (Southwick Associates 2008 in Kocovsky et al. 2012). As both major aquaculture products and widespread invasive species, hundreds of peer-reviewed studies have been published on the biology and ecology of bigheaded carps, and this research has been used to attempt to predict future invasions. Predictive models for bigheaded carps have taken a number of diverse approaches, including ecological niche models, which focus on habitat suitability based on multiple environmental characteristics (e.g., Herborg et al. 2007) and bioenergetics models, which use a mass balance approach to predict food limitation in a certain habitat (e.g., Cooke and Hill 2010). Predictive models, along with other biological information, have been used to develop risk assessments of bigheaded carps in the Great Lakes (Cudmore et al. 2012).

There are several challenges in developing predictive models for bigheaded carps specifically and for invasive species more generally. One challenge is accounting for the possibility of local adaptation of an invasive population in a new habitat. Bighead and silver carps were brought to the U.S. in the 1970s and, although the exact timing of their introduction to natural waters is unknown, they have been reproducing in the MRB since at least the early 1990s based on the earliest accounts of young-of-the-year fishes (Tucker et al. 1996). Recent evidence indicates that MRB and European populations of bighead and silver carps have genetically diverged from native Asian populations (Li et al. 2010, 2011), suggesting that phenotypic (e.g., morphological and ecological) divergence is highly probable as well. Local adaptation has been observed for many non-native freshwater fishes (e.g., Valiente et al. 2010; Westley et al. 2013), and some of this work shows that adaptive divergence can occur within only a few generations in populations located only a few kilometers apart on the landscape (Westley et al. 2013). Numerous cases of morphological divergence between bigheaded carp populations in Asia are documented (e.g., Karasev 1979; Shubnikova 1979) and, considering the temporal and spatial

extent of the bigheaded carp invasion in North America (Figs. 1, 2), it seems plausible that MRB bigheaded carps could have locally adapted as well. When phenotypic divergence occurs in key traits that affect fitness of an introduced species, it can alter the invasive capacity of a local population (e.g., Valiente et al. 2010).

Even in the absence of evolution, phenotypic plasticity is often observed when invaders enter new habitats (e.g., Ke et al. 2008), and this is especially true for opportunistic generalist species. For example, bighead and silver carp diets and consumption rates vary with temperature, stream velocity, body size, food particle size, plankton species composition, plankton density, light intensity, dissolved oxygen, and filter-feeding method (pump feeding or ram suspension feeding), among other factors (Kolar et al. 2007; Radenko and Alimov 1992; Shi et al. 1998). Hence, allometric and temperature-dependent consumption relationships—even those developed using data from well-replicated, carefully controlled experiments—may be limited in their predictive capabilities because lab-derived measurements may not apply to the field and consumption is likely to vary from habitat to habitat. Bigheaded carps also appear to have a broader spawning niche than earlier studies would suggest (Coulter et al. 2013; Deters et al. 2013). The possibilities of local adaptation and phenotypic plasticity have implications for predictive modeling, risk assessment, and management that have not been fully considered.

Given the substantial and wide-ranging body of research on bigheaded carps, modelers are also challenged by methodological differences and other variability among the studies they may be attempting to synthesize to parameterize a model. Studies may include native, introduced, or aquaculture populations of carp, and reported values for a parameter (such as optimum temperature for spawning) may be based on empirical data from controlled lab or aquaculture manipulations, in situ observations (following a careful protocol), or anecdotal observations (not replicated or following a protocol). Also, different studies examining the same question (e.g., the effect of stream flow on spawning) may focus on different parameters (e.g., gauging station hydrograph height vs. linear flow velocity) or response variables (e.g., eggs collected vs. larvae and juveniles collected).

Finally, it is difficult to predict the ecological effects of an invader when little is known about its current ecological effects in habitats it has already invaded. Most predictive models for bigheaded carps have focused on potential regions of spread rather than potential ecological effects (but see Attayde et al. 2010; Currie et al. 2012; Liu et al. 2007). A poor understanding of invader ecological effects is certainly not unique to bigheaded carps but, given the high likelihood of further spread throughout the MRB and to the Great Lakes, it is troubling that the ecological effects of bigheaded carps on plankton communities, native fishes, and trophic structure in the MRB are not well known (with a few exceptions, including Irons et al. 2007, Sampson et al. 2008, Schrank et al. 2003).

The objectives of this review are to (1) provide a comprehensive, tabulated review of bigheaded carp biological parameters, (2) assess how well predictive models for bigheaded carps account for the aforementioned challenges, and (3) suggest specific directions for further modeling efforts. Tabulating key biological parameters of bigheaded carps and noting the population source (native, introduced, or aquaculture) and methodological approach (empirical, observational, or anecdotal) associated with each parameter value could be useful for model developers because it will facilitate decisions of which values to use for specific modeling purposes. For example, a bioenergetics modeler simulating carp growth in the MRB may wish to exclude temperature-related parameter estimates from the Amur River in Russia due to the latitudinal and climatic differences between these regions. On the other hand, incorporating the full range of reported parameter values—including anecdotal extremes—in developing a model or running a simulation would result in a more conservative, comprehensive range of predictions. A review of biological parameters will also highlight cases where parameter estimates are lacking or are of questionable quality. Hence, this review may aid in future predictive studies and in developing strategies to minimize the spread and undesirable effects of bigheaded carps in regions where they have been introduced, especially Laurentian Great Lakes tributaries.

Methods for literature review of parameter values

I first reviewed the bigheaded carp literature to determine which types of parameters were used and

how they were used in predictive studies, as well as to identify existing reviews of parameter values. Based on nearly a dozen predictive models or other types of risk assessments for bigheaded carps, the biological parameters that were often used included velocity and temperature requirements for spawning (Tables 1, 2, 3); growth and condition parameters including von Bertalanffy growth parameters (Table 4), age at maturity (Table 5), and length-weight regressions; temperature requirements for feeding (Table 6); general thermal requirements (i.e., for maximum growth; thermal preferences; Table 7); fecundity (Tables 8, 9); and diet or feeding habits (Table 10).

To date, few peer-reviewed literature reviews have comprehensively synthesized values for all of these parameters. In a review of silver carp, Costa-Pierce (1992) compared spawning parameters among native and introduced populations and compared feeding parameters among natural waters, aquaculture ponds, and aquaria or tanks. Other earlier reviews include a U.S. Fish and Wildlife Service biological synopsis of bighead carp (Jennings 1988), a hatchery manual on Chinese and Indian carps (Jhingran and Pullin 1985), and a review of the feeding and ecological impacts of planktivorous fishes (Lazzaro 1987). More recently, Kolar et al. (2007) and a Canadian government report

(Kipp et al. 2011) provided biological synopses on bigheaded carps. For the current review I used the references within these earlier reviews to supplement literature searches in Web of Science, ProQuest, and Google Scholar. Search terms included "Asian carp", "bigheaded carp", "silver carp", "bighead carp", and "Hypophthalmichthys", which collectively yielded 1045 results in Web of Science (855 when food science topics were excluded) on 6 May 2014. Kolar et al. (2007) and earlier reviews cite gray literature, non-peer-reviewed literature, and other references not indexed by Web of Science or other major databases. I obtained and evaluated as much of this literature as possible, taking care to distinguish anecdotal, non-peer-reviewed observations from parameter values derived from peer-reviewed empirical and observational studies. Whenever possible, I also identified parameter values as deriving from native populations in natural waters, introduced populations in natural waters, or aquaculture populations (bred in hatcheries or aquaculture facilities). I included as much of the non-English language literature as possible by using translations, English abstracts, and an annotated bibliography of Russian literature (Naseka and Bogutskaya 2011).

To avoid redundancy, I did not include a table of length-weight regression parameters because a

Table 1 Minimum or range of velocity required for spawning of bigheaded carps

Source	Species	Velocity (m s^{-1})	Method	Notes	References
N	S	0.7	Obs.	Amur R. (Russia)	Reviewed in Abdusamadov (1987)
N	S	0.3–1.4	Obs.	Amur R. (Russia)	Krykhtin and Gorbach (1982)
N	S	1–1.8	Unk.	Amur R. (Russia)	Reviewed in Costa-Pierce (1992)
N	S	1.0	Unk.	Amur R. (China)	Makejeva 1963 in Costa-Pierce (1992)
I	S	0.5–0.8	Unk.	Tone R. (Japan)	Reviewed in Costa-Pierce (1992)
I	S	0.5–2.0	Unk.	Syr Darya R. (Russia)	Kamilov and Salikhov (1996) in Naseka and Bogutskaya (2011)
I	Both	0.9–1.2	Anec.	Kara Kum Canal (Turkmenistan)	Aliev 1976 in Kolar et al. (2007)
I	Both	0.5–1.9	Obs.	Terek region of Caspian basin	Abdusamadov (1987)
I	Both	0.15–0.25	Obs./Emp.	Based on multiple field and lab analyses	Murphy and Jackson (2013)
I	Both	0.22–1.07	Obs.	Eggs collected across this range of velocities in Missouri River	Deters et al. (2013)
Both	Both	0.3–3.0	Several	Based on review of multiple studies	Kolar et al. (2007)
I	Both	0.7	–	Used in spawning suitability model	Kocovsky et al. (2012)

Indicated are the population source (*N* natural waters in native range, *I* natural waters in introduced range), the species (*S* silver carp, *Both* both silver and bighead carp), and the study's methodological approach (*Obs.* observational study, *Emp.* empirical study, *Anec.* anecdotal observation, *Unk.* unknown/unclear methodology). The last entry shows the value used in a modeling study

Table 2 Optimal temperatures for spawning, including minimum (min.) and maximum (max.) temperatures for which spawning has been observed

