

Modeling the potential for managing invasive common carp in temperate lakes by targeting their winter aggregations

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Abstract Common carp (*Cyprinus carpio*) is one of world's most invasive fish and managers have long searched for practical control strategies for this species. In temperate systems, common carp forms large winter aggregations that can be located with telemetry and removed with seine nets. This has been viewed as an excellent management possibility, but its success has been mixed. Using a modeling approach, we demonstrate that the usefulness of winter seining in controlling common carp in temperate North American lakes depends on whether carp populations are driven by one of two distinct recruitment dynamics. In lakes where carp can easily recruit within systems from which they are being removed, such as within productive lakes with poor communities of micro-predators, winter seining is unlikely to be effective. Even very high removal rates (90 % adults annually) were not sufficient to reach management goal (biomass <100 kg/ha) in such systems. However, in regions with strong predatory communities where carp can recruit only in outlying, seasonally unstable marshes, removal rates as low as 30 % annually or 50 % every

other year were able to reduce carp biomass below the management threshold. Such removal rates are achievable as they fall within the range of empirically measured values. Because many carp populations are driven by external recruitment dynamics, strategically conducted winter removal could be used to control this species in a large number of systems across temperate North America and elsewhere.

Keywords *Cyprinus carpio* · Winter seining · Judas technique · Telemetry · Removal

Introduction

Common carp (*Cyprinus carpio*, or 'carp') is one of the world's most invasive fish (Matsuzaki et al. 2009) for which managers have long searched for sustainable control strategies (Moyle et al. 1950; Rach et al. 1994; Koehn 2004; Thresher et al. 2014). In temperate regions, the carp is known to form large winter aggregations, which create unique opportunities to remove large numbers of carp over short periods of time (Johnsen and Hasler 1977). Documented in carp's native range, winter aggregations have also been reported from ice-covered lakes of midwestern North America or from warmer temperate regions of south-eastern Australia (Johnsen and Hasler 1977; Jones and Stuart 2009; Bajer et al. 2011). By using the so-called "Judas technique", in which some

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individuals within a population are implanted with transmitters, carp winter aggregations can be easily located and up to 90 % of individuals can be removed in a single attempt, at least in small lakes (Bajer et al. 2011). However, the sustainability of winter seining, or physical removal in general, for managing carp populations remains questionable. While sustained removal had only a negligible effect on carp biomass in prairie lakes in North America or in the Murray-Darling River Basin in Australia (Moyle et al. 1950; Thresher 1996; Smith 2005; Weber et al. 2011), it resulted in a sustained population decline in a predator-dominated lake in Minnesota, USA (Bajer and Sorensen 2015) and in a shallow isolated lake in Tasmania (Donkers et al. 2012). We hypothesize that the success of physical removal in controlling common carp depends on differences in recruitment (i.e. survival of young) processes among geographic areas and ecosystem types to which this fish has been introduced.

Given the presence of vegetated spawning habitat, recruitment of carp is regulated primarily by processes associated with water productivity (most likely through increased abundance of larval food), abundance of small predators that forage on carp eggs and larvae (micropredators), such as the bluegill (*Lepomis macrochirus*), and abundance of adult carp (Bajer et al. 2012, 2015a; Weber and Brown 2013). Regional differences among these processes lead to distinct recruitment patterns that have important implications for managing carp via physical removal, or winter seining in particular. This can be illustrated by two different ecoregions of temperate North America. In lakes of the Great Plains ecoregion, which are very productive and typically have low abundance of micropredators (prairie lakes), carp recruitment is frequent (Bajer et al. 2015a) and is primarily regulated by the density of adults (recruitment tends to be especially high at low densities of adult carp) (Weber and Brown 2013; Bajer et al. 2015b). Such populations may be difficult to manage with removal because per-capita reproductive success increases as adult density is being reduced (Weber et al. 2011; Colvin et al. 2012). However, in lakes of the Temperate Forests ecoregion, which are less productive and typically have more abundant populations of bluegill, in-lake recruitment is very low and carp populations are sustained by spawning migrations of adults into winterkill-prone marshes in which communities of

micropredators are unstable and in which carp can periodically overcome recruitment bottlenecks (Bajer et al. 2015a, 2015b). Carp populations driven by such external recruitment dynamics may be more suitable for management via removal because recruitment is sporadic (it occurs only after winterkills when native micropredators perish) and also because out-migration rates of juveniles from marshes into lakes are often low (Bajer et al. 2015b).

