Compensatory response of invasive common carp *Cyprinus carpio* to harvest

Michael J. Weber [a,*], Matthew J. Hennen [a,1], Michael L. Brown [a], David O. Lucchesi [b], Todd R. St. Sauver [b]

[a] Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA
[b] South Dakota Department of Game, Fish and Parks, 4500 South Oxbow Avenue, Sioux Falls, South Dakota 57106, USA

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ABSTRACT

Invasive species are often mechanically removed to reduce or eliminate their populations. However, removal may release survivors from density-dependent mechanisms resulting in stable or increasing population abundance through compensatory processes. Additionally, immigration of new individuals into systems where removal is occurring may negate efforts to control population abundance. Thus, understanding population-level responses to removal and immigration rates are essential aspects of invasive species management. We evaluated how common carp *Cyprinus carpio* populations respond to removal through commercial harvest in three interconnected lakes over five years. Nearly 230,000 common carp (up to 55 fish/ha/year) were removed and exploitation rates ranged from <1 to 43% across three lakes over four years. Despite high removal rates in some years, carp population abundance, recruitment, and growth remained stable. Carp survival ranged between 54–79% and was inversely related to removal rate. However, survival only decreased by 25% at 43% exploitation, suggesting a partial compensatory rather than additive response. Emigration among lakes was low (<1%; >2000 carp), but varied among years in response to water level fluctuations. Our results indicate that carp control is difficult in large interconnected systems due to compensatory mortality and interbasin movement patterns, limiting the ability of removal-based management practices alone to control these invasive populations.

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1. Introduction

Successful invasions of non-native species are a primary source of irreversible change in ecological processes (Pimentel et al., 2000; Lodge et al., 2006) and present a formidable challenge to resource managers (Vitousek et al., 1996; Byers et al., 2002). The invasion and spread of non-native species into previously uninhabited environments can disrupt ecosystem structure and function at multiple levels by altering food webs (Hrabik et al., 1998; Weber and Brown, 2009), resulting in the loss of native species and biodiversity (Allan and Flecker, 1993; Weber and Brown, 2011a) and a homogenization of freshwater fauna (Rahel, 2002). Due to the deleterious effects of invasive species, there is a need to develop management strategies to reduce their adverse impacts. Harvest management (i.e., mechanical removal of individuals to suppress or eliminate a population) has been conducted on a wide range of taxa including aquatic invertebrates (Hein et al., 2006), fish (Peterson et al., 2004; Coggins et al., 2011), birds (Frederiksen et al., 2001), and mammals (Howald et al., 2007). Successful eradication or suppression of invasive species may reduce their ecological effects and serve as a restoration strategy in disrupted ecosystems (Hein et al., 2006; Weidel et al., 2007; Coggins et al., 2011). However, formal evaluations quantifying the success of eradication projects are rare, often only summarized in technical reports (Meronek et al., 1996; Simberloff, 2001), or been conducted on small, closed systems where eradication is likely to be successful (e.g., Peterson et al., 2004; Weidel et al., 2007; Bajer et al., 2011). In contrast, little is known concerning how populations respond to eradication projects in larger interconnected systems where animals are abundant, immigration and emigration occurs, and eradication is unlikely.

The goal of invasive species harvest management is population eradication or reduction to a level that minimizes the ecological impacts of the targeted species on invaded ecosystems. How-

* Corresponding author. Current address: Department of Natural Resource Ecology and Management, Iowa State University, 339 Science Hall II, Ames, IA 50011, USA. Fax: +515 294 2995.
  E-mail address: mjw@iastate.edu (M.J. Weber).
[1] Current address: Minnesota Department of Natural Resources, 650 Highway 169, Tower, MN 55790, USA.

ever, removal of individuals provides additional resources (e.g., food, habitat) to those that remain, potentially releasing them from density-dependent processes. If populations are regulated by density-dependent processes, survivors may compensate with increased levels of recruitment and growth or decreased natural mortality, resulting in stable (compensatory) or increasing (overcompensatory) population size (Brooks, 2002; Matsuda and Abrams, 2004; De Roos and Schellekens, 2007; Zipkin et al., 2008). Several theoretical models predict compensatory responses from populations subjected to harvest (Zipkin et al., 2008; Abrams, 2009; Colvin et al., 2012). However, empirical evidence of compensatory responses in natural populations subjected to harvest is rare (Abrams, 2009), but is needed to identify conditions under which compensatory responses occur.

Common carp *Cyprinus carpio* is a widespread invader worldwide that has been described as an ecosystem engineer due to its large-scale ecosystem disturbances (Koehn, 2004; Weber and Brown, 2009). Common carp are associated with physical, chemical, and biological alterations to shallow aquatic systems (Weber and Brown, 2009, 2011a). Direct effects of common carp (e.g., decreased water clarity and aquatic macrophyte coverage, increased suspended nutrient availability) can result in shifts in aquatic ecosystems between alternative equilibria from a heterogeneous, clear macrophyte-dominated state to a homogenous turbid, plankton-dominated state (Scheffer et al., 2001; Weber and Brown, 2009), which may indirectly result in changes in native fish assemblages and food web dynamics (Jackson et al., 2010; Weber and Brown, 2011a; Letvin, 2013).

