

# Partial migration to seasonally-unstable habitat facilitates biological invasions in a predator-dominated system

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Although partial migration, a phenomenon in which some individuals in a population conduct seasonal migrations while others remain resident, is common among animals, its importance in facilitating biological invasions has not been demonstrated. To illustrate how partial migration might facilitate invasions in spatially complex habitats, we developed an individual-based model of common carp *Cyprinus carpio* in systems of lakes and winterkill-prone marshes in the Upper Mississippi River Basin (UMRB). Our model predicted that common carp are unable to become invasive in lakes of the UMRB unless they conduct partial migrations into winterkill-prone marshes in which recruitment rates are high in the absence of native predators that forage on carp eggs and larvae. Despite low dispersal rates of juveniles and higher mortality rates of migrants, partial migration was adaptive across a wide range of migration rates and winterkill frequencies. Partial migration rates as low as 10% and winterkill occurrence as infrequent as once in 20 years were sufficient to cause invasiveness because of carp's reproductive potential and longevity. Consistent with the results of our model, empirical data showed that lake connectivity to winterkill-prone marshes was an important driver of carp abundance within the study region. Our results demonstrate that biological invasions may be driven by a small, migratory contingent of a population that exploits more beneficial reproductive habitats.

Partial migration is a common phenomenon among migratory animals in which some individuals in a population undergo a migration, often for reproductive purposes, while others remain resident (Dingle and Drake 2007, Chapman et al. 2011). Specific patterns vary greatly among species (Dingle and Drake 2007), but common attributes of partial migration involve its facultative nature (the same individuals may or may not migrate during consecutive years) (Brodersen et al. 2014) and the fact that the migrants and residents have sufficiently high gene flow to be considered a single population. Its origins can also be complex as partial migration may be ascribed to genetics (Biebach 1983), personality traits (Chapman et al. 2011) or nutritional status (Brodersen et al. 2008, 2011), and may or may not remain fixed through life (Kerr et al. 2009, Skov et al. 2010, Brodersen et al. 2014). Regardless of its drivers, one important function of partial migration is that it can increase the abundance, stability and resilience of native populations (Kerr et al. 2010). The extent to which this behaviour can play a similar role in facilitating biological invasions has not been addressed.

Partial migration may represent an important reproductive bet-hedging strategy for invasive species. Bet-hedging strategies increase fitness in variable environments (White et al. 2007, Sol et al. 2012) and may allow organisms to overcome recruitment bottlenecks in areas to which they

are introduced. For example, having both residents and migrants in a population is likely to increase chances of locating nursery habitats that may be spatially limited. Many of the world's most invasive vertebrates (global invasive species database; < [www.issg.org/](http://www.issg.org/) >) exhibit migratory tendencies and are likely to employ reproductive bet hedging. Yet partial migration has never been suggested as an important trait of a successful invader (Kolar and Lodge 2002, Garcia-Berthou 2007). This may be attributable to the fact that spatially and temporarily complex analyses are needed to demonstrate that partial migration is a clear driver of the invasion process. Population models capable of tracking the movement, survival and reproductive success of migrants and residents in large ecosystems are particularly well suited to conduct such analyses (Craft et al. 2008) but have rarely, if ever, been used for invasive species.

While broadly distributed, invasive species are able to become excessively abundant only in a relatively small number of locations to which they are being introduced (Hansen et al. 2013). Understanding processes that facilitate (or curb) the explosive increases in abundance is therefore of main interest to invasion ecologists. In this paper, we use both empirical data and an individual-based model to illustrate the role of partial migration in driving the abundance of one of the world's most invasive species, the common

