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Effects of crayfish density, body size and substrate on consumption of lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) eggs by invasive rusty crayfish [(*Orconectes rusticus* (Girard, 1852)]

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Summary

The density and size of benthic predators such as crayfish and the physical characteristics of aquatic habitats including benthic substrate size have been hypothesized to significantly affect levels of lake sturgeon (*Acipenser fulvescens*) egg consumption. The invasive rusty crayfish (*Orconectes rusticus*) was used to quantify consumption and apportion variation in egg loss in an experimental setting. Experiments consisted of large flow-through rectangular tanks (0.8 m wide, 2.96 m² total bottom surface area) receiving river water to mimic natural diel temperature regimes. Four crayfish densities were tested (5, 10, 15, 30 individuals or 1.7, 3.4, 5.1, 10.1 individuals/m²) that span the range of densities observed in natural settings. Crayfish were allowed to freely move among three substrates commonly found at spawning locations where lake sturgeon eggs are deposited (cobble, gravel and sand). After an acclimation period (15 min), 200 lake sturgeon eggs were randomly scattered over each substrate category (600 eggs per tank). Mean (± *SE*) egg consumption over 48 hr was 80 ± 3% (range 19–100% across 16 replicate trials). Egg consumption increased significantly as a function of increasing crayfish density. The effect of substrate size, however, depended significantly on crayfish density (substrate size × predator density interaction). Egg consumption significantly increased as substrate size decreased (e.g. from gravel to sand), at both high and low crayfish densities. Egg consumption also increased with increasing mean crayfish body size. Our results revealed that levels of lake sturgeon egg consumption by rusty crayfish are high in some settings. Further work is needed to determine if egg consumption in natural river settings is similarly high and whether egg consumption by crayfish and other egg predators could negatively affect population levels of recruitment.

1 | INTRODUCTION

Predation on eggs is a significant source of mortality early in life for many fishes (Dahlberg, 1979). Behavioral and life history strategies at the time of reproduction can help to reduce consumption of eggs by predators (Richardson, Hare, Fogarty, & Link, 2011). For example, parental behavior such as nest construction, egg guarding, burying and concealing eggs (Knouft, Page, & Plewa, 2003; Taborsky & Foerster, 2004; Wedekind & Muller, 2005), or the selection of specific spawning times and locations reduce the probability that eggs will be encountered and consumed (Ellrott, Marsden, Fitzsimons, Jonas, & Claramunt, 2007; Fitzsimons et al., 2006; Savino, Hudson, Fabrizio, & Bowen, 1999). Embryos may also exhibit early or induced hatching to the free-swimming larvae stage where the ability to respond and escape from

predators is enhanced (Chivers et al., 2001). Despite these behaviors, egg consumption can place limitations on the number of individuals surviving until hatch and to larval dispersal, even if eggs are deposited in a fashion (e.g. among substrates composed of gravel or cobble sized rock) expected to provide protection from predators (e.g. Ellrott et al., 2007; Fitzsimons et al., 2006, 2007).

Lake sturgeon, *Acipenser fulvescens*, is a threatened species throughout most of its native range. The species is long-lived and reaches sexual maturity late in life (12–27 year, depending on sex; Peterson, Vecsei, & Jennings, 2007). They are also highly migratory and highly fecund, spreading reproductive effort over multiple years, even delaying spawning until environmental conditions are appropriate. These traits allow populations to persist, even with high mortality during the egg and larval stages. Spawning in many Great Lakes tributaries occurs at the base of natural river barriers that frequently involve hydroelectric facilities where specific flows and substrate types are selected by spawning adults (Kerr, Davison, & Funnell, 2010), and where the abundance of native and introduced benthic egg predators can be unnaturally high (Bobeldyk & Lamberti, 2008; Butler & Wahl, 2011). Lake sturgeon eggs are relatively small (2.6–3.5 mm), negatively buoyant, adhesive and drift at variable distances and directions downstream from the spawning site, depending on water flow. Eggs often settle in discrete patches over a wide range of substrate types including clay, sand, gravel and cobble (Forsythe, 2010). As eggs settle, they adhere to substrate surfaces, many settling within interstitial spaces of river substrates (Forsythe, 2010). Following deposition, eggs are at risk to predation throughout their entire incubation period (5–14 days; Peterson et al., 2007).