Source	Species	Temp. (^{o}C)	Method	Notes	References
N	S	18–23	Unk.	Amur R. (Russia)	Reviewed in Costa-Pierce (1992)
N	S	18–20	Unk.	Lower Amur R. & Sungari R.	Gorbach and Krykhtin (1988) in Costa-Pierce (1992)
N	S	>18	Unk.	Amur R. (China)	Makejeva (1963) in Costa-Pierce (1992)
N	S	17–26.5	Obs.	Amur R. (Russia)	Krykhtin and Gorbach (1982)
N	B	26–30	Obs.	Yangtze R. in 1957	Chang (1966) in Kolar et al. (2007)
N	B	18.3–23.5	Obs.	Yangtze R. in 1953 & 1954	Chang (1966) in Kolar et al. (2007)
N	B	18 (min.)	Unk.	Han R.	Chunsheng et al. (1980) in Kolar et al. (2007)
N	B	14–15(min.)	Anec.	Russia; inferred from larvae	Opuszynski and Shireman (1995) in Kolar et al. (2007)
N	Both	18–24	Obs.	Middle Yangtze R.; used CART analysis	Li et al. (2013)
I/A	S	22–26	Unk.	Indian study	Kaul and Rishi (1993) in Kolar et al. (2007)
I	S	20–22	Unk.	Tone R. (Japan)	Reviewed in Costa-Pierce (1992)
I	S	18–20	Unk.	Syr Darya R. (Russia)	Verigin et al. (1978) in Costa-Pierce (1992), Kamilov and Salikhov (1996) in Naseka and Bogutskaya (2011)
I	S	18–20	Unk.	Kuban R. (Russia)	Motenkov (1966) in Costa-Pierce (1992)
I	S	22.8–23.8	Unk.	Murghab R.	Mitrofanov et al. (1992) in Naseka and Bogutskaya (2011)
I	S	14 (min.)	Anec.	Missouri R.; inferred from reproductive condition of adults	Papoulias et al. (2006)
I	B	22	Obs.	Lower Missouri R.	Schrank et al. (2001)
I	Both	18 (min.)	Obs.	Caspian basin	Abdusamadov (1987)
I	Both	27 (max.)	Obs.	Missouri R.; no eggs when temp. >27	Deters et al. (2013)
I	Both	18.5–29.7	Obs.	Wabash R.	Coulter et al. (2013)
I	Both	18 (min); 27 (max)	Obs.	Upper MRB; based on back-calculated birth dates of larvae	Lohmeyer and Garvey (2009)
I	Both	21	–	Used to estimate passable river length in spawning suitability model	Kocovsky et al. (2012)

Indicated are the population source (*N* natural waters in native range, *I* natural waters in introduced range, *A* aquaculture, *Unk.* unknown), the species (*S* silver carp, *B* bighead carp, or both), and the study's methodological approach (*Obs.* observational study, *Anec.* anecdotal or personal observation, *Unk.* = unknown/unclear methodology). *CART* classification and regression trees. Most values were determined based on in situ egg collections unless otherwise noted. The last entry shows the value used in a modeling study

comprehensive, recent review of such parameters was made by Cuddington et al. (2014). Cuddington et al. (2014) also presented a review of von Bertalanffy growth parameters, but I found seven additional sets of parameters that they did not include and combined their review with my findings (Table 4). Similarly, I have incorporated the spawning parameters reviewed by Costa-Pierce (1992) into the current review. Jennings (1988) and Jhingran and Pullin (1985)

presented tables summarizing age at maturity; values in those tables are not repeated here (Table 5 updates and supplements those values). Likewise, I have not repeated earlier reviews of feeding habits (Table 10 updates and supplements Table 3 in Costa-Pierce 1992 and the reviews of feeding habits in Kolar et al. 2007 and Lazzaro 1987). Bigheaded carp age at maturity and diet are difficult to summarize in tables because these parameters vary substantially

Table 3 Total degree-days (ADD_{T_0}) required each year for achieving sexual maturity and required in the pre-spawning period (usually late spring) for the onset of spawning

Source	Species	ADD_{T_0}	T_0 (°C)	Notes	References
Total annual degree-days for maturation					
N	S	2685	0	Amur R. (Russia)	Reviewed in Abdusamadov ([1987](#))
N	S	2865	0	Amur R. (Russia); range is 2655–3111	Gorbach and Krykhtin ([1980](#)) in Naseka and Bogutskaya ([2011](#))
Unk.	S	1000	15	Value may be for grass carp, not silver	Jhingran and Pullin ([1985](#)) in Kolar et al. ([2007](#))
Unk.	S	500	30	Value may be for grass carp, not silver	Jhingran and Pullin ([1985](#)) in Kolar et al. ([2007](#))
–	Both	2685	0	Used in spawning suitability model	Kocovsky et al. ([2012](#))
Total degree-days during pre-spawning period					
N	S	565	0	"immediately" prior to pre-spawning period (15 June)	Gorbach and Krykhtin ([1980](#)) in Naseka and Bogutskaya ([2011](#))
N	S	655	15	Amur R. (Russia)	Gorbach and Krykhtin ([1981](#)) in Kocovsky et al. ([2012](#))
N	S	919	Unk.	Amur R. (Russia)	Gorbach and Krykhtin ([1981](#)) in Naseka and Bogutskaya ([2011](#))
I	S	300	Unk.	Dnieper R. (Russia)	Mitrofanov et al. ([1992](#)) in Naseka and Bogutskaya ([2011](#))
I	B	1356	Unk.	Dnieper R. (Russia)	Mitrofanov et al. ([1992](#)) in Naseka and Bogutskaya ([2011](#))
–	Both	655	15	Used in spawning suitability model	Kocovsky et al. ([2012](#))

Degree-days are calculated by summing the mean daily temperatures (°C) for all days that exceed a given baseline temperature (T_0). Abbreviations are the same as in previous tables

with environmental conditions and many dozens of different values are reported across a wide range of studies. In particular, diet depends on fish age and size, fish stocking density, food availability (including plankton density and detritus load), and food particle size (Costa-Pierce [1992](#); Ke et al. [2008](#); Kolar et al. [2007](#)). Thus, the information on age at maturity and diet reviewed here should be considered a selection of the literature (representative of a range of habitats, populations, and methodological approaches) rather than exhaustive.

Comparison among studies with unique research objectives and varying methodology can be complicated, and so I have included key attributes of each study in the "Notes" column of each table to facilitate comparisons. I have included only the mean parameter values or range of values because, as others have noted (e.g., Cuddington et al. [2014](#)), many studies do not report error values or sample sizes with parameter estimates and, again, varying experimental designs make comparisons of error values across studies difficult.

Review of predictive studies

Spawning and recruitment suitability

The first evidence of bigheaded carp spawning in North American rivers was in the early 1990s (Tucker et al. [1996](#)), but determining specific habitats where spawning is possible (and favorable) remains a critical question, especially within the Great Lakes and their tributaries. A complex suite of factors must be considered when determining a habitat's spawning suitability (Murphy and Jackson [2013](#)), including temperature, hydrology, and turbidity. Hydraulics are particularly important for spawning and recruitment because most data suggest that sufficient flow is needed to prevent the semi-buoyant eggs from sinking to the benthos where they may be exposed to anoxia or predation (Kolar et al. [2007](#)). Kocovsky et al. ([2012](#)) modeled the spawning suitability of Lake Erie tributaries based on hydrological and thermal characteristics and estimated that many tributaries had sufficient temperatures and velocity to support spawning and

Table 4 Parameters for von Bertalanffy growth models: $l_t = L_\infty \times \left(1 - e^{-K(t-t_0)}\right)$ where l_t is the body length at time t, L_∞ is the maximum possible length in mm, K is a growth parameter, and t_0 is the time at which l_t is zero

Source	Species	L_∞	K	t_0	t_i	Notes	References
N	B	915.0[a]	0.2946	0.4849	4.21	Dahuofang Reservoir, China	Yuan and Shi (1993)
N	B	940.5[a]	0.1915	0.04	–	Biliuhe Reservoir, China	Jiang et al. (1994)
N	B	1176[a]	0.3088	0.5392	4	Lake Donghu, China	Ruan (1986)
N	S	881.2[a]	0.2318	0.1980	4.94	Dahuofang Reservior, China	Yuan and Shi (1993)
N	S	704.3[a]	0.2285	0.4773	–	Biliuhe Reservoir, China	Jiang et al. (1994)
N	S	998[a]	0.3040	0.4821	4	Lake Donghu, China	Ruan (1986)
N	S	702	0.234	0.156	–	Amur River, Russia	Nikolskii (1961) in Williamson and Garvey (2005)
I	B	1044	0.35	0.14	4	Middle Mississippi River 1998	Nuevo et al. (2004)
I	B	1093	0.28	0.098	4	Middle Mississippi River 1999	Nuevo et al. (2004)
I	B	1242	0.24	–	–	IL-MS River confluence	Garvey et al. (2006)
I	S	1127	0.179	0.271	–	Gobindsagar Reservoir, India	Tandon et al. (1993) in Williamson and Garvey (2005)
I	S	778	0.629	0.161	–	Missouri River	Williamson and Garvey (2005)
I	S	867	0.41	–	–	IL-MS River confluence	Garvey et al. (2006)
A	S	937.7[a]	0.2087	0.0311	5.14	National Original Breeding Farm, China	Yu et al. (2009)
N	B	915.0[a]	0.2946	0.4849	4.21	Used parameters from Yuan and Shi 1993	Currie et al. (2012)
Both	Both	955	0.3	0.16	–	Used median of multiple values	Cuddington et al. (2014)
Unk.	Both	Unk.	Unk.	Unk.	–	Did not specify which parameters used	Liu et al. (2007)

Also shown is the age of inflexion (t_i) after which growth rate declines. The last three entries show parameters used in modeling studies. Abbreviations are the same as in previous tables

[a] Values were reported in cm or assumed to be reported in cm (e.g., an L_∞ of 91.50 was converted to 915.0)

egg hatching. Kocovsky et al. (2012) used a linear velocity of 0.7 m s^{-1} as the threshold velocity value for spawning suitability in their model based on observations in multiple studies (Table 1; Abdusama-dov 1987). The authors note that shear velocity, not linear velocity, controls the suspension of carp eggs in a stream's current but, because in situ measurements of shear velocity are rarely available, linear velocity was used (Kocovsky et al. 2012). Since this study, however, Murphy and Jackson (2013) were able to calculate shear velocity for Lake Michigan and Lake Erie tributaries using a detailed fluvial egg drift model for bigheaded carps (Garcia et al. 2013). This analysis suggested that eggs may remain suspended at veloc-ities as low as 0.15 m s^{-1} (Table 1), which would expand the range of possible spawning tributaries (Murphy and Jackson 2013). Kocovsky et al. (2012) applied their predictive model using the best informa-tion available at the time, but only a few years after

publication it may already be worthwhile to revisit some of these predictions.

