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Variation in native micro-predator abundance explains recruitment of a mobile invasive fish, the common carp, in a naturally unstable environment

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Abstract Why certain species of fish become invasive is poorly understood and a key obstacle to restoring many of the world's ecosystems. In this study we tested whether variation in biotic resistance exerted by native predators might explain the reproductive success of the common carp, a large and fecund invasive species that typically spawns in outlying and unstable shallow habitat. An initial three-year study of the relative abundance of young-of-year (YOY) carp in interconnected lakes in the Upper Mississippi River Basin discovered that YOY carp are only found in shallow waters that experience winter hypoxia (winterkill) and have low densities of the native egg-predators that otherwise dominate these locales. A follow-up experiment tested if native fish predation on carp eggs could explain this distribution. It found that while carp eggs survived in winterkill lakes, they only survived in non-winterkill lakes when

protected by a mesh that excluded fish. Large numbers of carp eggs were found in the stomachs of native fish inhabiting lakes that did not winterkill. We conclude that common carp, and likely many other highly mobile and fecund invasive fish, have evolved life histories to avoid egg predators and can become invasive when they are absent.

Keywords Biological invasion · Common carp · *Cyprinus carpio* · Biotic resistance · Egg predation · Bluegill sunfish · *Lepomis macrochirus* · Winterkill · Hypoxia · Integrated pest management

Introduction

Dramatic increases in both the number and abundance of invasive fishes over the past few decades have caused precipitous declines in the biotic integrity of many aquatic ecosystems across the globe (Mack et al. 2000; Britton et al. 2010). While it is recognized that invasiveness in fish is often linked to complex combinations of local abiotic conditions and biotic resistance exerted by native competitors and predators, the precise nature of these relationships is poorly understood. Of special interest to aquatic ecologists and fisheries managers is whether native predators might control the abundance of invasive fish in natural ecosystems (Moyle and Light 1996a, b; Marchetti et al. 2004; Moyle and Marchetti 2006). Although it has been demonstrated that native predators can

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control invasive aquatic invertebrates and amphibians (Hill and Lodge 1999; DeRivera et al. 2005; Ward-Fear et al. 2010), no studies we know of provide direct (experimental) support for this possibility in fish. We speculate that one reason for this may simply be that the high mobility of many fishes coupled with the complexity of their life histories has made them difficult to study, which has precluded the development of meaningful biological control schemes.

The possibility that biotic resistance may often take the form of predatory pressure on eggs and larvae of invasive fishes (and thus impose a recruitment bottleneck) is compelling. First, although most invasive fishes are extremely fecund (Kolar and Lodge 2002), their eggs and larvae tend to be small and defenseless, suggesting that they are susceptible to predation. Second, the vulnerability of early life stages is suggested by the life histories of many invasive fishes, which often appear to employ predator-avoidance/swamping strategies (Ims 1990). In particular, many highly fecund invasive fishes have adult phases that are mobile and spawn in a synchronous fashion in unstable and peripheral areas that presumably have fewer predators. The common carp (*Cyprinus carpio*), Asian carps (*Hypophthalmichthys* sp.), sea lamprey (*Petromyzon marinus*), and northern pike (*Esox lucius*) are all invasive fish species in which highly fecund adults migrate long distances to disperse their gametes in seasonally-unstable peripheral habitats (Potter 1980; Koed et al. 2006; Lohmeyer and Garvey 2009; Bajer and Sorensen 2010). Whether this suite of life history characteristics evolved to reduce exposure to egg and/or larval predators does not appear to have been explicitly considered, nor does the possibility that differences in predator abundance might explain the success of invasive fishes in non-native habitats. Examples from the marine environment suggest that recruitment of fecund fishes (ex. cod [*Gadus morhua*]) can be controlled by egg and larval predators (Koster and Mollmann 2000).

The common carp (hereafter ‘carp’) is one of world’s most invasive fish (Britton et al. 2010) and a good model to address the role of egg predation and its role in invasiveness. This species evolved in large and seasonally unstable rivers of Eastern Europe, is extremely fecund (up to 3 million eggs/female), and performs annual spawning migrations into peripheral floodplains and marshes (Balon 1995; Barus et al. 2001). Over the course of the past century it has been

introduced worldwide and reaches extreme densities in temperate regions of North and South America and south-central Australia (Sorensen and Bajer 2011) where it is also extremely damaging to ecosystems (Weber and Brown 2009). These regions are both large and characterized by seasonal environmental extremes that include winter and summer hypoxia and spring flooding (King et al. 2003; Stuart and Jones 2006; Bajer and Sorensen 2010). Population-ageing studies conducted in the Upper Mississippi River Basin demonstrate that invasiveness of carp in this region can be attributed to punctuated and sporadic recruitment events (Phelps et al. 2008) that precisely coincide with severe winter hypoxia in peripheral shallow areas (Bajer and Sorensen 2010). Although several factors could explain this relationship, we have hypothesized that temporary reductions in biotic resistance triggered by winter hypoxia (winterkill) are the cause (Bajer and Sorensen 2010). In support of this possibility, we have described regular spawning movements of adult carp to and from seasonally-hypoxic areas (Bajer and Sorensen 2010). Furthermore, and most importantly, these areas are normally dominated by numerous species of centrarchids (sunfishes), which are voracious micro-predators (i.e. specialize in foraging on small particles; Gross and MacMillan 1981), but which are also sensitive to hypoxia and decline in abundance following winterkills (Rahel 1984).