Natural levels of lake sturgeon egg mortality are high (Forsythe, Scribner, Crossman, Ragavendran, & Baker, 2013; Kempinger, 1988), estimated to be between 80-99% in field-based studies. Egg mortality is due to various environmental sources including excessive siltation, and changes in water temperature, water velocity or water chemistry (Caroffino, Sutton, Elliott, & Donofrio, 2010a; Nichols et al., 2003). Egg mortality may also be due to consumption by benthic predators including resident crayfish, benthic fish omnivores, and co-migrating fish species (carp and sucker species) (Kempinger, 1988; Nichols et al., 2003), leading many studies to conclude that egg consumption plays a significant role in mortality (Biga, Janssen, & Marsden, 1998; Caroffino et al., 2010a; Chotkowski & Marsden, 1999). Egg consumption is likely to be a major cause of mortality in some situations but not all. Caroffino, Sutton, Elliott, and Donofrio (2010b) and Forsythe et al. (2013) came to the same conclusion for two different spawning populations; while egg consumption does occur on some eggs (16-18% of the total annual egg deposition), other sources (e.g. microbial infections that cause developmental arrest) cause much of the egg mortality (Fujimoto, Crossman, Scribner, & Marsh, 2013). Therefore, the role that egg consumption specifically plays in lake sturgeon egg mortality remains relatively uncertain and may depend on the surrounding ecological river conditions such as substrate size and the density and size of benthic predators. However, these ecological conditions as they pertain to variation in lake sturgeon egg consumption have not been evaluated specifically for any predator guild.

To complicate this story, the diversity and abundance of predacious aquatic invasive species have increased globally, and each invasion has negative implications for fish eggs during incubation (Lederer et al., 2008; Morse, Baldridge, & Sargent, 2013). For example, Findlay, Riley, and Lucas (2015) reported that egg consumption by a single exotic crayfish species of Atlantic salmon (*Salmo salar*) eggs significantly increased mortality, especially when the predator population was composed of larger bodied individuals that could effectively excavate redds and extract eggs. Rusty crayfish *Orconectes rusticus*, native to the Ohio River basin (Momot, Gowing, & Jones, 1978), have now become a prolific invasive species in many tributaries and lakes across the Great Lakes basin (Olden, Mccarthy, Maxted, Fetzer, & Jake, 2006). Rusty crayfish are capable of consuming more prey, including fish eggs (Morse et al., 2013), than most of their native counterparts (Hill & Lodge, 1994) due in part to their higher metabolic activity (Jones & Momot, 1983), faster growth (Olsen, Lodge, Capelli, & Houlihan, 1991), and a larger body size at maturity that energetically requires more resources (Hill, Sinars, & Lodge, 1993). The proliferation of rusty crayfish within the Great Lakes and tributaries has raised concerns over its impacts to recruitment and conservation of native fish.

The objectives of this study were to (1) estimate the levels of lake sturgeon egg mortality due to consumption by invasive rusty crayfish and (2) quantify the effects of rusty crayfish density, body size and substrate size on levels of egg consumption during incubation under controlled laboratory conditions. We hypothesized that rusty crayfish would consume lake sturgeon eggs if given the opportunity, but that levels of consumption would be significantly lower in situations with a smaller pool of predators (measured by body size or density), and with medium to larger rock substrates to provide interstitial spacing and opportunities for egg concealment. Crayfish are useful because they can account for as much of 60% of the total zoobenthic biomass of freshwater communities (Momot, 1995). Rusty crayfish in particular are reported to be a more effective predator of fish eggs than native crayfish species (Morse et al., 2013). Egg consumption studies focused on invasive rusty crayfish will also help inform the future directions of invasive crayfish management.

