

## Review

**Biological control of invasive fish and aquatic invertebrates: a brief review with case studies**

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**OPEN ACCESS****Abstract**

We review various applications of biocontrol for invasive fish and aquatic invertebrates. We adopt a broader definition of biocontrol that includes traditional methods like predation and physical removal (biocontrol by humans), and modern approaches like genetic engineering and use of microbes (including pathogens). While physical removal and predation (by native predators) are used relatively commonly, use of genetic technologies and microbes is in developmental stages. The two latter strategies are most advanced in case of the common carp (*Cyprinus carpio*), one of the world's most invasive fish; virus release to control carp might soon occur in Australia. Drawing from empirical examples in North America, we emphasize that biocontrol strategies are most likely to be successful if they include multiple approaches that target specific behaviors or weaknesses in pests' life histories. This is illustrated by reviewing case studies on the common carp and rusty crayfish (*Orconectes rusticus*) in Midwestern North America. In case of the common carp, basic research on movement patterns and recruitment bottlenecks identified a strategy where winter aggregations of adults were targeted for removal with nets, while native predators of carp eggs and larvae were instrumental in controlling carp's reproductive success. In the case of the rusty crayfish, basic research on interactions between crayfish, habitat, and native predators identified a successful strategy of stocking selected native predators to control juvenile crayfish in conjunction with physical removal of adult crayfish using traps. We are also reviewing the case of the round goby (*Neogobius melanostomus*) in the Great Lakes. In this example, multiple pieces of evidence (diet, bioenergetics) illustrate how initially abundant pest was brought under control (in some areas) by several species of native predators in a large, natural ecosystem. Overall, examples of successful biocontrol of aquatic pests have been rare and have relied on physical removal and predation. We expect that new technologies (e.g. genetic technologies) will occur in the next decade but will have to clear regulatory and ethical concerns before they are applied. While developing more sophisticated control techniques, we advocate for more basic research on the life history of the pests to identify behavioral or developmental weaknesses that could be targeted with specific tools to increase chances of success while minimizing impacts on native ecosystems.

**Key words:** biocontrol, invasive species, exotic, non-native, pest management

## Introduction

Broadly defined, biological control, or biocontrol, is a strategy in which living organisms control populations of pest species. Biocontrol agents may include predators (Symondson et al. 2002), parasites or pathogens (Saunders et al. 2010), consumers (Malecki et al. 1993), or genetically-modified organisms (i.e. organisms that carry genetic constructs used in biocontrol; Thresher et al. 2014a). Biocontrol of non-native pests has a long history of success in agricultural applications. For example, introduction of a South American parasitoid wasp (*Epidinocarsis lopezi*) was instrumental in curtailing the invasion of cassava mealybug (*Phaenococcus manihoti*) that threatened the production of cassava (*Manihot* spp.) in sub-Saharan Africa (Norgaard 1988). The introduction of another parasitic wasp (*Catolaccus grandis*), augmented by a natural spread of the fire ant (*Solenopsis* spp.), was also important in controlling the boll weevil (*Anthonomus grandis*), which invaded southern USA in late 1980s and reduced yields of cotton by some 50% within few years after arrival (Sterling 1978; Morales-Ramos et al. 1995; Lange et al. 2009). Traditionally (e.g. in agricultural pest control), biocontrol has taken three forms: importation, augmentation, and conservation. Importation, often called “classical” biocontrol, is used when the biocontrol agent is non-native, usually from pest’s native area (i.e. natural enemies). These natural enemies are organisms that co-evolved with the pest and control it in its native range. Natural enemies are generally screened, quarantined, and tested for specificity to minimize unintended consequences that might result from developing unforeseen associations with native organisms (Messing and Wright 2006). Augmentation involves release of more control agents to supplement an already existing population. Conservation involves conservation of existing natural enemies by, for example, creating habitat patches where they can survive and thrive. Shelterbelts of hedgerows, also known as “beetle banks”, are used in agriculture to provide habitat patches and conserve natural enemies (Collins et al. 2002).

Biocontrol is also being used with increased frequency in management of natural resources, including the management of invasive fish and aquatic invertebrates. In this field, approaches such as importation are generally not considered due to the risk of unintended consequences and the lack of closely co-evolved natural enemies (see below). Instead, native predatory species often play a key role in biocontrol strategies (Bajer et al. 2015). The use of pathogens and genetic technologies in aquatic pest control remains in developmental stages, with no known applications to date. Physical removal is applied often to manage invasive fish and aquatic invertebrates (Tsehaye et al. 2013) and we argue that this strategy should be included within broadly defined biocontrol strategies (biocontrol by

humans) because removal schemes grow increasingly complex and often exploit weaknesses in pests' life histories. For example, unique behaviors, such as social aggregations, and species-specific chemical cues (e.g. pheromones) are often used to affect removal of invasive fish (Johnson et al. 2009; Bajer et al. 2010, 2011). In some cases, aquatic pests are harvested for human consumption, a strategy termed "invasivory" (Nuñez et al. 2012; Barnes et al. 2014; Pasko and Goldberg 2014). Also, strategically conducted physical removal is sometimes needed to facilitate secondary biocontrol strategies. For example, modeling suggests that the use of genetic biocontrol technologies to control invasive fish needs to be jump-started by physical removal (Thresher et al. 2014a). Finally, physical removal strategies are typically non-controversial and do not require lengthy approval procedures.

