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Possible unintended effects of management at an invasion front: Reduced prevalence corresponds with high condition of invasive bigheaded carps

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ABSTRACT

Limiting the prevalence of invasive species is a global conservation priority. Invasive species can have varying ecosystem effects and responses to control throughout an invaded range, and removal near invasion fronts may inadvertently alter these characteristics. Bigheaded carp (bighead carp (*Hypophthalmichthys nobilis* Richardson) and silver carp (*H. molitrix* Valenciennes)) are invasive fishes from Asia invading North American freshwater ecosystems. We used mobile hydroacoustic surveys to examine bigheaded carp population characteristics from 2012 to 2015 across an invasion gradient in the Illinois River (USA), one of the most likely pathways to the Laurentian Great Lakes. These bigheaded carp species comprised 23–46% of fish community abundance and 45–78% of fish biomass across reaches, with lower contribution near the invasion front where intensive management by harvest occurs. Bigheaded carp prevalence in the community did not differ by habitat and comprised > 50% of community abundance and biomass throughout the river for most size classes. We identified negative relationships between density and relative weight (an index of body condition) of bigheaded carp, suggesting evidence of potential density-dependent intraspecific competition. Efforts to reduce invasive species abundances near invasion fronts may reduce prevalence. However, this could inadvertently release individuals from density-dependent competition and could enhance reproductive potential, growth or movements. By employing a suite of control efforts, including continuous removal efforts (including novel approaches) and by limiting movements (e.g., utilizing roads, fences, dams), it may be possible to offset undesired consequences of increased condition.

1. Introduction

Invasive species threaten ecosystems worldwide. Most invasive species exhibit high growth and survival rates that facilitate rapid population expansion in new ecosystems and result in negative ecological consequences. Once high relative abundance and biomass are achieved, competition with, or physical displacement of, similar native species can occur (Mooney and Cleland, 2001; Medley, 2010). In addition to community-level effects, high relative abundance and biomass of an invader can also lead to ecosystem-level consequences through homogenization of assemblages (McKinney and Lockwood, 1999; Olden et al., 2004) and redirecting or sequestering of energy and nutrients in their tissue (Hecky et al., 2004; Flecker et al., 2010). However, competitive dynamics of some invasive species can change with abundance, where interspecific competition, for example, occurs at low abundance of the invasive species and switches to intraspecific competition at high abundance (Kornis et al., 2014). Understanding the ecological consequences of an invasive species and developing appropriate management actions, therefore, requires assessing invasive populations across a range of abundances and available resources.

The duration of time an invasive species has been established is another important determinant of its influence on biodiversity, as increasing establishment time can not only increase prevalence of the invasive species but can alter its population demographics (Feiner et al., 2012). Newly established populations can be comprised of a specific demographic that eventually becomes more heterogeneous with time. For example, territorial invasive species in newly invaded systems may be comprised of recently displaced small individuals (Coulter et al., 2012), whereas large individuals of non-territorial species may initially invade new habitats due to abundant resources and low competition (Darling et al., 2011). Such homogenous demographics at the initial stages of invasion can influence how the invasive species affects the ecosystem and how natural resource managers target these individuals.

In order to manage current species invasions and to predict their

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future influences, it is essential to understand their prevalence relative to the existing biotic community and identify whether this changes across habitats and community demographics (e.g., size classes). Invasive species relative abundance and biomass can be used as a quantitative benchmark for evaluating management or conservation actions (Bronte and Sitar, 2008), and can be more biologically meaningful than evaluating absolute changes in invasive species abundance (e.g., a goal of maintaining invasive species relative abundance at 25% of the community versus maintaining a target density). Using percent composition of invasive species as an assessment index also accounts for changes in non-target species abundance. For example, harvest efforts could reduce an invasive species' density without changing its relative abundance in the community, if native species abundance also decreases due to unintentional management actions (e.g., by-catch) or an overarching factor affecting all species (e.g., drought). Identifying community demographics that are dominated by an invasive species can further refine management objectives, as is the case with size-selective harvest as an invasive species management tool (Tsehaye et al., 2013). Finally, invasive species relative abundance and biomass data can help develop or improve invasive species risk assessments. When evaluating an environment's vulnerability to a future invasion, risk assessments can incorporate the invasive species richness already present and their relative abundance or biomass in the community (Panov et al., 2009). Risk assessments also include the expected impacts (quantitative or qualitative) of an invasive species should they invade an environment. Combining results from controlled experiments (e.g., Collins and Wahl, 2017) with field-observed prevalence that the invasive species has obtained in other systems can help derive a metric of their likely impacts (Panov et al., 2009).

