Updated (2006–early 2011) Biological Synopsis of Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*)

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UPDATED (2006–EARLY 2011) BIOLOGICAL SYNOPSIS OF BIGHEAD CARP (*HYPOPHTHALMICHTHYS NOBILIS*) AND SILVER CARP (*H. MOLITRIX*)

by

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Kipp, R., Cudmore, B., and Mandrak, N.E. 2011. Updated (2006–early 2011) biological synopsis of Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2962: v + 51 p.

Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*) (collectively known as bigheaded carps) have been introduced worldwide from their native ranges in eastern Asia. They were introduced in the United States in the early 1970s. Subsequently, the distribution of both species expanded throughout the Mississippi River basin. Currently, authorities are concerned about their potential to invade the Great Lakes via waterways connected to the Mississippi River watershed, live trade, or other pathways. This biological synopsis is intended to update information on these species, specifically focussing on literature written between 2006 and early 2011. It outlines the invasion histories, taxonomy, ecology, and impacts of these species. This report emphasizes the longevity, physiological tolerance, diet, fecundity, adaptability, dispersal potential, and impacts of Bighead Carp and Silver Carp where they have been studied.

RÉSUMÉ

Kipp, R., Cudmore, B., and Mandrak, N.E. 2011. Updated (2006–early 2011) biological synopsis of Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2962: v + 51 p.

La carpe à grosse tête (*Hypophthalmichthys nobilis*) et la carpe argentée (*H. molitrix*) (connues sous le nom des carpes à grosse tête) ont été introduites à l'échelle mondiale à partir de leurs distributions d'origine en Asie de l'Est. Elles ont été introduites aux États-Unis au début des années 1970. Par la suite, la distribution des deux espèces s'est étendue à travers le bassin hydrologique de la Rivière Mississippi. Actuellement, les autorités s'inquiètent de la possibilité qu'elles envahissent les Grands Lacs par des voies maritimes connectées au bassin hydrologique de la Rivière Mississippi, le commerce des poissons vivants ou toute autre voie d'introduction. Cette synthèse de la biologie est destinée à mettre à jour les informations sur ces espèces de carpes asiatiques, en mettant l'accent spécifiquement sur la littérature produite entre 2006 et 2011. Elle résume l'historique d'invasion, la taxonomie, l'écologie et les impacts de ces espèces. Ce rapport souligne la longévité, la tolérance physiologique, la diète, la fécondité, l'adaptabilité, la dispersion potentielle et les impacts de la carpe à grosse tête et de la carpe argentée où des études ont été menées.

1 INTRODUCTION

Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*) are two of three carp species in the genus *Hypophthalmichthys* that Kolar et al. (2007) refer to as bigheaded carps in their biological synopsis and risk assessment and are referred to here, as such. The term Asian carps is used in this document to refer to bigheaded carps, Grass Carp (*Ctenopharyngodon idella*), and/or Black Carp (*Mylopharyngodon piceus*). Bighead Carp and Silver Carp have been introduced worldwide, including to North America, and are the focus of this report (Herborg et al. 2007). These two species warrant simultaneous treatment in a biological synopsis because of their similar taxonomy, ecology, and invasion histories.

This document is presented within the mandate of Fisheries and Oceans Canada's Centre of Expertise for Aquatic Risk Assessment (CEARA) to provide up-to-date biological synopses for use in risk assessments of potential invaders to Canada. There is now a vast amount of information on bigheaded carps in the scientific literature. This report concentrates on current literature from 2006 to early 2011, following the extensive review of literature published prior to this period by Kolar et al. (2007).

1.1 NAME AND CLASSIFICATION

From Froese and Pauly (2011), ISSG (2011), and ITIS (2011):

1.1.1 <u>Bighead Carp</u>

Kingdom: Animalia
Phylum: Chordata
Class: Actinopterygii
Order: Cypriniformes
Family: Cyprinidae
Genus and species: *Hypophthalmichthys nobilis* Richardson, 1845

Synonyms: *Aristichthys nobilis* Richardson, 1845*
Hypophthalmichthys mantschuricus Kner, 1867
Leuciscus nobilis Richardson, 1845

Common English name: Bighead Carp
Common French names: carpe à grosse tête, carpe marbrée

*Although Bighead Carp is still frequently referred to as *Aristichthys nobilis*, genetic evidence supports the use of the genus name *Hypophthalmichthys* (Li et al. 2009). The American Fisheries Society Names Committee continues to recognize this name (Nelson et al. 2004; Mandrak, Fisheries and Oceans Canada, Burlington ON, pers. comm.).

1.1.2 <u>Silver Carp</u>

Kingdom: Animalia
Phylum: Chordata
Class: Actinopterygii
Order: Cypriniformes
Family: Cyprinidae
Genus and species: *Hypophthalmichthys molitrix* Valenciennes, 1844

Synonyms: *Abramocephalus microlepis* Steindachner, 1869
Cephalus mantschuricus Basilewsky, 1855
Hypophthalmichthys dabry Guichenot, 1871
Hypophthalmichthys dybowskii Herzenstein, 1888
Leuciscus hypophthalmus Richardson, 1945
Leuciscus molitrix Valenciennes, 1844
Onychodon mantschuricus Basilewsky, 1872

Common English name: Silver Carp
Common French names: carpe argentée, amour argenté

1.2 DESCRIPTION

Bighead Carp and Silver Carp (Figure 1) are large cyprinid fishes that closely resemble each other. They are both deep-bodied and spindle-shaped; however, Silver Carp is more laterally compressed than Bighead Carp. Bighead Carp displays a smooth keel between the anal and pelvic fins, while Silver Carp exhibits a keel from the throat to the vent. The keeling in both fishes distinguishes them from most native North American cyprinids, which generally lack this feature. Bighead Carp is greyish on the dorsal surface and cream on the ventral surface, with blotches varying from grey to black on the dorsal and lateral surfaces. The mottling, however, is often absent in turbid water. Silver Carp is grey-black dorsally, olive to silver-shaded laterally, and silver ventrally. Both species have small, cycloid scales. The lateral line scale count for Bighead Carp is between 95 and 120, while for Silver Carp it ranges between 85 and 108. Bighead Carp exhibits smooth-surfaced, spoon-shaped pharyngeal teeth in a single row with four on each arch. Silver Carp exhibits finely striated pharyngeal teeth that are long and bluntly rounded. The gill rakers of Silver Carp are long, thin, fused, porous, and sponge-like, and are specifically adapted to filter phytoplankton. In contrast, the gill rakers of Bighead Carp are not fused and appear more like combs. They are adapted for general use, including filtration of some phytoplankton and zooplankton. Large individuals of both species can grow to sizes upwards of 40 kg. Bighead Carp can reach 1.5 m in length and approximately 16 years of age, while Silver Carp can attain lengths over 1.2 m and live 15–20 years (Chen et al. 2007a; Kolar et al. 2007).

Bighead Carp and Silver Carp are closely related and, as a result, have been known to hybridize. One study from a backwater of the Illinois River (Lamer et al. 2010) indicated that the gill rakers of F1 hybrids were twisted 88% of the time, while post-F1 hybrids were challenging to identify. In this study, 12.5% of a sample of individuals identified morphologically as either pure Bighead Carp or Silver Carp were actually hybrids. In general, gill rakers appearing like those of Bighead Carp, but showing clubbed ends or waviness, and those appearing like gill rakers of Silver Carp, but with incomplete fusion and raggedness, are indicative of hybrids (Kolar et al. 2007).

Larvae and eggs of bigheaded carps can be differentiated by a number of morphological characteristics from those of common North American species and have been described by Chapman and Wang (2006). The larvae of *Hypophthalmichthys* species exhibit 25–28 preanal myomeres and 12–14 postanal myomeres. These characteristics separate them from similar-looking catostomid larvae in much of the Mississippi River basin, where the bigheaded carps have been introduced. In general, most eggs of bigheaded carps are >4.9 mm in diameter, while native cyprinid eggs are usually at least 1.5 mm smaller. Newly hatched bigheaded carp larvae are around 6 mm in length. In contrast, larvae of native cyprinids are usually 4 mm or less. Bigheaded carp larvae exhibit eyes that are larger, more circular, and positioned more towards the anterior end in comparison to many native cyprinids and catostomids. The eyes of most native taxa are typically more dorsoventrally flattened. Bigheaded carp larvae also exhibit a dark spot on the inner ventral side of the eyes just before they undergo complete pigmentation. Finally, bigheaded carps show melanophore development at the preanal and anal finfold when they reach the one-chamber-gas-bladder or dorsal-fin-differentiation stage (Chapman and Wang 2006). This is unlike any other species in the region where they have been introduced in the United States. As seen in Figure 2, the patterns of these melanophores differ substantially, enabling this feature to be used to identify between species.

2 DISTRIBUTION

2.1 NATIVE DISTRIBUTION

Bighead Carp and Silver Carp are native to similar regions of eastern Asia. The native range of Silver Carp, however, is larger than that of Bighead Carp. The centre of evolution for Bighead Carp is in the Yangtze River (Li et al. 2010a). Both species have historically occupied the main channel of this river, as well as backwaters and thousands of lakes throughout its floodplain (Chapman and Wang 2006). The range of Silver Carp in China extends from the Pearl River in the south, to the Amur River in the north along the border with Russia. Silver Carp is native to North Korea and probably to Vietnam (Kolar et al. 2007). In contrast, Bighead Carp is native to the Yangtze, Yellow, and Pearl rivers in China, river mouths in southeastern Russia, and extreme northern North Korea. Despite these records, due to historical introductions, it is difficult to precisely define the native ranges of bigheaded carps (Chen et al. 2007a; Kolar et al. 2007).

2.2 NON-NATIVE DISTRIBUTION

2.2.1 Global

In China, bigheaded carps have been propagated by people beyond their native range limits. As a result, Silver Carp are now present throughout most of China. Bighead Carp occurs from Hainan Island in the south, to the Amur River in the north (Chen et al. 2007a).

Bigheaded carps have been introduced worldwide for aquaculture, improvement of fisheries, control of phytoplankton and zooplankton, and for research purposes (Tables 1 and 2). Current records indicate that Bighead Carp has been introduced to 80 countries or territories, and is established in at least 29 of these. Silver Carp has reached 94 countries or territories, and has become established in at least 29 of these. Either Bighead Carp or Silver Carp or both species are established in the following major Eurasian rivers: Danube, Amu Darya, Ural, Volga, Terek, Don, and Dniester. Populations frequently occupy lower sections of these rivers. Most introductions of both species occurred throughout the 1960s and 1970s (Kolar et al. 2007). Both species still continue to be propagated and expand their ranges worldwide. For example, Bighead Carp was found for the first time in the wild in the United Kingdom in 2006 (Britton and Davies 2007).

2.2.2 North America

Bighead Carp and Silver Carp were first introduced to the United States between 1971 and 1973. Reasons cited for intentional introduction range from biological control of plankton to research, fisheries, or aquaculture (Kolar et al. 2007). Additional introductions occurred accidentally when bigheaded carps escaped from facilities where they were being contained. At the same time, Asian carps continued to be introduced in many states for biological control. Flood events throughout the 1980s and 1990s contributed to their widespread dispersal and recruitment. Bighead Carp was recorded for the first time in the wild in 1981 in the Ohio River, while Silver Carp was recorded as early as 1974 or 1975 in Bayou Meto and the White River in Arkansas (Chen et al. 2007a; Kolar et al. 2007). Bigheaded carps have now been recorded in a number of states throughout the Mississippi River drainage, including main tributaries such as the Missouri, Ohio, and Illinois rivers (Figure 3). Although both species have been recorded outside of this drainage basin in North America, in most cases populations failed to establish. Although bigheaded carps occur throughout the Mississippi River watershed, they are not established in all tributaries. For example, they have not been detected in the Niobrara River, a tributary of the Missouri River in Nebraska (Wanner et al. 2010).

There are several artificial or manmade connections through which aquatic invasive species (AIS) can reach the Great Lakes from the Mississippi basin and vice versa. The Chicago Area Waterway System (CAWS), a permanent manmade link between Lake Michigan and the upper Illinois River, is considered the most important (GLMRIS 2011). The migration of bigheaded carp through the CAWS is a major concern (ACRCC 2010), and to prevent their dispersal into the Great Lakes basin through the Chicago Sanitary and Ship Canal, a part of the CAWS, an electric barrier has been deployed (Figure 4). Bigheaded carp populations in the Illinois River are large and, therefore, pose a serious invasion threat to the Great Lakes. Over the past decade, Silver Carp populations in this area increased exponentially; a study from the La Grange Reach in 2007–2008 indicated with 95% confidence that the Silver Carp population ranged from 231,226 to 484,474 individuals (Sass et al. 2010). This corresponds to 496–1,040 metric tonnes of biomass, and an average of 2,544 fish km^{-1}. In 2008, Silver Carp accounted for more than half the fish species collected.

Environmental DNA (eDNA) from bigheaded carps has been detected above the electric barrier in the Chicago Sanitary and Ship Canal (ACRCC 2010; Stockstad 2010; Jerde et al. 2011). According to Jerde et al. (2011), numerous eDNA samples suggested that the Silver Carp invasion front was in the Calumet Harbor of Lake Michigan and the Bighead Carp invasion front was in the Calumet River, within 13 km of Lake Michigan, in 2009–2010. However, these results could indicate the presence of adult bigheaded carps above the barrier, or could also reflect the transfer of eggs or DNA by other means (e.g., in bilge water, wastewater, or excrement of predators) from one side of the barrier to the other (ACRCC 2010; Jerde et al. 2011). In addition to eDNA, a live Bighead Carp specimen was found in the Chicago Sanitary and Ship Canal, potentially having breached the electric barrier in 2009 (Whitledge 2010). A second individual was found in 2010 in Chicago’s Lake Calumet, which drains into Lake Michigan. The individual found in 2009 appeared to have spent most of its life in the Illinois River, based on otolith chemistry (Whitledge 2010). However, the results for the individual found in 2010 suggested that it had spent much of its life in the Lake Calumet/Lake Michigan region (Whitledge 2010). These results were based on one specimen only and relied on the assumptions that otolith chemistry in this Bighead Carp was stable over time and was similar to patterns seen in other fish species in the region (Ziegler and Whitledge 2010).

FinallyA recent study examining mitochondrial DNA concluded that Bighead Carp established in the United States may have some genetic connection with populations in the Danube River basin (Li et al. 2010a). This study also showed that the American population exhibits relatively high values of nucleotide diversity, or the degree of polymorphism within the population, contrary to expectation. This could be due to the large size of the population, a high degree of adaptation, or multiple introduction events (Li et al. 2010a).