A variety of techniques have been applied to control common carp populations, including mechanical removal (e.g., netting and trapping), toxicants, water level manipulation, fish barriers, biotechnology, and immunological methods (Brown and Walker, 2004; Weber and Brown, 2009; Brown and Gilligan, 2014). Whole-lake chemical piscicide applications have been successful at reducing or eliminating invasive fish populations in small systems, but their use is limited by lake size, costs, and public concerns about effects on non-target fishes and risks to human health (Meronek et al., 1996; Harig and Bain, 1998). In contrast, mechanical removal of invasive species provides a species-specific alternative to chemical reclamation (Peterson et al., 2004; Hein et al., 2006; Zipkin et al., 2008), but formal holistic evaluations of its effectiveness at controlling invasive populations are scarce. The most widely attempted mechanical method to control common carp populations is commercial fishing using large seine nets (e.g., Weber and Brown, 2009; Bajer et al., 2011; Colvin et al., 2012). However, supporting population dynamic data for common carp is lacking and population-level effects of mechanical removal are unknown.

Controlling invasive species is a population-level phenomenon, but is rarely studied as such (Parker, 2000). The success of invasive populations depends on population growth, which fluctuates with recruitment, growth, mortality (natural and harvest), and immigration and emigration (Vermeij, 1996; Gotelli, 2001). Understanding population level mechanisms resulting in the success of invasive species is necessary to formulate control and recovery strategies (Parker et al., 1999; Sakai et al., 2001). Given the deleterious effects of common carp on aquatic ecosystems, there may be substantial ecological benefits to reducing their abundance in invaded lakes. However, very few manipulative approaches have been implemented to evaluate the effects of removal through harvest on populations. Here, we conducted a five-year manipulative experiment in three interconnected lakes to evaluate the effect of harvest on common carp abundance and population dynamics. Success of invasive species control depends upon the feasibility of population reduction, the potential for immigration, and the susceptibility to control measures (Myers et al., 2000). We assessed common carp population estimates and relative abundance, survival, inter-

basin movement, size structure, growth and recruitment and how they changed in relation to varying levels of removal. Our work was based on the premise of harvest management that predicts removing individuals from a population results in reduced survival and population size. Thus, we hypothesized that common carp survival and abundance would decline following harvest management. Alternatively, survival may decline at a lower rate than exploitation or may not be related to harvest and instead be constant through time or simply vary among lakes and years. If common carp survival and abundance were reduced following harvest, we hypothesized that recruitment and growth rates would increase and size structure would shift toward larger bodied individuals.

2. Methods

2.1. Study site

Common carp populations were sampled in an interconnected chain of natural lakes in southeastern South Dakota, USA (Fig. 1). Lake Herman forms the headwaters of the chain of lakes and connects to lakes Madison and Brant via Silver Creek. Lake Herman is intermediate in size (521 ha) compared to the other lakes, has a mean depth of 1.4 m and a maximum depth of 3.9 m. Lake Madison is the largest (1069 ha, mean depth = 2.4 m, maximum depth = 4.9 m) of the four lakes. Brant Lake, last in the chain, is 421 ha with a mean depth of 2.9 m and a maximum depth of 4.7 m and separated from Lake Madison by Round Lake (76 ha), which, due to its unimpeded connection with Brant Lake, was not considered a separate system in this study. A 1.5 m elevation change exists at the outlet of Lake Madison, prohibiting upstream movement from Lake Brant. All lakes are predominately silt bottoms with limited submerged macrophyte coverage.

2.2. Relative abundance

The relative abundance of adult and age-1 common carp was indexed using trap nets from 2004 through 2012 in lakes Herman, Madison, and Brant and in two control lakes where harvest did not occur, lakes Thompson and Sinai. Control lakes were selected because they are the only lakes comparable in size with similar fish communities that are located in close proximity (<30 km) to the study lakes. Carp catches in trap nets were positively correlated with population estimates from lakes Herman, Madison, and Brant from 2007 to 2010 ($n = 10$ lake/years; $r = 0.58$), indicating that trap nets provided a useful index of carp relative abundance. Trap nets were constructed with 19-mm bar mesh netting, frames were 0.9 m high by 1.5 m wide, and had 18.3-m-long leads. Experimental gill nets were 45.7 m long by 1.8 m deep with one 7.6-m panel each of 13-, 19-, 25-, 32-, 38- and 51-mm bar mesh monofilament netting. Effort deployed for each gear varied by lake as a function of lake surface area, but all locations were randomly selected and nets were soaked for 24 h. Common carp were counted in each gear and measured (nearest 1 mm). Von Bertalanffy growth curves indicate that age-1 common carp in these systems are 150–325 mm in length whereas those >350 mm are age-2 or older (Weber et al., 2011). Thus, individuals were categorized as age-1 or adult based on their length, and the relative abundance of each age group (age-1 and adult) captured in each gear was indexed as catch per unit effort (CPUE; number of fish per net night). We used a multiple site and year, before and after control and impact (BACI) design to test for differences in adult and age-1 common carp abundance in removal lakes following harvest. This approach compares differences in catch rates measured before and after a treatment in 'impacted' (lakes Herman, Madison, and Brant) and 'control' (lakes Thompson and Sinai) systems. BACI designs can be used to differ-