In this study, we used an individual-based model (Bajer et al. 2015b) to simulate the responses of carp populations to removal via winter seining in two model ecosystems that exemplified lakes of two temperate ecoregions in North America. The first ecosystem exemplified systems in which carp recruitment occurs within the lakes from which the adults are being removed (e.g. internal recruitment), versus the second ecosystem where populations are sustained by recruitment from external, seasonally unstable marshes (e.g. external recruitment); see methods for detailed description of each ecosystem. We evaluated a wide range of empirically demonstrated rates of physical removal in combination with two plausible removal regimes (every year and every other year). Although winter seining typically targets sexually mature carp, we also tested the importance of targeting juveniles (older than age-0, but not yet sexually mature), and age-0 carp to suggest alternative control strategies for systems where winter seining alone may not be sufficient to achieve management goals. Our results have implications for carp management in temperate regions of the world by suggesting that physical removal is likely to be effective in managing populations that are driven by intermittent, external recruitment dynamics.

Methods

Ecosystem types

We used two ecosystem types to demonstrate the effects of winter seining on the abundance and biomass of carp populations driven by internal versus external recruitment dynamics. The first ecosystem was representative of productive prairie lakes of the Great Plains ecoregion of North America, in which carp recruitment is pervasive and density-dependent (Kantrud et al. 1989; Weber and Brown 2013; Bajer

et al. 2015b). We modeled such ecosystems as an isolated 100 ha lake. We assumed that recruitment occurred annually and was regulated by the abundance of adult females following Ricker's stock-recruitment relationship (Weber and Brown 2013; Bajer et al. 2015b). If expressed per female, the number of recruits approached 800 at very low density of females and declined to zero at carrying capacity (approximately 300 females/ha) (Bajer et al. 2015b). The assumption that recruitment occurred annually was somewhat simplistic, but Weber et al. (2011) showed that more intermittent recruitment patterns had negligible effect on carp management via removal in prairie lakes due to density dependence.

The second ecosystem, in which recruitment occurred externally, represented interconnected systems of micropredator-dominated lakes and winterkill-prone marshes of the Temperate Forests ecoregion of North America (Rahel 1984; Bajer et al. 2012). In these systems, adult carp overwinter primarily in lakes but conduct spawning migrations into marshes during spring. Most adults return back to the lakes in early summer (Bajer et al. 2015b). Winterkills occur in marshes with moderate frequency (typically every 2–10 years) and are associated with declines in native micropredators, which allow carp eggs and larvae to survive in large numbers (Bajer et al. 2012). During a winterkill year, the number of recruits in marshes can be predicted by the same density-dependent relationship as in Ecosystem 1 (Bajer et al. 2015b), but recruitment is nil during non-winterkill years. Only a low percentage of age-0 carp out-migrate from marshes into lakes during the first or the second year, approximately one in 300 (Bajer et al. 2015b). More intense out-migration occurs in the third year and thereafter (50 %/year; Bajer et al. 2015b). Adult carp that do not conduct spawning migrations and spawn in lakes have low recruitment rate (<1 age-0/female; Bajer et al. 2015b). Adult carp form winter aggregations both in lakes and in marshes, but only lakes can be seined as marshes are too shallow. For simplicity, we assumed that the lake and marsh were of equal size (100 ha). We assumed that the marsh winterkilled, on average, once every 5 years because this winterkill frequency occurs commonly and is associated with highly abundant carp populations in lakes, thus our results are more conservative (Bajer et al. 2015b).