2.2.3 Predicted North American Range

A number of recent studies employed different modelling and mapping techniques to predict where bigheaded carps could establish or achieve high population densities in North America. These studies made predictions at different scales, ranging from the size of a river to the entire continent. In a smaller-scale study, Stainbrook et al. (2007) mapped preferred habitats of bigheaded carps in the upper Illinois Waterway, including the Illinois River, Des Plaines River, and Chicago Sanitary and Ship Canal. These authors highlighted where populations would encounter the most favourable conditions. The study found a decline in availability of preferred habitats towards Lake Michigan, especially between the La Grange pool at river mile 80 and the electric barrier in place in the canal at river mile 296. The decline in preferred habitats was based on measurements of lower productivity, Secchi depth, dissolved oxygen, and specific conductance in this stretch of the waterway compared to regions further downstream. Results also indicated a lack of long open river stretches with high velocity in upstream areas. All stretches were less than 56 km in length. One hundred km of uninterrupted river may be necessary for successful reproduction of bigheaded carps (Kolar et al. 2007); however, this requirement may be lower, potentially around 50 km (Hansen 2010, N. Mandrak, Fisheries and Oceans Canada, pers. comm.).

At the scale of the Great Lakes, two recent studies matched resource availability with bigheaded carp requirements, to attempt to predict establishment success. Cooke et al. (2009) first carried out a 37-day laboratory experiment testing Bighead Carp condition under a low density plankton treatment (700 μgL^{-1} dry zooplankton; 14 μgL^{-1} chlorophyll *a*) and a high density plankton treatment (1900 μgL^{-1} dry zooplankton; 25 μgL^{-1} chlorophyll *a*). Juvenile carps lost weight in the low density treatment and gained weight in the high density treatment. The lower density treatment employed lower overall plankton densities than those occurring in many regions of the Great Lakes proper. However, the authors noted that in shallows with higher plankton densities, establishment in the littoral zones could be possible. Furthermore, in the western and central basins of Lake Erie, phytoplankton densities can be 40 times higher than in the eastern basin and zooplankton densities can be twice as high, potentially facilitating successful establishment. The ability of Bighead Carp to survive on detritus and resuspended organic material could also aid establishment in some regions. Similarly, Cooke and Hill (2010) used bioenergetics models to predict changes in growth of bigheaded carps under different productivity regimes in the Great Lakes. Using a combination of experimental derivations and literature searches, they arrived at the conclusion that a 2400 g Bighead Carp requires 61.0 $kJday^{-1}$ to maintain body mass at rest at 20℃, while a similar-sized Silver Carp requires 91.0 $kJday^{-1}$. By matching the basic energy requirements with known productivity data from the Great Lakes, researchers were able to predict where positive growth could occur in this region (Table 3). In general, open water habitats did not allow the two species to achieve positive growth, while positive growth could be achieved in some productive embayments and wetlands. The authors noted, however, that these species can decrease their metabolism at low temperatures and still show positive growth.

Three recent studies opted for a broad-scale approach and made predictions with respect to potential establishment throughout North America. The first study (Whittier and Aitkin 2008) focussed on one variable, water hardness, and attempted to match potential habitats with bigheaded carp preferences, following up on the hypothesis that soft water may limit the reproduction of bigheaded carp. This hypothesis originated from a study undertaken in the Philippines, cited by Whittier and Aitkin (2008), which found that optimal water hardness values for hatching success of Silver Carp varied between 300 and 500 mgL^{-1} $CaCO_3$. Whittier and Aitkin (2008) determined that, with several exceptions, the median water hardness in areas where Bighead Carp was known to reproduce ranged from 116 to 254 mgL^{-1}; Silver Carp occupied a subset of these areas. They then classified ecoregions across the contiguous United States as soft water or hard water, relative to the reproduction of bigheaded carp. They found that, for many rivers of New England, the southeastern states, and western regions in the Pacific northwest, the 75th percentile of water hardness values was less than 65 mgL^{-1}. The authors noted most of the areas with bigheaded carp reproduction were located in the hard-water ecoregions; however, they cautioned it is possible that bigheaded carps have not established in the soft-water ecoregions because they might not have been introduced into these areas. See Section 3.2 for more updated information on greater tolerance to water hardness.

The final two studies employed niche-based modelling using a combination of environmental parameters and bigheaded carp preferences to predict potential North American range expansion. Chen et al. (2007a) employed Genetic Algorithm Rule-set Prediction (GARP) for their models and incorporated both topographic and climatic variables. These models predicted a broader geographic range for Silver Carp than Bighead Carp (Figure 5). Silver Carp models indicated ability to survive across the Mississippi River watershed, as well as Oregon, northern California, northern Idaho, eastern Montana, and some parts of southern Canada. The potential range included establishment in the Great Lakes drainage. For Bighead Carp, the predicted range did not reach southern Lake Michigan and did not encompass all known northern records at the time of the study. The authors attributed this mismatch to non-breeding individuals caught in the wild beyond the limits of established populations. However, Bighead Carp is currently established north of the range predicted (Figure 3).

Herborg et al. (2007) also used environmental niche-based GARP models to make similar predictions. For the bigheaded carp species, precipitation variables were the most important predictors of species presence. Mean daily precipitation contributed 60.5% to prediction accuracy in the Bighead Carp model and 34.7% in the Silver Carp model. The importance of precipitation was probably related to high spring flow requirements in large rivers. The authors noted that inclusion of flow data, water temperature, and water chemistry, if they had been available, could have improved the models. Based on the niche models, Silver Carp could expand across most of Canada, excluding the far north, while Bighead Carp could expand across much of this same territory, but would be more restricted in terms of northern expansion (Figure 6). Nevertheless, the Bighead Carp model successfully predicted establishment at the far northern edge of the current distribution, in contrast to the model by Chen et al. (2007a). Herborg et al. (2007) noted that the disparity could have resulted from the use of different criteria for selecting points in the native range. For example, the use of points based on museum records perhaps underestimates the extent of native range habitat, whereas, use of random points derived from range maps could result in an overestimation of range. Different model outcomes could have also been attributed to differences in the way environmental variables were selected.

3 BIOLOGY AND NATURAL HISTORY

3.1 AGE AND GROWTH

Although it is relatively difficult to accurately age bigheaded carps (Kolar et al. 2007), size and age data on these species has been summarized (Britton and Davies 2007; Williamson and Garvey 2005). These data should be interpreted with caution as sample sizes differed and aging techniques are not always reliable. Results indicate that both species grow relatively quickly in habitats to which they have been introduced in the United States in comparison to other regions (Figure 7). For example, Bighead Carp in the Missouri River reached around 700 mm by age 5; however, in Polish lakes and a lake in England, they attained similar lengths later, at age 7 or 8. Similarly, Silver Carp reached 700 mm in the Mississippi River around age 4, while they attained a similar length around age 5 in an reservoir in India, and never attained such lengths in the Amur River where they are native. Garvey et al. (2007) calculated *k*, the growth rate from a von Bertalanffy model characterizing length at age relationships. This study compared the Silver Carp growth rate (*k*) of 0.63 found in unimpounded middle reaches of the Mississippi River, with that of 0.41 found for Silver Carp at the confluence of the Illinois River with the Mississippi River, in an impounded pool. In contrast, Bighead Carp in the latter region showed a growth rate (*k*) of 0.24. Overall, Bighead Carp displayed slower growth, lower fecundity, higher survival, later maturity, and longer lifespan than Silver Carp.

Studies from introduced habitats in American rivers have recorded average and maximum sizes of bigheaded carps. Between 2003 and 2009, maximum size of adult Silver Carp varied across these studies 778–954 mm and 6.1–8.6 kg, depending on season and habitat (DeGrandchamp 2006; Garvey et al. 2007; Wanner and Klumb 2009a; Calkins 2010; Sass et al. 2010). Between 2003 and 2007, maximum size of adult Bighead Carp varied 865–1242 mm and 9.5–19.3 kg, depending on season and habitat (DeGrandchamp 2006; Garvey et al. 2007; Wanner and Klumb 2009a). On average, adult Silver Carp ranged 557–795 mm and 3.9–6 kg between 2004 and 2009, depending on habitat, season, sex, and type of fishing gear (DeGrandchamp 2006; Papoulias et al. 2006; Wanner and Klumb 2009b; Calkins 2010; Sass et al. 2010). On average, adult Bighead Carp ranged 531–827 mm and 5–5.7 kg between 2003 and 2007, depending on habitat, season, sex, and type of fishing gear (DeGrandchamp 2006; Papoulias et al. 2006; Wanner and Klumb 2009b). It is not uncommon for Bighead Carp to achieve lengths over 1 m in regions where they are commonly stocked. For example, Arthur et al. (2010) reported a maximum length of 1.1 m for individuals stocked in the Mekong region of Laos.

Male and female bigheaded carps may attain similar sizes in some habitats and years; however, when they differ, females are larger than males. For example, female Bighead Carp and Silver Carp were larger than males in the Missouri River between 2003 and 2005 (Papoulias et al. 2006). DeGrandchamp et al. (2007) showed that Bighead Carp females were larger than males in a flood year (2004) and a drought year (2005) in the lower Illinois River. However, Silver Carp females were larger than males only in the drought year.

Two studies published in 2009 from the hyperproductive Lake Taihu in China measured bigheaded carp growth rates and estimated daily gains in weight. The first study from Meiliang Bay (Zhou et al. 2009a) indicated that Silver Carp ranging in size 200–600 mm grew on average 5.4 g day^{-1} in 2004 and 3.5 g day^{-1} in 2005. Bighead Carp grew on average 7.3 g day^{-1} in 2004 and 5.6 g day^{-1} in 2005. Growth may have been lower in 2005 due to the proportion of protein-rich zooplankton in the diet declining from 2004 to 2005. In contrast, a second study from the same bay (Guo et al. 2009) found that Silver Carp mean wet weight ranged from around 0.2 kg in May to 1.0 kg in September 2005, and increased by 0.005 g day^{-1} [sic] between January and May and by 0.014 g day^{-1} [sic] from May to September. Bighead Carp ranged from around 0.2 kg in May to 1.1 kg in September, and growth rates ranged from 0.005 g day^{-1} [sic] to 0.013 g day^{-1} [sic] over this time period. These studies indicate that growth rates can be highly variable, even in similar habitats at similar times.

Using bioenergetics models, Cooke and Hill (2010) determined that bigheaded carps would likely exhibit more positive growth at lower temperatures if they were to establish in the Great Lakes due to slower metabolic rates. Positive growth could occur in regions with low productivity if temperatures were low. Weight loss would likely occur more at higher temperatures when metabolism increases. However, results indicated that Bighead Carp grew best at temperatures between 26℃ and 33℃, and exhibited reduced growth at temperatures of 7–15℃ (Afzal et al. 2008). Hogue and Pegg (2009) reported that bigheaded carps exhibit relatively high metabolic rates and require greater energy intake in comparison to native North American fishes occupying similar habitats. They found that oxygen consumption in bigheaded carps increases with size and water temperature.

3.2 PHYSIOLOGICAL TOLERANCE

Several studies have been carried out to determine the effect of water hardness on the hatching success of bigheaded carp eggs. Chapman and Deters (2009) showed experimentally that fertilized eggs of Bighead Carp displayed similar hatching success and attained similar sizes at a variety of water hardness values. Egg bursting never occurred in treatments with water hardness values ranging 28.5–259.0 mgL^{-1} $CaCO_3$ and 48.3–395.0 mgL^{-1} total dissolved solids. Hatching success was less than 50%. Chapman and Deters (2009) noted that it is theoretically possible for very low water hardness to cause egg bursting due to low osmotic concentrations, allowing excess pressure within eggs. Furthermore, egg bursting or mortality could occur if calcium ions, required for egg hardening, are lacking. They noted that hardness values are very low and range from 28 to 84 mgL^{-1} $CaCO_3$ in the native Yangtze River in China. Rach et al. (2010) experimentally tested Silver Carp egg enlargement and hatching success under different water hardness values ranging 50–250 mgL^{-1} $CaCO_3$. Although eggs swelled most in the water with hardness of 50 mgL^{-1} $CaCO_3$, they also exhibited the highest hatching success. Water hardness values during subsequent incubation had no effect on egg hatching success.

Bigheaded carps have evolved specific tolerances to toxins produced by cyanobacteria they may consume (Li et al. 2007, 2010b). They may be capable of inhibiting passage of the majority of such toxins from the intestinal wall into the internal organs (Zhang et al. 2009). However, a study by Chen et al. (2007b) found that microcystins produced by cyanobacteria were likely absorbed through the walls of the mid-gut of Bighead Carp. A study by Chen et al. (2006) noted that only the most toxic microcystins were inhibited from moving across the gut wall in Silver Carp. This study also showed that Silver Carp accumulated a lower concentration of microcystins in the liver in comparison to other animals at the same study site in Lake Taihu, China. In general, a number of studies indicate that Bighead Carp and Silver Carp exhibit a genetic basis for efficient microcystin detoxification (Liao et al. 2006; Li et al. 2008; He et al. 2010; Li et al. 2010c). Nevertheless, in spite of the relative tolerance of bigheaded carps to microcystins, consumption of cyanobacteria can still exert negative effects on these fishes. For example, a study by Qiu et al. (2009) from a hypereutrophic region of Lake Taihu in China, found negative consequences of cyanobacteria consumption on bigheaded carp livers and kidneys, as well as evidence for potential toxicogenomic effects.

A study by Pan et al. (2010) found a lectin molecule in Bighead Carp gills capable of exerting a negative effect on the growth of *Vibrio harveyi*, a pathogenic bacterium.

3.3 REPRODUCTION

The eggs of bigheaded carps are semi-transparent and exhibit thicker membranes than those of Grass Carp (*Ctenopharyngodon idella*) (Yi et al. 2006). Bigheaded carp eggs are very small when first released into the water (Yi et al. 2006; Chapman and Deters 2009). Subsequently, mature eggs are fertilized and their vacuoles are broken, which causes some fluid to be discharged. Water is then absorbed by the eggs, causing them to expand. In the native Yangtze River in China, Bighead Carp eggs range in size 4.9–6.7 mm, with most >5.5 mm, while Silver Carp eggs range in size 3.5–6.4 mm, with most >4.5 mm (Yi et al. 2006). In a study from the United States, Bighead Carp egg diameters ranged 5.5–6.8 mm (Chapman and Deters 2009).