Using these metrics to assess and manage invasive species will be particularly useful in riverine ecosystems due to the ability of invasive species to readily spread among connected waterways. Moreover, invasions in rivers typically exhibit a directional invasion pattern (i.e., dispersal corridor) that allows for invasive species' relative abundance, relative biomass, and demographics to be quantified across sites with varying invasive species abundance and time since invasion. Silver carp (*Hypophthalmichthys molitrix* Richardson) and bighead carp (*H. nobilis* Valenciennes; hereafter collectively termed bigheaded carp) are two fish species native to Asia that are rapidly invading North American aquatic ecosystems, especially rivers (Kolar et al., 2007). These species have spread throughout the Mississippi River and into its tributaries, where they have invaded most of the Illinois River and thereby threaten to invade the Laurentian Great Lakes (USACE, 2010). Their invasion has the potential to disrupt ecological processes due to the large amount of plankton they consume (Smith, 1989; Cooke and Hill, 2010) which, in combination with their fast individual and population growth rates (Williamson and Garvey, 2005), could result in interspecific competition with native fishes (Irons et al., 2007; Sampson et al., 2009; Nelson et al., 2017) and disruption of food web dynamics (Sass et al., 2014; Collins and Wahl, 2017).

Control of bigheaded carp is a priority in North America, particularly in the Illinois River which is divided by a series of locks and dams that have been shown to hinder movement (e.g., Lubejko et al., 2017). Differences in harvest efforts (the primary control strategy) and habitat availability among reaches likely also contribute to varying abundances of bigheaded carp, which generally decrease moving upstream (Sass et al., 2014; MacNamara et al., 2016). Additionally, bigheaded carp population demographics vary across reaches, where individual size increases farther upstream (MacNamara et al., 2016).

Understanding how population characteristics vary across an invasion gradient is critical for developing and enhancing invasive species management plans and risk assessments. We evaluated the prevalence of bigheaded carp relative to the existing fish community throughout the Illinois River (a 460 km navigable river). Our specific objectives were to 1) quantify the relative abundance and biomass of bigheaded carp in the fish community throughout the Illinois River over a four year period and determine whether this differed among reaches, 2) determine whether bigheaded carp prevalence in the fish community differed across habitats, 3) quantify the proportion of the fish community size distribution that was comprised of bigheaded carp and assess whether this varied among reaches and 4) examine relationships between bigheaded carp densities and body condition of bigheaded carp and other fish species as indicators of potential intraspecific and interspecific competition.

2. Methods

2.1. Study area

The Illinois River waterway is a floodplain river which has been altered by a series of locks and dams for flood control and navigation, and through changes in land-use (urban development in the most upstream reaches, agriculture throughout downstream reaches). Despite these anthropogenic alterations, the Illinois River functions as a natural river ecosystem comprised of natural side-channels and backwaters. Water quality in the Illinois River has improved since the 1970s (Pegg and McClelland, 2004) due in part to habitat improvement projects (O'Hara et al., 2008). The fish community throughout the river has been heavily dominated by native species, and native species richness and abundance increased from 1976 to 2009 (McClelland et al., 2012; Gibson-Reinemer et al., 2017). During this time, non-native fish species richness and abundance also increased, although until 2009 non-natives represented a relatively small proportion of the fish community (McClelland et al., 2012; Gibson-Reinemer et al., 2017). Bigheaded carp invaded the Illinois River from the Mississippi River and have spread upstream to the Dresden Island Reach (Irons et al., 2007; Gibson-Reinemer et al., 2017).

We sampled six reaches (Alton – Dresden Island) in the Illinois River (Fig. 1) where bigheaded carp are currently found (USFWS, 2015). Upstream from the invasion front in the Dresden Island Reach is the Brandon Road Reach and upstream from that, the Chicago Area Waterway System (CAWS) which provides a direct hydrological connection to Lake Michigan, albeit with man-made deterrents in place. Within the CAWS these deterrents include a series of electric dispersal barriers and fencing designed to deter fish movement between the Illinois River system and Lake Michigan (Parker et al., 2015). Bigheaded carp, along with native fishes, in the lower Illinois River (Alton – Peoria reaches) are subject to commercial harvest. However, commercial fishing in the upper Illinois River (Starved Rock – Dresden Island reaches) is prohibited, so bigheaded carp are managed through year-round intensive harvest performed by commercial fishers contracted and supervised by the Illinois Department of Natural Resources (USFWS, 2015; MacNamara et al., 2016). Native fishes collected with contracted harvest in the upper river reaches are released alive.

2.2. Hydroacoustic sampling

We assessed the Illinois River fish community by conducting hydroacoustic sampling in the six reaches of the Illinois River from 2012 to 2015. Mobile sampling was conducted from a 9 m research vessel using two split-beam BioSonics DT-X transducers (BioSonics Inc., Seattle WA, USA). We used different combinations of 70 kHz and 200 kHz transducers among years that were horizontally oriented due to the relatively shallow depth of all sampling locations. Transducers were angled so that one transducer sampled near the water surface and the other sampled directly below the upper beam, with automatic rotators maintaining transducer angles. We set a maximum distance of 50 m from the transducers for hydroacoustic data collection and used a ping rate of 5 pings s^{-1} and a 0.40 ms pulse duration.

Within each reach, we sampled standardized locations comprised of main channel, side-channel, backwater lake, harbor and tributary habitats that had ≥1.0 m water depth from September to November each