The model

To simulate the effects of winter seining on carp populations, we used an individual-based model that is capable of tracking the movement, reproductive success, survival, and growth of carp in lakes (Ecosystem 1) and lake-marsh systems (Ecosystem 2) (Bajer et al. 2015b). A list of model parameters and equations can be found in Bajer et al. (2015b; their Table 1). We modified the existing model slightly for the specific purpose of simulating winter removal. Specifically, because winter seining typically targets mature (large) carp, we simulated maturity based on the length of each carp (Online Resource 1). We also assigned gender to each mature individual using 1:1 sex ratio (Online Resource 1), which has also been used in other studies (Brown and Walker 2004). Because females comprise only half of the adult population, we multiplied the recruits per adult relationship in the existing model by two (the existing model calculates recruitment per adult rather than per female; Bajer et al. 2015b). To accelerate computations, the lengths of age-0 carp at the end of the first year were randomly distributed between 85.3 and 109.7 mm [mean \pm 1 SD reported in Phelps et al. (2008) and Osborne (2012)]. Growth in length and weight after the first year of life was density-dependent (Bajer et al. 2015b). Natural mortality was length-dependent (Charnov et al. 2012) and we modeled it as an annual mortality probability that decreased from approximately 0.66 for age-0 carp to 0.06 for carp that approached maximum size ($L_{\infty} = 712$ mm) (Bajer et al. 2015b).

In the Ecosystem 2, where spawning migrations occurred, we used empirically derived probabilities of adult carp migration from the lake to the marsh to spawn, their return to the lake, and the probability of juvenile dispersal out of the marsh and into the lake (Bajer et al. 2015b). Specifically, we allowed the probability of spawning migration to the marsh to vary from year to year as a random variable between 0.1 and 0.7. We allowed the return probability of adults to vary between 0.38 and 0.88 (also randomly generated each year) (Bajer et al. 2015b). The probability of age-0 and age-1 carp out-migrating from the marsh into the lake was 0.003 and it increased to 0.5 for age-2 and older carp (Bajer et al. 2015b). Finally, carp (all ages) that attempted to overwinter in the marsh incurred a high risk or mortality (0.95–1.00) if the marsh winterkilled (Bajer et al. 2015b). Annotated Java-

code for Ecosystem 1 and Ecosystem 2 is available in Online Resource 2.

Model runs

Modeling was conducted using annual time steps. The model runs began by removing a proportion of individuals according to background probability of natural mortality. The model then removed additional individuals in the marsh if winterkill occurred (Ecosystem 2 only). Following that, the model simulated a springtime spawning migration from the lake to the marsh and then a return back to the lake (Ecosystem 2 only). Recruitment, the number of age-0 carp/each female at the end of the summer, was then calculated (both Ecosystem 1 and 2). The model then simulated the dispersal of recruits from the marsh to the lake (Ecosystem 2 only). Following the dispersal, the model calculated the number of carp in each age class, overall carp density, and annual length and weight increments for each carp (which were density dependent). Total length was used to determine if carp reached maturity (Online Resource 1). Winter seining occurred at the end of each year. Depending on modeling scenario, sexually mature adults, juveniles, and age-0 were removed. Final outputs represented the number of carp in each age class, carp population density and overall carp biomass at the end of each year.