The purpose of this review is to familiarize aquatic ecosystem managers and aquatic ecologists with various forms of biocontrol and to review recent applications of various biocontrol strategies for invasive fish and aquatic invertebrates. To achieve this, we provide an overview of relevant and most common biocontrol strategies in the field, including the use of predators, physical removal, genetic engineering and pathogens. We also present three case studies to illustrate how various forms of biocontrol, in combination with other management techniques, have been applied to successfully control invasive fish and aquatic invertebrates in North America. It is not our intent to provide an exhaustive overview of the history, benefits, and risks of the broadly-defined biocontrol. For that, we direct the readers to three reviews by Simberloff and Stiling (1996), Messing and Wright (2006), and Meronek et al. (1996).

## **Types of biological control and application to invasive fish and invasive aquatic invertebrates**

### *1) Predators as a form of biocontrol*

Biocontrol of invasive fish and invasive aquatic invertebrates differs from that of agricultural pest insects in the use of native vs. non-native biocontrol agents. Due to their high diversity (> 1 million species), insects typically have highly co-evolved enemies in their native ranges, and it is unlikely that similarly effective biocontrol agents might be found in new geographic areas to which the pests are being introduced (but see Symondson et al. 2002). Fish are an order of magnitude less diverse and have few highly co-evolved predators or parasites (Lefèvre et al. 2009). Thus, the concept of natural enemies might not be broadly applicable in the management of invasive fish and aquatic invertebrates. Instead, invasive fish and aquatic invertebrates might be controlled by broad-spectrum predators found in areas to which they are being introduced (Balcombe et al. 2005). For example, the Japanese dace (*Tribolodon hakonensis*), which is an indigenous fish-egg predator in Japan, has been

shown to consume > 90% of eggs in the nests of invasive smallmouth bass (*Micropterus dolomieu*) (Iguchi and Yodo 2004). The native European eel (*Anguilla anguilla*) has been shown to be an effective predator of the invasive red swamp crayfish (*Procambarus clarkia*) in the Netherlands (Aquiloni et al. 2010; Musseau et al. 2015), while the native Eurasian perch (*Perca fluviatilis*) has been shown to be instrumental in controlling the population of invasive topmouth gudgeon (*Pseudorasbora parva*) in a large pond experiment in the United Kingdom (Davies and Britton 2015). In North America, native sunfish (*Lepomis* spp.) have been shown to be effective in controlling populations of invasive rusty crayfish (*Orconectes rusticus*) and common carp (*Cyprinus carpio*) (Roth et al. 2007; Tetzlaff et al. 2010; Bajer et al. 2012; Bajer et al. 2015). Burbot (*Lota lota*) was shown to consume over 60% of round goby standing stock annually in eastern Lake Erie (Madenjian et al. 2011). The concept of native biocontrol might at first seem paradoxical: if native predators can control invasive fish, why are those fish able to become invasive in the first place? Specifically, spatial and temporal habitat heterogeneity and disturbance events might explain this phenomenon. In regions dominated by predators, invaders are often able to exploit ephemeral patches of predator-free habitat to produce offspring. For example, Bajer et al. (2012, 2015) showed that in interconnected lakes systems of central Minnesota, invasive common carp successfully produce young in outlying marshes that winterkill and lack most native predators.

## 2) Application of genetic methods as a biocontrol measure

The use of genetic technologies to control invasive fish has progressed over the last decade, accompanied by political and social concerns (Sharpe 2014). Several options of genetic control have been identified and are at various stages of development (reviewed in Thresher et al. 2014a) with the most progress made in insect systems. Although many genetic technologies in consideration differ substantially on the molecular level, they can be grouped according to similarities in their effect on the organismal/population scale.

Sterile-male technologies are inspired by Sterile Insect Techniques (SIT) in which gamma irradiated male insects are released to mate with wild females (Dyck et al. 2005). SIT has had tremendous success in combating major pests such as screwworm flies in the Americas (Wyss 2000). Applying sterile-male release in fish may be accomplished by releasing males, which can fertilize wild-type eggs but do not generate viable offspring. For example, such an approach, where males are sterilized by injection with a chemical (bisazir) has been used in sea lamprey (*Petromyzon marinus*) control in the Great Lakes region (Twohey et al. 2003; Bergstedt et al. 2003). In this case, sterilized males spawn with wild females and fertilize their eggs but their offspring does not survive. The

released males may also be incompatible with the wild-type due to induced polyploidy (Piferrer et al. 2009) or the expression of a lethal gene in embryos developing in the absence of a chemical to repress the toxic gene. This was demonstrated in the model organism zebrafish (*Danio rerio*) and channel catfish (*Ictalurus punctatus*) (Thresher et al. 2009). Genetic incompatibility may also be established by engineering fish to express a programmable transcriptional activator targeting a DNA sequence only present in the wild-type. Hybridization between wild-type and engineered males results in lethal overexpression of a wild type gene in the embryo, although this has been only demonstrated as a proof on concept experiment in yeast (*Saccharomyces cerevisiae*) (Maselko et al. 2016).