In the present study we employed a combination of correlative observations and controlled experiments to test the hypothesis that recruitment (and invasiveness) of the common carp can be explained by localized reductions in biotic resistance associated with seasonal declines in native micro-predators in unstable spawning habitat (Bajer and Sorensen 2010; Sorensen and Bajer 2011). We found strong evidence that native micro-predators and bluegill sunfish (*Lepomis macrochirus*) in particular, are able to control carp recruitment by exerting strong predatory pressure on carp eggs. We also found no evidence that high propagule pressure that the carp exert on ecosystems can overwhelm this biotic resistance, unless the densities of native predators are reduced because of instability events (in this case winterkills). Our results appear to provide the first direct evidence that ecosystem invasions by the common carp, and possibly other species of mobile and highly fecund invasive fish, are fundamentally attributable to localized declines in biotic resistance.

Materials and methods

The study region and its fish

This study was conducted in the lake systems of the Upper Mississippi River Basin. This region is characterized by a dense network of lakes, marshes, and interconnecting streams, which drain into larger rivers and eventually the Mississippi River (Fig. 1). Adult carp inhabiting these systems typically overwinter in deeper lakes that have high oxygen concentrations but migrate in large numbers into shallow interconnected basins to spawn their adhesive eggs on floating vegetation in the spring (Bajer and Sorensen 2010; Fig. 1). Those carp that do not (or cannot) migrate, spawn at the edges of deeper lakes and propagule pressure is extremely high across entire watersheds (Bajer and Sorensen 2010; Fig. 1). Severe winters characterize this region and winter hypoxia commonly occurs in outlying shallow basins where oxygen levels often fall below 1.5–2 mg/L (Tonn et al. 1990). This level of oxygen is lethal to many native fish including the bluegill sunfish, which otherwise dominate these watersheds (Petrosky and Magnuson 1973; Rahel 1984). The bluegill is a relatively small (~15 cm TL) micro-predator that forages on invertebrates, zooplankton, fish eggs and larvae and typically comprises 50–70 % of the native fish biomass (Gross and MacMillan 1981; Roth et al. 2007; Spotte 2007). Other abundant species include the black crappie (*Pomoxis nigromaculatus*), green sunfish (*Lepomis cyanellus*), pumpkinseed (*L. gibbosus*), yellow perch (*Perca flavescens*) and black bullhead (*Ictalurus melas*), all of which have larger mouths and tend to forage on larger prey items and are also relatively tolerant of hypoxia (Spotte 2007).

Study 1: Reproductive success of carp in stable and unstable habitats with different densities of native micro-predators

Winter dissolved-oxygen (DO) levels, the relative abundance of native fishes, and the relative abundance of young-of-year (YOY) carp were measured in 19 lakes in five chains of interconnected lakes for three consecutive years (2008–2010). Not all lakes were sampled each year (Table 1). These chains are representative of the region and each included 2–7 lakes, approximately half of which are shallower than

5 m and frequently experienced winter hypoxia while the other half were deeper and did not (Table 1). Our study had three steps. First, we monitored oxygen levels in each lake each winter. Then we confirmed that adult carp were present in each lake each spring and estimated their abundance and fecundity (propagule pressure). Finally, we sampled each lake for YOY carp and native fish at each summer's end.

Dissolved oxygen (DO) was measured 1–2 times a month in each lake between December and March. Holes were drilled through the ice at two locations of each lake and oxygen measured using an electronic meter (YSI 85, Yellow Springs, Ohio, USA) from the surface to the bottom of the lake at 0.5 m intervals. These values were then used to calculate winter DO minima following established protocols (Rahel 1984; Bajer and Sorensen 2010).