In addition to river flow, minimum river length is a key variable that relates to hatching time (tributaries need sufficient length to suspend the eggs from fertilization to hatching). Previous estimates suggested that stream reaches need to be at least 100 km (Krykhtin and Gorbach 1982), but Murphy and Jack-son's (2013) analysis suggested that reaches as short as 25 km are sufficient and further analyses of the Sandusky River (Ohio) indicated that under ideal temperatures hatching could occur before egg settling begins approximately 15 km downstream of the impassable Ballville Dam (Garcia et al. 2013). Kocov-sky et al. (2012) defined length of passable river from the mouth or dam upstream to where width <5–7 m, which is appropriately conservative considering the smallest stream reach from which bigheaded carp eggs have been collected is ca. 30 m wide (Coulter et al.

Table 5 Age at maturity (in years) of bigheaded carp males and females (B × S = bighead × silver carp hybrids)

Source	Species	♀	♂	Method	Notes	References
N	S	3–4		Unk.	Rivers in south China	Konradt (1965) in Kolar et al. (2007)
N	S	4		Unk.	Yangtze River	Konradt (1965) in Kolar et al. (2007)
N	S	5–6		Unk.	Amur River; mean temp. 20.2 °C	FAO (1980) in Kolar et al. (2007)
N	S	7–8	5–7	Unk.	Amur River	Gorbach and Krykhtin (1981) in Abdusamadov (1987)
N	S	6–7	5–6	Unk.	Amur River; low water years	Gorbach and Krykhtin (1981) in Naseka and Bogutskaya (2011)
N	B	3–4		Unk.	Central China	Kuronuma (1968) in Kolar et al. (2007)
N	B	5–6		Unk.	Northeast China	Kuronuma (1968) in Kolar et al. (2007)
N	Both	4–5		Anec.	Southern latitudes in China	Huet (1970)
I	Both	6–7		Anec.	Romania	Huet (1970)
I	Both	8–9		Anec.	Kiev region	Huet (1970)
I	S	4		Anec.	Uzbekistan	Kamilov and Komrakova (1999) in Kolar et al. (2007)
I	S	4		Obs.	Amu Darya R. & Karakum Canal	Abdullayev and Khakberdiyev (1989) in Naseka and Bogutskaya (2011)
I	S	5	4	Obs.	Terek region of Caspian basin	Abdusamadov (1987)
I	S	2		Obs.	Middle Mississippi River	Williamson and Garvey (2005)
I	B	6	5	Obs.	Terek region of Caspian basin	Abdusamadov (1987)
I	B		2–4	Obs.	Middle Mississippi River	Nuevo et al. (2004)
I	B	3		Obs.	Missouri River	Schrank and Guy (2002)
I	B × S	4	3	Unk.	Krasnodar Kray Resevoir	Voropayev (1975) in Naseka and Bogutskaya (2011)
A	S	5		Unk.	Southern regions of Russia	Konradt (1965) in Kolar et al. (2007)
A	B	3–4		Unk.	Sub-tropical and tropical climate	Woynarovich and Horváth (1980) in Kolar et al. (2007)
A	B	6–8		Unk.	Temperate climates	Woynarovich and Horváth (1980) in Kolar et al. (2007)
A	B	≤2		Emp.	Reared in cages in the Philippines	Santiago et al. (1991, 2004)
A	B	3–4		Unk.	Arkansas aquaculture ponds	Henderson (1979) in Kolar et al. (2007)
Unk.	S	2		Unk.	Guangxi, China; mean temp. 27.2 °C	FAO (1980) in Kolar et al. (2007)
Unk.	S	2–4		Unk.	Guangdong, China; mean temp. 25 °C	FAO (1980) in Kolar et al. (2007)
Unk.	S	3–4		Unk.	Jiangsu, China; mean temp. 24 °C	FAO (1980) in Kolar et al. (2007)
–	Both	2–5	–		Varied this parameter in their model	Cuddington et al. (2014)

If sex was not indicated, value is centered between the male and female columns. The last entry shows the parameters used in a modeling study. Abbreviations are the same as in previous tables

2013). Also, temperature is integral to the calculation of minimum river length because of its influence on egg hatching time (George and Chapman 2013). The criteria of Kocovsky et al. (2012) included not only the minimum 5–7 m width, but also a minimum estimated mean summer temperature of 21 °C because hatch time generally increases below this value (reviewed in Kolar et al. 2007).

Prior to hatching, temperature is important for the onset of spawning. There is generally good agreement among studies regarding the range of temperatures at which bigheaded carp spawning has been observed, whether those observations are from their native or introduced habitats (Table 2). However, this range of temperatures (14–30 °C) is broad because the onset of spawning is determined not by temperature reaching a

Table 6 Optimum temperature for consumption for bigheaded carps

Source	Species	Temp. (°C)		Method	Notes	References
		Range	Min.			
I	S		4	Anec.	Missouri R.; full gut observed in collected fish	Kolar et al. (2007)
I	B	20–22	10	Anec.	Russian lakes	Negonovskaya (1980) in Kolar et al. (2007)
I	B		2.5	Anec.	Missouri R.; full gut observed in collected fish	Kolar et al. (2007)
A	S	10–19		Anec.	Israel	Leventer (1979) in Wrigley et al. (1988)
A	S		8–10	Unk.	India	Tripathi (1989) in Kolar et al. (2007)
A	Both	20–30	10	Anec.	Feeding observed in polyculture ponds	Ling (1977)
Unk.	S	15–30	4	Unk.	Summary table; population info not given	Kolar et al. (2007)
Unk.	Both	20–24	12–14	Unk.	Rapid decline in temp. caused 50 % decline in feeding activity	Negonovskaya et al. (1975) in Naseka and Bogutskaya (2011)
–	S	29		–	Used in bioenergetics model	Cooke and Hill (2010)
–	B	26		–	Used in bioenergetics model	Cooke and Hill (2010)

Min. = lowest temperature for which consumption was observed. Other abbreviations are the same as in previous tables. The last two entries show values used in a modeling study

specific critical level, but rather by the thermal load to which the fish has been exposed over its entire maturation period (Kocovsky et al. 2012; Murphy and Jackson 2013). This thermal load required for maturation is sometimes expressed in units of total annual degree-days (ADD_0), defined as the sum total of mean daily temperatures over 0 °C (Kocovsky et al. 2012). Additionally, total annual degree-days over 15 °C (ADD_{15}) determines the onset of spawning (Kocovsky et al. 2012). For their model, Kocovsky et al. (2012) used threshold values of 2685 ADD_0 and 655 ADD_{15}, which were required for maturation and spawning of silver carp in the Amur River in Russia (Abdusamadov 1987; Gorbach and Krykhtin 1981).

There are some inconsistencies, however, among maturation and pre-spawning ADD values reported in the literature (Table 3). First, it should be noted that the 2685 ADD_0 estimate was not determined by Abdusamadov in their 1987 study of the Caspian basin, but rather is a value they cite for the Amur River from the Russian language literature. It is unclear from which study this estimate originates, but it may be Gorbach and Krykhtin (1980). According to the annotated bibliography of Russian language literature (Naseka and Bogutskaya 2011), Gorbach and Krykhtin (1980) found that silver carp in the Amur River require a mean of 2865 ADD to attain sexual maturity (one has to wonder if Abdusamadov mistakenly cited

this figure), with a range of 2655–3111 ADD. They further note that 565 of these degree-days must immediately precede the pre-spawning period of 15 June (Gorbach and Krykhtin 1980 in Naseka and Bogutskaya 2011). Interestingly, in a different publication of silver carp reproduction in the Amur River these same authors state that "the sum of heat during the prespawning period (476–660 degree-days) and the main spawning period (515–685 degree-days) [does] not influence the success of the spawning of the silver carp" (Krykhtin and Gorbach 1982). Also, Kolar et al. (2007) cite the maturation rate of silver carp as requiring 1000 ADD_{15} and 500 degree-days at 30 °C, but the original source for these values, a hatchery manual published in the Philippines, reports only the 1000 ADD_{15} value and only for grass carp (*Ctenopharyngodon idella*), not silver carp (Jhingran and Pullin 1985). In some cases, the base temperature (T_0) for the degree-day metric (ADD_{T_0}) is not clearly defined, but is presumed to be 0 °C (Table 3).

Regardless of these discrepancies, Kocovsky et al.'s (2012) approach of using ADD_{T_0} as a thermal threshold for their model is sound, but it would be ideal to determine the thermal maturity requirements for bigheaded carps in the MRB rather than relying on values obtained in the Amur River using unclear methods. The Amur River is located close to the 50°N latitude, much farther north than bigheaded carps'

Table 7 Preferred (Pref.) or optimum (Opt.) temperatures for bigheaded carps

Source	Species	Temp. (°C)			Method	Notes	References
		Pref./Opt.	Min.	Max.			
N	B		5		Anec.	Russian lakes	Negonovskaya (1980) in Kolar et al. (2007)
I	S		12.1		Emp.	For embryonic develop.	George and Chapman (2013)
I	S		13.3		Emp.	For larval develop.	George and Chapman 2013
I	B		12.9		Emp.	For embryonic develop.	George and Chapman (2013)
I	B		13.4		Emp.	For larval develop.	George and Chapman (2013)
I	Both	2–4			Anec.	Adults in Missouri River	Kolar et al. (2007)
A	S		18	31	Anec.	Ovulation and hatching	FAO (1980) in Kolar et al. (2007)
A	S		16	40	Anec.	Larval preference	Tripathi (1989) in Kolar et al. (2007)
A	S	39		43.5–46.5	Emp.	Fry aged 3–50 d	Opuszynski et al. 1989
A	S	24–31			Emp.	Opt. for juvenile growth	Mahboob and Sheri (1997)
A	S	30–34			Emp.	Opt. for juvenile growth	Javed (1988) in Mahboob and Sheri (1997)
A	S	18–22			Emp.	Opt. for juvenile growth	Barthelmes and Jahnichen (1978) in Mahboob and Sheri (1997)
A	S		0		Anec.	Can overwinter in Alberta	Kolar et al. (2007)
A	S	31–33.5			Emp.	Depends on larval stage	Radenko and Alimov (1992)
A	B	25.0–26.9		38.8	Emp.	Pref.; age 1 fish	Bettoli et al. (1985)
Unk.	S	26–30			Unk.	Primary source in Polish	Panov and Khromov (1970) in Radenko and Alimov (1992)
Unk.	S	33		38	Emp.	Juvenile swimming activity	Heitmann and Siegmund (1992)
Unk.	B		1–8		Unk.	Overwintered in ponds for 6.5 months	Shcherbina and Giryayev (1990) in Naseka and Bogutskaya (2011)
Unk.	Both		16	44	Emp.	Lethal limits for fry aged 3–50 days	Lirski and Opuszynski (1988a, b)
–	S	29		43	–	Used in bioenergetics model	Cooke and Hill (2010)
–	B	26		38	–	Used in bioenergetics model	Cooke and Hill (2010)