Sex-ratio-biasing technologies impact the reproductive potential of a population by reducing the number of females. Female lethal technologies are similar to sterile-male approaches, except hybridization between the released male and wild females results in the death of any female offspring. The surviving F1 males may also have a genotype reducing the number of females in the F2 generation although the effect is diminished with each successive generation as the female lethal genetic elements segregate. However, modeling has shown that female-lethal technologies can reduce the number of females sufficiently for population collapse (Bax and Thresher 2009), and a female lethal technology has been demonstrated in zebrafish (Thresher et al. 2014b). The zebrafish were engineered with a lethal gene under the control of a female specific promoter that could be turned off in the presence of tetracycline (to allow for propagation). Alternative daughterless technologies depend on the release of fish where all of the offspring are male (as opposed to the females dying). By destroying the X chromosome during meiosis, all sperm cells will carry the Y chromosome and generate males, which has been demonstrated in mosquitoes (*Anopheles gambiae*) (Galizi et al. 2014). In species with XY sex determination systems such as common carp or brook trout (*Salvelinus fontinalis*), YY “supermales” or YY phenotypic females generated by hormone treatments only have YY or XY male offspring (Bongers et al. 1999). Lastly, genetic engineering can be applied to control hormone levels that determine sex in fish. The “daughterless carp” strategy involves blocking aromatase, an enzyme responsible for converting male-determining androgen hormones into female-determining estrogen hormones (Thresher et al. 2014a)

All of the above technologies are intrinsically “self-limiting”, meaning the allele frequency of the genetic constructs are governed by Mendelian inheritance and are not likely to persist since they are deleterious by design. This requires releasing a large number of animals for biocontrol applications and possibly repeat release events. These limitations may be overcome through the use of gene-drives which are self-propagating



genetic elements and have the potential to rapidly spread a deleterious trait (e.g. female lethal) throughout a population (Burt 2003). Theoretically, a single individual carrying a gene drive could result in its persistence (Marshall 2009). A cross between wild-type and the gene-drive carrier would generate a fish initially hemizygous for the gene-drive, however, the gene-drive contains components that copy itself and any additional adjacent genes, as desired, into the homologous chromosome. Therefore, all of the offspring become homozygous for the gene-drive and the process amplifies with each subsequent generation (Gantz and Bier 2015). Numerous groups are working on developing and/or controlling gene drives with recent success in fruit flies (*Drosophila melanogaster*) (Gantz and Bier 2015) and mosquitos (*A. gambiae*) (Hammond et al. 2016). However, recent excitement about gene-drives has been tempered by the rapid generation of resistance (Champer et al. 2017; Hammond et al. 2016). This may be a difficult challenge to overcome since resistant mutants arise from molecular steps also critical to copying the drive itself. Although any method using genetically engineered organisms will have to overcome public concerns, gene-drives face increased resistance since they may be difficult to control if there are unintended consequences (Lunshof 2015; National Academies of Sciences 2016; Webber et al. 2015).

Utilizing genetically engineered viruses is another promising self-propagating approach. Infecting lab mice with an engineered strain of Cytomegalovirus triggered an auto-immune response causing infertility in females (O'Leary et al. 2008). Similar attempts in rabbits (*Oryctolagus cuniculus*) and red fox (*Vulpes vulpes*) have been unsuccessful (Strive et al. 2007; van Leeuwen and Kerr 2007). These applications, have not been however tested in fish.

Advantages to genetic approaches are that they are far more species-specific than mechanical or chemical methods. Also, they may be used prophylactically by releasing small numbers of engineered fish into bodies of water at risk for invasion. Major challenges remain to the implementation of genetic technologies. Treatments to increase chromosome ploidy for sterile male release don't result in 100% sterility (Normand et al. 2008) and can drastically reduce fitness in some species (Piferrer et al. 2009). Likewise, transgenic traits can result in lowered fitness which hampers the ability of released animals to compete with wild-type for mates (Bongers et al. 1999; Irvin et al. 2004). Sterile male release, daughterless fish, or any other method dependent on a sustained release of fish also faces challenges to scaling production, although a combination of conventional methods to reduce populations (e.g. piscicides) followed by genetic approaches for elimination may mitigate scaling issues (Bax and Thresher 2009). Sterile male release and some daughterless technologies requires efficient separation of males from females, preferably at an early stage to reduce

costs. Nevertheless, genetic technologies in insects have recently completed field trials with impressive results (Carvalho et al. 2015; Harris et al. 2012) and applications in fish may only be a few years behind.

### 3) *Application of viruses*

The use of viruses to control invasive fish or invasive aquatic invertebrates has been considered for the common carp in the Murray-Darling basin in Australia due to lack of other realistic control measures in this large and interconnected system (McColl et al. 2014). Cyprinid herpesvirus-3 (also known as koi herpes virus; KHV) is being considered as a biocontrol agent in Australia because it appears to be specific to common carp (Hedrick et al. 2000) and was shown to cause large carp mortality outbreaks in Europe, Japan and Indonesia (Haenen et al. 2004; Sunarto et al. 2005; Uchii et al. 2009). Viruses were instrumental in facilitating the control of rabbits in Australia (McColl et al. 2014). However, this effort, or similar efforts to control cats on islands, showed that while targeted populations often suffer over 90% mortality immediately after virus release, they often gain resistance in 2–3 generations. Thus, use of viruses to control rabbit populations needs to be augmented by alternative strategies, including physical removal (Saunders et al. 2010). The use of viruses to control invasive fish or invertebrates might be different than the use of viruses in mammals. First, ectothermic immune response is temperature dependent (Wright and Cooper 1981). For example, common carp can effectively produce primary antibodies only at temperatures above 12 °C. Second, in fish, unlike in mammals, there is no transfer of immunoglobulins from the mother to the offspring making the fry more susceptible to the virus. Regardless, while adults may become resistant to the virus, early life stages might remain susceptible, which suggests that the virus could be used to control recruitment in invasive fish. Due to viral resistance, use of viruses, such as KHV in Australia, would be most effective within a broader framework of integrated pest management strategies, especially if combined with recombinant genetic approaches, such as “daughterless” carp and targeted physical removal (McColl et al. 2014).