2 | MATERIALS AND METHODS

This research was conducted using eggs collected from adult female *Acipenser fulvescens* from the Black Lake population, Michigan. Adult population size has been estimated to be ~1,100 (Pledger, Baker, & Scribner, 2013). The Upper Black River (UBR) is the largest tributary of Black Lake and contains 11.5 km of staging and spawning habitat downstream of Kleber Dam (built ca. 1949). Approximately 200–270 adults spawn annually (Forsythe, Crossman, Bello, Baker, & Scribner, 2012a). Lake sturgeon eggs and sperm were collected from spawning adults artificially fertilized using standard protocols (Crossman, Scribner, Davis, Forsythe, & Baker, 2014), and placed in incubation trays at a UBR streamside research facility for approx. 1 day before experiments were conducted. River water temperature was recorded
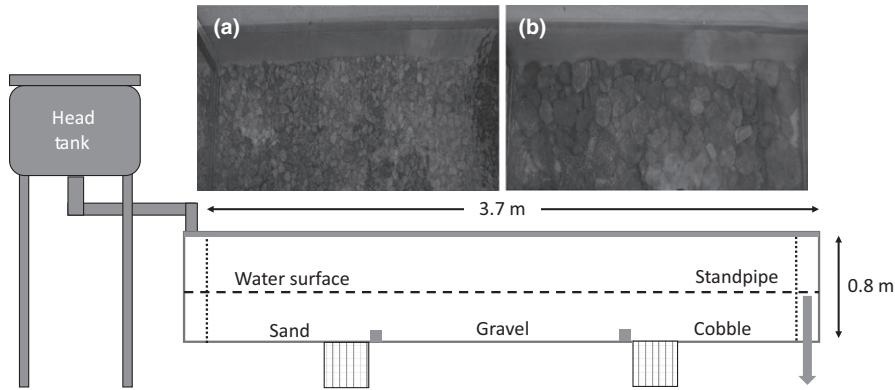
FIGURE 1 Flow-through tank experimental design used to evaluate lake sturgeon (*Acipenser fulvescens*) egg consumption. Water was taken directly from the Upper Black River, Michigan. Flow entering and exiting the system was equal and small gauge baffles (vertical dotted lines) were used to control unwanted hydrodynamics. Photos A and B illustrate the Gravel and Cobble substrate categories (Sand category not shown)

hourly using HOBO® data loggers (Onset Computer Corp.) placed at the streamside research facility.

Rusty crayfish were collected from areas of the UBR where spawning had not yet occurred (e.g. Kleber Dam; Forsythe et al., 2012a) to ensure that exposure to lake sturgeon eggs was unlikely. Crayfish were housed unfed in flow-through tanks for two days while lake sturgeon eggs and sperm were collected. Experimental tanks used for predation studies were 3.7 m long by 0.8 m wide (2.96 m^2 total bottom surface area) and received water taken directly from the UBR in order to induce changes in functional and metabolic activity of the focal crayfish that might accompany natural diel changes in water temperature (Fig. 1). It is important to note that the rectangular tanks (i.e. the experimental unit) were not designed to represent a flowing stream channel and no gradient was built in to the experimental design. The amount of water flowing out of the tank matched water flowing in (approx 3.5 L per minute), largely to minimize potential for oxygen stress of the crayfish predators and to keep the water level in the tank consistent. There was no perceivable water velocity within the main experimental arena as measured with a portable flow meter (Marsh–McBirney Model 2000 Flo–Mate).

Benthic substrates used for this experiment were collected from areas of the UBR where lake sturgeon had spawned in previous years (Forsythe et al., 2012b). Substrates were measured along the longest longitudinal axis and sorted into three categories as defined by Wentworth (1922) (*M* ± *SE*) including cobble (63.5 ± 18.4 mm), gravel (24.4 ± 5.87 mm), and sand (range = 0.6–2 mm). Recently deposited lake sturgeon eggs are associated with all three substrate categories in UBR spawning areas (see Forsythe, 2010). Sorted substrates were arranged into three equal size sections (approx. 1.2 m × 0.8 m) in the bottom of the experimental tanks so that all three substrate categories were available simultaneously within the tank (Fig. 1). Substrate categories were placed in a random order for each replicate to account for tank hydrodynamics surrounding the water intake, and novel crayfish were introduced to the experimental unit for each new replicate trial.