To estimate propagule pressure exerted by adult carp, we estimated the abundance of adult (sexually mature) carp in each lake. Precise population estimates of adult carp were available for ten of the study lakes from ongoing mark-recapture studies (Bajer and Sorensen 2010; Bajer et al. 2011; Osborne 2012; Table 1). In lakes for which mark-recapture data were not available, the abundance of carp was estimated using boat electrofishing in April–June and a regression relationship we developed using 4 years of census data [$\text{Density (carp/ha)} = -0.48 + 4.93 \times \text{electrofishing catch rate (carp/h)}$; P. G. Bajer, unpublished data]. We assumed that females comprised 50 % of each population and estimated the fecundity of females from their body lengths. To develop the length-fecundity relationship we collected 30 pre-spawning females of various lengths and counted mature (stage > 3) eggs in 1 g samples of their ovaries [$\text{Fecundity (millions of eggs)} = -0.90 + 0.0028 \times \text{length (mm)}$; $r^2 = 0.73$; $N = 30$; $P < 0.01$]. Our estimates of fecundity were in line with those previously reported for this region (Swee and McCrimmon 1966). We assumed that our calculations of propagule pressure are unbiased estimates of the actual propagule pressure (eggs spawned in each lake) because spawning and fertilization rates were unlikely to be influenced by winter DO.

Lastly, to estimate carp recruitment and native fish abundance, each lake was sampled in late summer using standard fish survey traps (9 mm bar mesh trapnets with a 10 m lead; Rahel 1984). These traps catch fish larger than approximately 40 mm in total length,

Fig. 1 Hydrography of the study region showing a network of interconnected lakes. The insert to the *right* shows Riley Creek chain of lakes, one of the five chains that we studied. Each year, between 20 and 40 % of adult carp move from lakes Susan and Riley, in which they overwinter, to spawn in the shallow, seasonally-hypoxic Rice Marsh Lake (*arrows*). The carp that do not move spawn along the edges of lakes Susan and Riley. The two upper lakes are isolated and inhabited by a smaller number of adult carp some of which also move between the two basins during spawning season. Propagule pressure (numbers next to lake names) ranges from 2.2 to 25.8 million eggs per ha. Numbers of adult carp in each lake and lake depths are presented in Table 1. For more details see Bajer and Sorensen (2010)

a size that carp typically surpass within 2 months in the region. Five traps were set at evenly spaced intervals around the entire perimeter of each lake for a 24-h period. Five traps per lake were deemed sufficient to collect representative samples of each lake's fish community as the study lakes were relatively small and catch rates were consistent between traps within each lake. Captured fish were identified to the species level, counted and measured. Catch rates of each species were averaged among the traps within each lake. Although 14 species of native fish were collected, four were included in the analysis (see below) because they comprised over 95 % of all fish collected. These species were the bluegill sunfish, black crappie, black bullhead and green sunfish. Native fish less than a year old (identified by length; Weaver et al. 1997; Pope and Willis 1998; Wolfe et al. 2009) were excluded from our analysis because they hatch after carp and thus could not have been foraging on carp eggs or larvae.

To analyze our data we produced scatter plots to examine possible relationships between YOY carp,

native fish, winter DO, and propagule pressure. Because these plots revealed that YOY carp catch rates were highly dispersed and included many zeros, we used logistic regression analysis to model the presence of YOY carp (i.e. recruitment). Single and multiple logistic regressions were developed to determine which combinations of explanatory variables were most robust in predicting the recruitment of carp. These logistic regressions were ranked using Akaike's Information Criterion (AIC) and Akaike's weights following Burnham and Anderson (2002). The best model had the lowest AIC score and the highest weight, but other models with scores within two AIC units were considered to have equal data support (Burnham and Anderson 2002). All model fitting was done in R (R Development Core Team 2011) using AICcmodavg (Mazerolle 2011). Although the data collection design suggested including random lake and year within lake effects, we did not include these effects in our analysis because the dominant ecological variables of winter oxygen and its effects on native fish were highly collinear with the lake and year

Table 1 Size, maximum depth, and adult carp abundance (mean estimate) in each study lake

Chain	Lake	Area (ha)	Depth (m)	Adult carp abundance		
				2008	2009	2010
Riley Creek	Lucy	35.0	6.1	NS	<u>642</u>	<u>105</u>
	Ann	44.4	13.7	NS	662	662
	Susan	37.5	5.1	<u>2,611</u>	<u>911</u>	<u>606</u>
	Rice Marsh	40.0	3.0	<u>2,065</u>	<u>178</u>	<u>178</u>
	Riley	120.0	14.9	<u>5,870</u>	<u>3,559</u>	<u>443</u>
Carver Creek	Goose	159.2	3.05	<u>708</u>	<u>10,707</u>	<u>9,239</u>
	Hydes	89.7	5.5	28,037	9,332	9,332
	Reitz	31.9	11.0	9,184	6,904	8,044
	Rice	50.0	2.5	<u>7,962</u>	<u>2,342</u>	<u>5,152</u>
Sandy Creek	St. Catherine	38.0	3.0	<u>169</u>	<u>4,712</u>	<u>2,342</u>
	Cynthia	80.0	3.1	45,588	24,381	23,330
Purgatory Creek	Wetland	70.0	1.5	NS	NS	<u>5,301</u>
	Staring	66.2	4.9	NS	NS	<u>26,228</u>
Phalen Creek	Casey	4.7	1.1	NS	NS	<u>2,585</u>
	Markham	7.0	2.0	NS	NS	<u>211</u>
	Kohlman	29.9	2.7	NS	<u>1,314</u>	<u>827</u>
	Gervais	94.5	12.5	NS	<u>4,115</u>	<u>2,613</u>
	Keller	29.0	2.4	NS	<u>1,275</u>	<u>802</u>
	Phalen	79.6	27.8	NS	2,316	2,316