### 4) *Application of traditional methods like physical removal*

While new forms of biocontrol are being invented and applied with increased frequency, physical removal (biocontrol by humans) remains to be a prominent element of many control strategies for aquatic invasive species (Mueller 2005). For example, commercial fishing is used in an attempt to manage the silver carp and bighead carp in the Illinois River (Tsehaye et al. 2013), while the Pacific lionfish (*Pterois* spp.) are harvested by divers with spear guns in the Caribbean Sea (de León et al. 2013). It is worth noting, however, that effectiveness and sustainability of these

control efforts remains to be demonstrated. Physical removal has also shown promise in controlling topmouth gudgeon in the United Kingdom (Davies and Britton 2015), and rusty crayfish in the US (Hein et al. 2006), the latter of which was convincingly demonstrated using a whole-lake experiment. However, successful strategies for physical removal highly depend on understanding the biology and behavior of the target species, thus, basic research should become an integral component for control strategies that involve physical removal.

Physical removal is sometimes augmented by the use of telemetry to locate seasonal aggregations of the pest. This strategy, which is often referred to as the Judas techniques (Campbell and Donlan 2005; Parkes et al. 2010), has been instrumental in controlling the common carp in lakes of Midwestern North America (Bajer et al. 2011) and in Tasmania (Donkers et al. 2012; Diggle et al. 2012). Bajer et al. 2011 reported that using the Judas technique allowed for highly efficient removal schemes for the common carp in small lakes in Minnesota, USA, where up to 94% of individuals within those lakes were removed in only one or two winter seines. Similar percentage of removal was also reported by Diggle et al. 2012 for the lakes in Tasmania. Molecular methods like measurements of DNA released by the fish (eDNA technique) can be integrated with the Judas method to confirm the presence and abundance of the target species in the induced aggregations (Eichmiller et al. 2014). Physical removal is sometimes augmented by the use of pheromones to lure aquatic pests into traps. Most notably, this strategy has been developed for the sea lamprey in the Great Lakes where migrating ovulated females are lured into traps by releasing a synthetic version of the male sex pheromone at the entrance to the trap (Johnson et al. 2009). Species-specific food attractants have also showed promise in inducing large aggregations of common carp in lakes (Bajer et al. 2010, Ghosal et al. 2018). These aggregations could be targeted for removal.

Below, we present three case studies that illustrate the successes and challenges associated with biocontrol of free ranging populations of invasive fish and invertebrates in freshwater systems of temperate North America.

### **Case studies demonstrating successful biocontrol of invasive fish and invasive aquatic invertebrates**

#### *Study 1: Common carp biocontrol in central Minnesota lakes*

Native to Eurasia, common carp (or “carp”) have been introduced to all continents except Antarctica and are considered to be one of the world’s most invasive fish (Vilizzi et al. 2015). This species is especially widespread and abundant in North America and Australia where its biomass commonly exceeds 400 kg/ha (Matsuzaki et al. 2009; Weber and Brown 2009). Carp feed primarily in benthic sediments and uproot aquatic vegetation,



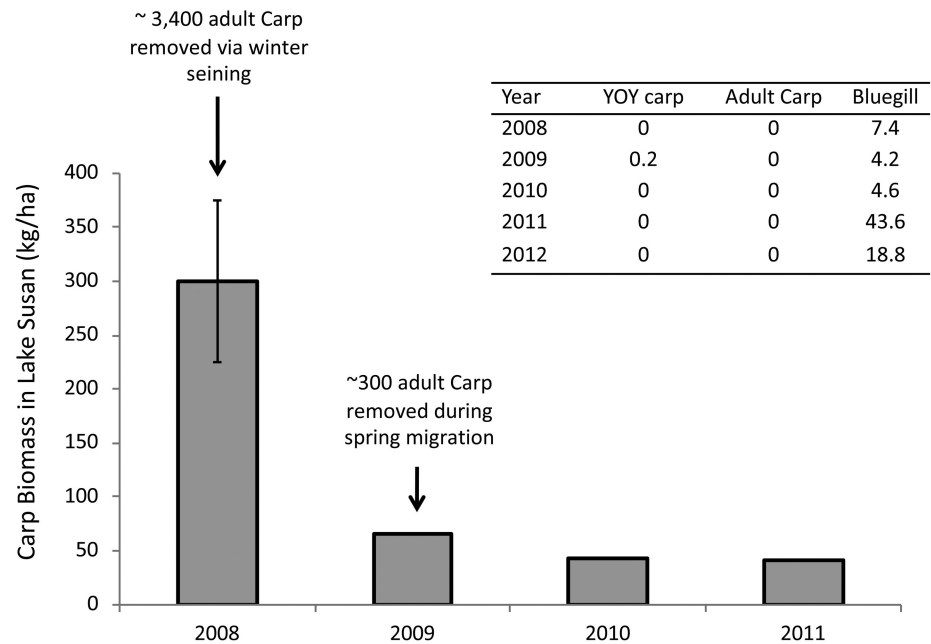


**Figure 1.** Left: common carp (*Cyprinus carpio*) spawning in a shallow vegetated area of Lake Keller, Minnesota, USA, Photo credit: Carrie Magnuson, Ramsey Washington Metro watershed District. Right: bluegill (*Lepomis macrochirus*), an abundant predator on common carp eggs and larvae in Minnesota, USA. Photo credit: Gretchen Hansen.