Asian carps usually migrate upriver in response to high spring flow, releasing eggs to float downstream into nursery habitats as they develop and hatch after about 35 hours (Chen et al. 2007a; Xie et al. 2007). Asian carp eggs exhibit low densities and are semibuoyant; they require a discernible current that creates turbulence to prevent them from sinking to the bottom (Kolar et al. 2007). Due to flow requirements, unobstructed stretches in large rivers of 50 km (Hansen 2010, N. Mandrak, pers.comm.) to 100 km (Kolar et al. 2007; Stainbrook et al. 2007) are traditionally considered necessary for Asian carp eggs to successfully develop. However, the exact length of river required probably depends on other parameters such as flow velocity and temperature (Kolar et al. 2007). Garvey (2007) used ultrasonic tagging of bigheaded carps and found that adults may need to migrate away from impounded pools and into unimpounded portions of the Mississippi River with current >0.7 ms^{-1} during low flow years to successfully reproduce. In a study conducted in the lower Illinois River (DeGrandchamp et al. 2007), bigheaded carp larvae were only present for 5% of sampling weeks in 2005 at average densities of 0.0006 m^{-3} between May and July, due to drought conditions with flow <0.2 ms^{-1}. In contrast, larvae occurred in 32% of sampling weeks in 2004, at average densities of 0.03 m^{-3} between May and July. In the latter year, there was considerable flow, and velocity was ≥0.7 ms^{-1} during flood conditions. In this study, the larval densities of bigheaded carps during peak densities in 2004 were still 100 times lower than total larval fish abundance.

Age at maturation in Bighead Carp may range from 2 to 8 years, and for Silver Carp, from 2 to 6 years, with males maturing one year earlier than females (Kolar et al. 2007). In both species, older age at maturity is typically recorded in colder climates, as maturation rate depends on water temperature (Kolar et al. 2007). A study from the Mississippi River found mature Silver Carp females as young as age 2 in unimpounded reaches (Garvey et al. 2007). In contrast, age at maturity in an impounded reach was three for Silver Carp females and four for Bighead Carp females.

Although spawning events in bigheaded carps are typically triggered by rising floodwaters, they also occur at water temperatures between 18℃ and 30℃ in native and some introduced habitats (Chen et al. 2007a; Kolar et al. 2007; Duan et al. 2009), such as the Upper Mississippi River (Lohmeyer 2008; Lohmeyer and Garvey 2009). Even so, Silver Carp spawning has been observed in the Missouri River once temperatures reached 14℃ in late March (Papoulias et al. 2006).

Spawning periods typically range from April or May to July in the native range (Chen et al. 2007a; Duan et al. 2009). Spawning events in the native Yangtze River are not synchronous between the two species (Yi et al. 2006). In studies in the United States, multiple spawning events have been recorded throughout the summer and as late as October. In the Missouri River, female bigheaded carp ovaries were either partially or completely spent over the spring to fall season (Papoulias et al. 2006). This indicates that some females may have spawned more than once (Kolar et al. 2007). In the Upper Mississippi River, larvae occurred during peaks in discharge in late May to early June in both 2005 and 2006 (Lohmeyer 2008; Lohmeyer and Garvey 2009). In 2005, a second spawning event was recorded as larvae were again present during an increase in discharge in late August. This also corresponded to a decline in temperature from 32℃ to 27℃.

Bigheaded carps exhibit high fecundity. In general, the number of eggs females can produce increases with age, length, and weight (Kolar et al. 2007). In a study from the lower Illinois River in 2004 (DeGrandchamp et al. 2007), the mean number of eggs per female Bighead Carp across summer months was 180,000, while 280,000 eggs were recorded per female Silver Carp. In 2004, the river exhibited relatively high water levels. In 2005, a year of drought, these numbers increased to 750,000 and 1,600,000, respectively. The increase likely indicated that individuals did not spawn during the drought year, resulting in higher observed egg quantity, while many of the females caught in 2004 had already partially spawned. Similarly, in a 2004 study from the Mississippi River (Garvey et al. 2007), female Bighead Carp caught in an impounded reach harboured 4,792–473,200 eggs, while Silver Carp females harboured 26,650–

598,767 eggs. In the 2005 drought year, when all eggs were resorbed, Bighead Carp females produced 88,133–1,938,333 eggs and Silver Carp females produced 274,917–3,683,150 eggs. These numbers are substantially higher than maximum fecundities known for native species such as: Channel Catfish (*Ictalurus punctatus*), which produces a maximum of around 70,000 eggs; Paddlefish (*Polyodon spathula*), which produces a maximum around 142,000 eggs; and, Gizzard Shad (*Dorosoma cepedianum*), which produces a maximum around 350,000 eggs (Garvey et al. 2007). The data suggest that the reproductive potential of bigheaded carps was higher than that of native fishes in the region.

As previously mentioned, Bighead Carp and Silver Carp are closely related and may hybridize. Lamer et al. (2010) surveyed populations from the backwaters of the Illinois River, finding that 22.5% of 120 fishes caught showed hybridization. They found F1 and post-F1 hybrids with a high level of introgression. Consequently, the authors noted that a hybrid swarm could develop, with the potential to negatively affect fitness and condition of these fish species.

Papoulias et al. (2006) found intersex individuals of bigheaded carps in the Missouri River. They concluded this could have occurred because of contaminants in the water.

3.4 FEEDING AND DIET

Kolar et al. (2007) reported that Bighead Carp probably uses a combination of feeding methods, including: pump feeding, during which individuals hang almost vertical to the water surface, employing the buccal pump to push water through the gill rakers and trap particles; and, ram suspension, during which individuals swim horizontally, holding the mouth open and forcing water through the gills. Bighead Carp is typically zooplanktivorous, but can be very opportunistic, consuming a variety of prey items (Kolar et al. 2007). In a 2002–2003 study in backwater lakes of the Illinois and Mississippi Rivers, Bighead Carp positively selected for *Keratella* spp. (rotifers), Bosminidae, Chydoridae, cyclopoid copepods, and ostracods (Sampson et al. 2009). In contrast, one western Chinese study in a pond-wetland system recorded that stocked Bighead Carp consumed 100% algae, 90% of which were cyanobacteria (Wu et al. 2010). Larval and juvenile Bighead Carp are known to feed on both zooplankton and phytoplankton (Guo et al. 2008; Cooke et al. 2009).

Silver Carp uses pump feeding and can filter smaller particles than Bighead Carp (Kolar et al. 2007). In general, adults are phytoplanktivorous, but they are also opportunistic feeders and can consume a variety of zooplankton (Kolar et al. 2007). Silver Carp populations alter the length of their gut in response to environmental conditions as they grow (Ke et al. 2008a). When feeding on more phytoplankton, gut length increases in order to enhance uptake of nutrients from phytoplankton. In the Mississippi River, Calkins (2010) compared the concentration of chlorophyll *a* in the diet with that available in the environment. The study concluded that concentrations in the foregut were generally high despite environmental variability. This suggested that Silver Carp was capable of consuming high amounts of phytoplankton even when resources were scarce. Similarly, a study by Pongruktham et al. (2010) in an oxbow lake of the

Mississippi River found that Silver Carp guts generally contained much higher concentrations of phytoplankton relative to the euglenoid algae, cyanobacteria, and diatoms available in the water column. A study from the Mississippi River (Garvey et al. 2007) showed that chlorophyll *a* concentrations in gut mucus were higher in August and September, but declined by October and November. Silver Carp consumed large amounts of phytoplankton, but also consumed cladocerans, rotifers, and detritus. Finally, in backwater lakes of the Illinois and Mississippi Rivers in 2002–2003, Silver Carp positively selected for three rotifers (*Keratella* spp., *Brachionis* spp., and *Trichocera* spp.) (Sampson et al. 2009).

In some instances, Silver Carp may selectively feed on specific particle sizes or taxa. Zhou et al. (2011) studied Silver Carp feeding in the Three Gorges Dam Reservoir in China, showing that this species was unable to efficiently filter phytoplankton <10 μm. In this study, Silver Carp consumed rotifers and copepods, but not cladocerans, possibly because of low densities of the latter taxon that would have resulted in low encounter rates. Ma et al. (2010) found that Silver Carp consumed large colony-forming *Microcystis* phytoplankton most efficiently. It filtered phytoplankton ranging in size 5–20 μm some of the time, and rarely filtered phytoplankton <5 μm such as the green algae *Chlamydomonas* and *Platymonas*. In an oxbow lake off the Mississippi River, Pongruktham et al. (2010) reported that Silver Carp selectively fed on euglenoid algae and avoided cyanobacteria. In this study, some euglenoid algae and pinnate diatoms also survived passage through Silver Carp digestive tracts, in contrast to rotifers, the dominant zooplankton present.

Bighead Carp and Silver Carp lack stomachs and are typically capable of efficiently digesting and assimilating zooplankton more easily than most phytoplankton. A 2004 study in a highly productive bay in Lake Taihu, China (Zhou et al. 2009a), indicated that Bighead Carp diet was comprised of 21.8% phytoplankton and Silver Carp diet was comprised of 45.4% phytoplankton. In 2005, these fish species consumed 45.3% and 79.0% phytoplankton, respectively. The remainder in all cases was zooplankton, and growth for both carps was slower in the year when fewer zooplankton were consumed.

A second study from the same region of Lake Taihu (Guo et al. 2009) recorded that Silver Carp generally consumed more plankton in proportion to body weight than Bighead Carp, especially during periods of high productivity. In this study, both species consumed green algae and cyanobacteria in differing proportions depending on the season. Cladocerans always dominated in the zooplankton component of the diet of both species. Phytoplankton dominated Silver Carp diet at 80–85%, regardless of time of year. However, for Bighead Carp, 90% of the diet in May was zooplankton, compared to less than 50% in September. In the latter month, there was an outbreak of large, easily consumed colonies of *Microcystis*. Decreased water clarity may also have exerted an effect on selective feeding of Bighead Carp, favouring phytoplankton consumption over zooplankton consumption. Finally, a study conducted in the same Chinese lake (Ke et al. 2007), recorded filtration rates of phytoplankton by Bighead Carp and Silver Carp of 0.02–0.68 $Lg^{-1}h^{-1}$ and 0.22–1.53 $Lg^{-1}h^{-1}$, respectively. Filtration rates of zooplankton were 0.08–1.41 $Lg^{-1}h^{-1}$ and 0.24–0.44 $Lg^{-1}h^{-1}$, respectively.

3.5 HABITAT

In their native habitat, bigheaded carps primarily occupy large rivers and associated floodplain backwaters and lakes. They have also been introduced to many ponds, lakes, reservoirs, and canals. In general, a large river channel is considered necessary for successful spawning, while juveniles typically utilize nursery areas in floodplain backwaters and lakes (Chen et al. 2007a; Kolar et al. 2007).

A large number of studies have focussed on documenting habitat use of bigheaded carps in areas they have invaded in North America. One study (Stainbrook et al. 2007) combined a literature review with an expert questionnaire to estimate the range of preferred habitat variables of bigheaded carps in invaded regions. The following preferences were reported: 578–726 μScm^{-1} conductivity; 30–97 μgL^{-1} chlorophyll *a*; 7–10 mgL^{-1} dissolved oxygen; >3 m depth; 0–1.5 ms^{-1} flow velocity; 21–30℃ water temperature; and <0.6 m water clarity. Overall, preferred habitat types reported in the survey were confluences with tributaries, backwaters, regions below dams, side channels, and channel borders.

A study from the Mississippi River (Calkins 2010) found that Silver Carp occurred more frequently in backwaters and channel borders with lower current speed and higher chlorophyll *a* concentrations than in other areas of the river. Similarly, Garvey (2007) found that bigheaded carps typically preferred channel borders or side channels in the Mississippi River. A lower Illinois River study (DeGrandchamp 2006; DeGrandchamp et al. 2008) found that bigheaded carps preferred channel borders during low summer flow. Mean depth selected by both species varied between 3.8 and 4.1 m in spring and summer, and mean velocity preferred was 0.2 ms^{-1}. In spring, Bighead Carp selected river reaches with mean temperature of 16.1℃, while Silver Carp selected areas with mean temperature of 17.7℃. In summer, these preferences changed to 27.0℃ and 27.1℃, respectively. Mean dissolved oxygen content in preferred spring habitats was 9.9 mgL^{-1} and 9.0 mgL^{-1} for Bighead Carp and Silver Carp, respectively. These values changed to 6.0 mgL^{-1} and 6.4 mgL^{-1} for each, respectively, in summer.

A study by Schultz et al. (2007) on Lower Swan Lake, a backwater of the Illinois River, found that Bighead Carp <300 mm immigrated into this waterbody in winter, and did not consistently prefer one region of the water column. Silver Carp <300 mm was caught most frequently in this backwater in the fall and winter, and consistently preferred channel edges and middle and lower depths in the water column.

Finally, one study from the Mississippi River focussed on larval bigheaded carp habitat use (Lohmeyer 2008; Lohmeyer and Garvey 2009). It found that larval density was higher in open river reaches than in impounded ones in 2005 and 2006. However, in 2007, during a high flow year when gates in the study region were open for longer, a high density of larvae occurred in an impounded pool. This was attributed to the high spring flood that year in comparison with the lower spring flows in 2005 and 2006. During low flow years, and especially when lock and dam gates were closed, bigheaded carp larvae were more restricted in their habitat use.

3.6 INTERSPECIFIC INTERACTIONS

No research has examined predation in North America by fishes or birds on bigheaded carp juveniles. Most research on interspecific interactions between bigheaded carps and other species has examined predation of bigheaded carps on plankton and potential competitive effects through diet overlap between bigheaded carps and other fish species (see Section 4.1).

A few studies have examined competitive interactions between Bighead Carp and Silver Carp. A stable isotope study from the Illinois and Mississippi Rivers (Rogowski et al. 2009) showed that Bighead Carp fed higher up the food chain than Silver Carp. This diet differentiation may enable coexistence between the species and decrease competition. A stable isotope study by Zhou et al. (2009b) from a hypereutrophic bay in Lake Taihu, China, indicated that the two species occupied the same trophic level and consumed very similar amounts of phytoplankton and zooplankton. Ke et al. (2008b) manipulated bigheaded carp densities in an experiment in China. Their results indicated that, when fish densities were low and food resources were plentiful, both species consumed more zooplankton, although Silver Carp diet always included more phytoplankton. When fish densities increased, the diet breadth of Bighead Carp also increased. Competition increased, as both species consumed more phytoplankton. Chen et al. (2010a) found that there was trophic overlap between Bighead Carp and Silver Carp in an unproductive reservoir and a highly productive reservoir in southern China. In two southern Chinese systems with average productivity and watershed size, there was segregation in terms of trophic level. The trophic overlap in the unproductive reservoir probably resulted from the limited availability of resources, while that in the highly productive reservoir was due to the very high abundances of resources that both species preferred. In the two watersheds with moderate productivity, neither of these scenarios occurred, and Bighead Carp generally fed at a higher trophic level than Silver Carp.

3.7 BEHAVIOUR AND MOVEMENTS

In the native range in Asia, migration behaviours have been disrupted due to river impoundment, causing alterations in timing of environmental triggers such as flooding and low flow (Xie et al. 2007). For example, egg maturation may now occur asynchronously with upstream spawning runs in response to flooding, reducing spawning success. Migration back to main channels from feeding grounds in response to low flow conditions may now occur before energy has been stored sufficiently for the overwintering period (Xie et al. 2007).