Crayfish were allowed to move freely among substrate types. Experimental crayfish numbers selected for this study (5, 10, 15, 30 total individuals or 1.7, 3.4, 5.1, 10.1 individuals/m^2) represented the range reported from published field studies (Kuhlmann, 2016; Kuhlmann & Hazelton, 2007). Crayfish were sorted visually by carapace length to reduce body size variation across replicates. Crayfish

predators were initially placed randomly among the three substrate categories so that each substrate had a similar number of predators. After a 15-min acclimation period, 200 fertilized eggs were randomly scattered across each substrate category (600 eggs per tank or approx. 202 eggs/m^2 for the entire experimental unit). Experimental egg densities were chosen to reflect those reported for deposited lake sturgeon eggs in in the UBR (approx. range: 0–365 eggs/0.5 m^2; Forsythe, 2010). Eggs were observed resting on the top of substrates and within interstitial spaces of gravel and cobble, similar to field based observations (Forsythe, 2010). The proportion of crayfish occupying each substrate type and their activity (e.g. foraging, refuging or searching) were recorded every four hours. After 48 hr, crayfish were removed and carapace length (mm) recorded from each individual. Small gauge screen dividers were then placed between substrate sections to preclude egg drift. Substrates were searched and remaining eggs counted. This experimental process was replicated 16 times with 9,600 individual eggs and 225 rusty crayfish by completely disassembling, cleaning and reassembling the tank (four tanks were run simultaneously).

Due to diel variation in crayfish substrate selection and foraging activity, a second experiment was conducted where crayfish were limited to a single substrate. This experiment was conducted in tanks roughly the same size as one subsection from the first experiment (1.2 m × 0.8 m; 0.96 m^2 bottom surface area). Five crayfish (approx. 1.7 individuals/m^2) were housed unfed for 48 hr then placed randomly in a tank containing one of the three substrate categories. Two-hundred eggs were released after a 15-min acclimation period. The experimental protocol was repeated as previously described for a total of 18 replicates.

Data for both experiments were analyzed in a whole-plot split-plot design using a general linear mixed model within the MIXED procedure of SAS Version 9 (Littel, Milliken, Stroup, Wolfinger, & Schabenberger, 1996). Crayfish density was treated as the whole plot factor and the substrate category as the subplot factor. The proportion of eggs remaining (arcsine square root transformed dependent variable) after 48 hr was modeled as a function of crayfish density, substrate size and the interaction between these main effects. Mean crayfish size was used as a covariate to account for non-uniform differences in body size and associated behaviors of crayfish across replicates. Pair-wise comparisons were investigated using least square means and post hoc differences were computed using Tukey's HSD (α = 0.05). Because the

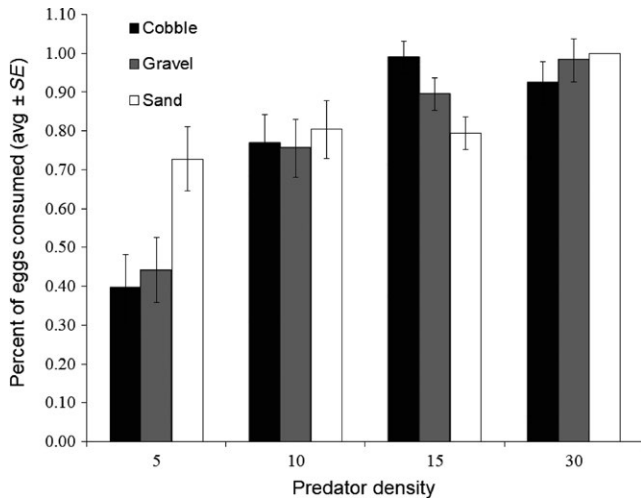**FIGURE 2** Percent of lake sturgeon (*Acipenser fulvescens*) eggs consumed (±*SE*) in treatments containing 5, 10, 15 or 30 rusty crayfish (*Orconectes rusticus*) predators and across sand, gravel and cobble substrate categories. Crayfish were allowed to move freely within experimental tanks. (Number of eggs at trial start = 200)

assumptions of normality were met, a traditional analysis of variance was used to test for differences in the mean proportion of time crayfish were observed in each substrate category when movement was unrestricted during Experiment 1.