The abundance of adult carp was estimated using mark-recapture (underlined values) or boat electrofishing; for details on mark-recapture estimates see Bajer and Sorensen (2010) and Bajer et al. (2011). *NS* indicates lakes that were not sampled. Italicized values denote lakes in which carp recruitment was observed

effects. Instead, we included only the ecologically meaningful variables. To corroborate that our analysis was not biased by sampling some lakes multiple times, we conducted a separate model selection analysis in which only a single data point from each lake was used (see online Resource 1).

Study 2: Testing predation by native fish on carp eggs in stable versus unstable habitats

This experiment tested whether the presence (or absence) of YOY carp in lakes that winterkill (or not) could be explained by native fish predation on carp eggs. It was conducted in two hypoxic lakes (winter DO < 1.5 mg/L; lakes Markham and Casey; Table 1) and two normoxic lakes (winter DO > 1.5 mg/L; lakes Keller and Riley; Table 1). These lakes were selected from the systems included in Study 1. We first confirmed that these lakes contained native fish communities representative of hypoxic and normoxic systems by collecting five ~ 100 m² littoral seine hauls in each lake approximately 2 weeks before carp spawning season began (Table 2). The experiment then began in early May 2010 by monitoring daily carp

spawning activity in each lake. When carp were observed spawning they were captured using an electrofishing boat and their eggs stripped into plastic containers and mixed with sperm (Billard 1999). Fertilized eggs, which are adhesive, were then placed onto 30-cm long pieces of artificial vegetation (green yarn) tied in loose clumps. Carp eggs were added to create densities similar to those found on natural vegetation (one per ~ 1 cm). Clumps of yarn with 200 (±20) eggs were then attached to anchored lines with small floats to mimic floating plants on which carp typically spawn. Each clump included several empty strings of yarn to control for the possibility that spawning carp might deposit new eggs on our clumps, which did not occur. Eight clumps were placed (~ 10 m apart) into each of two areas of each lake where spawning had recently been observed, while another set of 8 was inserted into either coarse- mesh bags to exclude fish (3 mm bar mesh, 4 per site), or fine-mesh bags to also exclude macroinvertebrates (0.5 mm mesh, 4 per site) and also placed in the spawning sites. These clumps were then examined on a daily basis and the number of attached eggs was counted before the clumps were placed back in the water (eggs that fell off

Table 2 Species composition and biomass (g/m²) of native fish in the two hypoxic and two normoxic lakes used in Experiment 2 estimated using beach seines

Fish species	Hypoxic		Normoxic	
	Casey	Markham	Riley	Keller
Bluegill sunfish	0.0	0.0	9.81	23.66
Black crappie	0.0	0.0	0.0	0.18
Yellow perch	0.0	0.0	0.20	0.68
Largemouth bass	0.0	0.0	0.64	0.36
Northern pike	0.0	0.0	0.68	0.0
Pumpkinseed	0.06	0.0	0.05	0.18
Green sunfish	0.42	0.0	0.0	0.05
Black bullhead	3.18	0.0	0.0	0.0
Other native fish	0.0	0.09	0.0	0.0

Lake characteristics are presented in Table 1

the yarn were also counted for the fine mesh controls). This procedure continued until larvae were noted in the fine-mesh controls.

For data analysis, survival to hatch date was calculated as the proportion of eggs that were still found on the yarn on the last day before larvae were observed. Egg survival was then analyzed using a nested ANOVA (SAS 9.2) to test for lake-type effects (hypoxic vs normoxic), treatment type (open, coarse-mesh, fine-mesh), and interactions. In addition to monitoring egg survival, we monitored the feeding habits of local fishes. Fish were collected from carp spawning sites in one of the normoxic lakes using an electrofishing boat and their stomach contents examined for carp eggs using gastric lavage. Finally, each lake was surveyed for YOY carp in late summer to confirm that the egg predation we observed could explain the presence or absence of YOY carp.

