



Predictors of bigheaded carp drifting egg density and spawning activity in an invaded, free-flowing river



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ABSTRACT

Successful reproduction of non-native species is a critical step in the invasion process, influencing establishment and spread. Predicting invasive species' reproduction is often based on information collected from species' native ranges; however, environmental variables within the invaded range may provoke different responses. Bigheaded carp (*Hypophthalmichthys* spp.) have successfully invaded many water bodies worldwide and are currently threatening the Laurentian Great Lakes. We examined bigheaded carp spawning in a mostly unregulated, invaded ecosystem (Wabash River, IN, USA) which has similarities to multiple Great Lakes tributaries; it can therefore provide insights into the potential spawning of bigheaded carp in the Great Lakes. Spawning was protracted, and while initiation of spawning has been reported to require changes in discharge in their native ranges, this association was not observed in the Wabash River. However, changing discharges did appear to influence egg density, with rises in late spring producing high drifting egg densities. Cumulative growing degree-day (sum of days where [(max temperature – min temperature / 2) – 10 °C base temperature] is >0) was the most influential factor predicting spawning initiation. Overall, it appears that bigheaded carp exhibit the ability to spawn under a variety of environmental conditions, with changing discharges targeting spawning to periods when reproductive success may be more likely. The successful establishment of invasive species may hinge on their ability to reproduce across wide-ranging environmental conditions. The reproductive plasticity displayed by bigheaded carp could therefore contribute to their successful reproduction in multiple invaded ecosystems, including Great Lakes tributaries.

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Introduction

Invasive species are often studied to determine the traits that contribute to the species' successful invasion of and establishment in novel environments (e.g., Garcia-Berthou, 2007; Lee, 2002; Marchetti et al., 2004). There is no question that reproductive success is necessary for establishment and promotes spread through increased propagule pressure. Thus, reproductive ecology (e.g., maturity, spawning requirements, spawning length, fecundity) often plays a major role in the successful establishment of an invasive species (Deacon et al., 2011; Gozlan et al., 2003; Marchetti et al., 2004), and individuals may even allocate more energy toward reproduction during invasions (Hawkes, 2007). However, differences in environmental cues of introduced versus native ecosystems may provoke novel reproductive strategies. It is therefore important to examine reproductive ecology of invasive species in

invaded ecosystems and examine how reproductive plasticity may facilitate establishment and spread.

Successful invasive species often exhibit high levels of plasticity in multiple traits (e.g., length-at-maturity, fecundity; Alcaraz et al., 2005; David et al., 2004; Deacon et al., 2011). This plasticity makes it difficult to predict when and where non-native species may become established in novel environments. Timing of spawning is often mediated by environmental variables such as temperature (Achor et al., 2007; Dahl et al., 2004; Keefer et al., 2009) and can coincide with plentiful food resources or improved environmental conditions that can contribute to reproductive success and enhance recruitment (Anderson, 1988; Hinrichsen et al., 2003), thus positively impacting reproductive outcomes favoring establishment and spread. Therefore, examining reproductive ecology of invasive species across both native and novel environments could lead to improved understanding and predictions of which species are most likely to successfully invade.

One approach to invasive species prevention and control is modeling the vulnerability of waterbodies to aquatic invasive species (AIS) based on ecology and life history, usually based on data from a species' native range or populations in other ecosystems. For example, Lake Erie tributaries have been examined using this approach to determine their

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suitability for grass carp (*Ctenopharyngodon idella*) reproduction, and evidence of recruitment has since been detected in one of the tributaries predicted to be most vulnerable (Kocovsky et al., 2012; Chapman et al., 2013). This approach is a necessary first step in predicting reproductive success of AIS in invaded environments. However, reproductive plasticity in response to novel environmental metrics can facilitate successful establishment over a much wider range of environments than may be initially apparent, weakening the ability of this approach to accurately predict invasion success in some cases.

While regulations have helped in slowing non-native species introductions, the Laurentian Great Lakes have been affected by a large number of AIS, some of which have had severe deleterious impacts including reduced condition of native species (Irons et al., 2007). Big-headed carp (silver carp [*Hypophthalmichthys molitrix*], bighead carp [*Hypophthalmichthys nobilis*], hybrids [*H. molitrix* × *H. nobilis*], and backcrosses of these species, hereafter, collectively BHDC) exhibit multiple traits of successful invasive species including early maturity, rapid growth and high fecundity (Chick and Pegg, 2001; Kolar et al., 2007), have known negative impacts on invaded ecosystems (Chick and Pegg, 2001), and are currently threatening to invade the Great Lakes Basin. Considerable resources have been invested in early detection, rapid responses, and preventative efforts such as the electric barriers near Chicago, IL. The rapid population growth exhibited by invasive BHDC (Chick and Pegg, 2001) indicates that high reproductive success is likely an important component of their invasion success and will likely contribute to their future success in the Great Lakes. Elements of BHDC reproductive ecology, including environmental factors thought to influence reproduction, are therefore important for models seeking to predict their invasion success in novel environments. Multiple efforts have been made to develop such models based on bioenergetics, habitat suitability and the river length required for successful spawning for the Laurentian Great Lakes. These efforts have led to the broad conclusion that BHDC are likely to successfully establish in this system given sufficient introductions, leading to a myriad of negative impacts on native species (e.g., Chen et al., 2007; Cooke and Hill, 2010; Kocovsky et al., 2012; Long et al., 2014). However, there is no complete agreement regarding these predicted outcomes (Wittmann et al., 2014). Regardless, these assessments assume reproductive ecology in the Great Lakes and other invaded ecosystems will be similar to the species' native ranges. It is possible that altered reproductive ecology in response to novel environments could result in unexpected outcomes in newly invaded ecosystems.