3 | RESULTS

3.1 | Experiment 1

Water temperature entering experimental tanks ranged from 11.5 to 17.5°C (*M* = 14.4°C). Carapace length of rusty crayfish ranged from 19.4 to 35.2 mm and some replicates differed significantly in terms of crayfish average body size (*p* < .05). A total of 7,718 eggs (80%) were consumed by 255 crayfish across all replicates where predators had unrestricted access to each substrate category. Crayfish density was a significant predictor of the number of eggs consumed over 48 hours ($F_{3,11}$ = 6.9, *p* < .005). Egg consumption increased by approx. 20% on average for each experimental increase in crayfish density. Average egg consumption with a density of 15 and 30 crayfish predators was 89% (range: 75–100%) and 96% (range: 24–100%), respectively (Fig. 2).

The main effect of substrate size did not explain a significant portion of the variation in egg consumption in the statistical model ($F_{3,24}$ = 0.9, *p* = .39). However, a density-by-substrate interaction was detected ($F_{6,24}$ = 3.5, *p* = .049) and exploration of this interaction revealed some significant differences (*p* < .05). For example, mean (± *SE*) consumption was significantly lower in replicates of the cobble treatment (mean percent consumed = 39 ± 4%) compared to the gravel (mean percent consumed = 44% ± 5%) and sand substrates (mean percent consumed = 73% ± 5%) when crayfish densities were low (five individuals; Fig. 2). Significant (*p* < .05) and comparable differences among substrate types were also found at a high crayfish

density (30 individuals). However, at intermediate crayfish densities, substrate size either had no effect on the number of eggs consumed (10 individuals) or the effects were the opposite, based on significant pairwise comparison (15 individuals; Fig. 2).

We noted that crayfish use and residency time in each substrate category was non-random; crayfish spent significantly more time (32 out of 48 total hours) associated with and seeking refuge in cobble substrates, especially during daytime ($F_{2,68}$ = 28.1, *p* < .001; Fig. 3). However, there was 17% shift in substrate occupancy to gravel and sand substrates at night (Fig. 3). This shift in occupancy was accompanied by higher activity levels, including foraging (P.S. Forsythe, personal observation). Egg consumption was also related to the average carapace length of crayfish used in an experimental replicate ($F_{1,11}$ = 15.0, *p* < .01; Fig. 4). Significantly more eggs were consumed in replicates populated by larger crayfish, especially when the mean carapace length exceeded 24 mm. Although consumption rates by
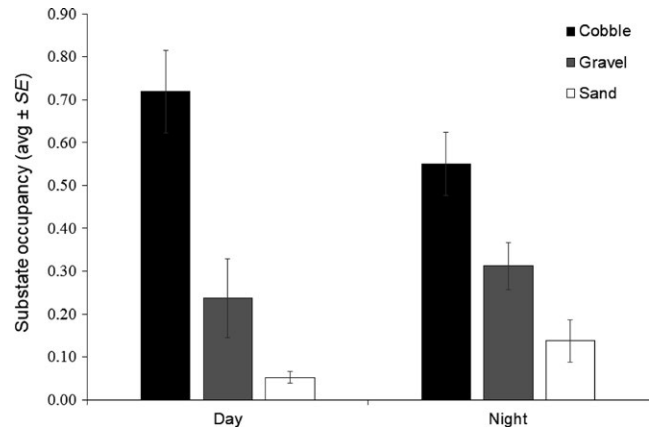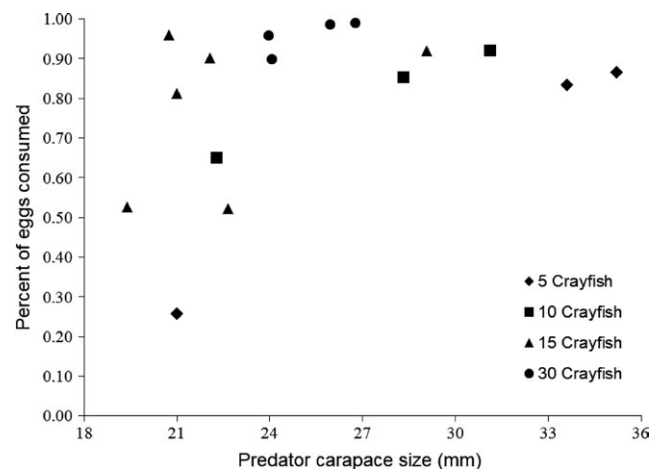