Results

Study 1

Winter DO appeared to have a strong influence on both YOY carp and native fish; with one exception, YOY carp were found only in lakes in which winter DO fell below ~1.5 mg/L (Fig. 2). The opposite trend was observed for bluegill sunfish, the dominant native species; while bluegill sunfish comprised 65 % of the median fish catch in lakes with oxygen levels >1.5 mg/L they were largely absent from lakes with

DO < 1.5 mg/L (6 % of median catch) (Fig. 2). As a result, a strong reciprocal relationship was observed between bluegill sunfish and YOY carp (Fig. 3). Other species of native fish were captured in lower abundance (typically < 10 per trap-net); black crappie tended to be absent in lakes with DO < 1.5 mg/L while green sunfish tended to be more abundant in those systems (Fig. 2). Overall, the median number of native fish was 2.5 times higher in lakes with DO > 1.5 mg/L. Propagule pressure varied between 10 and 100 million eggs per ha (Fig. 2) but there was no clear evidence that carp recruitment was attributable to higher propagule pressure (Fig. 3).

The AIC model selection analysis indicated that five logistic regression models had relatively strong support ($\Delta\text{AIC} < 2.0$) and all of these included bluegill sunfish (Table 3). In contrast, all models that excluded bluegill sunfish had very little support ($\Delta\text{AIC} > 6.3$; $w_i < 0.02$). The simple model that included bluegill sunfish as the sole predictor variable was able to correctly classify 87 % of all recruitment events (Table 3). The model that fit best included bluegill sunfish and green sunfish and indicated that carp recruitment was negatively related to bluegill sunfish and positively related to green sunfish, both of which were attributable to the effect of winter hypoxia on native fish. This model correctly classified 91 % of all recruitment events (Table 3).

Study 2

While 47 % of unprotected eggs survived to hatching in hypoxic lakes, only 0.8 % of unprotected eggs survived in normoxic lakes and over 90 % of these disappeared within the first 24-h (Fig. 3, $P < 0.05$). In contrast, nearly 70 % of the eggs placed into either fine-mesh or coarse-mesh bags survived to hatching (4 days) in both the hypoxic and normoxic lakes (Fig. 4). Nested ANOVA showed that survivorship was highest among eggs placed in coarse or fine mesh bags, followed by unprotected eggs in hypoxic lakes, followed by unprotected lakes in normoxic lakes (Fig. 4). Carp larvae were observed in the fine-mesh bags after 4 days and we estimated that no more than 5 % of eggs fell off the yarn. Electrofishing surveys of carp spawning habitats in the normoxic lake captured 74 native fish including 45 bluegill sunfish. Thirty five of the bluegills were large enough for their diets to be examined and 29 of these had carp eggs in their

Fig. 2 Trap-net catch rates of young-of-the-year (YOY) carp, trap-net catch rates of native fish species, and propagule pressure versus winter dissolved oxygen minima in the study lakes. All *Y* axis variables, except for propagule pressure, were log +1 transformed

stomachs (on average 71 eggs per bluegill). We also captured 8 yellow perch of which 6 were found to have consumed carp eggs (an average of 118 eggs per fish). Late summer trap-net surveys caught an average of 3.0 (SE = 1.58) and 4.75 (SE = 2.86) YOY carp per trap-net in both of the hypoxic lakes, but no YOY carp were sampled in the two normoxic lakes.

Discussion

Although it has been previously demonstrated that native predators can control invasive invertebrates and amphibians (Hill and Lodge 1999; deRivera et al. 2005; Ward-Fear et al. 2010), our study appears to provide the first direct evidence for a fish. Using both

Fig. 3 Trap-net catch rates of YOY carp versus bluegill sunfish in the study lakes (*top*), and catch rates of YOY carp versus propagule pressure (*bottom*). All Y axis variables were log +1 transformed

correlative analyses and controlled experiments in complex and large systems, we demonstrate that although carp exert high propagule pressure across wide range of habitats, they successfully recruit only in lakes that experience severe instability events (in this case winterkills). This appears to be caused by reduced densities of native predators, and bluegill sunfish in particular, in winterkill lakes. Seemingly, the inability of carp to recruit in more stable and predator-rich communities is attributable to the fact that bluegill sunfish (and possibly also other

native fish) exert very high predatory pressure on carp eggs. This scenario appears to explain the invasiveness of carp in large portions of the Upper Mississippi River Basin and possibly other regions, such as the Murray Darling Basin (Australia) that are also characterized by expansive and highly interconnected watersheds which have seasonal extremes such as floods, droughts and summer hypoxia, and likely extreme spatial variation in predator abundance (King et al. 2003). We speculate that the carp evolved to grow large and migrate into outlying shallow floodplains of the Ponto-Caspian region to escape predation by cyprinids native to this region whose proclivity for carp eggs has already been noted (Koblitskaya 1977; Barus et al. 2001).