A number of studies in the non-native range in North America have documented movements through time and space to build a picture of bigheaded carp dispersal. Upstream colonization has already occurred in many places, such as the Missouri River (Klumb 2007). Brooks et al. (2009) carried out a study in the Mississippi River examining the ability of Silver Carp to migrate when lock and dam gates were closed or open. The study found little influence of “open” or “closed” river conditions on the ability of this species to disperse. However, the authors noted more downstream movements in spring and more upstream movements in summer. Mean maximum distance travelled upstream was 162 km in comparison to 386 km downstream in one sampling season. Peters et al. (2006) tracked Bighead Carp with radio transmitters in the Illinois River, finding that adults moved at a rate of 1.70 km day^{-1} on average, with a maximum observed upstream migration of 163 km over 35 days. In another Illinois River study (DeGrandchamp et al. 2008), movement rates were correlated with flow. In this study, Bighead Carp moved on average of 6.8 km day^{-1} and Silver Carp moved on average of 10.6 km day^{-1} between April and June over a 32 km river reach. Maximum total recorded displacement over an entire sampling season was greater than 460 km for one Bighead Carp and greater than 410 km for one Silver Carp (DeGrandchamp 2006). Finally, a bioenergetics modelling study by Cooke and Hill (2010) found that large movements within the Great Lakes could be possible for both species without loss of biomass, with the possibility that juveniles and adults could disperse around 30–40 km over a 30 day period (Table 4).

As previously mentioned, an electric barrier in the Chicago Sanitary and Ship Canal acts to impede fish dispersal between the Great Lakes and the Mississippi River basin. The barrier is a micro-pulsed, graded DC electric field that is strongest near the centre and weak around the edges. In this way, fishes can sense the electric field before they are stunned, and are repelled (Stainbrook et al. 2007). Prior to construction of the electric barrier, studies examined other potential methods to deter fish movements in this area. Lovell et al. (2006) examined the effectiveness of implementing a species-specific acoustic barrier. In this study, bigheaded carps were found to exhibit higher sensitivities to sonic frequencies across a wider range at lower intensities than native species, including Paddlefish and Lake Sturgeon (*Acipenser fulvescens*). This is because all minnows, including bigheaded carps, are hearing specialists, with a connected swim bladder and inner ear, causing them to respond to sound pressure. In contrast, the two native species tested hear by way of detecting changes in water pressure. A previous study had shown that movements could be prevented with 95% effectiveness using such a barrier (Taylor et al. 2005).

Subsequent studies have also examined the potential for using chemical markers in fish otoliths to track movements across the electric barrier in the canal. Whitledge (2008) found that it would be possible to discern from which rivers, such as the Fox, Des Plaines, and Illinois rivers, fishes had originated. This is possible because otolith chemistry reflects chemical composition of the water and surrounding habitat. Employing such methods, Ernat et al. (2010) found that Silver Carp caught just below the electric barrier originated from the Illinois River itself, the Middle Mississippi River, and floodplain lakes of the lower Illinois River valley.

Reeves and Galat (2010) carried out a study in the Missouri River documenting diel cycles of a number of fish larvae. They found that bigheaded carp larvae did not show diel cycles of movement through the water column during the summer, nor did the larvae of most cyprinids. The larvae of a few less common taxa did show such movements. One hypothesis suggests that diel cycles are lacking or less pronounced for fish larvae in more turbid waters like those of the Missouri River. However, it was not possible to test if the lack of drift patterns was due to turbidity or innate species behaviour.

Bigheaded carps may be relatively difficult to capture, consequently, a combination of fishing gear, including experimental gill nets, hoop nets, mini-fyke nets, electrofishing, and trammel nets deployed frequently through space and time may be required to estimate relative population densities and size structures (Wanner and Klumb 2009b).

Silver Carp is, however, more sensitive to the sound of boat motors than Bighead Carp (Kolar et al. 2007; Hansen 2010). This pelagic and schooling species frequently leaps into the air when disturbed by outboard motors, often landing in boats, causing damage and injuries. Bighead Carp typically displays jumping behaviour only when spawning or due to electrofishing. Bighead Carp can frequently be seen surface feeding; this behaviour is rarely observed in Silver Carp (Kolar et al. 2007).

3.8 DISEASES AND PARASITES

A large number of disease-causing organisms are known to infect bigheaded carps (Table 5; updated from Kolar et al. 2007). In Iran, a number of non-native *Dactylogyrus* spp., which are trematodes infecting cyprinid gills, have been introduced to various waterbodies with bigheaded carps (Shamsi et al. 2009). In Bangladesh, a study by Hossain et al. (2008) found that a variety of parasites can cause disease and mortality in juvenile bigheaded carps. The trematode *D. catlarias* and the protozoan *Trichodina domerguei* were particularly prevalent. Bigheaded carps can also host the trematode *Clonorchis sinensis*, which can subsequently be transmitted to humans (Chen et al. 2010b). Infection rates in Guangdong province in China, especially in the Pearl River Delta region, are relatively high amongst people. The infection rate of metacercariae in Bighead Carp reached 21.65%, while that in Silver Carp was 9.52%. Grass Carp in this study was actually the most important host for the parasite, being infected at a rate of 52.42% (Chen et al. 2010b). Finally, a study in Vietnam on rural fish farming found the presence of trematodes, including *Haplorchis pumilio*, *H. taichui*, and *Centrocestus formosanus* in Asian carps (Chi et al. 2008). These trematodes may infect mammal or bird definitive hosts, including humans.

4 RECORDED IMPACTS ASSOCIATED WITH INTRODUCTION

4.1 FISHES

A wide variety of studies from Eurasia have documented alterations to native fish communities upon introduction of bigheaded carps. These were summarized by Kolar et al. (2007). In all instances, competition was not experimentally tested but was surmised to have played a role in declines in native planktivores after introduction of Bighead and/or Silver Carp. Similarly, Jiang et al. (2009) indicated that, in the Chinese Lake Dianchi and White Dragon spring at Chenggong, Kunming (which flows into Lake Dianchi), a native cobitid fish known as Yi Se Yun Nan Qiu (*Yunnanilus discoloris*) is now endangered. The presence of invasive Grass, Bighead, Silver, and Black (*Mylopharyngodon piceus*) carps has negatively affected this fish. An experimental polyculture study by Kadir et al. (2006) in Bangladesh recorded negative effects of

Silver Carp on Roho Labeo (*Labeo rohita*) and Catla (*Catla catla*) growth and yield, as well as on the yield of Pool Barb (*Puntius sophore*) and Mola Carplet (*Amblypharyngodon mola*).

In North America, a variety of studies have focussed on diet overlap and potential competitive effects of bigheaded carps on native species. For example, in the Missouri River, a stable isotope study (Gu et al. 2006) indicated a strong potential for competition between hybrid Bighead Carp x Silver Carp with native Paddlefish because of similar trophic position. The potential for competition was greater between hybrid bigheaded carps and Paddlefish than between either bigheaded carp species and the native fishes. A study by Sampson et al. (2009) on backwater lakes of the Illinois and Mississippi Rivers showed that Gizzard Shad was more susceptible to competition with bigheaded carps than either Bigmouth Buffalo (*Ictiobus cyprinellus*) or Paddlefish, due to greater diet overlap on rotifer species. However, because productivity was very high, resources may not have been limiting and competition may not have been important. Irons et al. (2007) reported that in the relatively productive Missouri River, bigheaded carps have increased since 2000 and now dominate the fish assemblage. There is substantial diet overlap between bigheaded carps, Gizzard Shad, and Bigmouth Buffalo in this area. A long-term study indicated a decline in body condition of the former native species by 7% and of the latter by 5% between 2000 and 2006. Temperature, chlorophyll *a*, and discharge were not correlated with these negative changes in body condition, while the increase in bigheaded carps was correlated with the negative effects. The authors suggested that competition with bigheaded carps may be responsible for the negative effect on body condition in these two native fishes.

In contrast to these studies, a combined observational and experimental study carried out in Mekong region in Laos examined the effects of non-native stocked Nile Tilapia (*Oreochromis niloticus*), Mrigal Carp (*Cirrhinus cirrhosus*), Roho Labeo, and Bighead Carp on native fish communities. It found no negative effects on native fish biomass, species richness, diversity indices, species composition, or feeding guild composition, except for a marginally negative impact on Simpson diversity and equitability. Overall total fish biomass increased 49–180% after stocking (Arthur et al. 2010).

Negative effects on native fish species can also be exerted by bigheaded carps through the transmission of harmful parasites. For example, as previously noted, a number of *Dactylogyrus* spp. have been introduced with bigheaded carps to Iran (Shamsi et al. 2009). It is unknown to what extent these species could jump hosts, but seeing as most native species in Iran are also cyprinids, the possibility cannot be ruled out (Shamsi et al. 2009). Finally, a fish tapeworm, *Bothriocephalus acheilognathi*, which may occur in both bigheaded carp species (Kolar et al. 2007) and is widely distributed in North America (Marcogliese 2008), is known to exert negative impacts on native fishes in the United States (e.g., Koehle and Adelman 2007).

4.2 MACROINVERTEBRATES

Effects of bigheaded carps on macroinvertebrates have not been studied well. Kolar et al. (2007) described how some authors have speculated that competition for food could occur with native freshwater mussels, many of which are threatened in North America (Baker and Levinton 2003; Metcalfe-Smith and Cudmore-Vokey 2003; Strayer 1999). On the other hand, a study on pearl culture in freshwater mussels (Yan et al. 2009) found that stocking bigheaded carps increased mussel production due to filtration of harmful cyanobacteria. The addition of these species also caused an increase in dominance of smaller phytoplankton species, which were more easily consumed by mussels. The authors speculated that because Silver Carp may overlap more in diet with mussels than Bighead Carp, the latter may have exerted more of the positive effect on mussel production than the former. A similar study by Wang et al. (2009) also found that the presence of Bighead Carp and Prussian Carp (*Carassius gibelio*) enhanced pearl yield and mussel production. The authors speculated that positive effects on mussels could have resulted from mussels feeding on fish waste products or benefiting from fish activity.

4.3 PLANKTON

Zooplankton frequently decline or undergo alterations in community composition in the presence of bigheaded carp species. A 37-day laboratory experiment (Cooke et al. 2009) examined the effects of juvenile Bighead Carp on zooplankton and phytoplankton. It found that stocking triggered a change in zooplankton dominance from *Daphnia* to copepods, possibly because the latter were more evasive than the former, and the carps, therefore, fed more on *Daphnia*. An increase in dominance of chydorids and ostracods also occurred at lower zooplankton densities of 700 μgL^{-1} dry mass but not at 1900 μgL^{-1} dry mass. This may have been because grazing on preferred *Daphnia* was not substantial enough in the high density treatment to release chydorids and ostracods from competition. These authors also made a point of noting that the zooplankton densities they employed were much higher than those in the Great Lakes. Therefore, impacts of Bighead Carp juveniles in the Great Lakes could be quite different. In experiments in Lake Taihu, China, Ke et al. (2007, 2009) found that stocking Bighead Carp and Silver Carp resulted in declines in crustacean zooplankton. Silver Carp also caused a decline in zooplankton biomass in the eutrophic Lake Shichahai in Beijing (Zhang et al. 2006).

Bigheaded carps exert a variety of different effects on phytoplankton abundance. An enclosure experiment conducted by Zhou et al. (2011) in the Three Gorges Reservoir in China found that a reduction of some zooplankton, such as rotifer and copepod, by Silver Carp, resulted in a trophic cascade, releasing phytoplankton from herbivory and allowing it to increase. The trophic cascade was probably also magnified by the small size of the phytoplankton present, which were perhaps too small to filter consistently when zooplankton were plentiful. Similarly, Ke et al. (2008b) performed an experiment in a Chinese lake by stocking Bighead Carp and Silver Carp. They concluded that phytoplankton density declined only when bigheaded carp densities were very high and zooplankton resources were scarce; otherwise, zooplankton were preferentially consumed. A study by Wang et al. (2008) in 45 shallow lakes in China concluded that when lakes had higher yields of Bighead Carp and Silver Carp, they also exhibited higher chlorophyll *a* concentrations and lower visibility. This could have occurred because smaller and less vulnerable phytoplankton species not consumed by bigheaded carps increased in abundance, or because feeding and excretion by the bigheaded carps increased nutrient cycling and phytoplankton growth.

A modelling study in Lake Qiandaohu in China found that frequent stocking of bigheaded carps would likely result in a decline in phytoplankton (Liu et al. 2007). An experimental study in a eutrophic Chinese reservoir found a negative effect on the nanophytoplankton species (<20 μm) *Scenedesmus quadricauda* (Xiao et al. 2010). An experimental study in Lake Taihu, China (Ke et al. 2009), showed that stocking Bighead Carp and Silver Carp resulted in declines in *Microcystis* cyanobacteria but not the green alga *Ulothrix*. Finally, a restoration study in a pond system in western China (Wu et al. 2010) involved stocking Bighead Carp and Barbel Chub (*Squaliobarbus curriculus*), as well as planting macrophytes. Over time, cyanobacteria declined. Bighead Carp probably contributed to this decline, as at least 90% of their diet was comprised of these taxa.

Bigheaded carps do not always have an immediate effect on phytoplankton. For example, Tucker (2006) found that Silver Carp stocked in earthen ponds with Channel Catfish in the United States exerted no detectable effect on chlorophyll *a* between April and October. Silver Carp did not eliminate cyanobacteria in the genera *Oscillatoria* and *Anabaena*. It is possible that the densities of 75 and 250 Silver Carp ha^{-1} the study employed were too low for an effect to be measured. In another study within enclosures in a highly eutrophic Chinese lake (Chen et al. 2009a), Silver Carp were stocked to help reduce phytoplankton. Piscivores were also stocked to help remove fishes that would normally graze on zooplankton, thereby increasing zooplankton grazing on phytoplankton. Phytoplankton biomass declined, but only after a three-year period. Water quality nutrient parameters showed a more rapid response to the biomanipulation than phytoplankton biomass.

Ma et al. (2010) found that Silver Carp stocking in the pre-sedimentation pond of a drinking water reservoir in China resulted in removal of large colony-forming *Microcystis* cyanobacteria. However, there was no effect on smaller unicellular phytoplankton, resulting in a shift in phytoplankton dominance towards smaller species. A study on freshwater pearl culture in Chinese mussels found that stocking bigheaded carps resulted in a decline in phytoplankton size (Yan et al. 2009). This occurred because of direct consumption of larger phytoplankton and/or carp grazing on zooplankton. Zooplankton normally feed on smaller algae. If zooplankton grazing declines, smaller algae could increase. Similarly, Zhang et al. (2006) found that picophytoplankton biomass increased with Silver Carp stocking density in the eutrophic Lake Shichahai, Beijing, probably because zooplankton declined and grazing was suppressed. *Microcystis* spp., in contrast, were effectively controlled by Silver Carp.