increase turbidity, and increase transport of nutrients from the sediments into the water column (Zambrano et al. 2001; Bajer et al. 2009; Vilizzi et al. 2015). If excessively abundant (> 100 kg/ha), carp can “flip” shallow lakes from a clear water state with submerged aquatic vegetation into turbid systems that lack aquatic vegetation and are dominated by algae (Bajer et al. 2009). This leads to reduced numbers of waterfowl (Haas et al. 2007), amphibians (often through predation on tadpoles), insects, and possibly also fish (Jackson et al. 2010; Kloskowski 2011).

Carp are large (typically 40–80 cm in length), fecund (up to 3 million eggs), long-lived (commonly > 20 years old), and mobile. They are known for their spawning migrations that can span tens of kilometers (Jones and Stuart 2009). Spawning usually occurs in shallow, ephemeral areas that are sheltered, productive and have few predators. In their native range, carp migrate out of large lowland rivers into seasonally flooded meadows and marshes to spawn (Balon 1995). In non-native regions of temperate North America (Minnesota), carp often migrate from lakes into adjacent shallow marshes (Bajer et al. 2012). Carp spawn in relatively synchronized events, which might function to swamp predators, over a period of several days in mid- to late spring (Figure 1). Because of rapid growth of carp larvae (Phelps et al. 2008), biocontrol through predation is believed to be most effective at the egg and larval stage (Bajer et al. 2012; Silbernagel and Sorensen 2013). Carp do not employ parental care strategies to protect their eggs or larvae.

Carp recruitment dynamics in lakes of central Minnesota suggested that predation may play a role in controlling carp. In those systems, common carp were unable to recruit in most lakes due to high predation on carp eggs and larvae by native fishes, primarily bluegill (Figure 1) (Bajer and Sorensen 2010; Bajer et al. 2012; Silbernagel and Sorensen 2013; Bajer et al. 2015). Carp were able to recruit only in adjacent marshes that winterkilled and lacked bluegills and most other native predators (Bajer and Sorensen



**Figure 2.** Successful control of common carp in Lake Susan in central Minnesota. Approximately 80% of adults were removed in winter 2008/09 using winter seining guided by telemetry to locate carp aggregations. Additional 300 adults were removed the following spring during their spawning migration from the lake to an adjacent marsh (the stream was blocked with a temporary barrier to facilitate removal). Insert table shows mean catch rates of young-of-year and adult carp and bluegills (biocontrol agent) in Lake Susan. Lack of significant carp recruitment, despite plentiful spawning substrate and intense spawning activity by the remaining adults, is attributable to native fish predation on carp eggs and larvae. Data from Bajer and Sorensen (2015).

2010). This spatially complex life cycle suggested that restricting access to winterkill-prone marshes by adult carp would curb carp recruitment. In addition, efforts were also made to better understand and exploit social behaviors of adult carp in lakes to affect control through physical removal. Because adult carp form tight wintertime aggregations, up to 90% can also be removed from small lakes using targeted winter seining (Bajer et al. 2011). Prolonged baiting can be used to condition the carp to aggregate in small areas of lakes during summers creating additional opportunities for large-scale, selective removal (Bajer et al. 2010).

A proof of concept experimental control of common carp population that combined predation with physical removal was conducted in Lake Susan, a small eutrophic lake in central Minnesota (lake area = 35.1 ha; max depth = 5.1 m). In 2007, the lake was inhabited by over 4,100 carp whose biomass exceeded 300 kg/ha (Bajer and Sorensen 2015); approximately 3-times over a threshold that causes damage to lake ecology (Bajer et al. 2009). In March of 2009, ~ 80% of the carp population was removed from Lake Susan using winter seining after an aggregation of carp was located under the ice using telemetry (Figure 2). Also, in April 2009 a temporary carp barrier was placed in the stream that connected Lake Susan with a winterkill-prone marsh to curb carp spawning migrations and recruitment (Chizinski et al. 2016). Adults (~ 300) attempting to migrate to the marsh to

spawn were captured and removed in 2010. Overall, carp abundance was reduced from ~ 4,100 carp in 2008 to ~ 750 in 2009 and fewer than 400 in 2010 (Figure 2; Bajer and Sorensen 2015). Carp biomass was reduced from 307 to ~ 40 kg/ha (Figure 2; Bajer and Sorensen 2015). Trapnet surveys conducted annually revealed very low rates of carp recruitment within Lake Susan, as only one juvenile was captured over the course of four years following adult removal (Figure 2).

The Lake Susan experiment demonstrated that simple means of physical removal can be used to control common carp populations in systems where the recruitment of this species is limited by native predators and where predator-free habitat patches that comprise key carp nurseries can be isolated using temporary barriers. It also showed that propagule pressure (eggs spawned by adults in Lake Susan) is not always a good predictor of carp recruitment. Despite intense annual spawning activity, there was clear evidence that carp could not produce young in Lake Susan. Thus, thorough understanding of pest life history was key to developing sustainable management schemes that incorporated biocontrol using native predators.