At the beginning of each run, each lake (both Ecosystem 1 and 2) was seeded with 400 carp/ha, or approximately 500 kg/ha (a density observed in high abundance carp lakes; Bajer and Sorensen 2012) and ages were randomly distributed between 1 and 15. The populations were then allowed to equilibrate for 30 years using default model settings (no removal) to create a realistic age structure and biomass. This was followed by 75 years of management via winter seining. Four removal probabilities were simulated: baseline conditions (0.0), low (0.3), medium (0.5) and high (0.9). These values are similar to previous models (Weber et al. 2011) and to empirical observations (Bajer et al. 2011); e.g. removal probability of 0.9 meant that each fish had 90 % chance of being removed from the population whenever removal was applied. Intermediate removal probabilities (0.6, 0.7, 0.8) were added as necessary to increase model

resolution. Removal occurred either every year or every other year. We ran ten simulations of each scenario for Ecosystem 1 and 15 for Ecosystem 2 because model results were more variable in this scenario due to the stochastic nature of winterkills, adult spawning migrations and juvenile dispersal. For each scenario, we calculated the mean (\pm SD) biomass at year zero (immediately before management started) and then 5, 10, 25, 50, and 75 years after management commenced. At each of these time intervals, we examined whether the biomass of carp declined below 100 kg/ha, which represents an ecologically non-damaging level, i.e. management threshold (Crivelli 1983; Bajer et al. 2009; Bajer and Sorensen 2015).

Results

In Ecosystem 1, the management goal of 100 kg/ha was never reached if only adults were targeted, even if 0.9 removal probabilities were applied annually (Fig. 1). The management goal was reached if adults and juveniles were targeted with a 0.7 or higher probability or when all life stages were targeted with a 0.6 or higher probability annually (Fig. 1). When removal frequency was reduced to every other year, only the highest removal probability (0.9), and only when it was applied to target all life stages, resulted in reaching the management goal (Fig. 2).

In Ecosystem 2, reaching and sustaining the management goal of 100 kg/ha was observed over a broader range of scenarios. Annual removal probabilities as low as 0.3 resulted in reaching the management goal by year 75 regardless of whether only adults or other life stages were targeted (Fig. 3). Annual removal probabilities of 0.5 allowed for reaching management goals in 10 years even if only adults were targeted. Annual removal probability of 0.9 resulted in extremely low carp biomass by year 5 (Fig. 3) and population quasi-extinction (<1 individual) by year 25. If removal frequency was reduced to every other year, the management goal was reached by year 10 at removal probability of 0.5 or higher, regardless if only adults or also other life stages were targeted (Fig. 4).