carp *Cyprinus carpio*, in lakes of the Upper Mississippi River Basin (UMRB). Common carp (henceforth 'carp') is a large, long-lived, fecund fish that is native to large Eurasian rivers (Balon 1995) in which it employs partial spawning migrations to seasonally-inundated floodplains (Balon 2004). Similar behaviours have been noted in the UMRB (Bajer and Sorensen 2010). The UMRB encompasses approximately 0.5 million km<sup>2</sup> with more than 10 000 lakes and over 4 million ha of marshes drained by networks of streams and rivers. Lakes in this region are dominated by several species of predacious sunfishes (Rahel 1984). However, severe winters in hypoxia-prone marshes of the UMRB lead to fish kills (winterkills) (Rahel 1984). This natural disturbance creates pockets of largely predator-free habitat within the landscape. Carp in the UMRB show strong partial migration tendencies, and move out of the lakes in which they overwinter to spawn in hypoxia-prone marshes (Bajer and Sorensen 2010). The migrants that exploit such areas have much higher recruitment success than residents that spawn in lakes, and whose eggs and larvae appear to suffer heavy predation by native fishes, especially the bluegill *Lepomis macrochirus* (Bajer et al. 2012, Silbernagel and Sorensen 2013). It has been thus hypothesized that partial migrations to winterkill-prone marshes drive carp invasiveness (i.e. excessive abundance) within the lakes of UMRB by functioning as a predator avoidance mechanism (Bajer et al. 2012).

To test this hypothesis, we developed an individual-based model that simulated the movement, survival and reproductive success of resident and migratory carp as well as the survival and dispersal of their offspring in lakes and marshes of the UMRB. We used our model to simulate the abundance and biomass of carp in winterkill-free lakes of the UMRB within the context of documented partial migration rates to winterkill-prone marshes. To evaluate partial migration as a facilitator of invasion, we also included theoretical scenarios in which partial migration was not permitted. We then tested the predictions of our model using empirical data on carp abundance in winterkill-free lakes of the UMRB that were either connected to winterkill-prone marshes (partial migration occurs) or isolated (partial migration does not occur). Our results suggest that biological invasions in variable environments might often be driven by small, migratory contingents within populations that exploit unique reproductive habitats.

## Methods

### Carp population dynamics model

We developed an individual-based, age structured population dynamics model of carp in lakes of the UMRB (Minnesota, USA). Model structure and parameters are based on a decade of research in systems of interconnected lakes and marshes (Supplementary material Appendix 1). Each carp in the model is a separate 'object' that has biological properties such as age, length, weight, current location, and natal location. While analytically complex, our model can be conceptually represented by two habitats (winterkill-free lakes and winterkill-prone marshes) and two life stages (adults and juveniles). The marsh habitat is identical to the lake habi-

tat when winterkill does not occur. However, occurrence of winterkill in the marsh, which drastically reduces the densities of native predators that forage on carp eggs and larvae (Bajer et al. 2012), increases the reproductive success of adults that decide to migrate there during that particular year. This scenario occurs only during the first season after a winterkill because populations of native predators recover quickly (through increased recruitment) and by the next year are typically as high as in the surrounding lakes (Bajer et al. 2012). Adult carp that migrate to winterkill-prone marshes run an increased risk of mortality (they may perish during subsequent winterkills if they attempt to overwinter in the marsh). Adult carp conduct partial migrations from the lake to the marsh each year regardless of whether winter hypoxia occurs in the marsh.

Adults (age 3 and older) conduct partial spawning migration into marshes with a probability  $\alpha$ , which we assumed to be independent among individuals and years. Adults return from the marsh after the spawning with a probability  $\beta$ . Adults that remain in the marsh for the winter incur an additional cost of mortality that is the product of winterkill probability ( $\omega$ ) and the probability of dying during a winterkill ( $\epsilon$ ). Recruitment is expressed as the number of offspring per adult at the end of the summer ( $\tau$ ) and is a function of winterkill and adult density (recruitment increases after a winterkill; Table 1). Juveniles disperse with a probability  $\kappa$  (Table 1). All juveniles that had dispersed refrain from migrating until they mature at the end of their second year of life. Carp (all ages) gain length and mass with a rate that is population density-dependent (Supplementary material Appendix 1). Natural mortality rate ( $\nu$ ) is also length- and density-dependent (Charnov et al. 2013). We estimated all model parameters empirically (Supplementary material Appendix 1).

### Modelling scenarios

To examine the role of partial migration in facilitating carp invasiveness in lakes of the UMRB, we modelled carp in a lake that was connected to a winterkill-prone marsh of the same area. For this scenario, we conducted model runs using the lowest-observed (0.1), mean (0.3) and highest observed (0.7) probabilities of adult carp partial migration into the marsh over the full range of possible winterkill probabilities (0.0 to 1.0) in the marsh (Table 1). We also conducted additional model runs using a theoretical scenario in which partial migrations were not permitted. These scenarios were used to determine under what conditions carp populations inhabiting lakes of the UMRB are likely to reach excessively high abundance and biomass, which we defined as  $>100$  kg ha<sup>-1</sup> (Bajer et al. 2009). In each scenario, we seeded the lake with 10 adult carp per hectare (a density observed in low-abundance carp lakes in the region; Bajer and Sorensen 2012) and simulated 50 years of population dynamics. We replicated each scenario ten times so that we could express variation in our estimates of density and biomass.