Although we have not examined the effects of all native predators on all developmental stages of carp, our data strongly suggest that predation by native fish, and bluegill sunfish in particular, on carp eggs largely explains the invasiveness of carp in the Upper Mississippi River Basin. Bluegills are typically very abundant in this region, specialize in foraging on small prey in vegetated habitats (Keenleyside 1972; Werner and Hall 1974), and have been previously shown to be voracious egg predators (Gross and MacMillan 1981). We do not propose that bluegills necessarily consume all carp eggs, but rather that the extremely high predatory pressure they typically exert on eggs allows other sympatric predators to control the remaining eggs, larvae and fry. Laboratory experiments also show that bluegills are very effective predators on larval carp (Silbernagel 2011). The specific role of bluegill sunfish versus other native predators in controlling the survival of carp eggs and larvae needs to be further addressed. However, while sympatric predators (including larger piscivores) may have additive effects, the strong reciprocal relationship between bluegill sunfish and YOY carp in our study lakes and the results of model selection analysis suggest that the bluegill sunfish is the keystone element of biotic resistance in lakes of the Upper Mississippi region. This hypothesis is also supported by our carp aging studies (Bajer and Sorensen 2010). Interestingly, bluegill sunfish have also been shown to play a role in controlling the early life stages of the invasive rusty crayfish (*Orconectis rusticus*) (Roth et al. 2007).

As demonstrated by this study, explaining invasiveness of fish in specific locales may often not be

Table 3 Results of the logistic regression model selection analysis

Variables in the model	AIC	Δ AIC	w_i	% Concordant
BGS, GSF	45.36	0	0.19	90.1
BGS, BCP, GSF	46.21	0.85	0.12	91.1
BGS, BCP	46.25	0.89	0.12	87.1
BGS	46.40	1.03	0.11	87.1
BGS, PCP, Propagule	46.84	1.48	0.09	91.1
Best model without BGS as a predictor variable				
BCP, GSF	51.75	6.39	0.02	77.7

Predictor variables are: bluegill sunfish (BGS), black crappie (BCP), green sunfish (GSF), and propagule pressure (Propagule). The five best models (Δ AIC < 2.0) among a total of 28 possible models are shown along with the best model that did not include bluegill sunfish as a predictor variable. Percent concordant shows the percentage of carp recruitment events correctly classified by each model. Each model was fitted using the same 42 data points (different combinations of lakes and years)

Fig. 4 Number of carp eggs that survived to hatching in normoxic and hypoxic lakes. Eggs were subjected to one of three treatments: (1) eggs placed into open water within carp spawning areas without any protection, (2) eggs placed into coarse-mesh bags that excluded fish, (3) eggs placed into fine-mesh bags that excluded both fish and invertebrates. Vertical bars represent standard deviation. Letters indicate statistical differences (nested ANOVA; $p = 0.05$)

possible without considering specific life history requirements and behaviors exhibited by invaders in local habitats (Korsu et al. 2007). Key to the success of the carp is its propensity to move into shallow unstable areas to spawn (King et al. 2003; Bajer and Sorensen 2010). However, this strategy may only be effective in ecosystems where unstable nurseries that lack predators are at least periodically connected with stable overwintering/foraging habitats. Adaptations of native predators to instability events in shallow waters may also help explain the success of carp in different areas of the world. In our study region, the success of carp

appears to be explained by high sensitivity of the dominant egg predators to hypoxia. On the other hand, the fact that carp are typically not invasive in large tropical rivers in which summer hypoxia commonly occurs, may be explained by unique adaptations of native species in these systems to survive hypoxia (Welcomme 1995; Chippari-Gomes et al. 2005). Notably, although hypoxia has previously been shown to play a major role in structuring native fish assemblages in North America (Tonn and Magnuson 1982; Rahel 1984; Tonn et al. 1990), it seemingly has not been considered as an explanation for the success of invasive fishes.

Many of the world's most invasive fish are mobile and complete their life cycles over large areas using specialized nursery habitats. Of special interest are the silver (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*), which invaded the Mississippi River Basin and now threaten the Laurentian Great Lakes. These species employ long upstream migrations to spawn in open river habitat during spring floods, and their larvae drift into backwater flooded habitats located up to 200 km downstream (Lohmeyer and Garvey 2009). Flooded backwaters would be expected to have fewer predators. Another example is the northern pike, which is highly invasive in western North America and has a life history similar to that of the common carp as it also migrates to shallow peripheral regions to spawn after winterkill (Koed et al. 2006). Similarly, invasive salmonids and land-locked sea lamprey migrate into shallow streams to spawn (Potter 1980). Whether these behaviors function to protect their young from predators has not been explicitly studied, although it has been suggested for

the lamprey (Potter 1980). Our study shows that this possibility needs to be examined to explain invasiveness of these fish in different regions of the world.