Min. lower limit, *Max.* upper limit. The last two entries shows the parameters used in a modeling study. Other abbreviations are the same as in previous tables

current distribution in the MRB and potential distribution in the Great Lakes. It is not surprising, then, that some MRB and Amur River bigheaded carp populations exhibit significant genetic differentiation according to haplotype analyses of mitochondrial DNA (Li et al. 2010, 2011), and it is possible that local adaption has occurred in ways relevant to maturation, spawning, and development. For example, silver carp growth and maturation rates in the MRB are greater than those in the Amur River (Tables 4, 5; Williamson and Garvey 2005). Additionally, the presence of bigheaded carp eggs in the Wabash River (Indiana, US) was unrelated to mean daily water temperature and

hydrology, suggesting plasticity in spawning traits (Coulter et al. 2013). Similarly, spawning in the Missouri River occurred when discharge was low and at a wider range of sites than in the Yangtze River, China (Deters et al. 2013), although analysis of fecundity and larval density in the Illinois River suggested bigheaded carp reproduction is linked to river flow (DeGrandchamp et al. 2007). Plasticity in spawning traits is also suggested by varying observations of the role of turbidity. While some studies have found no influence of turbidity (e.g., Krykhtin and Gorbach 1982), evidence from Serbian rivers suggested that "suspended alluvium" was more important

326   S. L. Cooke

Table 8 Mean, minimum (min.), and maximum (max.) observed gonadosomatic index (I_G) for male (M) and female (F) bigheaded carps

River	Species	Sex	Mean	Min.	Max.	Notes	References
MO	B	M	0.3	0.4	1.1	No correlation w/length	Schrank and Guy (2002)
MO	B	F	3.9	0.2	14.7	Correlated w/length	Schrank and Guy (2002)
MO	B	M		0.1	1.5	Data indicate a protracted spawning period spanning early spring to fall	Papoulias et al. (2006)
MO	B	F		1.0	9.6		Papoulias et al. (2006)
SD	B	F			22.55	Each female measured up to 1 m in length, 18 kg; caught in May	Miroshnichenko and Kamenetskaya (1978) in Naseka and Bogutskaya (2011)
SD	S	F			35		
MO	S	M		0.3	1.8	Data indicate a protracted spawning period spanning early spring to fall	Papoulias et al. (2006)
MO	S	F		2.3	14.5		Papoulias et al. (2006)
MS	S	F	3.71	0.55	13.3	Jul–Nov; no seasonal trend; correlated w/length & weight	Williamson and Garvey (2005)
Ili	S	F		0.57	1.51	Balkhash-Ili basin in Russia; late April	Karpov et al. (1989) in Naseka and Bogutskaya (2011)
Ili	S	F		4.14	17.7	Balkhash-Ili basin in Russia; late May	
IL	Both	F	1.7			Apr–Aug 2004; no seasonal trend	DeGrandchamp et al. (2007)
IL	Both	F	5.4			Apr–Aug 2005; no seasonal trend	DeGrandchamp et al. (2007)
IL	Both	M	0.17			Apr–Aug 2004; no seasonal trend	DeGrandchamp et al. (2007)
IL	Both	M	0.39			Apr–Aug 2005; no seasonal trend	DeGrandchamp et al. (2007)

All values are from observational studies of non-native populations in natural waters, except values from the Syr Darya River in Uzbekistan (SD) are anecdotal observations of a single individual of each species

for silver carp spawning than hydrology (Jankovic 1992 in Kolar et al. 2007). Also, although they did not examine turbidity in their lab experiments with bigheaded carp embryos and larvae, George and Chapman (2013) speculate that turbidity may be important to provide protection from sight feeding predators during the early larval stage. Turbidity often co-varies with discharge, making it difficult to separately examine these factors.

Collectively, these observations suggest that spawning traits are plastic and differ among bigheaded carp populations, especially between introduced and native populations. Thus, predictive spawning models may be difficult to accurately parameterize, although recent detailed physiological studies will likely facilitate these efforts (e.g., Garcia et al. 2013; George and Chapman 2013; Murphy and Jackson 2013). It is notable that grass carp are now reproducing in the Lake Erie basin, and that the Sandusky River, which has a flow length of 26 km, is presumed to be the spawning location (Chapman et al. 2013). Although grass carp eat macrophytes and bigheaded carps are

filter-feeding planktivores, the two have similar spawning and early life history requirements, and successful spawning of grass carp in the Sandusky River would support the notion of less restrictive spawning requirements for bigheaded carps (Chapman et al. 2013).

Bioenergetics models

As the bigheaded carp invasion front approaches the Great Lakes, some question if these filter-feeding planktivores would be food limited in meso-oligotrophic habitats (Cooke and Hill 2010). Bioenergetics models attempt to address food limitation questions based on zooplankton and phytoplankton densities, temperature, and probable swimming distances in a given habitat. Cooke and Hill (2010) presented bioenergetics models for silver carp and bighead carp and used these models to assess the potential for both species to inhabit the Great Lakes. They estimated that productive embayments, wetlands, and the western basin of Lake Erie contain

Table 9 Absolute fecundity (number of eggs produced per female $\times 10^3$) of bigheaded carps

Source	Species	Mean	Min.	Max.	Method	Notes	References
N	B	1100			Unk.	Yangtze River; 18.5 kg body weight	Chang (1966) in Kolar et al. (2007)
N	B		478	549	Unk.	Russia; original source in Russian	Sukhanova (1966) in Schrank and Guy (2002)
N	S	1540	597	4330	Unk.	Russian reservoir; 6.4–12.1 kg; original source in Russian	Karimov (1980) in Singh (1989)[a]
N	S		467	532	Unk.	Amur R.; aged 7–10 years	Vogaefski (1948) in Singh (1989)[a]
N/A	B	280			Unk.	Russia; fecundity at first spawn	Vinogradov et al. (1966) in Kolar et al. (2007)
A	B	150	97	182	Hor.	Growth experiments; 2.2–3.8 kg	Santiago et al. (2004)
A	B	810	204	1659	Hor.	Parental stock from China; size not given	Verigin et al. (1990)
A	S	572	103	1298	Hor.	Parental stock from China; 3.4–8.7 kg	Verigin et al. (1990)
A	S		114	255	Unk.	Unclear if hormone injection used; 0.76–1.35 kg	Singh (1989)
I	B	226	12	770	Obs.	Missouri R.	Schrank and Guy (2002)
I	B	180			Obs.	Illinois R. (2004)	DeGrandchamp et al. (2007)
I	B	750			Obs.	Illinois R. (2005); correlated with weight and length	DeGrandchamp et al. (2007)
I	B	930	316	1861	Obs.	Terek region of Caspian	Abdusamadov (1987)
I	S	812	315	1340	Obs.	Terek region of Caspian; 4.2–9.3 kg	Abdusamadov (1987)
I	S		308	1387	Obs.	Amu Darya R. & Karakum Canal	Abdullayev and Khakberdiyev (1989) in Naseka and Bogutskaya (2011)
I	S		299	5400	Unk.	Syr Darya R. (Russia)	Kamilov and Salikhov (1996) in Naseka and Bogutskaya (2011)
I	S		1576	2184	Obs.	Balkhash-Ili basin in Russia	Karpov et al. (1989) in Naseka and Bogutskaya (2011)
I	S	280			Obs.	Illinois R. (2004)	DeGrandchamp et al. (2007)
I	S	1600			Obs.	Illinois R. (2005); correlated with weight	DeGrandchamp et al. (2007)
I	S	156	57	329	Obs.	Middle Mississippi River; age 2	Williamson and Garvey (2005)
–	Both	150	15	1500	–	Used in population model	Cuddington et al. (2014)

Hor. = aquaculture study in which fish were given hormone injections to stimulate reproduction. Other abbreviations are the same as in previous tables. The last entry shows the parameters used in a modeling study

[a] Note that Singh (1989) incorrectly cites fecundity values from another study and these references could not be confirmed

sufficient plankton food resources (at least at certain times of year) to theoretically support bigheaded carp growth and swimming activity, but plankton densities in most pelagic regions would be insufficient for carp to simply maintain their basic metabolic needs (Cooke and Hill 2010). Recently, however, bighead × silver hybrids in low productivity Lake Balaton, Hungary were found to exhibit higher condition than bighead carp in the MRB, suggesting sufficient food resources in an ecosystem with a chlorophyll a maximum of 8–23 µg L^{-1} (Boros et al. 2014). By comparison, chlorophyll a ranges from <1 to ca. 20 µg L^{-1} in some nearshore sites of Lake Michigan depending on influences from river plumes (Tomas Höök, unpublished data), and a range of 8–39 µg L^{-1} has been reported in the Middle Mississippi River (Williamson and Garvey 2005). It should be noted, however, that Lake Balaton has a very unusual limnology, with

Table 10 Preferred food item (*phyto* phytoplankton, *zoop* zooplankton, *detr* detritus) of bigheaded carps