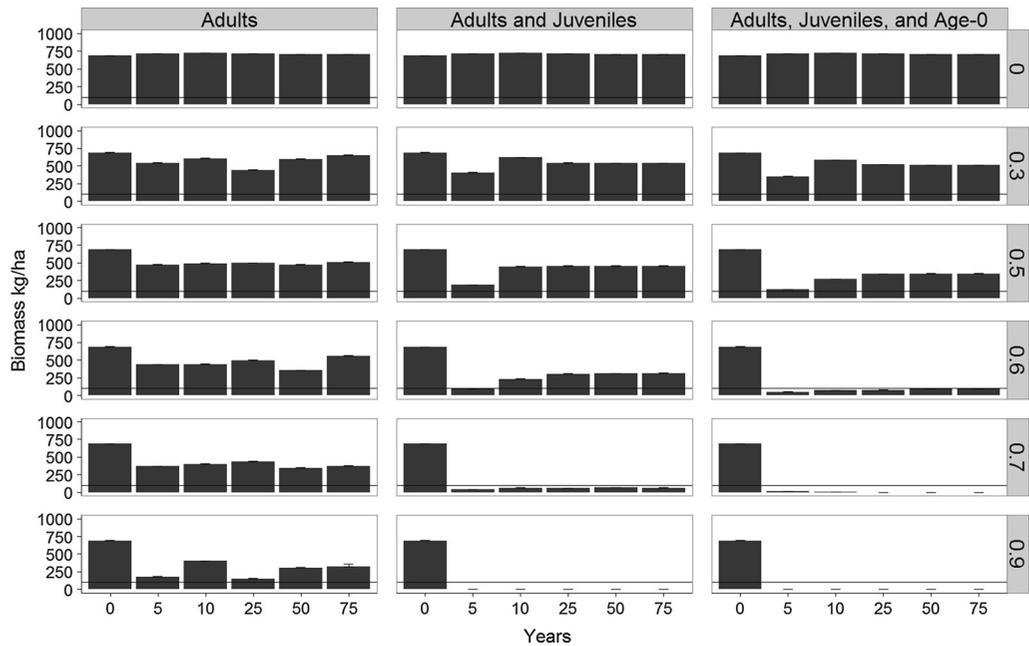


Fig. 1 Mean \pm SD biomass of common carp in a lake driven by internal, density-dependent recruitment in which winter seining occurs every year. Six removal probabilities (right) are shown ranging from 0 to 0.9; removal probability of 0.9 means that each fish has a 90 % chance of being removed each year. Targeted life

stages (top) included adults, adults and juveniles, and adults, juveniles, and age-0 carp. Values on x-axis show years since winter seining commenced. Horizontal line represents the management goal of 100 kg/ha

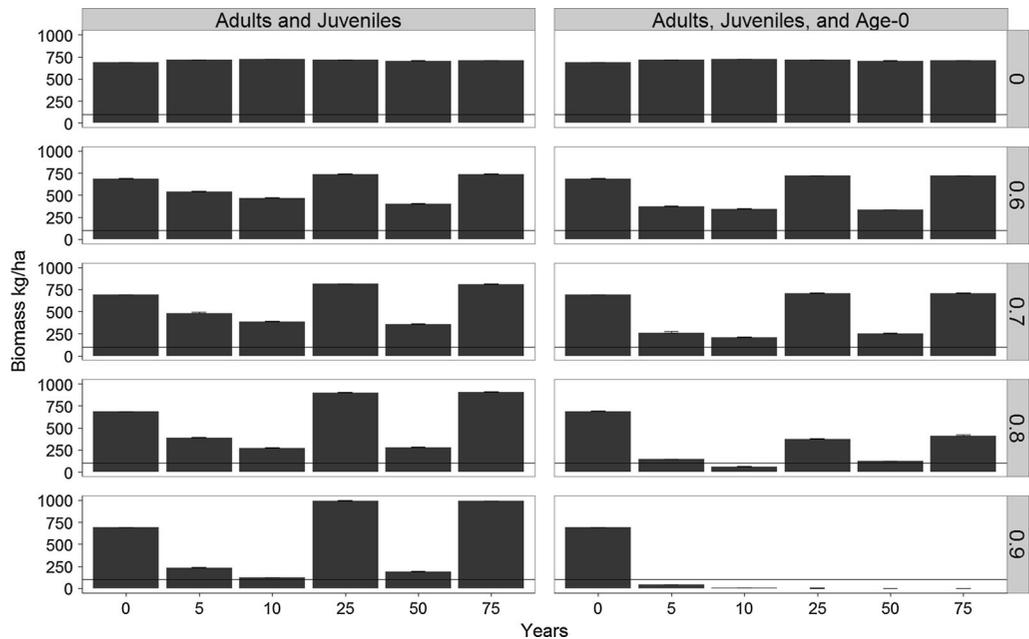


Fig. 2 Mean \pm SD biomass of common carp in a lake driven by internal, density-dependent recruitment in which winter seining occurs every other year. Five removal probabilities (right) are shown ranging from 0 to 0.9. Targeted life stages (top) included adults and juveniles, and adults, juveniles, and age-0 carp.