Propagule pressure has been shown to play an important role in explaining biological invasions in terrestrial and marine ecosystems. In these ecosystems it has been shown that high propagule pressure can overwhelm even highly resistant communities (Von Holle and Simberloff 2005; Hollebone and Hay 2007). Although our study was not designed to explicitly test this hypothesis, observed trends and logistic regression analysis suggest that propagule pressure plays only a relatively minor role in explaining the recruitment of carp (also see Bajer and Sorensen 2010). Alternative explanations for the lack of carp recruitment in normoxic systems are not apparent as lake productivity (total phosphorus) and habitat characteristics (water clarity and vegetation density) changed little from year to year in our systems, and YOY carp were only present following hypoxic events. Lakes that had YOY carp also typically had high densities of YOY of native species suggesting that competition for planktonic food plays a relatively minor role in the survival of YOY carp. In fact, a post hoc analysis showed that the densities of YOY of native fish species were, on average, 3.5 times higher in hypoxic lakes (t test; $P < 0.001$). Low abundance of YOYs of native fish in normoxic lakes further suggests that extremely high predation rates on fish eggs and larvae exist in these ecosystems.

Finally, this study suggests new and sustainable paths to control the common carp, which to date have been controlled using nonspecific toxins, barriers and water draw-downs (Marking 1992; Wiley 2008). While poisons, barriers and drawdowns may on occasion provide short-term improvements in carp numbers and water quality, they may also reduce biotic resistance and enhance the need for continuing intensive management. The present study suggests that the common carp, and possibly other invaders that employ similar life histories, could instead be controlled using approaches that strengthen native fish communities.

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References

- Bajer PG, Sorensen PW (2010) Recruitment and abundance of an invasive fish, the common carp, is driven by its propensity to invade and reproduce in basins that experience winter-time hypoxia in interconnected lakes. *Biol Invasions* 12:1101–1112
- Bajer PG, Chizinski CJ, Sorensen PW (2011) Using the Judas technique to locate and remove wintertime aggregations of invasive common carp. *Fisheries Manag Ecol* 18:497–505
- Balon EK (1995) Origin and domestication of the wild carp, *Cyprinus carpio*—from Roman gourmets to swimming flowers. *Aquaculture* 129:3–48
- Barus V, Penaz M, Kohlmann K (2001) *Cyprinus carpio*. In: Barnescu PM, Paepke H-J (eds) *The freshwater fishes of Europe*, Vol. 5. Cyprinidae – 2. AULA-Verlag, Wiebelsheim, Germany, pp 85–179
- Billard R (1999) *Carp biology and culture*. Springer, New York
- Britton JR, Cucherousset J, Davies GD, Godard MJ, Copp GH (2010) Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. *Freshw Biol* 55:1130–1141
- Burnham KP, Anderson DR (2002) *Model selection and multi model inference: a practical information-theoretic approach*. Springer, New York
- Chippari-Gomes AR, Gomes LC, Lopes NP, Val AL, Almeida-Val V (2005) Metabolic adjustments in two Amazonian cichlids exposed to hypoxia and anoxia. *Comp Biochem Phys B* 141:347–355
- deRivera CE, Ruiz GM, Hines AH, Jivoff P (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology* 86:3364–3376
- Gross MR, MacMillan AM (1981) Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). *Behav Ecol Sociobiol* 8:163–174
- Hill AM, Lodge DM (1999) Replacement of resident crayfishes by an exotic crayfish: the roles of competition and predation. *Ecol Appl* 9:678–690
- Hollebone A, Hay M (2007) Propagule pressure of an invasive crab overwhelms native biotic resistance. *Mar Ecol Prog Ser* 342:191–196
- Ims RA (1990) On the adaptive value of reproductive synchrony as a predator-swamping strategy. *Am Nat* 136:485–498
- Keenleyside MHA (1972) Intraspecific intrusions into nests of spawning longear sunfish (Pisces: Centrarchidae). *Copeia* 1972:272–278
- King AJ, Humphries JP, Lake PS (2003) Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Can J Fish Aquat Sci* 60:773–786
- Koblitskaya AF (1977) The succession of spawning communities in the Volga Delta. *J Ichthyol* 17:534–547