FIGURE 3 Occupancy of three different substrate categories (sand, cobble, gravel) of crayfish predators (*Orconectes rusticus*) as a percent of the total during the day (07.00–19.00) and night (20.00–06.00) hours

FIGURE 4 Percent of lake sturgeon (*Acipenser fulvescens*) eggs consumed as a function of rusty crayfish (*Orconectes rusticus*) mean carapace size in treatments containing 5, 10, 15 or 30 individuals. (Number of eggs at trial start = 200)
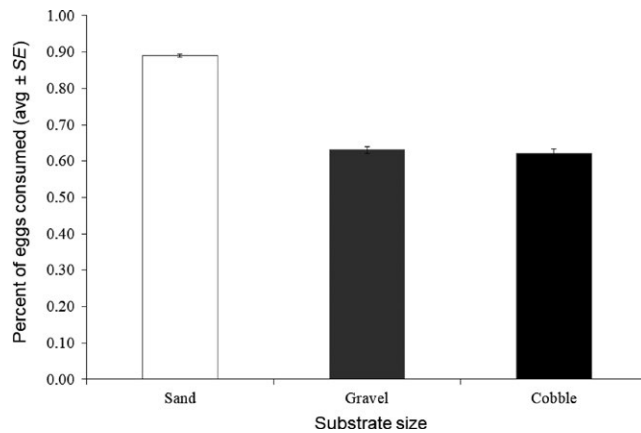
FIGURE 5 Percent of lake sturgeon (*Acipenser fulvescens*) eggs consumed (±*SE*) across sand, gravel and cobble substrate categories. Density of rusty crayfish (*Orconectes rusticus*) was fixed to five individuals and substrate category. (Number of eggs at trial start = 200)

individual crayfish were not measured directly, we estimated that eggs were consumed up to a maximum individual level of 104 eggs/day (*M* ± SE, 40.2 ± 6.7 eggs per individual per day).

3.2 | Experiment 2

Consumption of lake sturgeon eggs was also high when predator density and movement were fixed within a specific substrate category. A total of 2,495 eggs representing 69% of the total were consumed by 90 crayfish predators. This is comparable to the 77% total egg consumption observed in Experiment 1 at a similar crayfish density. In this case, however, substrate size was a significant predictor of egg consumption ($F_{2,15}$ = 3.85, p = .045), with lower levels of consumption in the cobble (62%) and gravel (63%) treatments relative to treatments with a sand bottom (89%) (Fig. 5). We estimated that 28 eggs/crayfish were consumed on average during this experiment. Carapace length of crayfish predators was also a significant predictor of the number of eggs consumed ($F_{1,17}$ = 7.26, p < .01) with larger crayfish on average within a replicate experiment consuming more eggs.

4 | DISCUSSION

Results from this study confirmed that rusty crayfish are an important predator of lake sturgeon eggs and can cause high egg mortalities under experimental conditions. Previous field-based studies (e.g. Caroffino et al., 2010b; Forsythe et al., 2013 and Kempinger, 1988) have documented high mortality during the egg stage for lake sturgeon, but were not able to partition mortality among sources (e.g. predators, microbial colonization and developmental arrest, etc.). The levels of consumption that we estimated were over four times the mean egg consumption reported for crayfish in the Peshtigo River, Wisconsin (Caroffino et al., 2010a). Our estimates of individual egg consumption averaged from both

experiments (38 eggs/individual) were also higher than reported for other Great Lakes fishes, where recruitment is reported to be negatively affected by egg predators. For comparison, Savino and Henry (1991), Chotkowski and Marsden (1999), and Mason and Evans (2011), reported that mean consumption rates of lake trout eggs were generally less than 10 eggs/individual/day for two crayfish species (*O. propinquus* and *O. virillis*), mottled sculpin (*Cottus bairdii*), round gobies (*Neogobius melanostomus*), and slimy sculpins (*Cottus cognatus*).