Source	Species	Main diet item	Method	Notes	References
N	S	zoop; phyto	Emp.; gut contents	Chinese lake; low stocking density = zoop; high stocking density = phyto	Ke et al. (2008)
N	S	rotifers	Emp.; plankton density	Mesocosms in a Chinese lake	Shao and Xie (2003)
N	S	phyto; detr	Obs.; gut contents	Amur R.; juveniles; phyto, but switch to detr in spring	Borutskiy (1950) in Naseka and Bogutskaya (2011)
N	S	phyto	Obs.; stable isotope	Detr was main source in eutrophic lake	Jayasinghe et al. (2014)
N	B	zoop	Obs.; stable isotope	Detr was main source in eutrophic lake	Jayasinghe et al. (2014)
N	Both	zoop	Obs.; stable isotope	Chinese lake	Xu and Xie (2004)
I	S	diatoms; zoop	Obs.; gut contents	Amu Darya R. & Karakum Canal; switch to zoop in late spring/early summer	Abdullayev and Khakberdiyev (1989) in Naseka and Bogutskaya (2011)
I	S	phyto	Obs.; gut contents	MRB; adults	Calkins et al. (2012)
I	S	phyto	Obs.; gut contents	MRB; adults/subadults	Pongruktham et al. (2010)
I	S	phyto	Obs.; gut contents	Middle MRB; age 1+	Williamson and Garvey (2005)
I	S	cladocerans	Emp.; plankton density	Mesocosms in a reservoir	Domaizon and Devaux (1999)
I	S	phyto	Obs., gut contents	Russian reservoir; no age- or sex-related differences in dietary preferences	Mukhamedova and Kalinina (1986) in Naseka and Bogutskaya (2011)
I	S	zoop; phyto; detr	Obs., gut contents	Fed on zoop until 10–15 cm length then switch to phyto & detr	Pavlov et al. (1994) in Naseka and Bogutskaya (2011)
I	S	phyto	Obs., gut contents	Ili R.; young-of-year; mostly green and blue–green algae	Karpov et al. (1989) in Naseka and Bogutskaya (2011)
I	S	phyto; detr	Obs.; gut contents	Age 2 + , fed on benthic sediments	Danchenko et al. (1980) in Naseka and Bogutskaya (2011)
I	B	zoop	Obs.; gut contents	Age 1+; did not feed on phyto or detr	Danchenko et al. (1980) in Naseka and Bogutskaya (2011)
I	B	zoop	Emp.; plankton density	Mesocosms in U.S.; age 0	Schrank et al. (2003)
I	B	*Daphnia*	Emp.; gut & plankton	Mesocosms in U.S.; juvenile	Cooke et al. (2009)
I	B	zoop; blue–green algae	Obs.; gut contents	Karakum Canal; zoop inMay–Aug, switch to blue–green in Sept.	Aliyev (1974) in Naseka and Bogutskaya (2011)
I	Both	phyto	Obs.; gut & plankton	Lakes in Italy	Sekulic et al. (1998)
I	Both	rotifers	Obs.; gut contents	IL and MS R. backwater lakes; adults	Sampson et al. (2008)
I	B × S	detr	Unk.	Adults in Lake Balaton, Hungary	Boros et al. (2014)
A	S	phyto	Emp.; plankton density	Juveniles in aquaria	Dong and Li (1994)

Table 10 continued

Source	Species	Main diet item	Method	Notes	References
A	B	large phyto	Emp.; gut contents	Ponds in FL; juveniles	Opuszynski and Shireman (1993)
A	B	small phyto	Emp.; gut & plankton	Ponds in FL; range of ages	Opuszynski et al. (1991)
A	B	zoop; phytp; detr	Obs.; gut contents	Larvae fed on zoop; switch to phyto & detr as carp aged	Lazareva et al. (1977)
A	Both	*Microcystis*	Emp.; gut & plankton	Mesocosms in a reservoir; juveniles	Datta and Jana (1998)
A	Both	phyto	Obs.; stable isotope	Ponds in China; age not specified	Gu et al. (1996)
A	B × S	large phyto	Emp.; gut contents	Ponds in Alabama; adults/subadults	Bayne et al. (1991)
Unk.	S	small zoop	Emp.; plankton density	Juveniles in aquaria	Smith (1989)
N	S	phyto	Ecopath model	Set diet as 10 % zoop, 75 % phyto, 15 % detr	Liu et al. (2007)
N	B	zoop	Ecopath model	Set diet as 95 % zoop, 3 % phyto, 2 % detr	Liu et al. (2007)
I	Both	varied	Bioenergetics model	Set diet according to plankton availability	Cooke and Hill (2010)
I	Both	varied	Ecopath model	Explored five diets, including one based on plankton availability	Currie et al. (2012)

"Gut contents" means that the alimentary tract contents were examined via dissection to determine diet, "plankton density" means the diet was inferred from sampling plankton density before and after feeding, and "stable isotope" means $\delta^{13}C$ and $\delta^{15}N$ values were used to infer on which trophic levels carp feed. The last several entries below the line show the parameters used in modeling studies. Other abbreviations are the same as in previous tables

extremely high concentrations of suspended carbonates, which may constitute attachment sites for bacteria that could be digested by bigheaded carps.

The parameters of a bioenergetics model include mass- and temperature-dependent coefficients for consumption, egestion and excretion, and respiration. Respiration parameters for bighead and silver carps were experimentally derived (Hogue and Pegg 2009), but consumption parameters were derived from the literature on bigheaded carps and tilapia (*Sarotherodon* spp. and *Oreochromis* spp.), planktivores biologically similar to bigheaded carps (Cooke and Hill 2010). There are multiple reports of the effects of temperature on bigheaded carp consumption, but these values are largely based on anecdotal observations made in aquaculture facilities (Table 6). Also, several of the reported temperature ranges for optimum feeding are broad and non- overlapping (e.g., 10–19 vs. 20–30 °C; Table 6). Hence, Cooke and Hill (2010) used the temperature-dependent consumption parameter from tilapia. The specific dynamic action variable

for tilapia was also borrowed, and egestion and excretion parameters were obtained from *Oncorhynchus* spp. (Cooke and Hill 2010). "Parameter borrowing" across species is not uncommon in bioenergetics modeling, but it should be avoided (Chipps and Wahl 2008; Hansen et al. 1993).

Even when parameters are used from literature on bigheaded carps and not other species, deciding which values to use can be problematic. Cooke and Hill (2010) relied on bigheaded carps' general thermal requirements (e.g., for growth and survival) as proxies for optimum and maximum feeding temperatures (Table 7). There are some consistencies among the studies summarized in Table 7, including the fact that the maximum temperatures for larvae or fry are generally close in range. But there are also discrepancies among values, such as optimum temperature for juvenile silver carp growth in aquaculture (reported values range from 18 to 34 °C). Most of the values in Table 7, however, cannot be compared to one another because they represent thermal requirements of

different response variables. Additionally, some studies reported preferred temperatures (e.g., where carp spend most of their time in thermal selection experiments) while others reported optimum temperatures (e.g., temperature at which maximum growth rate occurred), and the two are not always the same (Radenko and Alimov 1992). Also, most studies focused on larvae, fry, or juveniles and few reported thermal requirements for adults. Clearly, more basic physiological research on bigheaded carps is needed.

Some argue, however, that laboratory experiments to determine physiological parameters may not be sufficiently representative of field conditions for bioenergetics predictions to be reliable (Hansen et al. 1993). This may be particularly true for generalist omnivores like bigheaded carps. For example, free-swimming bighead carp in aquaculture ponds filtered algae 30 times more efficiently and grew faster than caged bighead carp within the ponds (Opuszynski et al. 1991), indicating that feeding rates obtained from aquarium or mesocosm experiments may not be representative of bighead carp feeding in natural waters. Also, temperature-dependent growth curves for larval silver carp fed artificial formula feed differed from those fed live zooplankton (Radenko and Alimov 1992). Furthermore, bigheaded carp consumption rates vary with time of day (Shi et al. 1998), food particle size (Smith 1989), dissolved oxygen (Shi et al. 1998), and light intensity and spectral composition (Heitmann and Siegmund 1989; Radenko and Alimov 1992), which are factors not considered in most bioenergetics models. Presumably, these factors may effect egestion and excretion as well.

Bigheaded carp diets are also highly variable (Table 10), depending on food availability (which varies seasonally and across habitats), carp life stage, and carp density, among other factors (Ke et al. 2008; Kolar et al. 2007). Cooke and Hill (2010) assumed that diets mirrored plankton availability in their simulations. This may be a somewhat safe assumption although, in reality patchy plankton distribution may lead to selective feeding and low plankton densities may cause a switch from plankton to detritus (and the energy content of the latter is presumed to vary greatly). Detritus appears to sustain bighead × silver hybrids in meso-oligotrophic Lake Balaton (Boros et al. 2014). These complexities should be accounted for to ensure that bioenergetics simulations are as realistic as possible.

However, another issue with fish bioenergetics modeling is that physiological responses differ between populations and this information on local adaptation is often lacking for many species (Chipps and Wahl 2008). All models are simplifications of the real world, but bioenergetics models, in particular, have been criticized for lacking sufficient detail to reliably predict occurrences in nature (Hansen et al. 1993). The model developed by Cooke and Hill (2010) borrows many of its parameters from other species, although the model has recently been modified and improved by incorporating more species-specific parameters (Anderson et al. 2015). With such improvements, bigheaded carp bioenergetics models may still be of some value, especially if parameters are developed from research on MRB populations (or other invasive populations of current interest), the models are empirically evaluated, and hypothesis-based parameter testing is implemented to reduce uncertainty in model applications (Chipps and Wahl 2008).

Multivariate models

While focusing on single biological attributes such as bioenergetics and spawning has merit, other modeling approaches for bigheaded carp invasions consider a more comprehensive set of biological, life history, invasion history, and environmental factors. For example, one of the earliest quantitative modeling efforts to predict if bigheaded carps could become established in the Great Lakes considered 13 species characteristics, five habitat requirements, and six aspects of invasion history (Kolar and Lodge 2002). Overall, the model predicted that silver carp (but not bighead carp) could become established in the Great Lakes, but it would not spread quickly or be a nuisance. Kolar and Lodge (2002) cautioned, however, that the model may not be "robust" to deviations such as silver carp's jumping behavior and that the model was only for the Great Lakes themselves and not tributaries.

More recently, another multivariate approach was used to determine if bigheaded carps could become established in the Great Lakes given varying founding population sizes and access to suitable spawning rivers (Cuddington et al. 2014). The researchers parameterized a life stage- and river-structured population model that considered the probability of locating a

suitable spawning river and various containment breach scenarios under varying levels of environmental stochasticity. The model results suggested that establishment is likely even for a small founding population (<20 individuals) in a lake with 10 or less spawning rivers, although the model assumes that individuals within that small founding population will be in close enough proximity to find a mate.