- Koed A, Balleby K, Mejlhede P, Aarestrup K (2006) Annual movement of adult pike (*Esox lucius* L.) in a lowland river. *Ecol Freshw Fish* 15:191–199
- Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science* 298:1233–1236
- Korsu K, Huusko A, Muotka T (2007) Niche characteristics explain the reciprocal invasion success of stream salmonids in different continents. *P Natl Acad Sci USA* 104:9725–9729
- Koster FW, Mollmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES J Mar Sci* 57:310–323
- Lohmeyer AM, Garvey JE (2009) Placing the North American invasion of Asian carp in a spatially explicit context. *Biol Invasions* 11:905–916
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Marchetti MP, Light T, Moyle PB, Viers JH (2004) Fish invasions in California watersheds: testing hypotheses using landscape patterns. *Ecol Appl* 14:1507–1525
- Marking LL (1992) Evaluation of toxicants for the control of carp and other nuisance fishes. *Fisheries* 17:6–12
- Mazerolle MJ (2011) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.17. <http://CRAN.R-project.org/package=AICcmodavg>
- Moyle PB, Light T (1996a) Biological invasions of fresh water: empirical rules and assembly theory. *Biol Conserv* 78:149–161
- Moyle PB, Light T (1996b) Fish invasions in California: do abiotic factors determine success? *Ecology* 77:1666–1670
- Moyle PB, Marchetti MP (2006) Predicting invasion success: freshwater fishes in California as a model. *Bioscience* 56:515–524
- Osborne J (2012) Distribution, abundance, and overwinter survival of young-of-year carp in a Midwestern watershed. MS Thesis, University of Minnesota
- Petrosky BR, Magnuson JJ (1973) Behavioral responses of northern pike, yellow perch and bluegill to oxygen concentrations under simulated winter conditions. *Copeia* 1973:124–133
- Phelps QE, Graeb BDS, Willis DW (2008) Influence of the Moran effect on spatiotemporal synchrony in common carp recruitment. *T Am Fish Soc* 137:1701–1708
- Pope KL, Willis DW (1998) Early life history and recruitment of black crappie (*Pomoxis nigromaculatus*) in two South Dakota waters. *Ecol Freshw Fish* 7:56–68
- Potter IC (1980) Ecology of larval and metamorphosing lampreys. *Can J Fish Aquat Sci* 37:1641–1657
- Rahel FJ (1984) Factors structuring fish assemblages along a bog lake successional gradient. *Ecology* 65:1276–1289
- Roth BM, Tetzlaff JC, Alexander ML, Kitchell JF (2007) Reciprocal relationships between exotic rusty crayfish, macrophytes, and *Lepomis* species in northern Wisconsin lakes. *Ecosystems* 10:74–85
- Silbernagel JJ (2011) Field and laboratory studies suggest that recruitment of the invasive common carp is controlled by native fish in stable lakes of the Upper Mississippi Basin. MS Thesis, University of Minnesota
- Sorensen PW, Bajer PG (2011) The common carp. In: Simberloff D, Rejmanek M (eds) *Encyclopedia of invasive introduced species*. University of California Press Berkeley, California, pp 100–103
- Spotte S (2007) Bluegills: biology and behavior. American Fisheries Society, Bethesda, MA
- Stuart IG, Jones M (2006) Large, regulated forest floodplain is an ideal recruitment zone for non-native common carp (*Cyprinus carpio* L.). *Mar Freshw Res* 57:333–347
- Swee UB, McCrimmon HR (1966) Reproductive biology of the carp, *Cyprinus carpio* L., in Lake St. Lawrence, Ontario. *T Am Fish Soc* 95:372–380
- Tonn WM, Magnuson JJ (1982) Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149–1166
- Tonn WM, Magnuson JJ, Rask M, Toivonen J (1990) Intercontinental comparison of small-lake fish assemblages - the balance between local and regional processes. *Am Nat* 136:345–375
- Von Holle B, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3212–3218
- Ward-Fear G, Brown GP, Shine R (2010) Using a native predator (the meat ant, *Iridomyrmex reburrus*) to reduce the abundance of an invasive species (the cane toad, *Bufo marinus*) in tropical Australia. *J Appl Ecol* 47:273–280
- Weaver MJ, Magnuson JJ, Clayton MK (1997) Distribution of littoral fishes in structurally complex macrophytes. *Can J Fish Aquat Sci* 54:2277–2289
- Weber MJ, Brown ML (2009) Effects of common carp on aquatic ecosystems 80 years after “carp as a dominant”: ecological insights for fisheries management. *Rev Fish Sci* 17:524–537
- Welcomme RL (1995) Relationships between fisheries and the integrity of river systems. *Regul River* 11:121–136
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052
- Wiley RW (2008) The 1962 rotenone treatment of the Green River, Wyoming and Utah, revisited: lessons learned. *Fisheries* 33:611–617
- Wolfe MD, Santucci JJ Jr, Einfalt LM, Wahl DH (2009) Effects of common carp on reproduction, growth, and survival of largemouth bass and bluegills. *T Am Fish Soc* 138:975–983

Supplementary material follows.

Biological Invasions

Variation in native micro-predator abundance explains recruitment of a mobile invasive fish, the common carp, in a naturally unstable environment

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Table 1. AIC model selection results using full data set from all lakes and years combined (N=42) and a reduced data set that includes only one data point per lake (N=19; first time each lake was sampled). Predictor variables are: bluegill sunfish (BGS), black crappie (BCP), green sunfish (GSF), and propagule pressure (Propagule).

Model	AIC full data set	AIC reduced data set
BGS, GSF	45.36	6.13
BGS, BCP, GSF	46.21	8.08
BGS, BCP	46.25	6.10
BGS	46.40	4.26
BGS, PCP, Propagule	46.84	8.04
Best model without BGS as a predictor variable		
BCP, GSF	51.75	17.57