We note that our experimental results should be interpreted in the context of the imposed experimental conditions. Specifically, trials were conducted using a single predator and single prey. Negative interspecific interactions among benthic predators, or the threat of predation by a top predator (e.g. largemouth bass, *Microbterus salmoides*), can reduce egg consumption in field and laboratory settings (Garvey, Stein, & Thomas, 1994). For example, Miller, Savino, and Neely (1992) showed that crayfish consumption of rainbow trout (*Oncorhynchus mykiss*) eggs was reduced by up to 50% in the presence of slimy sculpin (*Cottus cognatus*). Red swamp crayfish (*Procambarus clarkii*) significantly reduced foraging time in the presence of conspecifics and fish predator odors (Gherardi, Mavuti, Pacini, Tricarico, & Harper, 2011). Our study also used no alternative prey. Waraniak (2017) has shown that predation of lake sturgeon larvae varied as a function of the relative abundance of co-distributed sucker and macroinvertebrate prey. Thus, consumption of lake sturgeon eggs may be significantly reduced in the natural stream environment, especially where alternative prey are available during incubation. Although crayfish in our study displayed much of their natural behaviors (e.g. spent 63% of the time refuging in cobble), mixed predator-prey experiments should be evaluated to quantify the magnitude of lake sturgeon egg consumption under more complex predator-prey scenarios.

Our research suggests that levels of egg consumption significantly increase with increasing rusty crayfish density, even up to 100% in some experimental conditions. However, complete elimination of eggs does not appear likely for some Great Lakes spawning populations. For example, low levels of egg consumption were reported by Caroffino et al. (2010a) and are consistent with our relatively low projections of egg consumption at an estimated density of crayfish (all species) on the Peshtigo River, Wisconsin of approx. 4.1 crayfish/m². Rusty crayfish density in Upper Black River spawning areas also appears to be relatively low (e.g. less than five crayfish/m²) during reproduction (P. Forsythe, personal observation) and both the Peshtigo and Upper Black rivers consistently recruit individuals to the larval and juvenile stages despite the presence of benthic egg predators. Further research is needed to extend our experimental data to determine the non-native crayfish population abundance required to reduce egg numbers (given a density of spawning females and size depositional area) below levels desired by management to achieve annual recruitment goals.

Higher densities of crayfish (greater than 200 individuals/m²) have been reported for many other Great Lakes tributaries where lake sturgeon spawn (Kuhlmann & Hazelton, 2007), especially at the base of dams where the abundance of native and introduced crayfish predators is often high (Bobeldyk & Lamberti, 2008; Butler & Wahl,

2011). High and localized crayfish densities would be detrimental to egg survival based on our data, and should be a serious concern for managers seeking to rehabilitate populations, particularly where abundance of spawning adult lake sturgeon has been severely depressed (e.g. Grand and Kalamazoo rivers, Michigan). Other introduced and prolific benthic predators to the Great Lakes are likely to be important if the magnitude of mortality is similar. For example, Nichols et al. (2003) used video and recorded round goby densities of 25 individuals/m² on a spawning reef in the Lower St. Clair River, Michigan. Hatching rate of lake sturgeon eggs in devices that excluded round gobies was 16% higher than unprotected eggs (Nichols et al., 2003). Recruitment to the larval stage on the Fox River (DePere Dam, Wisconsin), which supports large populations of numerous resident native and invasive crayfish, benthic and adfluvial fish egg predators (e.g. common carp, *Cyprinus carpio*), appears to be a major impediment to lake sturgeon recruitment to the larval stage (P. S. Forsythe, unpublished data).

The importance and availability of larger substrates with interstitial spacing downstream from known lake sturgeon spawning areas was reinforced by this study. We observed that lake sturgeon eggs deposited on sand, which does happen in natural areas (Forsythe, 2010), were quickly consumed by crayfish at all densities. Influence of substrate size on the magnitude of consumption across the predator densities tested was conflicting, however, and our results should be interpreted as a function of substrate type and predator size. For example, the highest consumption of lake sturgeon eggs (mean 93% consumption) actually occurred on cobble substrate when predator density was 5.1 individuals/m² (or 15 crayfish, total). It is possible that agonistic interactions among crayfish of different body sizes (i.e. dominance) at high density accelerated the egg consumption (Gruber, Tulonen, Kortet, & Hirvonen, 2016). However, the rusty crayfish selected for use in these trials were among the smallest available (by 6 mm CL on average), and thus likely able to forage more effectively within interstitial spaces of cobble and gravel treatments. The role that substrate size plays in mitigating egg predation also varies among fish species. For example, Palm et al. (2009) reported the highest rates (83%) of Atlantic salmon (*Salmo salar*) egg consumption by European sculpin (*Cottus gobio*) on large substrates, suggesting that such habitats were selected for refuge and also allowed greater access to eggs. Corkum and Cronin (2004) reported that when food resources were unlimited (which might be the case during peak lake sturgeon spawning), larger substrate size led to greater egg consumption rates by decreasing intraspecific aggressive interactions between predators.