The model included a comprehensive set of parameters and the authors note that they used a "considerable range" of literature data to parameterize the model (Cuddington et al. 2014). For growth (size at each stage), they used a von Bertalanffy growth model parameterized using median values from multiple studies (Table 4; not all of these values were used by Cuddington et al. 2014). Growth curves were also used to simulate variation in age at maturity by varying the growth parameter (K) of the von Bertalanffy equation from 0.4 to 0.15 (corresponding to age at maturity of 2 and 5, respectively) and assuming that sexual maturity only occurred when individuals were >400 mm. This range in K brackets the 14 values listed in Table 4, but age at maturity can vary from 2 to 9 years (Table 5), depending on environmental conditions (Kolar et al. 2007).

Similar to age at maturity, fecundity can vary greatly with body size, age, and, in some cases, season (Tables 8, 9). The variation of values in Tables 8 and 9 also suggests that fecundity varies within and among sites, with no clear differences between native and introduced populations. To "conservatively bracket" the reported ranges, Cuddington et al. (2014) used minimum, mean, and maximum absolute fecundity values of 15,000, 150,000, and 1,500,000 eggs per female, respectively, although maximum absolute fecundity values several times greater than this (e.g., 5,400,000) have been reported in Russian waters (Table 9).

Of all of the factors used in the model, early sexual maturity may influence establishment risk the most (Cuddington et al. 2014). The model suggested that if first reproduction is delayed until age 5 or older then establishment in the Great Lakes is unlikely. While ages at maturity >5 have been observed in the Amur River and other north temperate systems in Asia, most observations in North American rivers are 2–4 years (Table 5). Cuddington et al. (2014) cautioned, however, that large river systems (from which they obtained much of the data used to parameterize their

model) differ from the Great Lakes and, thus, it is important to determine the effects of "lake conditions" on age at maturity. The challenge, of course, with any effort to predict invasion risk in the Great Lakes is that few of bigheaded carps' current habitats closely mimic large, deep, moderately cool, dimictic, meso-oligotrophic lakes and such conditions are difficult to replicate in a lab, hatchery, or aquaculture facility. Also, research in large Chinese lakes and reservoirs may be limited in applicability because these systems are usually eutrophic or hypereutrophic with stocked populations of bigheaded carps.

Environmental niche models

The overall approach of environmental niche models is to use the environmental conditions of a species' native range or current distribution to predict the suitability of habitats to which the species may spread (thus, it differs from the previously discussed models in that biological parameters are not directly used). Several different environmental niche models have predicted Great Lakes drainage basins as well as the Great Lakes themselves to be suitable habitats for bighead and silver carps. Chen et al. (2007) used the Genetic Algorithm for Rule-set Prediction (GARP) model, which identifies associations between the occurrence of a species and environmental parameters. This analysis included 15 environmental variables, and the model was trained using only native distribution data (Chen et al. 2007). They found that silver carp, but not bighead carp, could survive in Great Lakes drainages (Chen et al. 2007), although their model did not accurately predict bighead carp establishment in regions where they were already abundant at the time of the study. Herborg et al. (2007), on the other hand, found that the entirety of the Great Lakes drainage basin is highly suitable for both silver and bighead carp establishment, with the Great Lakes themselves also being highly suitable for silver carp. They developed their GARP model using both Asian and North American distribution data, although their suite of environmental parameters was more limited. They found that precipitation was a key predictor for invasion, which could be related to flow and other hydrological characteristics (Herborg et al. 2007).

A comparison of four environmental niche modeling methods, including GARP, used 20 environmental predictors and found that silver carp could spread

beyond its current distribution in the MRB into habitats with slow flow, low sand content, and little vegetative cover, particularly the Ohio River basin and other regions east of their current distribution (Poulos et al. 2012). These habitat conditions are characteristic of many Great Lakes tributaries, but Poulos et al. (2012) suggested that much of the Great Lakes would be too cold for silver carp establishment. However, their models did not focus on the Great Lakes themselves and it seems that bigheaded carps could have broader thermal requirements than previously believed (Tables 2, 3, 6, 7). Poulos et al. (2012) suggested that abundance-based models could be a useful next step in identifying more specific habitats likely to support high numbers of invaders. Ecological niche models have been used to predict the abundance and impact of common carp (*Cyprinus carpio*) (Kulhanek et al. 2011), although there are probably insufficient ecological effects data to adequately replicate this approach for bighead and silver carps.

Models to predict ecological effects

While substantial efforts have been made to predict further spread of bigheaded carps, considerably less is known about their current and potential ecological effects. In their risk assessment for the Great Lakes, Cudmore et al. (2012) predict detrimental ecological effects based on presumed competition with planktivorous fishes in each lake, but the extent of dietary overlap and competition between these native species and bigheaded carps has not been experimentally tested in most cases. Invader impacts are generally difficult to predict because their effects may not increase linearly with abundance and usually vary across different habitat types (Thiele et al. 2010). Hence, predicting the trophic consequences of bigheaded carps in the Great Lakes and other novel ecosystems may be the most challenging task of their invasion risk assessment. Additionally, the trophic ecology of filter-feeding planktivores is not as well studied as that of visually feeding planktivores, and the two groups are expected to have different effects on plankton communities (Lazzaro 1987).

Part of the reason that few ecological impact models have been developed is that the effects of bigheaded carps on plankton communities in different types of habitats are varied, complex, or unknown, which is not surprising given their broad diet and feeding habits (Tables 6, 10). Only a few studies have examined the effects of bigheaded carps on plankton communities in the MRB. Silver carp catch-per-unit-effort was negatively associated with cladoceran density in Mississippi and Illinois River backwater lakes, although rotifers were the most common prey item consumed according to gut content analyses (Sampson et al. 2008). A study of silver carp from a Mississippi River oxbow lake also found high consumption of rotifers, along with evidence of selective planktivory on euglenoid algae compared to cyanobacteria (Pongruktham et al. 2010). In a five-week mesocosm experiment with different zooplankton densities, zooplankton shifted from *Daphnia* to copepods in the presence of juvenile bighead carp (of Missouri River broodstock), but the effects of bighead carp on zooplankton community composition varied with initial zooplankton density (Cooke et al. 2009). Collectively, the U.S. research suggests that bigheaded carp effects on plankton communities in MRB ecosystems are difficult to predict but could be substantial. Also, Delong (2010) points out that the synergetic effects of bigheaded carps and other invaders in the MRB (e.g., dreissenid mussels, *Daphnia lumholtzi*) have not yet been considered.

Some generalizable trophic models of planktivorous fishes may provide insight into the ecological effects of bigheaded carps on plankton communities. Attayde et al. (2010) developed a model to explore omnivory by filter-feeding planktivorous fishes. Tilapia was the focus of model development, but the model is applicable to silver carp (Attayde et al. 2010). The model results suggest that high biomass of omnivorous fishes does not necessarily lead to collapse of zooplankton, even if the fish have a strong preference for zooplankton. Omnivory can actually have a stabilizing effect because prey switching (from zooplankton to phytoplankton as the former becomes depleted) prevents collapse of zooplankton communities (Attayde et al. 2010). Ultimately, the model suggested that omnivores like bigheaded carps can decrease or increase algal biomass depending on their density and the initial productivity of the ecosystem, which is consistent with the mixed results observed across many studies. For example, in several long-term (ca. 2 month) enclosure experiments in which silver carp biomass was manipulated, algal biomass was lowest in the fishless treatment, although algae decreased over time in all treatments (Lu et al. 2002;

Tang et al. 2002). But in a 10-week enclosure experiment, algal biomass declined the most in the high silver carp treatment (Xiao et al. 2010). The omnivory model does have some limitations, including failure to account for fish dynamics, nutrient recycling by consumers, and size structure of the phytoplankton, zooplankton, and fish (Attayde et al. 2010). It should be noted that studies conducted in ponds, lakes, and enclosures consistently show that silver carp reduce zooplankton abundance and/or stimulate a shift to smaller-bodied zooplankton (Kolar et al. 2007).

Theoretically, however, invasion by a planktivorous fish could actually lead to an increase in zooplankton densities (a phenomenon dubbed "paradoxical top-down control") in addition to the more typical response of a decrease in zooplankton followed by an increase in phytoplankton (Morozov et al. 2005). A model developed by Morozov et al. (2005) indicates that the paradoxical mechanism may be caused by indirect effects occurring in ecosystems with sufficient nutrient influx. Whether a planktivorous fish invasion results in the typical response or the paradoxical response depends on numerous factors, including the time scale. One reason that paradoxical top-down control is rarely documented is that the time scale of experiments or observations is often too short (Morozov et al. 2005). For example, in a 10-week enclosure experiment, high silver carp biomass was associated with increased predation on rotifers and the dominance of small cladocerans (Shao and Xie 2003), but increases in rotifer densities and decreases in cladocerans were observed over four decades following dense stocking of bigheaded carps in Lake Donghu, China (Shao et al. 2001).

Liu et al. (2007) evaluated the role of heavily stocked bighead and silver carps in the trophic structure of a large Chinese reservoir using Ecopath, a widely used mass-balance modeling method for quantifying food web interactions and fisheries ecosystem dynamics. In Ecopath, trophic functional groups consisting of a single species or group of closely related species are designated, and the input variables are the biomasses and diet composition of each group. The production to biomass (P/B), production to consumption (P/Q), and consumption to biomass (Q/B) ratios are then estimated for each functional group. The biomasses of bighead and silver carp were estimated in part by using von Bertalanffy

growth functions (Liu et al. 2007), but the parameters of those functions were not given (Table 4). Silver and bighead carp diet compositions (Table 10) were estimated or derived from long-term monitoring data in the focus reservoir. The model results showed that bighead and silver carps play active roles in several food chains, exhibiting ecotropic efficiencies (the proportion of production used by a trophic functional group) of 0.953 and 0.981, respectively, and effective trophic level scores of 2.97 and 2.10, respectively (phytoplankton and detritus had a score of 1 and top predators had a score of 3.89; Liu et al. 2007).