Silver Carp can also exert other effects on phytoplankton species. In one experiment, when the cyanobacteria *Microcystis aeruginosa* were exposed to Silver Carp kairomones, or water-borne chemical cues, microcystin production levels increased (Ha et al. 2009). In an experiment by Jančula et al. (2008), photosynthetic activity of cyanobacteria, which were mostly *Microcystis* spp., increased after passage through the gut of Silver Carp. In contrast, photosynthetic activity declined 92–95% after passage through the gut of Nile Tilapia.

Finally, Delong (2010) pointed out that no studies to date have examined potential synergistic impacts between bigheaded carps and other non-native phytoplanktivores such as *Dreissena* spp. or *Daphnia lumholtzi*. It is possible that impacts on available primary productivity in the water column could be magnified when such invaders are present together; however, no mechanism for such synergistic effects was proposed.

4.4 ABIOTIC VARIABLES

Kolar et al. (2007) summarized the effects of stocking bigheaded carps on abiotic variables, documenting that water column nutrient concentrations responded negatively or positively in different studies. A study on polyculture in Bangladesh (Kadir et al. 2006) found that additions of Silver Carp resulted in resuspension of particles in the water column and increased nitrification. A restoration study by Gao et al. (2009) found a reduction over time in surface sediment nutrient concentrations when bigheaded carps and other filter feeders were stocked. The authors speculated that filter feeding may have contributed to reducing nutrient transfer to the sediments. However, the study also involved macrophyte harvesting and the use of a biomimetic net to increase adsorption of organic matter, both of which could have contributed to the decline in surface sediment nutrients (Gao et al. 2009).

4.5 HUMANS

Bigheaded carps may harbour toxins in their flesh from cyanobacteria they consume that are potentially harmful to humans. A study from the highly eutrophic Chinese Lake Taihu (Zhang et al. 2009) examined bioaccumulation of toxins from *M. aeruginosa* in tissues of various fish species that are traditionally consumed in this area. Only tissue from Common Carp (*Cyprinus carpio*) in one instance exhibited microcystin concentrations exceeding the recommended levels for safe consumption by the World Health Organization (WHO). Silver Carp was tested but tissue concentrations were below the safe consumption level. Researchers noted that if they were to be consumed over long periods, adverse human health effects could be possible even at safe contamination levels. A study by Chen et al. (2007b) found that 25% of muscle samples taken from Bighead Carp in Lake Taihu were above the WHO recommended daily intake level. Finally, Woo et al. (2009) reported that the bacterium *Laribacter hongkongensis* is harboured in the intestine of healthy Grass Carp and Bighead Carp. It is likely transmitted to humans when they are consumed, and can cause gastroenteritis.

5 HUMAN USE

Asian carps are used worldwide by the food industry. People in China have been culturing Grass, Bighead, Silver, and Black carps in aquaculture for at least one thousand years, since the Tang Dynasty. People commonly captured larvae and raised them in ponds. More recently, artificial spawning has become a routine practice (Chapman and Wang 2006; Kolar et al. 2007). These four species of carp are the most important freshwater fishes in China from an economic perspective (Yi et al. 2006). Low-value freshwater fishes, which include Bighead Carp and Silver Carp, account for more than 60% of the yield in Chinese freshwater fisheries. Most of the industry sells frozen or live carps, but attention is now being paid to developing more innovative processing techniques (Zhang et al. 2007). In China, Asian carp species are used to adulterate products claiming they contain other fish species (Chen et al. 2009b). Globally, Silver Carp showed the highest aquaculture production of any species worldwide in 2008, while Bighead Carp was ranked sixth (FAO 2010). Many countries other than China have introduced Asian carp species to augment fisheries, and many continue to harvest bigheaded carps from stocked reservoirs (Kolar et al. 2007).

Asian carps are also extensively used as a means of biocontrol and to enhance production of other fish species in polyculture. Silver Carp has been extensively stocked worldwide in the hopes that this species will control algae in wastewater ponds, reservoirs, warm eutrophic lakes, and aquaculture facilities (Ke et al. 2008b; also see Table 2). Bighead Carp is also sometimes stocked for similar purposes, although the emphasis is often more on zooplankton control. Polyculture, which maintains that raising a number of fish species together can be more productive than raising a single taxon at a time, has been common in Asia for hundreds of years. Polyculture in Asia, Europe, and Africa still occurs today, relying on bigheaded carps to help clean the water and provide faeces as a food source to other fishes. Such enterprises are often very productive (Kolar et al. 2007). Afzal et al. (2007), in a study where Bighead Carp, Catla, Grass Carp, Mrigal Carp, Roho Labeo, and Silver Carp were raised together, found that Bighead Carp showed the highest growth rates, followed by Silver Carp.

In North America, the use of bigheaded carps is more recent. In the United States, Bighead Carp has frequently been raised in some states and transported to others for live sale in specialty food markets. Most of the time, the states in which this species is sold are not those in which it is raised. Shipping to Canada for sale in live fish markets was also a common practice (Conover et al. 2007; Kolar et al. 2007; Stephens et al. 2011). Legislation has now banned possession of Asian carps in Ontario, although live individuals may still be available illegally at certain fish markets (Herborg et al. 2007). In many states, similar legislation now only permits the sale of dead Asian carps in fish markets (Kolar et al. 2007).

Presently, available piscicides such as rotenone and antimycin would not allow for selective targeting of Asian carp species in the wild, and native fish species would also be adversely affected (Rach et al. 2009). Consequently, the feasibility of creating a more mainstream consumer market for bigheaded carps in the United States is being considered, in order to promote harvesting populations as a means of control (Garvey et al. 2010). Currently, fisheries occur on the Mississippi, Missouri, and Illinois rivers (Kolar et al. 2007). More studies on contaminant concentrations in bigheaded carps are currently underway in order to ensure the suitability of these species harvested in the United States for human consumption (ACRCC 2010).

6 CONSERVATION STATUS

Bigheaded carps have not yet been evaluated by the International Union for the Conservation of Nature (IUCN) and are both listed as potential pest species (Froese and Pauly 2011). In 2007, Silver Carp was added to the list of injurious wildlife under the *Lacey Act* in the United States; Bighead Carp was added in 2010 (USDA 2011). The *Lacey Act* gives jurisdiction to the United States Fish and Wildlife Service to ban import and transport of live bigheaded carp between states.

In contrast to North America, conservation of bigheaded carps is of increasing concern throughout their native range. During the planning phase of the Three Gorges Dam on the Yangtze River, significant consideration was given to building structures which may exert a detrimental effect on bigheaded carp spawning and migration (Chapman and Wang 2006). Despite these considerations, results indicate that harvest levels (2003-2005) of Bighead, Black, Grass and Silver carps below the dam declined 50–70% prior to impoundment (Xie et al. 2007). In the middle Yangtze River, 3.59 billion carp larvae were observed in drift samples (1997), 1.90 billion (2001, 2002), but only 105 million in 2005 (Duan et al. 2009). Bighead, Black, Grass, and Silver carps only accounted for 4.6% of total fish larvae present in the Pearl River (2006 -2008)(Tan et al. 2010). Population declines since 1931 have been partly attributed to damming.

Genetic diversity of bigheaded carps has also become a concern for Chinese aquaculturists. Recent studies have examined ways of conserving and/or improving genetic resources. This is an important issue because species, such as Bighead Carp, now exhibit problems related to growth, size, and disease when they are farmed. These are symptomatic of years of cultivation with little attention being paid to conserving genetic diversity (Ye et al. 2008).

7 SUMMARY

Since the introduction of bigheaded carps to the United States in the 1970s, these species have spread throughout the Mississippi River basin. They have also been introduced to a number of other drainage basins, where establishment typically failed. The populations now established throughout major tributaries of the Mississippi River are large and are threatening to expand into the Great Lakes through connected waterways and other potential pathways. Efforts continue to stave off introduction to the Great Lakes, including the construction of an electric fish barrier in the Chicago Sanitary and Ship Canal, intensive monitoring, and population control.

This biological synopsis was required to update current information on these invaders, as the body of scientific literature has expanded over recent years. It surveyed studies from 2006 to early 2011. As described in this report, bigheaded carps are long-lived species with broad physiological tolerance. They have high fecundities and are opportunistic planktivores typically occupying large river basins. They are capable of migrating large distances and have been associated with negative impacts on a variety of taxa and foodwebs. These species are also widely used by people worldwide for food and plankton control. Recent legislation in both Canada and the United States has begun to control human-mediated movements of Asian carps, including bigheaded carps, to deter future introductions and spread.

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Table 1. Countries and territories where Bighead Carp (*Hypophthalmichthys nobilis*) has been introduced

Status: E = established, PE = probably established, PN = probably not established, N = not established, and ? = unknown. Data are from Kolar et al. (2007), with updated information from Froese and Pauly (2011). Occasionally, each set of authors disagreed in regards to the status of populations. In such cases, the less conservative description is reported, as each set of authors found the most reliable references possible.

Country	Status	First year or period of introduction	Source	Reason for introduction (note that biocontrol typically refers to control of plankton)
Afghanistan	E	Unknown	Unknown	Biocontrol
Albania	PE	Unknown	Unknown	Aquaculture
Algeria	PN	1985-1991	Hungary	Fisheries & research
Argentina	?	1970-1979	Unknown	Aquaculture
Armenia	E	Unknown	Moldova, Russia, Uzbekistan	Unknown
Austria	NE	Unknown	Unknown	Aquaculture
Bangladesh	PN	1981	Nepal	Aquaculture, research
Belarus	E	1965	Unknown	Aquaculture
Belgium	E	Unknown	Unknown	Aquaculture
Bhutan	N	1983, 1985	Nepal	Aquaculture
Bolivia	N	1990, 1991	Israel?	Aquaculture
Brazil	N	1979, 1983, 1984	China, Hungary	Aquaculture
Brunei	PE	Unknown	Unknown	Unknown
Bulgaria	PE	Unknown	Unknown	Aquaculture
Cambodia	E	1981	Vietnam	Aquaculture
Canada	?	Unknown	Unknown	Possibly due to live food trade
China	E	Historical	China	Aquaculture
Colombia	N	1988	Taiwan	Aquaculture
Costa Rica	N	1976	Taiwan	Aquaculture
Croatia	?	Unknown	Unknown	Unknown
Cuba	N	1968, 1976	USSR	Aquaculture
Czech Republic	E	1965	Russia	Aquaculture, fisheries
Denmark	E	Unknown	Unknown	Unknown
Dominican Republic	N	1981	Taiwan	Aquaculture
England	N	1975	Austria	Inadvertent
Egypt	N	1975-1976	China	Aquaculture
Estonia	PN	2002	Unknown	Unknown
Fiji	N	1968	Malaysia	Research
France	PN	1975, 1976	Hungary, Asia	Aquaculture
Germany	N	1964	Hungary	Aquaculture
Greece	PN	Unknown	Unknown	Unknown
Guam	N	Unknown	Unknown	Unknown
Haiti	?	1987, 1990	Dominican Republic, Panama	Unknown
Hong Kong	N	Historical?	China	Aquaculture
Hungary	E	1963-1968	China, USSR	Accidental, aquaculture
India	PN	1987	Japan, Bangladesh	Aquaculture, fisheries
Indonesia	E	1969	Taiwan	Aquaculture
Iran	E	1968, 1969, 1992	China	Aquaculture
Iraq	E	1966-1969	Unknown	Aquaculture
Israel	PN	1973	Germany	Aquaculture
Italy	E	1975-1999	Eastern Europe	Sport fishing
Japan	E	1878-1945	China	Aquaculture
Jordan	N	1973	Germany	Aquaculture
Kazakhstan	E	Unknown	China	Aquaculture
Korea	N	1963	Taiwan	Aquaculture
Laos	E	1968	China	Aquaculture

Country	Status	First year or period of introduction	Source	Reason for introduction (note that biocontrol typically refers to control of plankton)
Latvia	PN	1990, 1992	Unknown	Unknown
Lesotho	N	1990	Unknown	Aquaculture
Luxembourg	?	Unknown	Unknown	Unknown
Madagascar	PN	1982	Hungary	Unknown
Malaysia	N	1800s	China	Aquaculture
Mexico	PE	1975	Cuba	Aquaculture
Moldova	E	Unknown	Unknown	Aquaculture
Morocco	N	1981	Hungary	Aquaculture
Mozambique	N	1991	Cuba	Aquaculture, fisheries
Myanmar	E	1987	China?	Aquaculture
Nepal	N	1971	Hungary	Aquaculture
Netherlands	PE	1983	Germany	Range expansion
Pakistan	?	Unknown	China	Unknown
Panama	N	1978	Taiwan	Aquaculture
Peru	N	1979	Israel, Panama	Aquaculture
Philippines	E	1968	Taiwan	Aquaculture
Poland	PE	1965	USSR	Aquaculture
Romania	E	1960-1962	China	Aquaculture
Russia	E	1949	China	Aquaculture
Singapore	N	1900s	China	Aquaculture
Slovakia	PE	1955	Russia	Aquaculture, fisheries
Slovenia	E	Unknown	Unknown	Aquaculture?
Sri Lanka	N	1948	China	Aquaculture, biocontrol
Sweden	PE	Unknown	Unknown	Range expansion
Switzerland	N	1970	Unknown	Biocontrol
Taiwan	N	<1700s	China	Aquaculture
Thailand	E	1932	China	Aquaculture
Turkey	E	Unknown	Unknown	Aquaculture, biocontrol
Turkmenistan	E	Unknown	China	Unknown
Ukraine	E	Unknown	Russia?	Aquaculture?
United States	E	1972-1986	Taiwan	Aquaculture
Uzbekistan	E	1964	China	Aquaculture
Vietnam	E	1958	China	Aquaculture
Yugoslavia	N	1963	Romania, Hungary, USSR	Aquaculture

Table 2. Countries and territories where Silver Carp (*Hypophthalmichthys molitrix*) has been introduced

Status: E = established, PE = probably established, PN = probably not established, N = not established, and ? = unknown. Data are from Kolar et al. (2007), with updated information from Froese and Pauly (2011). Occasionally, each set of authors disagreed in regards to the status of populations. In such cases, the less conservative description is reported, as each set of authors found the most reliable references possible.