#### *Study 2: Rusty crayfish control in a Northern Wisconsin lake*

Rusty crayfish (*Orconectes rusticus*; Figure 3) are native to streams of the Ohio River basin of the United States (Taylor et al. 1996). Over the past half-century they have been introduced outside of this range primarily via bait-bucket introductions, and spread to lakes and streams throughout the United States and Canada (Capelli and Munjal 1982; Hobbs et al. 1989; Olden et al. 2006). Crayfish prefer cobble substrates that provide refuge from fish predation, particularly during juvenile life stages and during molting (Lorman 1980; Capelli and Magnuson 1983). Mature rusty crayfish mate in late summer or early fall (Hobbs and Jass 1988) and juveniles hatch in the spring. After hatching, juvenile crayfish remain attached to the mother's abdomen for protection for several weeks as they grow and molt. Females are relatively sedentary and remain under cover during this time to avoid predation (Thorp and Covich 2010). Eventually, juvenile crayfish leave the mother and molt several times before maturing in their first or second year (Hobbs and Jass 1988).

The negative ecological impacts of invasive rusty crayfish are well-documented (Lodge et al. 2000). Crayfish are omnivores that interact with multiple food web components simultaneously and therefore their impacts are far-reaching (Momot et al. 1978; Diehl 1995; Dorn and Wojdak 2004). Rusty crayfish compete with native virile crayfish (*Orconectes virilis*) for shelter, thereby increasing predation on native crayfish by native predators (Capelli 1982; Capelli and Munjal 1982; DiDonato and Lodge 1993) leading to reduced densities or even extirpation (Lodge et al. 1986; Olsen et al. 1991). Invasive rusty crayfish act as ecosystem engineers (Crooks 2002) by removing



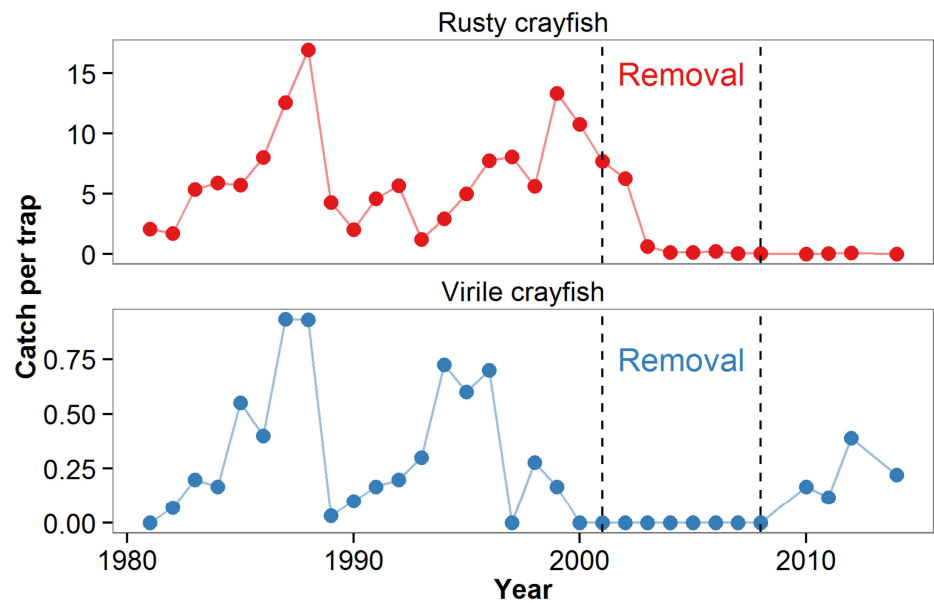


**Figure 3.** Rusty crayfish (*Orconectes rusticus*). Top: female with juveniles attached. Bottom: rusty crayfish obtained from trapping. Photos credit: Gretchen Hansen.

aquatic macrophytes used by other species as a refuge from predation and/or a food source (Magnuson et al. 1975; Crowder and Cooper 1982; Olsen et al. 1991; Lodge et al. 1994; Rosenthal et al. 2006). As a result of their destruction of aquatic plants combined with direct interactions, invasive rusty crayfish reduce the densities of bluegill and pumpkinseed (*Lepomis gibbosus*) (hereafter *Lepomis*) sunfish (Wilson et al. 2004; Roth et al. 2007) and invertebrate populations, particularly snails, (Olsen et al. 1991; Lodge et al. 1994). However, the effects of rusty crayfish on non-snail macroinvertebrates are highly variable across lakes (Wilson et al. 2004; McCarthy et al. 2006; Hansen et al. 2013a), in part due to high variability in the abundance of invasive rusty crayfish (Vander Zanden and Olden 2008; Hansen et al. 2013c).

Although they are capable of achieving extremely high densities, rusty crayfish do not become abundant in all invaded lakes and streams (Hansen et al. 2013c), at least in part due to control by fish predators (Roth et al. 2007; Tetzlaff et al. 2010). Crayfish densities are generally lower in lakes with high densities of *Lepomis* (Wilson et al. 2004; Roth et al. 2007) and rusty crayfish make up a significant portion of the diets of *Lepomis* and other native fishes such as smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) (Hein et al. 2006; Roth et al. 2007; Tetzlaff et al. 2010). Theoretical models of ecosystem dynamics suggest that alternative states govern the abundance of rusty crayfish and their fish predators, mediated by aquatic plant cover and intraguild predation (Roth et al. 2007; Horan et al. 2011; Baldrige and Lodge 2013). Together, these observations led to an experimental project to control rusty crayfish in Sparkling Lake, a 64 ha mesotrophic seepage lake in Vilas County, Wisconsin, USA (46.008°N; 89.701°W).