A limitation of the Ecopath model as used by Liu et al. (2007) is that its static nature does not permit explorations of alternative scenarios such as changing carp stocking densities over time. However, the dynamic version of the model, Ecopath with Ecosim (EwE) can be used for such purposes. EwE has been used in a preliminary assessment of potential trophic consequences of bigheaded carps in offshore Lake Ontario (Currie et al. 2012). The effects of a range of carp biomasses and food items were simulated under scenarios of high dreissenid biomass (HDM) and low dreissenid biomass (LDM), considered proxies for high and low productivity, respectively, of lower trophic levels. To estimate P/B for bigheaded carps, von Bertalanffy growth parameters were used from Dahuofang Reservoir in China (Table 4) because it is located at the same latitude as Lake Ontario (Currie et al. 2012), although this reservoir is eutrophic and in a semi-arid climate (Xu et al. 2009). Additionally, seasonal diet data (proportions of detritus, bacteria, phytoplankton and zooplankton) were derived from bigheaded carps caught in another eutrophic Chinese system (Lake Donghu), but zooplankton species groups were based on Lake Ontario communities. Also, four additional diets were considered: equal proportions of detritus, microbes, phytoplankton and zooplankton, and diets dominated by detritus, phytoplankton, or zooplankton (Currie et al. 2012). The model results suggest that high biomass of bigheaded carps could be sustained in offshore Lake Ontario, resulting in disruptions of carbon flow to lower trophic levels. Low bigheaded carp biomass, on the other hand, would probably have minimal consequences (Currie et al. 2012).

In addition to their effects on plankton communities, the competitive effects of bigheaded carps on other fishes are also not well known. Currie et al.

(2012) found with their Ecopath model that high bigheaded carp biomass would result in reduced alewife (*Alosa pseudoharengus*) biomass and a possible population collapse, which would lead to a collapse of Chinook salmon (*Oncorhynchus tshawytscha*). However, the results depend on dreissenid biomass (i.e., productivity of lower trophic levels) and bigheaded carps' diet, among other factors. Currie et al. (2012) emphasized that the many uncertainties and assumptions in the model make food web consequences "impossible to predict with any degree of confidence." Williamson and Garvey (2005) speculated that competition of silver carp with early life stages of native fish species in the MRB could be a concern, given the rapid growth and maturation rates of young silver carp. Mesocosm experiments in Missouri indicated that bighead carp could compete with paddlefish (*Polyodon spathula*) for zooplankton food resources (Schrank et al. 2003). Foregut analyses found little dietary overlap between these two species collected from backwater lakes of the Illinois and Mississippi Rivers, but found substantial overlap between bighead carp and gizzard shad (*Dorosoma cepedianum*) and bigmouth buffalo (*Ictiobus cyprinellus*) (Sampson et al. 2008). There was evidence of reduced body condition of both gizzard shad and bigmouth buffalo coincident with increased bigheaded carps in the Illinois River (Irons et al. 2007), indicating that the dietary overlap observed by Sampson et al. (2008) may translate to competition. Lipids (an indicator of condition) and reproductive success are reduced in some native fish species in regions of the Mississippi River where bigheaded carps are abundant, but there is no evidence of population-level effects (Gutreuter et al. 2011 in Cudmore et al. 2012).

Similarly, in other countries where bigheaded carps have been introduced, there is only correlative evidence that they compete with native species, and the correlations are often complicated by other fish introductions. Catches of native fishes in the Danube delta have declined since the introduction of silver carp and other cyprinids (Cowx 1997). Likewise, several economically valuable native fishes in Pakistan have declined since the introduction of bighead and silver carps, but at least half a dozen other introduced species could also be responsible for the decline (Khan et al. 2011). A multi-decade assessment of a small German lake found that the native fish community was largely resistant to stocking of silver carp, common carp, and European eel (*Anguilla anguilla*), even though silver carp substantially reduced the zooplankton (Barthelmes and Bramick 2003). A manipulative study in the Mekong basin of southeastern Asia examined the effects of stocking bighead carp and Nile tilapia (*Oreochromis niloticus*) on native fishes, many of which are planktivorous or omnivorus (Arthur et al. 2010). After 1 year, biomass, species richness, and species composition of native fish communities did not significantly differ between stocked wetlands and reference wetlands, although there was a 24 % reduction in Simpson's diversity index in the stocked wetlands (Arthur et al. 2010). In Lake Kinneret, Israel dietary overlap based on gut analyses suggested silver carp may compete with commercially valuable native fish species (Spataru and Gophen 1985).

Despite some of these mixed results, it seems reasonable to hypothesize that bigheaded carp competition with native planktivores would be substantial, even in highly productive habitats, given their rapid feeding and growth rates. Also, based on their dietary overlap, bighead and silver carps could compete with each other. In southeast China bighead and silver carps exhibited trophic niche overlap in both oligotrophic and hypereutrophic habitats, but exhibited trophic niche separation in mesotrophic ecosystems according to stable isotope analysis (Chen et al. 2011). But given the paucity of data, it remains uncertain how trophic state (as a proxy of plankton food availability) may affect bigheaded carps' role as competitors and whether they are stronger competitors in introduced habitats compared to their native range.

An additional unknown is the possibility of predators on the early life stages of bigheaded carps in novel habitats. Currently, there is little evidence in the published literature that the Great Lakes or other regions in North America harbor any piscivores that would prey on young carp, although this is an active area of research (Duane Chapman, personal communication). As potential predators are assessed, it is important to not rule out invertebrate predators, as cyclopoid predation on early stage silver carp larvae can be substantial, depending on the densities of predator and prey (Sukhanova 1968 in Naseka and Bogutskaya 2011).

Despite the many unknowns and complexities of bigheaded carp ecological effects, dynamic trophic models such as EwE should be developed and used to
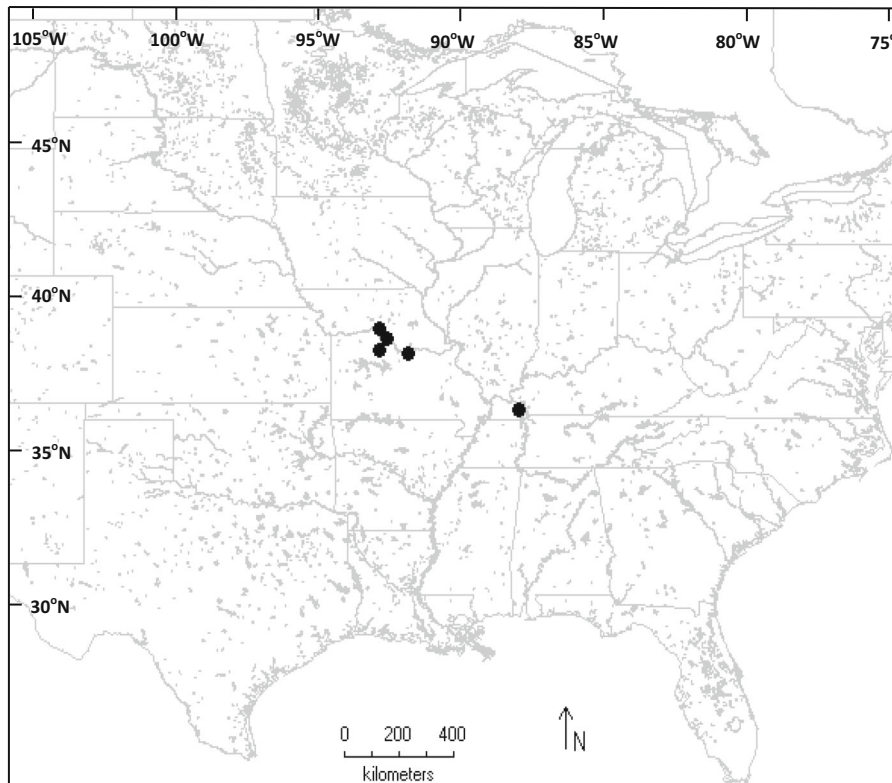
Fig. 3 Distribution of established populations of silver carp × bighead carp hybrids in the United States. Data obtained from the United States Geological Survey Nonindigenous Aquatic Species database and used with permission

explore possible ecological consequences of invasion scenarios in the MRB, the Great Lakes, and other habitats at risk of invasion. Our understanding of food web dynamics in the upper MRB (Delong 2010) and in many regions of the Great Lakes (e.g., Hossain et al. 2012; Krause et al. 2009) has been advanced by early population and diet studies, more recent experimental studies, the use of stable isotopes, and ecological network theory. In some cases this knowledge has been used to construct food web models and predict trophic effects of aquatic invaders that are already present in the Great Lakes, such as *Bythotrephes longimanus* (e.g., Miller et al. 2010). One could argue that, unlike *Bythotrephes*, preliminary ecological effect data of bigheaded carps in the Great Lakes are unavailable and, therefore, their trophic effects cannot be adequately simulated. But, perhaps, bigheaded carp modelers could adopt a model called Rank Proportion Algorithm (RPA), which has been used to predict prey preferences for yet-to-arrive marine invaders in novel habitats (Pinnegar et al. 2014). The predicted diet

composition from the RPA analysis is then used as input to an EwE model (Pinnegar et al. 2014). Also, the challenges of incorporating invasive species into Great Lakes EwE models have recently been assessed, with recommendations for initiating invader biomass at low levels as a more simplistic and realistic approach when seeking to determine the effects on fisheries management (Langseth et al. 2012).

Other considerations for predicting bigheaded carp spread and effects

An examination of the reviewed parameter values shows that bighead carp and silver carp are largely similar, but it also reveals some differences between the species (e.g., Table 3). Hence, another factor that should be considered when developing or applying predictive models is the apparent prevalence of hybrid bigheaded carps in North American habitats (Fig. 3). Although a few occurrences of natural hybridization

have been observed in Russian rivers (multiple references in Naseka and Bogutskaya 2011) including recent molecular confirmation of three hybrid backcrosses in the Amur River (Lamer et al. 2014), bighead carp x silver carp hybrids are generally rare in their native range (Kolar et al. 2007). But an allozyme analysis found that hybrids comprised 22.5 % of 120 *Hypophthalmichthys* spp. collected near the Mississippi-Illinois River confluence (Lamer et al. 2010). Only four genetic loci were examined in this study, meaning this high percentage is likely a conservative value that may underestimate the true occurrence of hybrids. Additionally, both first generation (F1) and post-F1 hybrids were found, which suggests the possibility of introgression and a hybrid swarm.