Multiple lines of evidence contend that the reproductive ecology of invasive species in invaded ecosystems often departs from that reported either in the native range or across different invasive populations, often the result of high levels of phenotypic plasticity in response to environmental cues (e.g., Fox et al., 2007; Gutowsky and Fox, 2012; Feiner et al., 2012; Fox and Copp, 2014; Hórková and Kováč, 2014). Such plasticity must be examined to improve model performance and enhance management decisions. For example, successful BHDC spawning and embryo development, including hatching, was thought to require approximately 48–100 km of free flowing river (Kolar et al., 2007; Nico et al., 2005); however, recent evidence demonstrates that this distance may be much shorter (García et al., 2013). Additionally, BHDC have been found to spawn in a smaller watershed than previously thought possible (Coulter et al., 2013) and to be less specific in their spawning site selection (Deters et al., 2013).

Our study goal was to determine the environmental factors that influence BHDC reproductive ecology in an invaded ecosystem. We thus examined several aspects of BHDC reproduction across multiple years to determine whether specific environmental factors can predict spawning initiation and cessation and drifting egg density. We also examined whether invasive BHDC exhibit reproductive ecology driven by responses to environmental conditions that may produce differences in spawning timing and triggers across invaded ecosystems.

Materials and methods

Drifting BHDC eggs were collected at Wabash River Kilometer (RKM) 499 near West Lafayette, IN, USA. from 2012–2014. The Wabash River a tributary to the Ohio River in the Mississippi watershed and contains approx. 600 RKM of free-flowing water below its single mainstem dam (Fig. 1). The watershed land use is over 60% agriculture and encompasses just over 100,000 km². Mean discharge is 1000 m³/s but averages 88 m³/s at RKM 499 where observations were made. The upper free-flowing portion of the Wabash River has predominantly bedrock substrate, while substrate in the middle and lower Wabash River, including the sampling location, is mostly sand. The Wabash River channel is approx. 90 m wide at RKM 499, and water depth was similar throughout the sampling transect, averaging 1 m during summer months and up to 5.3 m during high flow events.

Paired bongo nets (60 cm diameter, 500 μm mesh) were towed in the river Thalweg starting at the same location for each pull (Lenaerts et al., 2015). Triplicate bongo net pulls were conducted weekly after water temperatures were greater than 15 °C and continued until no eggs were collected for three consecutive weeks. The net was towed with the current from the bow of a 4.9 m boat piloted downstream at 8 km h⁻¹ for approx. 5 min. Water velocity was measured (Marsh-McBirney Flo-Mate model 2000, Marsh-McBirney Inc., Frederick, Maryland) at 30 cm below the water surface (approx. velocity at the center of the bongo net) in 2012 only. These velocity measurements averaged 0.43 m/s. The volume of water sampled was quantified using a flowmeter (standard rotor, G. O. Environmental, Miami, Florida) mounted inside the mouth of the bongo nets. The net was towed just below the water surface and thus sampled the upper 60 cm of the water column. This was done to standardize sampling, match the depth at which water temperature was taken, and avoid collection of sand and debris during low flows.

Collected samples were taken to the lab and eggs were sorted and counted. Genetic verification was done of 30 BHDC eggs collected on each sampling date (Lenaerts et al., 2015). Mean egg density (eggs/m³) was calculated using flowmeter measures calculated according to manufacturer's instructions. Mean volume of water sampled in each bongo net pull was 80.2 m³ ± 10.9 SD (Max: 93.2 m³, Min: 54.0 m³). The flowmeter malfunctioned in July 2012, and so average sample volumes were calculated from the flowmeter measures from the surrounding dates (August) with similar river discharge (USGS #03335500), and the resulting mean volume sampled was used to determine egg density for July sampling dates. Every effort was made to sample in a consistent manner each week (i.e., location, duration, and speed of bongo net pulls), but volumes of water may still have varied. However, these sampling methods appeared to be effective in helping standardize water volume sampled as volumes of individual bongo net pulls in August, which had a similar discharge to July (August discharge: 29 m³/s–37 m³/s; July discharge: 22–37 m³/s), were all between 82 m³ and 92 m³.

Environmental variables were also measured for each sampling event. Water temperature (alcohol thermometer ± 0.25 °C) was measured during weekly sampling activities at a depth of 40–60 cm at the location where all bongo net pulls began. Discharge data were gathered from the river gage at Lafayette, IN (USGS #03335500) for each sampling date. Discharge data were not available from this gage prior to late July 2012; therefore, discharge values for April–July 2012 were estimated, using linear regression, from a downstream river gage at Covington, IN (USGS #03336000). There are no major tributaries entering the Wabash River between these gages and there was a strong relationship between the values from later in 2012 (Lafayette discharge = 0.954 * Covington discharge – 5.51; R² = 0.94).

For fishes, water temperature greatly influences growth, maturity, and survival, but instantaneous temperature measures generally do not accurately represent the thermal regimes that individuals experience, especially in temperate freshwaters. One method for quantifying

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