### Observed carp abundance in connected and isolated lakes

If partial migration to winterkill-prone marshes facilitates carp invasiveness in lakes of the UMRB, then carp abundance

Table 1. Model parameters. Partial migration was modelled using three empirically-derived levels (low, mean, high); return probability and mortality probability during a winterkill were modelled as random variables drawn from a uniform distribution between minimum and maximum mean values observed in different lakes; winterkill probability was modelled using discrete levels: 0, 0.05, and then 0.1 to 1.0 every 0.1;  $k \in (0,1,2,3\dots)$  is the number of possible recruits per adult that follows a Poisson distribution;  $S$  is parental stock (number of adults per hectare);  $L$  is carp length (mm),  $L_{\infty}$  is the theoretical maximum length (mm);  $D$  is carp density (number of carp older than age-0 per hectare). Detailed description of each parameter is included in the Supplementary material Appendix 1.

Parameter	Symbol	Estimate
Partial migration probability	$\alpha$	0.1, 0.3, 0.7
Return probability	$\beta$	random (0.38, 0.88)
Winterkill probability	$\omega$	0 to 1.0
Mortality probability during a winterkill	$\epsilon$	random (0.95, 1.0)
Recruitment in a lake or in a marsh during non-winterkill year	$\tau$	$\tau = \frac{0.24}{k!} \times e^{-k} - 0.01S$
Recruitment in a marsh during a winterkill year	$\tau$	$\tau = 106.6 (3.92 \times e^{(-0.01S)})$
Juvenile dispersal probability	$\kappa$	$\kappa = 0.003$ if age 0 or 1 $\kappa = 0.5$ if age $\geq 2$
Annual natural mortality probability	$\nu$	$\nu = 1 - e^{\left(-0.06 \left(\frac{L}{L_{\infty}}\right)^{-1.5}\right)} + 10^{-4} \times D$

should be higher in lakes that are connected to winterkill-prone marshes than in lakes that lack such connections. To explore this hypothesis, we analysed mid-summer (August and September, after migrants return back to the lakes) gillnet catch rates of common carp in lakes in central and southern Minnesota during 1994–2012. We selected a group of 50 lakes (water bodies deeper than 6 m and larger than 10 ha to exclude marshes prone to winter hypoxia), all of which were located in southern Minnesota where carp are especially pervasive and abundant, and for which we had documented catches of common carp to ensure that they were historically introduced to all of those systems. We included only lakes for which we could determine hydrological connectivity with confidence. We then divided these lakes into two groups: isolated lakes that had no significant inlets, outlets or connections to marshes that winterkill ( $n = 24$ ), and connected lakes ( $n = 26$ ) that had at least one permanent inlet or outlet and were located within larger systems of connected bodies of water that included winterkill-prone marshes located within a distance of 2 km. All lakes included in the connected group were spatially independent from one another as they occurred in separate chains of lakes (22 lakes) or, if they occurred within the same chain (four lakes), they were separated by a distance of at least 10 km from each other. Lake connectivity and presence of marshes was determined using aerial imagery and GIS layers that included lakes and marshes, watershed delineations, national wetland inventory, streams and dams (source: <<http://deli.dnr.state.mn.us/>>). In each of the selected lakes, we calculated mean catch rate of carp over the entire sampling period (1994–2012; each lake was surveyed every three to five years). Because carp abundance has been suggested to also be influenced by nutrient concentrations, lake morphometry, and native predators (Kulhanek et al. 2011, Bajer et al. 2012), we calculated mean values of summer-time Secchi depths (an index of nutrient concentrations; Mercado-Silva et al. 2006), lake area, lake maximum depth, and the catch rates of six dominant species of native predatory fishes: bluegill, crappies *Pomoxis* spp., yellow perch

*Perca flavescens*, bullheads *Ameiurus*, spp., walleye *Sander vitreus* and northern pike *Esox lucius*. Together, these species comprised 80% of fish captured in standardized surveys conducted by the Minnesota Dept of Natural Resources.