Country	Status	First year or period of introduction	Source	Reason for introduction (note that biocontrol typically refers to control of plankton)
Afghanistan	E	Unknown	Unknown	Aquaculture, weed control
Albania	PN	Unknown	Unknown	Aquaculture
Algeria	PN	1985, 1986, 19911	Hungary	Fisheries
Argentina	?	Unknown	Unknown	Aquaculture
Armenia	PE	Unknown	Far East	Aquaculture
Austria	N	Unknown	Unknown	Aquaculture
Bangladesh	PE	1969	Hong Kong, Japan	Aquaculture
Belgium	PN	1975	Yugoslavia	Biocontrol
Bhutan	PE	1984	Unknown	Aquaculture
Brazil	PN	1968, 1979, 1982, 1983	Japan, China, Hungary	Aquaculture
Bulgaria	N	Unknown	Unknown	Aquaculture
Cambodia	E	1969	Vietnam, Taiwan	Aquaculture
Colombia	?	1988	Taiwan	Aquaculture
Costa Rica	PN	1976	Taiwan	Aquaculture
Cuba	PE	1967, 1978	USSR	Aquaculture
Cyprus	E	1976	Israel	Biocontrol, sport fishing
Czech Republic	E	1953, 1961	Unknown	Range expansion
Denmark	PN	Unknown	Unknown	Aquaculture
Dominican Republic	PE	1971-1981	Taiwan	Fisheries, aquaculture
Egypt	N	1962	Japan	Research
Estonia	N	1980-1989	Hungary, Russia	Weed control
Ethiopia	E	1975	Japan	Stocking, aquaculture
Fiji	PN	1968	Malaysia	Research
France	PE	1950, 1975	Asia, Hungary	Biocontrol
Germany	PE	1964, 1970, 1972	Hungary, China	Aquaculture, biocontrol
Greece	PE	1980	Poland	Fisheries
Guam	?	1974	Taiwan	Aquaculture
Haiti	?	1991	Panama	Unknown
Honduras	PN	1976	Taiwan	Aquaculture
Hungary	E	1963, 1964, 1968, 1973-1983	China, Russia	Aquaculture
India	E	1959, 1963	Japan, Hong Kong, China, Southeast Asia	Escape during flooding, aquaculture, fisheries
Indonesia	N	1964, 1969	Japan, Taiwan	Aquaculture
Iran	E	1968, 1969, 1992	China, Romania	Aquaculture, fisheries, biocontrol
Iraq	E	1966-1969	Unknown	Aquaculture, research
Israel	E	1960s, 1979-1981	Japan, unknown	Aquaculture, biocontrol, research, fisheries
Italy	E	Unknown	Unknown	Aquaculture
Jamaica	?	1978	Unknown	Aquaculture
Japan	E	1878-1940, 1969	China	Aquaculture, accidental
Jordan	?	Unknown	Unknown	Weed control
Kazakhstan	E	1958-1961	China	Accidental

Country	Status	First year or period of introduction	Source	Reason for introduction (note that biocontrol typically refers to control of plankton)
Korea	PE	1963	Japan	Aquaculture, research
Kyrgyzstan	E	Unknown	China	Accidental
Laos	PE	1960s	Thailand, Vietnam, China	Aquaculture
Latvia	E	Unknown	Unknown	Unknown
Lebanon	E	Unknown	Unknown	Aquaculture, weed control
Lesotho	N	1988	South Africa	Aquaculture
Luxembourg	N	Unknown	Unknown	Unknown
Madagascar	N	1982	North Korea	Research
Malawi	N	1970	Israel	Aquaculture
Malaysia	N	1800s	China	Aquaculture
Mauritius	?	1976	India	Unknown
Mexico	PN	1965	China	Aquaculture, biocontrol
Mongolia	PE	Unknown	Unknown	Unknown
Morocco	PE	1980, 1981	Bulgaria, Hungary	Biocontrol
Mozambique	N	1991	Cuba	Aquaculture, fisheries
Moldova	PN	Unknown	China	Stocked
Myanmar	PE	1967	Unknown	Aquaculture
Nepal	N	1965, 1967	India, Japan	Aquaculture
Netherlands	PN	1966	Hungary	Unknown
New Zealand	PN	1969	Hong Kong	Biocontrol, research
Nigeria	N	1984	Unknown	Aquaculture
Pakistan	E	1982-1983	Nepal, China	Fisheries, aquaculture
Panama	PN	1978	Taiwan	Aquaculture
Papua New Guinea	?	Unknown	Unknown	Aquaculture
Peru	PN	1979	Panama	Aquaculture
Philippines	N	1964, 1968	China, Taiwan	Aquaculture
Poland	E	1964, 1965	USSR	Aquaculture
Puerto Rico	PE	1972	United States	Accidental
Romania	E	1960-1962	China	Biocontrol, aquaculture
Russia	E	1953,1959, 1961	China	Biocontrol, accidental
Rwanda	PN	1979	Korea	Aquaculture
Saudi Arabia	E	Unknown	Unknown	Aquaculture, weed control
Serbia (former Yugoslavia)	E	1963	Romania, Hungary, USSR	Aquaculture
Singapore	N	1900s	China	Aquaculture
Slovakia	E	Unknown	Unknown	Range expansion
South Africa	PE	1975	Israel	Increase production, aquaculture
Sri Lanka	N	1948	China	Aquaculture, weed control
Sweden	PN	Unknown	Unknown	Aquaculture
Switzerland	N	1970	Unknown	Biocontrol
Tajikistan	E	Unknown	Unknown	Unknown
Taiwan	N	<1700s	China	Aquaculture
Tanzania	N	1981	India	Aquaculture
Thailand	PE	1913	China, Hong Kong	Aquaculture, research
Tunisia	PN	1981	Hungary	Biocontrol
Turkey	E	Unknown	Unknown	Aquaculture, weed control
Turkmenistan	E	1958-1961	China	Aquaculture
Ukraine	?	Unknown	Unknown	Aquaculture
United Kingdom	PN	Unknown	Unknown	Aquaculture
United States	E	1971, 1973, 1980	Taiwan	Biocontrol, aquaculture, fisheries
Uzbekistan	E	1960, 1961, 1964-1975	China	Aquaculture, intentional introductions
Vietnam	E	1958	China	Aquaculture
Zambia	?	Unknown	Unknown	Aquaculture
Zimbabwe	?	Unknown	Unknown	Aquaculture

Table 3. Projected growth of Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*Hypophthalmichthys molitrix*) in different habitats

Values are based on bioenergetics models of juvenile (10cm, 10g) and adult (60cm, 2400g) non-swimming Bighead Carp (BC) and Silver Carp (SC) foraging on zooplankton (Zoop.) and phytoplankton (Phytop.) for 30 days at different times of year and in different non-native regions. Note that Spr = spring and Sum = summer. Table and caption are modified from Cooke and Hill (2010). References providing productivity data for the bioenergetics calculations can be found in Cooke and Hill (2010).

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Location	Time of year, water temp. (℃)	Phytop. wet mass (mg L^{-1})	Zoop. wet mass (mg L^{-1})	Predicted % biomass gain or loss over 30 days			
				10 g BC	10 g SC	2400 g BC	2400 g SC
Lake Michigan							
Southern basin, nearshore	May, 8.8	0.69	0.024	-15	-9	-3	-3
	Jul, 19.4	0.69	0.15	-29	-30	-6	-10
	Sep, 20.2	0.69	0.79	-20	-23	-4	-9
Within production pulse	Apr, 3.4	0.52	0.18	-9	-2	-2	-1
Outside production pulse	Apr, 3.6	0.19	0.045	-17	-11	-4	-3
Green Bay*	Apr, 13.4	5.5	0.16	+63	+66	+15	+13
	Jun, 20.3	5.5	4.72	+120	+113	+28	+23
Lake Superior*							
Western arm	May, 3.4	0.31	0.16	-13	-6	-3	-2
	Aug, 9.4	0.32	0.59	-12	-6	-2	-3
Chippewa Park (wet)	Jul, 22.5	1.42	2.52	+13	+5	+4	-3
Pine Bay (wet)	Jul, 22.5	1.13	2.22	+3	-4	+2	-5
Hurkett Cove (wet)	Jul, 22.5	0.07	3.19	+2	-5	+1	-5
Lake Huron							
Collingwood Harbour (Georgian Bay)	Jul, 22.5	1.42	1.83	+2	-5	+1	-5
Oliphant Bay (wet)	Jul, 22.5	0.57	0.056	-38	-43	-9	-15
Baie du Dore (wet)	Jul, 22.5	0.07	0.024	-46	-51	-10	-16
Lake Erie							
West basin*	Spr, 6.1	3.31	0.69	+46	+50	+10	+9
	Sum, 21.0	3.12	1.74	+31	+25	+8	+2
Central basin*	Spr, 6.1	0.63	1.14	+8	+14	+2	+2
	Sum, 21.0	1.21	0.95	-12	-16	-2	-7
East basin*	Spr, 6.1	1.82	0.29	+13	+20	+3	+3
	Sum, 21.0	1.06	0.62	-20	-23	-2	-9
Rondeau Prov. Park (wet)	Jun, 22.5	0.14	0.46	-38	-43	-9	-15
Long Point Prov. Park (wet)	Jul, 22.5	0.36	0.40	-36	-41	-8	-14
Lake Ontario							
Sodus Bay embayment*	Jul, 20.0	1.87	5.91	+82	+77	+20	+14
Sodus Bay nearshore*	Jul, 20.0	0.29	0.81	-26	-28	-6	-10
Sandy Point embayment*	Jul, 20.0	1.11	6.06	+72	+67	+17	+12
Sandy Point nearshore*	Jul, 20.0	0.64	0.76	-21	-24	-4	-9
Frenchman's Bay (wet)	Jun, 22.5	8.94	1.57	+116	+104	+28	+21
Bronte Creek (wet)	Jun, 22.5	1.84	0.42	-14	-20	-3	-9
Middle Mississippi River							
Chester*	Aug, 22.0	5.00	0.05	+30	+23	+8	+2
Grand Tower*	Oct, 16.0	10.0	0.01	+130	+130	+30	+26
Upper Mississippi River	Sum, 27.0	8.77	3.75	+127	+102	+31	+19
Missouri River	Sum, 23.0	5.30	1.39	+37	+27	+9	+2

*Zooplankton data for these regions excluded rotifers.

Table 4. Maximum potential distance travelled by Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*Hypophthalmichthys molitrix*) in different habitats
Values are based on bioenergetics models, and are for juvenile (10cm, 10g) and adult (60cm, 2400g) Bighead Carp (BC) and Silver Carp (SC) over 30 days in various habitats at different times of year (Spr = spring; Sum = summer). Open-water habitats near wetlands are indicated after the site name (wet). Table and caption modified from Cooke and Hill (2010).
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Location	Time of year, water temp. (℃)	Maximum distance of travel over 30 days (km)			
		10g BC	10g SC	2400g BC	2400g SC
Lake Michigan					
Green Bay	Apr 1999	27.0	29.8	28.8	22.8
	Jun 1999	33.4	31.4	35.0	24.4
Lake Superior					
Chippewa Park (wet)	Jul 1998	5.7	2.1	7.5	
Pine Bay (wet)	Jul 1998	1.6		2.4	
Hurkett Cove (wet)	Jul 1998	1.0		2.9	
Lake Huron					
Collingwood Harbour	Jul 1998	0.8		2.6	
Lake Erie					
West basin	Spr, 6.1	26.7	33.7	28.5	26.7
	Sum, 22.0	13.2	10.6	14.8	3.9
Central basin	Spr, 6.1	6.5	14.5	8.8	8.0
East basin	Spr, 6.1	10.9	18.7	13.0	12.2
Lake Ontario					
Sodus Bay embayment	Jul 1997	26.7	25.1	28.5	18.1
Sandy Pond embayment	Jul 1997	24.9	23.1	26.4	16.3
Frenchman's Bay (wet)	Jun 1998	30.8	27.2	32.7	20.5
Rivers					
Middle Mississippi River (Chester)	Aug, 22.0	12.4	9.3	14.3	2.6
Middle Mississippi River (Grand Tower)	Oct, 16.0	38.1	38.9	39.9	32.1
Upper Mississippi River	Sum, 27.0	29.3	22.8	31.1	15.6
Missouri River	Sum, 23.0	14.0	10.1	15.8	3.4

Table 5. Disease-causing agents of Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*Hypophthalmichthys molitrix*) known to date

Table and caption modified from Kolar et al. (2007). Additions are made from Thien et al. (2007), Chi et al. (2008), Hossain et al. (2008), Khalil et al. (2009), Shamsi et al. (2009), Woo et al. (2009), and Chen et al. (2010b). Scientific names were maintained as written in the literature and therefore may have undergone subsequent name changes; however, spelling was changed when noted to be incorrect.

(Table reproduced with the permission of the American Fisheries Society)

Bighead Carp	**Silver Carp**
BACTERIA	BACTERIA
Aeromonas hydrophila	*Aeromonas hydrophila*
Edwardsiella spp.	*Citrobacter freundii*
*Laribacter hongkongensis**	*Edwardsiella tarda*
Proteus rettgeri	*Flavobacterium* spp.
Pseudomonas dermoalba	*Proteus rettgeri*
P. fluorescens	*Pseudomonas aeruginosa*
VIRUSES	*P. dermoalba*
Rhabdovirus carpio	*P. fluorescens*
FUNGI	*Vibrio fluvialis biovar* III
Saprolegnia spp.	*Staphylococcus aureus*
PROTOZOANS	*Yersinia ruckeri*
Apiosoma spp.	VIRUSES
Chilodonella spp.	*Rhabdovirus carpio*
C. cyprini	FUNGI
C. hexasticha	*Achlya bisexualis*
C. cucullulus	*Alternaria*
Cryptobia agitate	*Aspergillus flavus*
C. branchialis	*Aphanomyces*
Eimeria sinensis	*Fusarium*
E. cheni	*Penicillium*
Frontonia acuminata	*Saprolegnia parasitica*
F. leucas	PROTOZOANS
Glaucoma scintillans	*Apiosoma amoebae*
Ichthyophthirius multifilis	*A. cylindriformis*
Myxobolus pavlovskii	*A. piscola*
M. koi	*Chilodonella cyprini*
Trichodina spp.	*C. hexasticha*
T. domerguei	*C. uncinata*
T. pediculus	*Chloromyxum cyprini*
T. nigra	*Cryptobia agitata*
T. ovaliformis	*C. branchialis*
T. reticulata	*Dexiostoma campylum*
Trichodinella epizootica	*Eimeria aristichthysi*
T. minuta	*E. carpelli*
Tripartiella bulbosa	*E. hypophthalmichthys*
T. lieni	*E.* [=*Goussia*] *sinensis*
Trypanosoma aristichthysi	*Glaucoma scintillans*
TREMATODES	*Glossatella cylindriformis*
Centrocestus formosanus	*Ichthyophthius multifilis*
Clonorchis sinensis	*Myxidium hemiculteri*
Dactylogyroides tripathi	*M. sarcocheilichthysi*
Dactylogyrus aristichthys	*Myxobolus cerebralis*
D. catlarius	*M. dispar*
D. extensus	*M. drjagini*
D. nobilis	*M. ellipsoides*
D. spathaceum	*M. koi*
D. taihuensis	*M. latus*
Haplorchis pumilio	*M. macrocapsularis*
Posthodiplostomum spp.	*M. pavlovskii*
P. cuticola	*M. phylloides*
CESTODES	*M. saurogobioi*
Bothriocephalus acheilognathi	*Myxosoma mai*

Bighead Carp	**Silver Carp**
Diagramma interrupta	*M. sachalinensis*
Ligula intestinalis	*M. sphaerica*
COPEPODS	*Sphaerosporida lieni*
Lernaea spp.	*Sessilia* spp.
L. cyprinacea	*Trichodina domerguei*
L. piscinae	*T. mutabilis*
Synergasilus lieni	*T. nigra*
S. major	*T. nobilis*
S. polycolpus	*T. ovaliformis*
	T. pediculus
	T. reticulata
	Trichodinella epizootica
	T. minuta
	Trichophrya piscium
	Tripartiella bulbosa
	T. copiosa
	T. lieni
	Trypanoplasma cyprini
	TREMATODES
	Allocreadium hypophthalmichthydis
	Camallanus hypophthalmichthys
	Centrocestus formosanus
	Clonorchis sinensis
	Dactylogyroides tripathi
	Dactylogyrus catlarius
	D. chenshuchenae
	D. extensus
	D. hypophthalmichthys
	D. magnihamatus
	D. vaginulatus
	D. skrjabini
	D. suchengtaii
	D. yinwenyingae
	Diplostomum spathaceum
	Diplozoon paradoxum
	Gyrodactylus hypophthalmichthydis
	Haplorchis pumilio
	H. taichui
	Posthodiplostomum cuticola
	Rhabdochona denudata
	Sanguinicola spp.
	Tetracotyle spp.
	CESTODES
	Bothriocephalus acheilognathi [=*gowkongensis*]
	Triaenophorus nodulosus
	COPEPODS
	Lamproglena orientalis
	Lernea bhadraensis
	L. cyprinacea
	Sinergasilus lieni
	S. major
	S. polycolpus

*From the intestines of healthy Bighead Carp. Causes gastroenteritis in humans.