Modeling scenario that targeted only adults is not shown because it was not successful at reaching the management goal even at highest (0.9) removal probability applied annually (Fig. 1). Values on x-axis show years since winter seining commenced. Horizontal line represents the management goal of 100 kg/ha

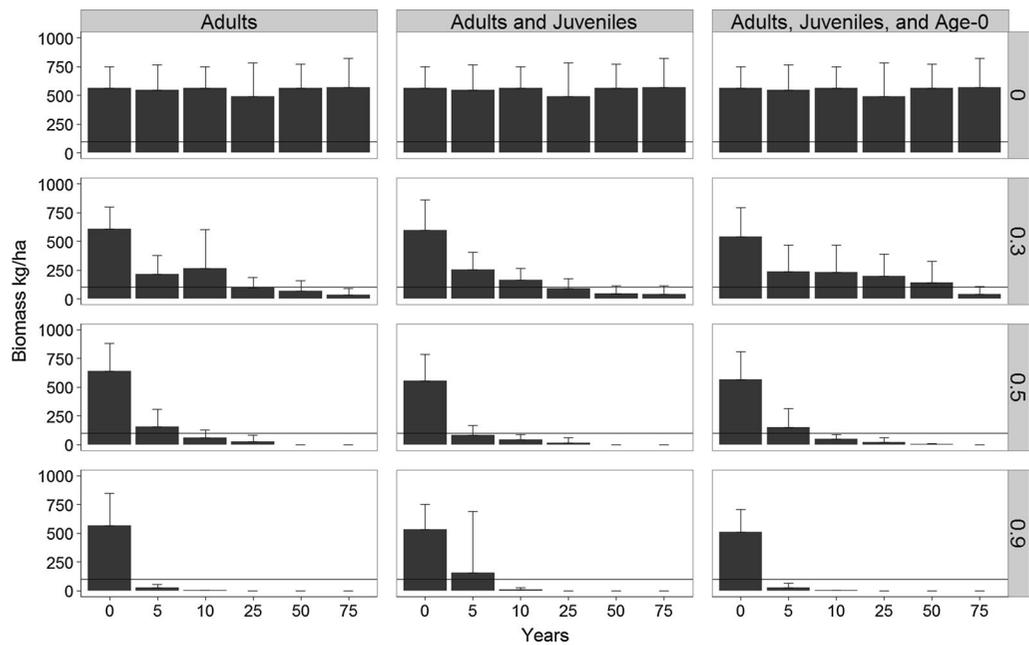


Fig. 3 Mean \pm SD biomass of common carp in a lake driven by external recruitment from a winterkill-prone marsh. Winter seining and removal occurred in the lake every year. Six removal probabilities (right) are shown ranging from 0 to 0.9. Targeted

life stages (top) included adults, adults and juveniles, and adults, juveniles, and age-0 carp. Values on x-axis show years since winter seining commenced. Horizontal line represents the management goal of 100 kg/ha