Our research shows that lake sturgeon egg consumption increases significantly with increasing crayfish size (as measured by carapace length). Egg consumption was greater than 80% in every trial where mean crayfish body size was above 24 mm. This result was anticipated, given that larger individuals often require more energy (Jones & Momot, 1983), and that larger crayfish tend to forage more actively during all hours in the presence of conspecifics (Bondar, Zeron, & Richardson, 2006). Morse et al. (2013) reported a similar positive correlation between rusty crayfish body size and foraging success on bluegill sunfish (*Lepomis macrochirus*) eggs in nests guarded by attending males. Larger rusty crayfish resumed their consumption of eggs much sooner after periods of perceived predation risk by the guarder, and foraged for longer periods of time (Morse et al., 2013). Interestingly, size-based foraging was not observed for *O. virilis*, a native congener in the Great Lakes region (Morse et al., 2013). Management biologists working to mitigate the impacts of rusty crayfish might be compelled to recommend targeted removals of the largest individuals before spawning occurs in the spring. However, crayfish populations (invasive or native) are often composed of small individuals, and since lake sturgeon eggs remain unguarded by adults after spawning, our research suggests that a dense population of smaller rusty crayfish may pose a more serious threat to egg survival if they indeed forage more efficiently for incubating eggs within interstitial spaces as previously discussed.

As is true with most laboratory studies, abiotic factors existing in natural aquatic environments are not entirely represented. For example, our experimental tanks had relatively low flow rates compared to the specific areas of natural streams where lake sturgeon spawn. However, while increasing stream water velocity and the associated increase in water turbidity that tends to reduce predation rates of visual aquatic predators (Ward, Morton-starner, & Vaage, 2016), the same is not always true for chemosensory predators like crayfish (Lunt & Smee, 2015). Clark, Kershner, and Montemarano (2013) also showed that the distribution and density of crayfish within stream channels were often size dependent, with larger individuals found in the deep pools with large substrate. Further, LaHaye, Branchaud, Gendron, Verdon, and Fortin (1992) and Forsythe (2010) showed that lake sturgeon eggs are deposited in discrete clumps across multiple substrates, directly downstream from spawning areas. Thus, access to and consumption of lake sturgeon eggs broadcast over a relatively large area will not be uniform across the stream channel. Smaller crayfish may consume eggs deposited in shallow stream margins while larger crayfish may consume eggs in deeper water. All sizes of crayfish may be chemically drawn to large aggregates of deposited eggs (Forsythe, 2010), resulting in higher levels of egg consumption.

The natural recovery of many lake sturgeon populations around the Great Lakes has been slow or negligible. Given the comparatively lower density of lake sturgeon eggs from a significantly reduced stock of spawning adults and the high density and diversity of (natural) egg predators found at the time of spawning, it is plausible that egg consumption may be impeding the recovery efforts. While we demonstrate that crayfish alone can be a significant additive source of egg mortality, other known predators of lake sturgeon eggs should be evaluated in a similar way. Kempinger (1988) and Caroffino et al. (2010b) reported lake sturgeon egg predators including white sucker (*Catostomus commersonii*), northern hog sucker (*Hypentelium nigricans*), yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), and mudpuppy (*Necturus maculosus*), to actively consume eggs. Our research indicates that expanding populations of benthic-introduced egg predators (e.g. rusty crayfish and round goby) may exacerbate the effect of egg consumption on some populations of broadcast spawning Great Lakes fishes, in particular depressed populations like the lake sturgeon (Phillips, Vinebrooke, & Turner, 2009).

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