We log + 1 transformed the carp catch rates to achieve co-linearity with the predictor variables and fitted linear models (all possible combinations of predictor variables) to determine the importance of lake connectivity and other predictor variables in explaining observed carp catch rates. Due to small sample size, we did not include interactions among predictor variables to avoid model overfitting. We used Akaike's information criterion (AICc; Burnham and Anderson 2002) to rank individual models and examined whether the best models ( $\Delta AICc < 2$ ) included lake connectivity. We also conducted model averaging using all models for which  $\Delta AICc < 2$  to quantify the relative importance of lake connectivity among other predictor variables. We used 'MuMIn' package (Barton 2010) in R (<[www.r-project.org/](http://www.r-project.org/)>) to conduct model selection and model averaging.

## Results

Our modelling results showed that common carp are unlikely to become excessively abundant in lakes of the UMRB unless they conduct partial migrations to marshes that winterkill (Fig. 1). If carp in the simulation did not employ partial migration or if the marsh did not winterkill, carp densities were predicted to be  $\sim 5$  individuals  $ha^{-1}$  ( $SD = 0.26$ ) and their biomass was approximately  $10$   $kg$   $ha^{-1}$  ( $SD = 1.5$ ) (Fig. 1). These values are an order of magnitude lower than the threshold associated with invasiveness (Bajer et al. 2009). However, the abundance and biomass of carp increased to 2–7 times over this threshold when carp employed partial migration to marshes that winterkilled with low to moderate probability (0.05–0.6) (Fig. 1). Carp were predicted to reach this high biomass across the entire range of observed partial migration rates (0.1–0.7) (Fig. 1). Partial migration did not

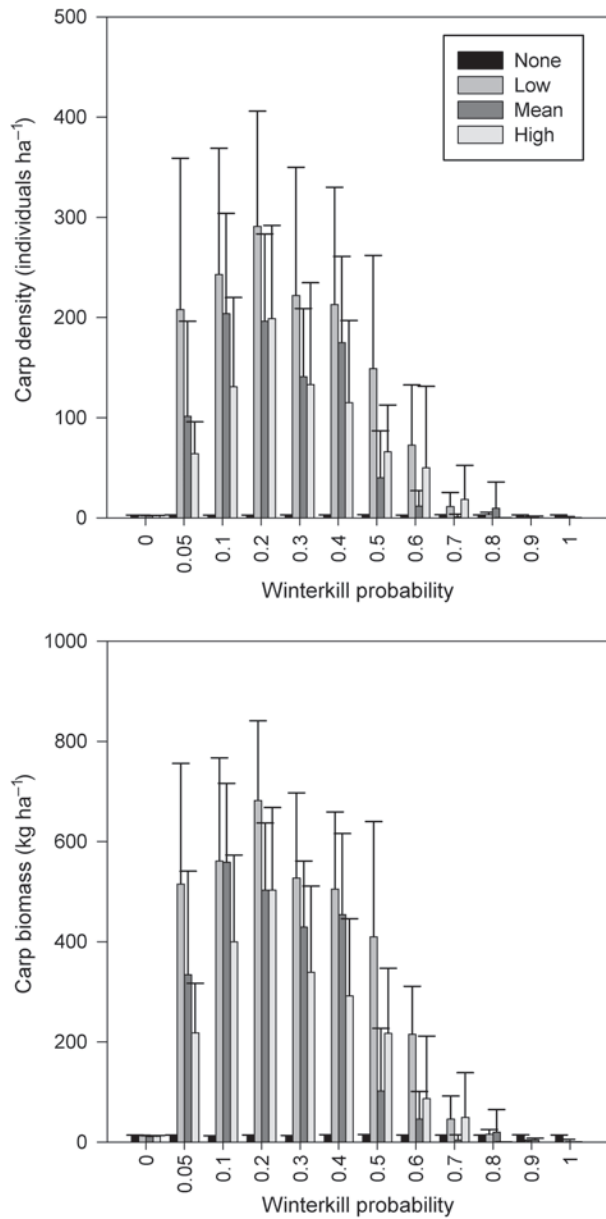


Figure 1. The mean density (top panel) and biomass (bottom panel) of common carp predicted by the individual-based model in a lake connected to a marsh that winterkills with an annual probability of 0.0–1.0. Separate predictions are generated for low (0.10, lowest observed), mean (0.3), and high (0.70, highest observed) probabilities of partial migration from the lake to the marsh. We also include a theoretical scenario in which none of the individuals migrate (None). Vertical bars represent  $\pm 1$  SD. Carp are considered invasive if their biomass exceeds  $100 \text{ kg ha}^{-1}$  (Bajer et al. 2009).