Control of rusty crayfish in Sparkling Lake was attempted via two primary mechanisms: control of juvenile crayfish by fish predators and the physical removal of adult crayfish through trapping (Hein et al. 2006, 2007; Hansen et al. 2013a). Native predators were augmented by changing fishing regulations in 2001 to reduce angler harvest and increase fish predation on juvenile rusty crayfish (Hein et al. 2006); the length limits of smallmouth bass and walleye (*Sander vitreus*) were increased to 45 cm and 70 cm, respectively, and angler bag limits were decreased to 1 for both species (compared with a statewide bag limit of 5 and length limits of 35 cm and 38 cm, respectively). These regulations were in effect through 2014. Additionally, trapping of adult crayfish occurred from early June through late August in each year from 2001–2008, with 30–313 traps deployed daily (mean = 149) around the perimeter of the lake. All rusty crayfish collected in traps were removed from the lake, and all native virile crayfish were released unharmed. Rusty crayfish catch rates declined by over 99% by 2008 (Hansen et al. 2013a), and rusty crayfish densities remained low even following the cessation of trapping (Figure 4; Hansen et al. 2013a). Native crayfish densities increased concurrently with declines in rusty crayfish densities, and native crayfish densities exceeded those of rusty crayfish from 2010–2014 (Figure 4). The densities of aquatic macrophytes, *Lepomis*, and many aquatic invertebrates also increased as a result of the rusty crayfish control, although some responses were unexpected due to changing interactions between native fish and invertebrates (Hansen et al. 2013a). Both predation by native fishes and trapping of adult crayfish contributed to the collapse of rusty crayfish in Sparkling Lake. In 2003, fish predation removed an estimated 51% of the crayfish population, while trapping removed 4% of the total population (Hein et al. 2006). Fish predation targeted juvenile crayfish, which comprised the majority (91%) of



**Figure 4.** Catch rates (number of crayfish per trap) of invasive rusty crayfish (top) and native virile crayfish (bottom) in Sparkling Lake from 1981–2014. Control via manual removal occurred from 2001–2008, and fish predators were protected from 2001–2014. Data courtesy of the North Temperate Lakes Long Term Ecological Research Program (<https://lter.limnology.wisc.edu/>).

the population, while trapping targeted adult crayfish only. At the same time, trapping removed crayfish with the highest reproductive value and was extremely effective at removing the majority of adult crayfish (over age 2), although these age classes comprised only 3–4% of the total population (Hein et al. 2006). Rusty crayfish in Wisconsin exhibit an apparently linear stock-recruitment relationship (Hansen et al. 2013a), and therefore removing adults via trapping was a necessary component of the control effort. Additionally, the capacity of native fishes to control rusty crayfish abundance appears to be mediated by available habitat, which in Sparkling Lake fluctuates dramatically as a function of variable water levels (Hansen et al. 2013b). Therefore, the efficacy of biocontrol of rusty crayfish in other systems is likely to vary depending on habitat conditions.

Experimental evidence, theoretical models, and cross-lakes comparisons all suggest that biological control of rusty crayfish is possible under certain conditions (Hein et al. 2006, 2007; Roth et al. 2007; Hansen et al. 2013a). The successful control program of rusty crayfish in Sparkling Lake led to dramatic recovery of ecosystem function, including increased density of aquatic plants, *Lepomis* spp., snails, and native crayfish (Hansen et al. 2013a). The effort required to trap at the necessary intensity was substantial. Traps were emptied and re-set daily, and this level of effort may be difficult to replicate in larger systems. Furthermore, the success of this effort appeared to be linked to the available habitat for rusty crayfish (Hansen et al. 2013b). The widespread applicability of biocontrol of rusty crayfish requires further testing in different systems with a variety of habitat types.





**Figure 5.** Round goby (*Neogobius melanostomus*). Photo credit: Matthew Kornis.

### *Study 3: Round goby control by piscivores in the Great Lakes region*

The round goby (*Neogobius melanostomus*; Figure 5) is a small (~ 20 cm) benthic fish native to the Ponto-Caspian region that was introduced via ballast waters of international shipping vessels to transoceanic shipping centers in the Laurentian Great Lakes, the Baltic Sea, and numerous European rivers (Hensler and Jude 2007; Hayden and Miner 2009; Kornis et al. 2012). Following initial introductions in early 1990s, round gobies rapidly spread within each invaded system through natural dispersal, commercial shipping, and accidental bait-bucket releases. In North America, round gobies are in the midst of a secondary invasion into Great Lakes' tributaries (Kornis and Vander Zanden 2010; Poos et al. 2010; Campbell and Tiegs 2012), finger lakes in upstate New York, the Flint and Shiawassee Rivers in Michigan, and the Susquehanna River (U.S. Geological Survey Nonindigenous Aquatic Species Database).