Lamer et al. (2010) suggested that an increasing prevalence of hybrids could mitigate the bigheaded carp invasion in the MRB, given the reduced fitness of post-F1 hybrids as described in older Russian literature cited by Lamer et al. (2010). According to these studies, post-F1 hybrids exhibit reduced jumping behavior, twisted gill-rakers, less efficient food conversion, and lower disease resistance compared to parental species in some aquaculture settings (Lamer et al. 2010). But the possibility that heterosis could instead promote the invasion should also be considered. Other aquaculture studies showed that silver carp × bighead carp reciprocal crosses had higher survival and biomass than parental species (Hulata 1995; Naseka and Bogutskaya 2011). In a recent study of bigheaded carps in Lake Balaton, Hungary, all individuals sampled were morphologically determined to be hybrids with good condition factors (mean 1.55) that exceeded those of MRB adult bighead carp (Boros et al. 2014). Also, larger gill-raker spacing and lower algal grazing efficiency have been observed in aquaculture hybrids (Hulata 1995), which implies that hybrids could affect plankton communities and compete with native planktivores differently compared to parental species. Bettoli et al. (1985) found that F1 hybrids of bighead carp and grass carp (*Ctenopharyngodon idella*) in aquaculture had a significantly higher preferred temperature and critical thermal maximum compared to either parental species—the difference was nearly 3 °C in the case of preferred temperature.

An additional consideration for predictive studies and risk assessments is the role of disease and parasites in regulating bigheaded carp populations and their effects in North American waters. The bacterial pathogen *Lactococcus* spp. was confirmed in a silver carp specimen obtained from a Mississippi River fish kill dominated by bigheaded carps, but researchers could not confirm that *Lactococcus* spp. was responsible for the kill (Khoo et al. 2014). Spring viremia of carp virus (SVCV) infects cyprinids, especially common carp, as well as other fish species. SVCV was discovered in common carp in a Wisconsin lake (Dikkeboom et al. 2004), a Minnesota tributary to the Mississippi River (Phelps et al. 2012), and Hamilton Harbour of Lake Ontario (Garver et al. 2007), although the complete extent of its distribution in North American natural waters is not well known. While both bighead and silver carps can be infected by SVCV, it is unlikely to be an effective control agent (Kolar et al. 2007). Rather, it seems more likely that bigheaded carps, because of their high densities and rapid movement rates, would promote the spread of SVCV to native species, such as paddlefish (Pegg et al. 2009). There is also concern that bighead and silver carps could facilitate the transmission of parasites such as the Asian carp tapeworm (*Bothriocephalus acheilognathi*), which has infected native fishes in the southwestern U.S. (e.g., Kolar et al. 2007) and the Great Lakes (Marcogliese 2008). Largely, however, much of the bigheaded carp disease research has only been done in the context of aquaculture and may be limited in its applicability to invasive populations in the wild.

Summary, synthesis, and research priorities

Part of the rationale in tabulating bigheaded carp biological parameters was to gain insight into whether values differ among native, introduced, and aquaculture populations, which has been suggested by other studies and could be indicative of local adaptation. For example, Williamson and Garvey (2005) noted that growth parameters differ between silver carp populations in India, the Amur River, and the MRB. However, a more comprehensive look at growth parameters reveals variability even within the same system or region (Table 4). Indeed, with the possible exception of velocity requirements for spawning (which seem to be broader in the MRB and more constrained in the Amur River; Table 1), bigheaded carp biological parameters vary greatly across and within systems in their native and introduced ranges

(and in aquaculture). Although this is not unexpected for traits that are known to depend on environmental conditions, such as age at maturity and diet, future predictive studies that use any biological parameters should be cognizant of this within- and among-system variation. It seems advisable to use data from the focal system or region when possible (e.g., if aiming to predict the spread of carp to Great Lakes tributaries, one should use recent data from Illinois River populations rather than older data from Russian populations).

Tabulating biological parameters also reveals important knowledge gaps. For example, as noted earlier, the total annual degree-days (ADD_{T_0}) required for achieving sexual maturity has only been determined for populations from the Amur River (Table 3), a climatically different system from the MRB. Similarly, the preferred and optimum temperatures for growth and consumption for MRB populations are largely unknown or based on anecdotal observations (Tables 6, 7). Some potentially useful parameters for modeling were not tabulated because data are lacking. These include survivorship, which is a component of the multivariate model used by Cuddington et al. (2014), and egestion/excretion allometric relationships and other bioenergetics modeling parameters.

Considering these knowledge gaps and the other potential difficulties with model parameterization highlighted at the outset of this review, bigheaded carp predictive models for the most part are carefully parameterized using the best information available. Some models, however, such as bioenergetics and EwE, need to be substantially improved before they can be considered reliable and realistic. Certain elements of some predictive tools can be updated using existing data (e.g., velocity requirements in the spawning suitability study of Kocovsky et al. 2012) but, in other cases, further research is needed. In light of this review, I recommend the following research priorities:

1. Better understand bigheaded carp phenotypic plasticity.

Enhancing our understanding of how and why certain traits vary among and within systems could improve predictive models. Spawning requirements and other life history attributes would be good initial targets for this research considering some of the differences observed between native and non-native populations, as well as between different non-native populations (e.g., spawning in the Wabash River vs. the Mississippi River). Local adaptation studies of bigheaded carps could take a number of approaches. Valiente et al. (2010) simultaneously compared genetic variation and life history traits (e.g., age determination from scales) of brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) populations from different sub-basins to determine if traits associated with invasive capacity differed between demes (they found that invasiveness did indeed differ between demes). A similar approach could be used to compare silver and bighead carp sub-basin populations throughout the MRB. Reciprocal transplant and common garden experiments are also advocated for local adaptation research, whereby, individuals from different populations are directly compared under the same environmental conditions (Kawecki and Ebert 2004). This approach was actually used in earlier morphological studies conducted in Asia (e.g., Shubnikova 1979) but, to my knowledge, no such experiments have been done since the development of genetic technologies for bighead and silver carps.

Studies of phenotypic plasticity should also include continued attention to bighead × silver hybrids in natural waters. Hybrids have become more prevalent in the MRB and other systems (e.g., Lake Balaton, Hungary), but it is still unclear how hybridization may affect bigheaded carps' invasive capacity. Earlier aquaculture studies found differences in survivorship, growth, gill-raker spacing, optimum temperature, and maximum temperature between hybrids and parental species (Bettoli et al. 1985; Hulata 1995; Naseka and Bogutskaya 2011). Hence, researchers should begin by comparing these traits among parental species, F1 hybrids, and post-F1 hybrids from natural waters (as opposed to aquaculture-raised specimens).

Additionally, research on phenotypic plasticity and local adaptation should extend beyond the MRB. Part of the reason this review focused on the imminent Great Lakes invasion is that there is a relative shortage of research on invasions outside North America. For example, bighead carp is established in the Danube River in Hungary (Kolar et al. 2007) but, aside from a report that bighead carp comprised more than 10 % of the fish biomass in two sections of the river from 2006 to 2008 (Florea 2012) and some commercial fisheries analyses (e.g., Jarić et al. 2014), there are few recent studies on Danube populations. Likewise, silver carp

have been established in South Africa since at least 1992, but little is known about invasions in this region, not to mention the African continent as a whole. However, ecological niche modeling was recently used to predict that silver carp could spread beyond their current distribution to large regions of northeastern South Africa (Lubcker et al. 2014). Because biological traits and invader effects seem to vary across habitats and regions, it is important to not neglect introduced populations outside North America.

2. Determine key biological traits of bigheaded carp populations in high risk habitats.

There are some populations in "high risk" habitats (i.e., where the spread of established populations to not-yet-invaded habitats is likely) for which important biological traits are unknown and, consequently, predictive models have used parameters from other, potentially phenotypically divergent, populations. For example, because ADD_{T_0} is useful for predicting suitable spawning habitat (Kocovsky et al. 2012), it would be preferable to determine the thermal maturity requirements for bigheaded carps in the MRB rather than using values obtained in the Amur River. As a preliminary estimation of required ADD_{T_0}, existing observations or estimations of spawning and maturity in the MRB (e.g., Coulter et al. 2013; DeGrandchamp et al. 2007; Williamson and Garvey 2005) could presumably be combined with U.S. Geological Survey (USGS) temperature data. Perhaps other temperature monitoring data from academic institutions could also be used if USGS temperature data are temporally or spatially mismatched with spawning observations in the MRB.

Similarly, the preferred and optimum temperatures for growth and consumption of bigheaded carps in the MRB are fundamental characteristics that are needed to refine bioenergetics and trophic models. Thermal requirements for embryonic and larval development have recently been determined (George and Chapman 2013), but more work is needed on adults (Table 7). Earlier I noted the limitations of laboratory-derived consumption rates but, perhaps, an awareness of these limitations could lead to the development of better methods for consumption experiments (e.g., measurements on free-swimming carp in temperature-controlled ponds or large tanks rather than cages or

smaller aquaria). As mentioned previously, egestion and excretion allometric relationships also need to be determined. Additionally, the food quality of different prey types in different habitats could be better studied to improve the accuracy of bioenergetics simulations.

3. Study the ecological effects of bigheaded carp in a range of habitats.

To better predict the potential ecological effects of bigheaded carps in the Great Lakes and other systems at risk of invasion, more research is needed on their effects on plankton and fish communities in large river channels, small streams, backwater lakes, reservoirs (of varying sizes and depths), large lakes (such as Lake Balaton in Hungary) and other habitats. Continuous monitoring in habitats at and near invasion fronts is especially critical, as understanding ecological conditions before movement into the habitat during the initial colonization phase and after establishment could help elucidate the full range of ecological effects. This monitoring should ideally include the density and taxonomic composition of plankton communities; concentrations of detritus; and condition, CPUE, and diet of native fish species. Also, potential indirect interactions with other invasive species, such as dreissenid mussels (*Dreissena polymorpha*) in the MRB, should be explored. Finally, as noted earlier, it would be worthwhile to assess the potential of native Great Lakes fishes and invertebrates (as well as native species in other systems at risk of invasion) to prey on larval and juvenile bigheaded carps. All of this knowledge could then be used to develop new EwE models and abundance-based ecological niche models. It could also highlight potential disease transmission pathways between bigheaded carps and native fishes.

In their review of fish bioenergetics models, Hansen et al. (1993) concluded with an important piece of wisdom: "A model is a lie that helps you see the truth" (a quote attributed to Robert H. MacArthur). All models are imperfect simplifications that have acknowledged limitations, and it is not the intention of this review to overemphasize these drawbacks. Instead, I hope that underscoring the strengths and shortcomings of predictive models and prioritizing research needs will lead to improved predictive tools, thereby aiding managers and other decision-makers in anticipating (and hopefully counteracting) the spread and effects of invasive bigheaded carps.

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