drive invasiveness when the probability of winterkill in the marsh was  $> 0.6$  (Fig. 1).

To better understand how partial migration to marshy regions contributes to carp biomass increase in lakes, we examined in detail a scenario in which carp employed partial migrations to a marsh that had winterkill probability of 0.2 (an often encountered scenario in UMRB lakes; Bajer and Sorensen 2010). In this scenario, carp biomass rapidly increased and then exhibited fluctuations that corresponded to winterkill events in the marsh (Fig. 2). Carp

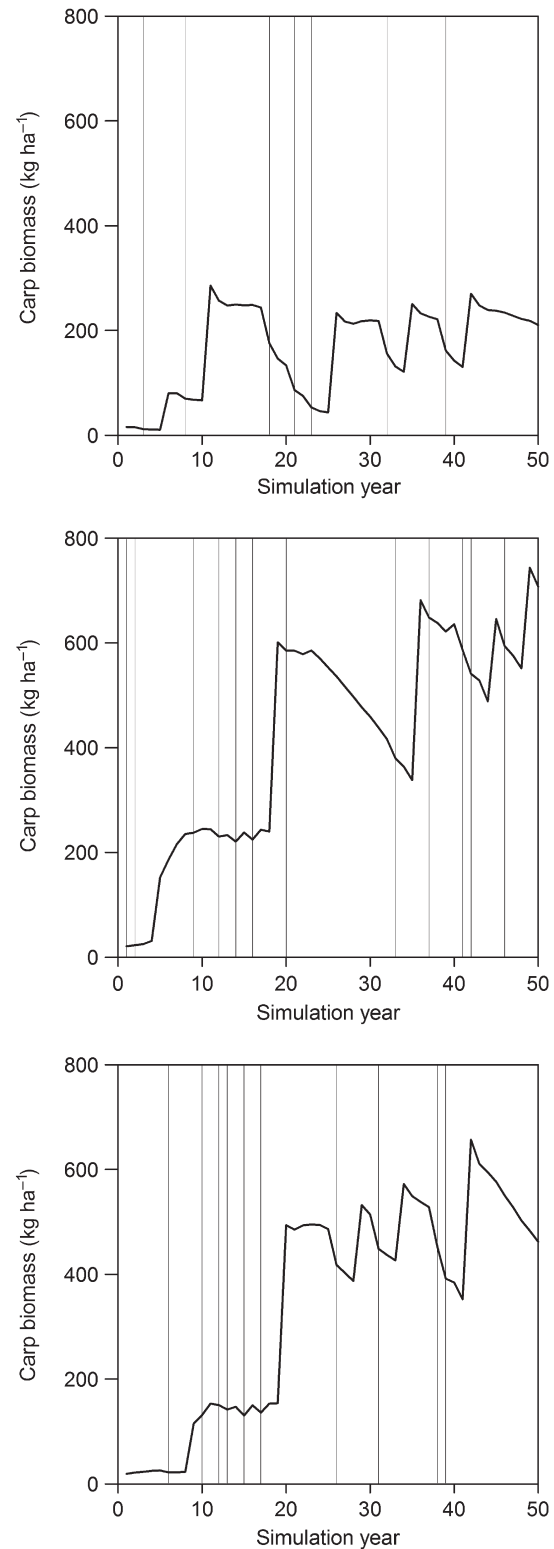


Figure 2. Common carp biomass in a lake connected to a winterkill-prone marsh. Each panel represents a separate model run with identical parameter values including a winterkill probability of 0.20 in the marsh (an often observed value; Bajer and Sorensen 2010) and a probability of adult carp partial migration from the lake to the marsh of 0.3 (mean observed). Vertical lines represent winterkill events in the marsh. Initial carp biomass in the lake was the same for each run, approximately  $20 \text{ kg ha}^{-1}$ .