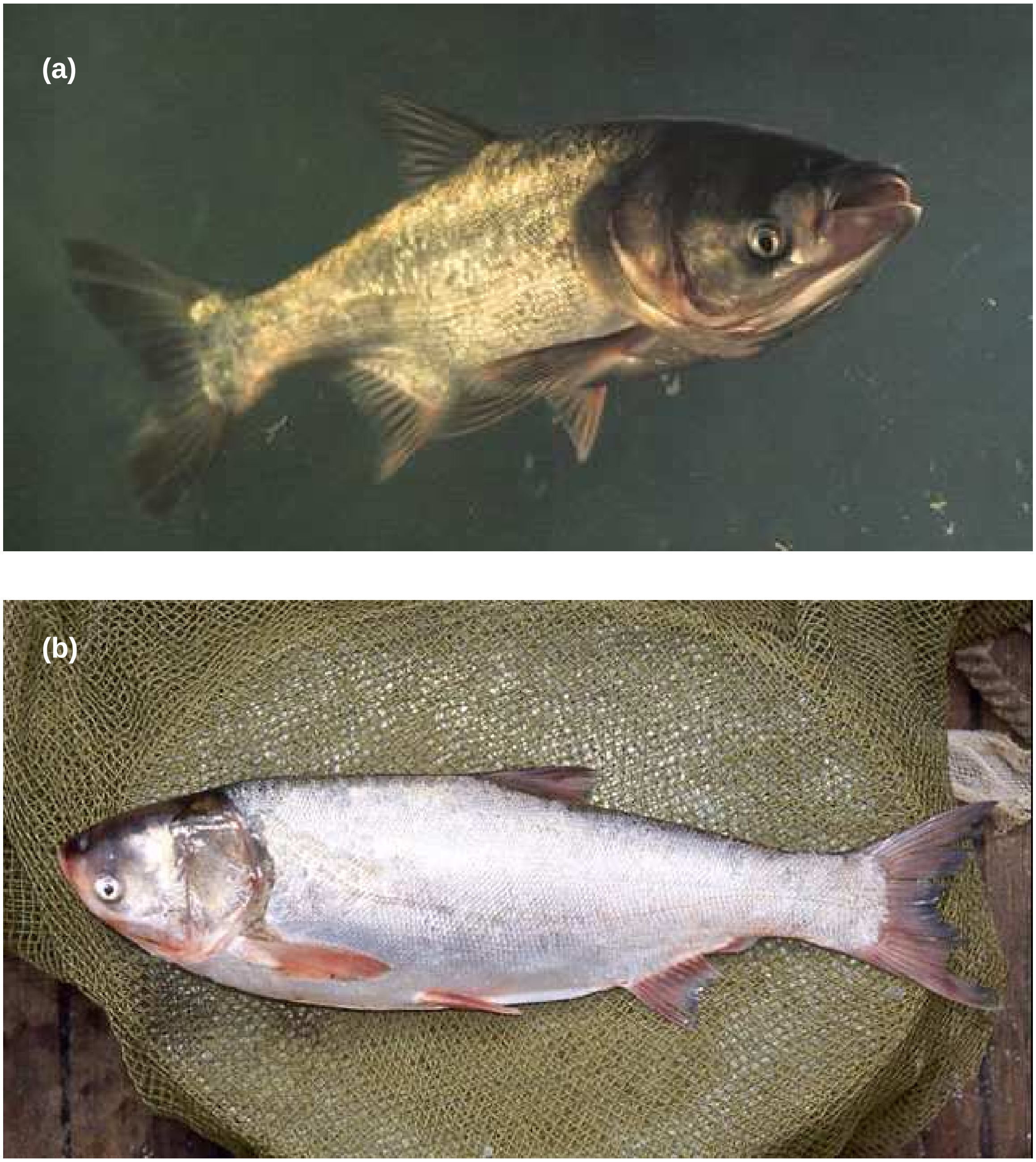
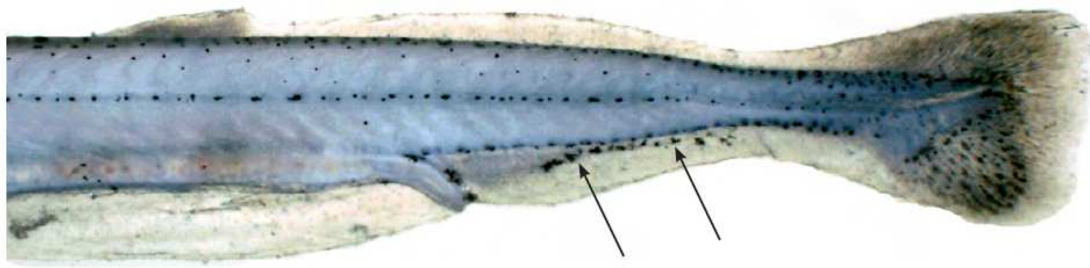


Figure 1. Photographs of (a) Bighead Carp (*Hypophthalmichthys nobilis*) and (b) Silver Carp (*Hypophthalmichthys molitrix*)

For web access to these photos, see (http://fishbase.org/Photos/PicturesSummary.php?ID=275&what=species) and (http://fishbase.org/Photos/PicturesSummary.php?StartRow=4&ID=274&what=species&TotRec=7), respectively (Froese and Pauly 2011). Photos not to scale.

(Figure 1(a) provided courtesy of the Chinese Academy of Fishery Sciences); Figure 1(b) reproduced courtesy of Dr. Alexander Naseka, Russian Academy of Science)

(a)



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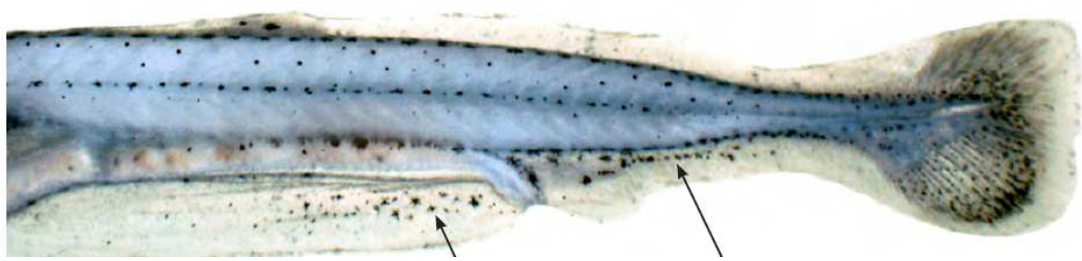


Figure 2. Melanophore patterns in young (a) Bighead Carp (*Hypophthalmichthys nobilis*) and (b) Silver Carp (*Hypophthalmichthys molitrix*)
Refer to the arrows for the subtle distinctions. Pictures specifically depict individuals in the one-chamber-gas-bladder or dorsal-fin-differentiation stage. Figure and caption modified from Chapman and Wang (2006).
(Photo courtesy of the U.S. Geological Survey)

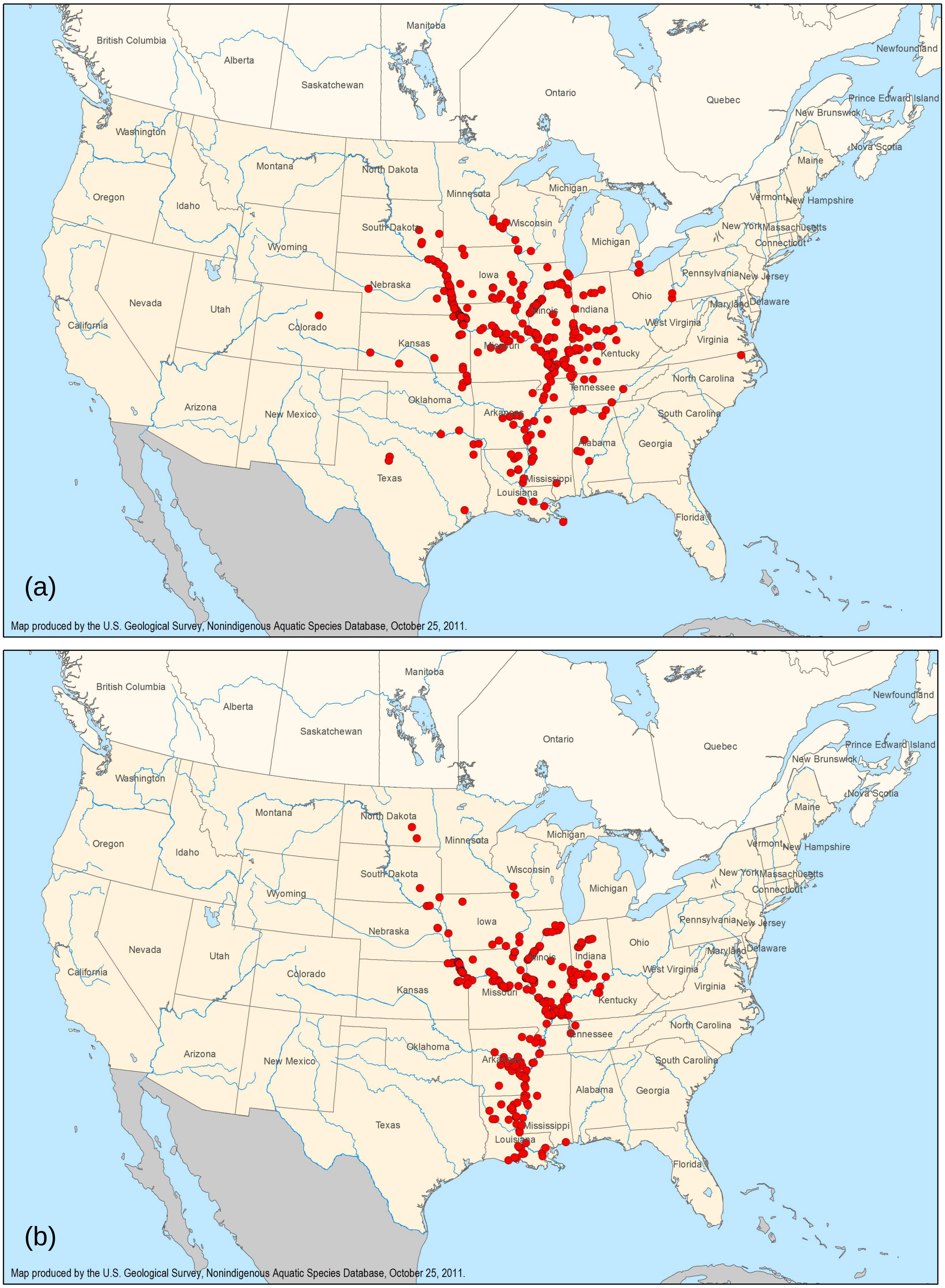


Figure 3. Non-native occurrences of (a) Bighead Carp (Hypophthalmichthys nobilis) and (b) Silver Carp (Hypophthalmichthys molitrix) in the United States

Dots represent confirmed sightings and collections, not necessarily established populations.