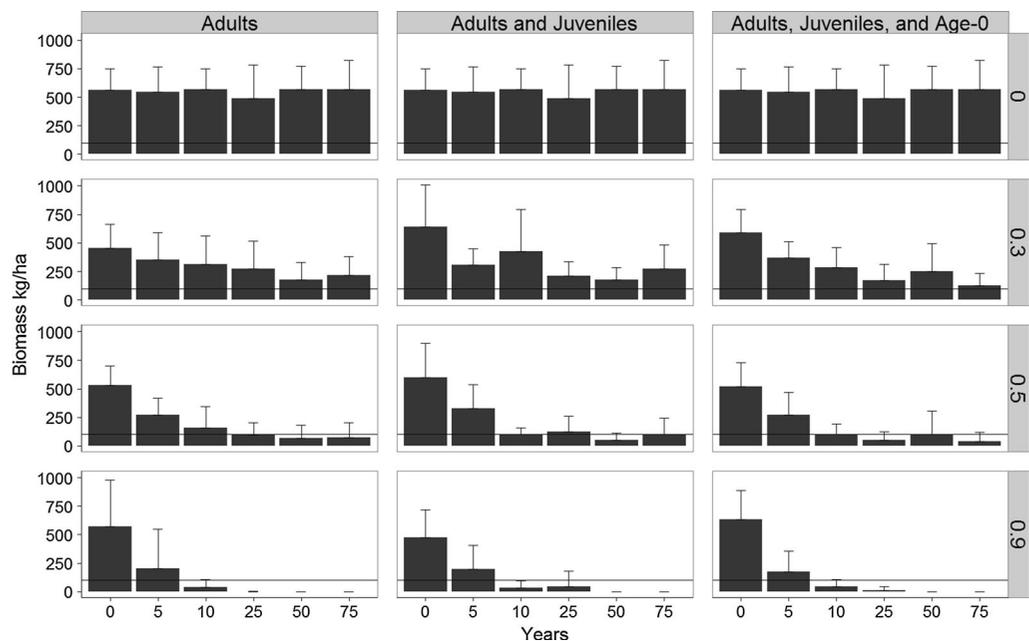


Fig. 4 Mean \pm SD biomass of common carp in a lake driven by external recruitment from a winterkill-prone marsh. Winter seining and removal occurred in the lake every other year. Four removal probabilities (right) are shown ranging from 0 to 0.9. Targeted

life stages (top) included adults, adults and juveniles, and adults, juveniles, and age-0 carp. Values on x-axis show years since winter seining commenced. Horizontal line represents the management goal of 100 kg/ha

Discussion

Using telemetry to locate and remove seasonal aggregations has been an important strategy to manage invasive mammals inhabiting islands or 'habitat islands' (Taylor and Katahira 1988; Cruz et al. 2009). Our study suggests that this strategy, often referred to as the Judas technique, might also be used to implement simple and practical strategies to manage common carp in system where this species' recruitment is restricted to outlying, seasonally unstable habitats from which the young disperse in limited numbers. Because many carp populations are driven by such external recruitment dynamics (Bajer et al. 2015a, b), physical removal might allow for sustained control of carp populations in numerous temperate ecosystems, including lakes of the Eastern Forests ecoregion in North America. This is supported by a case study in Lake Susan (MN, USA), in which a single winter seine resulted in a substantial (80 %) and long-lasting reduction in carp biomass (Bajer and Sorensen 2015). The amount of effort that is required to achieve the management goal of 100 kg/ha is relatively low (30 % removal annually or 50 % every other year) and well within the range of empirically documented removal rates (Bajer et al. 2011). This strategy could be further improved by reducing the frequency of instability events (such as winterkills) that promote carp recruitment and by reducing juvenile dispersal rates from unstable habitats.

Several factors could hinder or accelerate carp management in systems driven by external recruitment, such as lake-marsh systems in temperate North America described in this study (our Ecosystem 2). Carp can learn to avoid nets if repeatedly targeted (Hunter and Wisby 1964), thus, the effectiveness of winter seining may decline over time. Nonetheless, it should remain high for the newly recruited fish. Carp populations can rebound quickly after being reduced to low levels. Colvin et al. (2012) showed that carp biomass can double in 2.7 years, and Bajer et al. (2015b) showed that carp biomass can increase from approximately 10 to 200 kg/ha in 2–3 years after a recruitment event in adjacent marsh. Therefore, the frequency of winter seining will need to appropriately match the frequency of winterkill events and recruitment events in the marsh. Monitoring recruitment dynamics and/or the abundance of adults using rapid-assessment methods, such as boat electrofishing (Bajer

and Sorensen 2012), could determine when seining is needed and how many individuals need to be removed. Behavioral deterrents, such as bubble curtains, that have the potential to reduce the out-migration of juvenile carp from nurseries into lakes without impacting native fish movement (Zielinski and Sorensen 2015), might substantially extend the periods between seinings even if only moderately effective. Reducing the frequency of winterkills by installing aeration systems (if practical) would also increase the sustainability of carp management in lake-marsh systems.