age structure in the lake was composed of 2–5 age classes that corresponded to the most recent winterkill events in the marsh. Not every winterkill in the marsh resulted in an increase in carp biomass in the lake or the presence of a year class in the lake. If, by chance, winterkill was frequent (e.g. occurred during consecutive years), the biomass of carp in the lake declined because the adults that remained in the marsh perished during the winter (the probability of returning from the marsh into the lake by the end of the year varied between 0.38 and 0.88; Supplementary material Appendix 1 Table A1) and only the last winterkill resulted in a year class due to low dispersal rates of juveniles during the first years of life. This pattern likely explains low carp abundance and biomass when winterkill probability in the marsh exceeded 0.6 (Fig. 1).

Empirical data from across the study region supported our modelling results. Model selection analysis showed that all of the best models ( $\Delta\text{AICc} < 2$ ) included lake connectivity as a predictor variable (Supplementary material Appendix 1 Table A6). All of these models also included bluegill and crappie catch rates. Some also included northern pike, bullhead and yellow perch catch rates and Secchi depth (Supplementary material Appendix 1 Table A6). AICc scores showed that models that excluded lake connectivity were not supported by the data ( $\Delta\text{AICc} > 5.24$ ), regardless of which combinations of the remaining predictor variables they included (Supplementary material Appendix 1 Table A6). Model averaging conducted on our best models ( $\Delta\text{AICc} < 2$ ) showed that carp catch rates were influenced by (from most to least important) lake connectivity, bluegill catch rates, crappie catch rates, Secchi depth, northern pike catch rates, bullhead catch rates, and yellow perch catch rates (Table 2). Coefficient values showed that carp catch rates were higher in lakes that were connected, had lower catch rates of bluegills, northern pike and bullheads, had lower Secchi depths, and had higher catch rates of crappies and yellow perch (Table 2); the latter two species may benefit from increased productivity and turbidity often found in lakes with higher carp abundance.

Table 2. Results of AIC model selection analysis to explain observed patterns in adult common carp catch rates in a group of 50 lakes that included 24 lakes that were isolated and 26 that were connected to winterkill-prone marshes in southern Minnesota (a sub region of the Upper Mississippi River Basin). Parameter estimates, significance, and relative importance were estimated by averaging all models that were highly supported by the data ( $\Delta\text{AICc} < 2$ ; Supplementary material Appendix 1 Table A6). Predictor variables include lake connectivity, catch rates of bluegills (BLG), crappies (CRP), northern pike (NOP), bullheads (BUL; log + 1 transformed), and yellow perch (YEP), and Secchi depth.

Variable	Estimate	SE	Z	p	Relative Importance
Intercept	0.62	0.18	3.44	<0.001	
Connectivity (isolated)	-0.30	0.10	2.96	0.0031	1.00
BLG	-0.014	0.0047	2.98	0.0028	1.00
CRP	0.032	0.013	2.46	0.013	1.00
Secchi	-0.082	0.055	1.48	0.13	0.44
NOP	-0.017	0.016	1.05	0.29	0.24
log (BUL + 1)	-0.054	0.067	0.81	0.42	0.19
YEP	0.0051	0.0056	0.89	0.37	0.10

## Discussion

This study used model simulations and empirical data to demonstrate the importance of partial migration in facilitating common carp invasiveness in spatially heterogeneous lake systems of the UMRB. This appears to be the first study to demonstrate the importance of partial migration to invasion success. Our results may be broadly applicable because partial migration is common among migratory animals. For example, of the eight fish species included among the 100 world's worst invaders (< www.issg.org/ >) at least three are known to employ partial migration: *Salmo trutta* (Olsson and Greenberg 2004), *Oncorhynchus mykiss* (Olsen et al. 2006), and the common carp. It has been recently demonstrated that partial migration plays a key role in the abundance, stability and population resilience of native fishes (Kerr et al. 2010). We suggest that this behaviour may also help to explain the success of some invasive species.