(Maps courtesy of the U.S. Geological Survey)

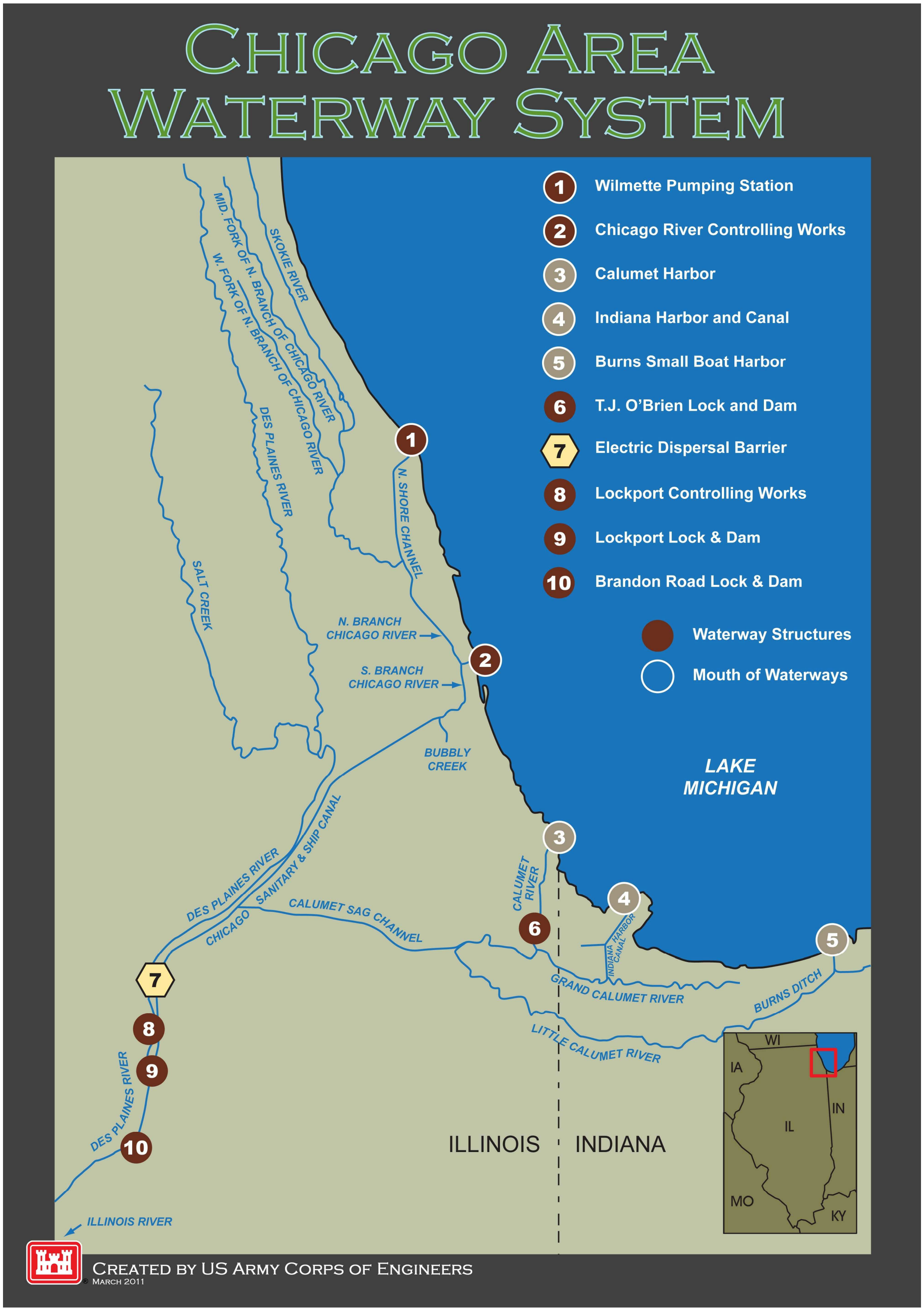
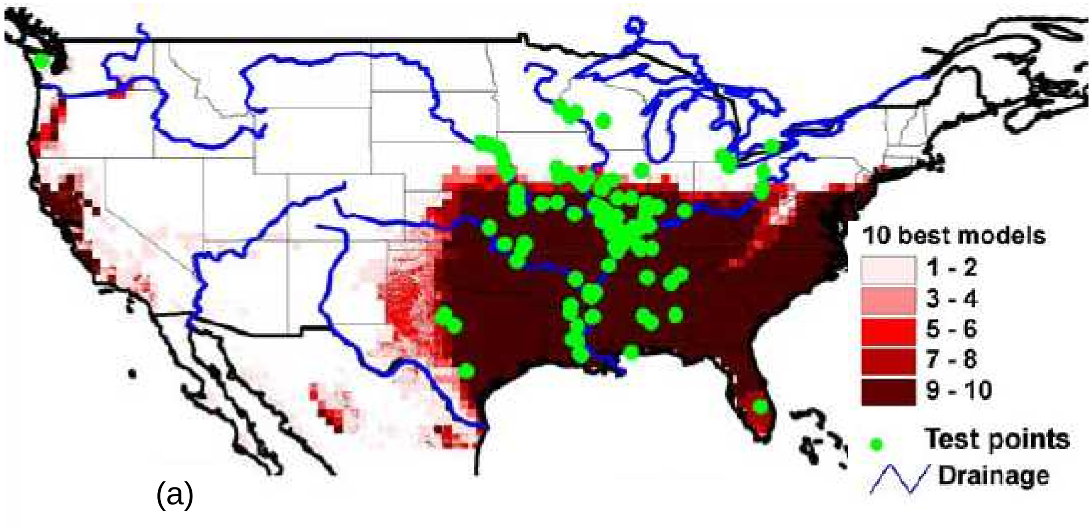


Figure 4. Map of the Chicago Area Waterway System (CAWS)
(Image reproduced courtesy of USACE)



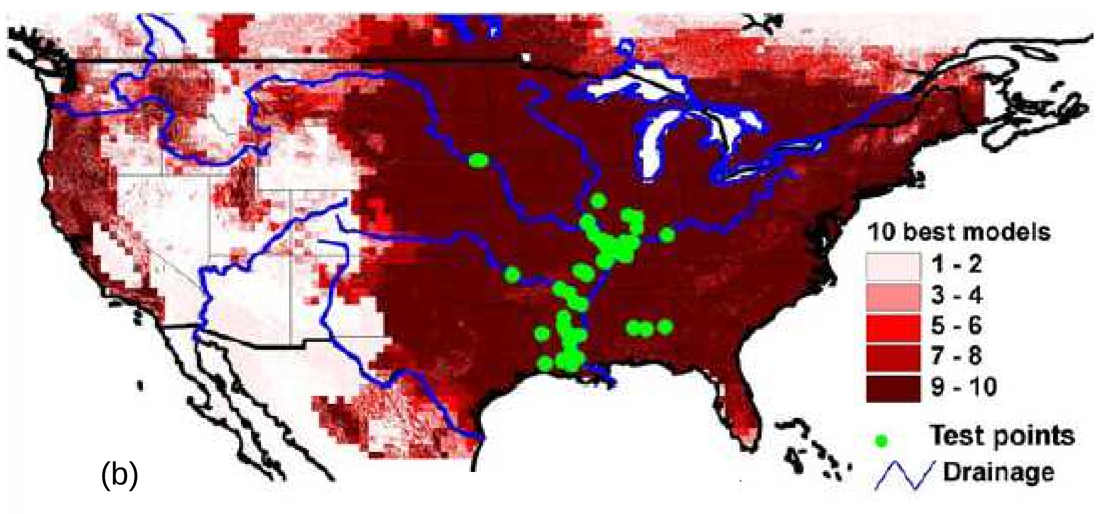


Figure 5. Predicted distribution of (a) Bighead Carp (*Hypophthalmichthys nobilis*) and (b) Silver Carp (*Hypophthalmichthys molitrix*) in North America

The maps show the 10 best distributions according to Genetic Algorithm for Rule-set Prediction (GARP). GARP used niche-based modelling based on such variables as topography and climate, and extrapolated the potential non-native ranged based on ability to predict the native range. Figure and caption modified from Chen et al. (2007a, Figures 1and 2).

(Figure reproduced with kind permission from Springer Science+Business Media B.V.)

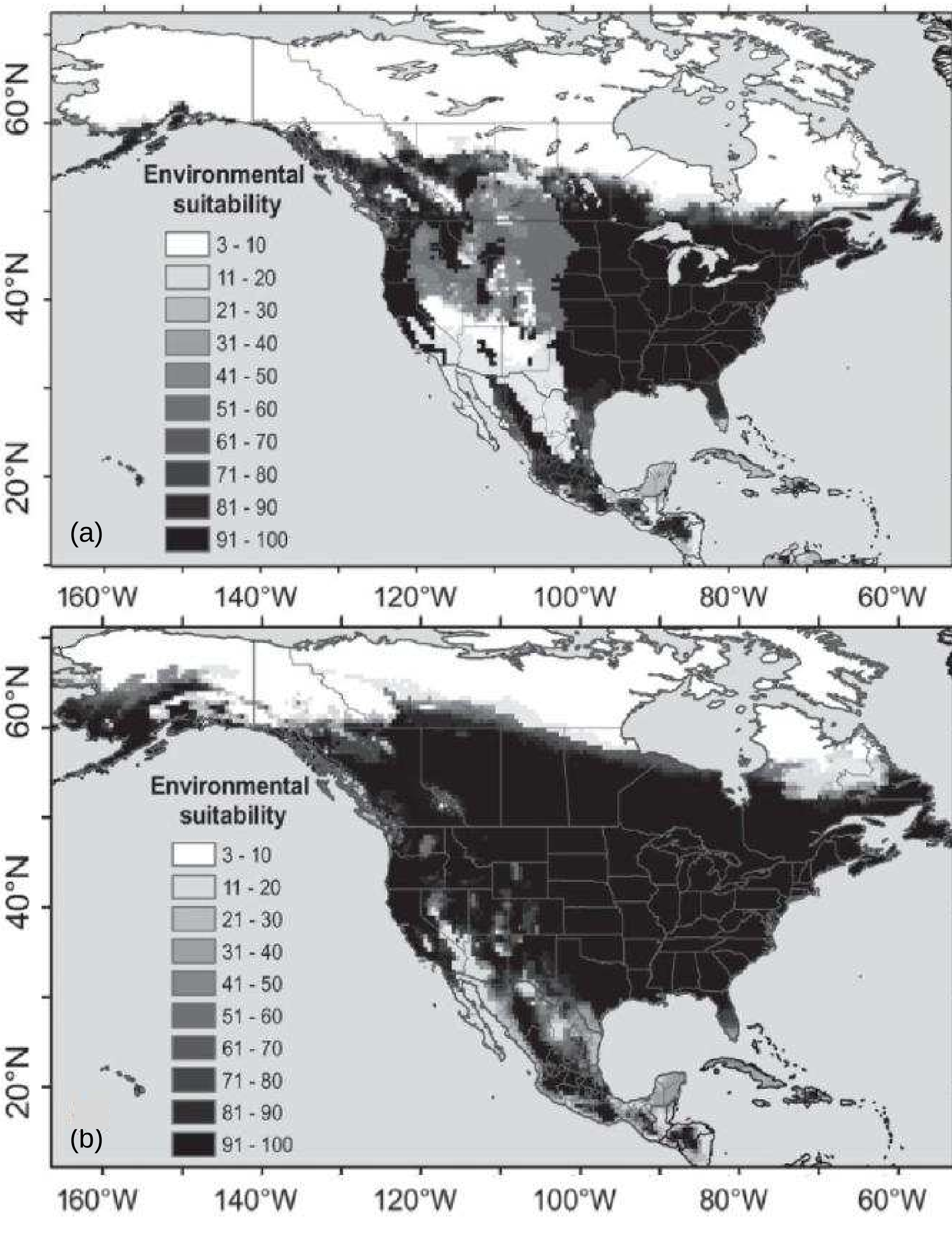


Figure 6. Potential distribution of (a) Bighead Carp (*Hypophthalmichthys nobilis*) and (b) Silver Carp (*Hypophthalmichthys molitrix*) in North America

Maps are based on environmental suitability, or the number out of a maximum of 100 niche-based models that predicted a certain area as appropriate. Figure and caption modified from Herborg et al. (2007).

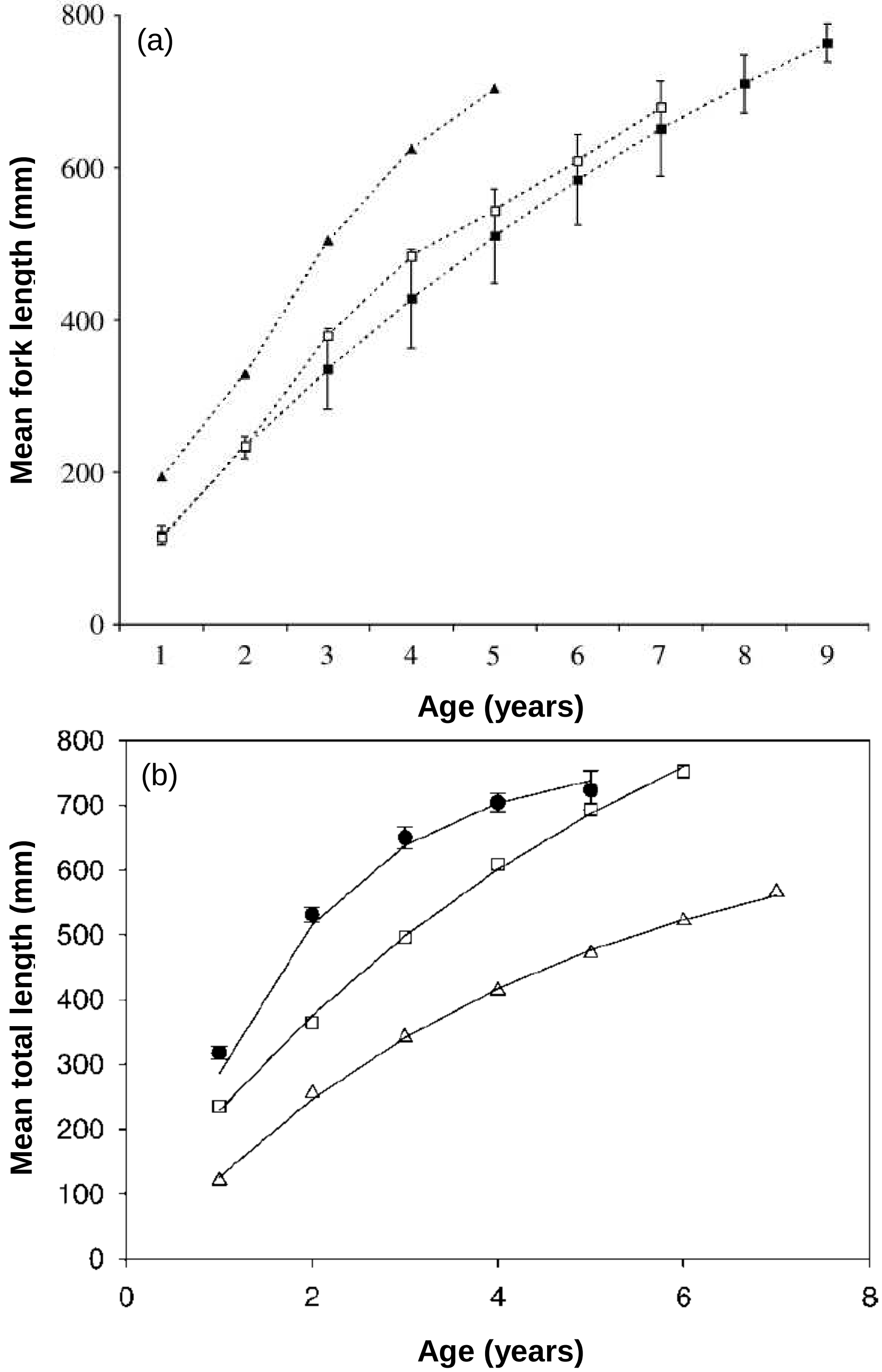


Figure 7. Size at age for (a) Bighead Carp (*Hypophthalmichthys nobilis*) and (b) Silver Carp (*Hypophthalmichthys molitrix*) in different habitats

Mean fork length at age (±S.D.) of Bighead Carp in the Lower Missouri River (▲; data from Schrank and Guy 2002), Polish lakes (□; data from Jennings 1988), and an eastern English lake (■). Figure and caption modified from Britton and Davies (2007)**; (b)** Mean total length at age (±95% CIs) of Silver Carp in the Middle Mississippi River (●; data from Williamson and Garvey 2005), an Indian reservoir (□; data from Tandon et al. 1993), and the Amur River (∆; data from Nikolskii 1961). Figure and caption modified from Kolar et al. (2007), who reproduced a figure from Williamson and Garvey (2005).