Our results show that winter seining may not be sufficient to reach management goals in many lakes of the Great Plains ecoregion in North America (prairie lakes) or other systems where carp recruitment is internal, frequent, and density dependent, as also suggested by others (Weber et al. 2011). In such types of ecosystems, removing 90 % of adults each year may not be sufficient to reduce the biomass below 100 kg/ha. Targeting all life stages annually with at least a moderate probability (0.6) appears to be necessary to reach management goals in such ecosystems, which may not be achievable with simple removal schemes. Although genetic technologies or pathogens may play a significant role in controlling such populations in the future (Thresher et al. 2014), toxins may offer the only feasible control strategy for now. Antimycin A, a piscicide that the carp are seemingly unable to detect, could be incorporated into carp-selective baits to allow for targeted and effective control of multiple life stages at the same time (Rach et al. 1994). Selective antimycin A delivery media could be developed given carp's gustatory preferences, but plant seeds (e.g. corn; *Zea mays*) or their products could be used as relatively effective surrogates in the short term (Bajer et al. 2010). For example, Bajer et al. (2010) showed that over half of carp population could be trained to aggregate in one area of a small lake and consume corn in <1 week. Because all post-larval life stages of carp share similar diet, the same toxin delivery system could be used for age-0, juvenile and adult carp. This possibility should be further explored to create meaningful management possibilities for ecosystems where natural processes, such as predation, are unable to control the recruitment of carp.

While focusing on lakes in midwestern North America, our analysis has important implications for

carp management in other regions of the world. Our modeling results are supported by empirical evidence that successful carp management via removal is most likely to occur in situations when this species' recruitment is suppressed and sporadic. Physical removal was successful in eradicating carp from Lake Crescent in Tasmania, which was isolated from other waterbodies and in which carp spawning habitats could be blocked off with nets (Donkers et al. 2012). This was similar to successful carp control in Lake Susan in Minnesota, USA, which was also relatively isolated and in which recruitment was controlled by stabilizing native micropredators using winter aeration (Bajer and Sorensen 2015). Pinto et al. (2005) also showed that modest and sustained removal effort was sufficient to reduce carp biomass in Sydney's Botany Wetlands, a system of ponds and channels, although processes that drove recruitment there were not described. In contrast, physical removal has not been successful in systems where carp can easily evade recruitment bottlenecks. Over a decade of intense removal resulted in no appreciable decline in carp abundance in several prairie lakes in southern Minnesota, USA (Moyle et al. 1950). Physical removal is also thought to be insufficient to reach management goals in the Murray-Darling River Basin in southeastern Australia (Thresher 1996; Gilligan et al. 2005; Smith 2005). In that system, adult carp overwinter in deeper areas of the river and move to outlying floodplains to spawn in the spring. Large numbers of young-of-year carp leave the floodplains and join the riverine population few months later as floodwaters recede (Stuart and Jones 2006; McNeil and Closs 2007), making it more similar to our Ecosystem 1. That, and the sheer size and connectedness of Murray-Darling, make it unsuitable for control via removal. Processes that regulate carp recruitment vary greatly among geographic locations, but surveys of 1000+ lakes in three ecoregions in North America demonstrated that only a small fraction of lakes (<10 %) showed evidence of carp recruitment (Bajer et al. 2015a). This shows that carp faces strong recruitment bottlenecks in many locations creating opportunities for management via removal. We urge managers to determine local nuances of carp life history and recruitment dynamics, e.g. adult spawning migration patterns and locations of carp nurseries, before embarking on removal efforts.

Common carp has invaded large geographic areas across the globe (KoeHN 2004; Kulhanek et al. 2011a, b) and may be responsible for reducing water quality and biodiversity in lakes and rivers of entire ecoregions (Haas et al. 2007; Kloskowski 2011; Kulhanek et al. 2011b; Vilizzi et al. 2015). Managing carp populations in thousands of lakes across large areas may not be feasible even if practical management strategies existed for many of them, as suggested by this study. However, by carefully selecting ecosystems in which carp populations may be especially suitable to control by winter seining or other means of physical removal, areas of increased biodiversity could be created within broader landscapes (Suski and Cooke 2007). If so, the impacts of carp on native biodiversity and ecosystem function could be substantially lessened with a more manageable amount of effort.

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