This study supports our previous hypothesis that partial migration to winterkill-prone, unstable marshes that lack egg and larval predators is largely responsible for carp becoming invasive in lakes of the UMRB (Bajer and Sorensen 2010). Our model also shows that partial migration is adaptive if winterkills occur with low to moderate frequency (0.05–0.6). Marshes that winterkill very frequently (> 0.6) may become population sinks from which few adult carp return, and few juveniles disperse. Previous studies suggested that shallow lakes in the UMRB usually winterkill once every few years (Bajer and Sorensen 2010, Bajer et al. 2012). Therefore, partial migration is overall likely to be adaptive for carp. Also, systems of lakes and marshes of the UMRB are relatively large and complex and the frequency and severity of winterkill is likely to vary among individual marshes. This heterogeneity in the frequency and severity of winterkills is likely to enhance the size and stability of carp populations in lakes of the UMRB.

The common carp is one of the world's most widely distributed fishes (Balon 1995) but processes that determine its invasiveness in specific regions are still poorly understood. Results of this and several recent studies allow for the formation of hypotheses to explain carp invasiveness in different regions. In lakes of the UMRB, in which the native fish community is dominated by bluegills, partial migration to winterkill-prone marshes that lack these predators appears to be important for overcoming recruitment bottlenecks. On the other hand, in the prairie pothole region of North America that is characterized by shallower lakes in which bluegills are often not very abundant (Weber and Brown 2013), partial migration is likely to be less important because both resident and migratory carp have high reproductive success and carp recruitment there appears to be largely determined by the density of adults (Weber and Brown 2013). Our findings about the importance of partial migration may extend to regions in which winter hypoxia does not occur, such as Australia or South Africa. In those regions, summer hypoxia or dry-season water depletion may create pockets of predator-free habitats that the carp might be able to exploit for reproduction. In the Murray Darling River Basin in Australia, partial migration may be also important to locate vegetated areas with abundant spawning substrate that appear to be

restricted to periodically inundated floodplains and forests (Stuart and Jones 2006, Humphries et al. 2008).

Sustainable management approaches are urgently needed for invasive fish. However, with the exception of the sea lamprey *Petromyzon marinus* in the Great Lakes, few, if any, of such strategies have been developed. Our study suggests that common carp populations in lakes of the UMRB can be controlled by efforts that focus on preventing winterkills in connected water bodies to maintain high densities of native fishes that forage on carp eggs and larvae (Silbernagel and Sorensen 2013) and/or blocking migration routes to or from nursery areas. In systems that rarely winterkill and produce few year classes, carp populations could likely be managed by targeting winter aggregations of adults for removal every few years (Bajer et al. 2011). Barriers to migration and physical removal have been used with some success in individual lakes in the study region, but our model should allow for the development of more efficient carp management strategies for larger systems of lakes. It is encouraging that our model was able to predict values of carp biomass, density and age structure that closely match empirical estimates from the region across a wide range of ecological conditions (Bajer and Sorensen 2010, 2012). This suggests that the model is sufficiently robust to be used in carp management.

Introduced fishes have been responsible for rapid and widespread biological invasions worldwide (Fausch and Garcia-Berthou 2013). For example, common carp invaded the largest river system in Australia in less than 30 years (Koehn 2004) and bigheaded carps (*Hypophthalmichthys* sp.) have invaded most of the Mississippi basin within a similar time frame (Chick and Pegg 2001). Our understanding of processes associated with different phases of fish invasions has also increased (Garcia-Berthou 2007), but why certain fish species are able to reach extremely high densities in some areas but not in others is still relatively poorly understood. Fish invasions are driven by interactions between life history traits of the invader, physical habitat, and native biotic community (Moyle and Light 1996, Alcaraz et al. 2008). But the specific nature of these interactions has remained obscure. Our study illustrates how such interactions enable carp to become invasive in lakes of the UMRB. Partial migration allows carp to exploit peripheral shallow habitats, and winterkills make this strategy successful by reducing densities of native predators in outlying marshes (Bajer et al. 2012). High fecundity allows carp to generate strong recruitment pulses in winterkill-prone marshes while longevity allows the carp to capitalize on winterkills as infrequent as once every 20 years. All of these elements, when present, act synergistically to result in an invasion. Given the role of partial migration in this process, we suggest that partial migration be added to the list of traits that influence invasion success.

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Supplementary material (available online as Appendix oik.01795 at <[www.oikosjournal.org/readers/appendix](http://www.oikosjournal.org/readers/appendix)>). Appendix 1.