Round gobies can have a multitude of negative effects on invaded ecosystems. Direct effects include diminishing invertebrate populations through predation (Lederer et al. 2008), reducing the abundance of native bottom-oriented fish as a result of competition for food and habitat (Janssen and Jude 2001; Lauer et al. 2004; Balshine et al. 2005; Bergstrom and Mensinger 2009), and consumption of the eggs and larvae of fish species with benthic eggs, including smallmouth bass (Steinhart et al. 2004a), walleye (Roseman et al. 2006), lake trout *Salvelinus namaycush* (Chotkowski and Marsden 1999; Fitzsimons et al. 2009a, b), and lake sturgeon (*Acer fulvescens*) (Nichols et al. 2003). As co-evolved predators of

invasive *Dreissenid* mussels that are associated with a heavy contaminant burden and which occur in habitats appropriate for botulism (*Clostridium botulinum*), round gobies can amplify bioaccumulation of toxic contaminants (Kwon et al. 2006; Hogan et al. 2007; Ng et al. 2008; Ng and Gray 2009; Azim et al. 2011) and increase the incidence of avian botulism (Yule et al. 2006a, b, c; Hannett et al. 2011). Ecological impacts appear to be much lower in river systems than in lakes (Kornis et al. 2013; Janáč et al. 2018). In rivers, round goby densities may be kept low by reduced availability of preferred *Dreissenid* forage and a density-dependent dispersal mechanism (Kornis et al. 2014).

Round gobies employ life history strategies typical of small fish with relatively complex parental care strategies. Round gobies spawn multiple times a year, from April through September, on the underside of overhanging hard substrate, providing excellent refuge against predators (Charlebois et al. 1997; Meunier et al. 2009). The eggs are relatively large (3.2 mm diameter on average) but not very numerous; a single female produces between 100 and 1400 eggs (Kovtun 1978; MacInnis and Corkum 2000). Male round gobies aggressively defend the nests against intruders, including piscivores (Wickett and Corkum 1998), and provide a high level of parental care through frequent inspection of eggs and by ventilating the nest using sweeping fin motions (Meunier et al. 2009). Eggs hatch rates often exceed 90% (Charlebois et al. 1997). Little is known about the behavior of the larvae of round gobies, except that in lentic environments, round goby larvae are nocturnally pelagic, exhibiting diel vertical migration to prey on zooplankton (Hensler and Jude 2007; Hayden and Miner 2009). It is not known if this behavior functions to avoid predators, as seen in zooplankton (Zaret and Suffern 1976; Bollens et al. 1992; Loose and Dawidowicz 1994). Juvenile round gobies might be especially vulnerable to predation because they are often displaced by the adults out of the preferred rocky substrates to sub-optimal soft substrates where they cannot easily find shelter (Charlebois et al. 1997; Ray and Corkum 2001; Belanger and Corkum 2003). Adults are also vulnerable to predators due to their small size, especially where shelter is difficult to find outside rocky habitats.

Round gobies are likely too abundant and widespread in large systems such as the Laurentian Great Lakes for eradication to be an attainable management goal (Kornis et al. 2012). Management efforts targeting round gobies have typically focused on prevention or early detection/rapid response. For example, an electric barrier was constructed in the Chicago Sanitary and Ship Canal in part to prevent the spread of round goby into the connected waters of the Mississippi River catchment (Steingraeber and Thiel 2000), and the effort would have likely succeeded if round gobies had not crossed the barrier prior to its activation. Rotenone and other piscicides have also occasionally been used in attempts to eradicate recently

detected round goby populations, although with limited success (Corkum et al. 2008; Schreier et al. 2008). Regulations aimed at reducing aquatic invasive species in general, such as requiring mid-ocean ballast water exchange from vessels entering the Great Lakes (Costello et al. 2007) or state or provincial regulations on use of bait for angling, also curtail future round goby introductions. Pheromones have potential for selectively trapping and controlling round gobies, but have not been field tested (Corkum et al. 2008) and would likely require a high level of sustained effort as observed in examples of successful control of other aquatic invasive species via trapping (Hein et al. 2006, 2007).

Although eradication of round gobies appears unlikely, natural control of round gobies through predation is prominent in many locations throughout introduced round goby populations in North America and Europe. Predators with especially heavy reliance on round gobies include Burbot (Johnson et al. 2005; Hensler et al. 2008), lake trout (Happel et al. 2018), yellow perch and European perch (*Perca flavescens* and *P. fluviatilis*) (Johnson et al. 2005; Truemper et al. 2006; Almqvist et al. 2010), smallmouth bass (Steinhart et al. 2004b; Johnson et al. 2005), cod (*Gadus morhua*) (Almqvist et al. 2010), lake whitefish (*Coregonus clupeaformis*) (Pothoven and Madenjian 2013; Lehrer-Brey and Kornis 2013) and several bird species (Bzoma 1998; Jakubas 2004; Johnson et al. 2010).

Several studies on the abundance and population dynamics of the round goby in the Laurentian Great Lakes can be synthesized in a case study of native predators controlling an invasive fish in large ecosystems. For example, Madenjian et al. (2011) notes that round goby abundance in Lake Erie increased dramatically during 1999 – 2004, but declined from 2004–2008, coinciding with round gobies being observed in burbot diet. Bioenergetics models estimated that adult burbot in eastern Lake Erie annually consumed 1361 metric tons of round goby, equal to 61% of the estimated round goby standing stock, strongly suggesting burbot had high potential to exert predatory control on round goby (Madenjian et al. 2011). Additionally, annual round goby mortality was estimated to be 79 to 84% in three areas of Lake Michigan, suggesting round goby populations may be under predatory control from a suite of piscivorous species (Huo et al. 2014). Time series of round goby density and biomass in Lakes Michigan, Huron, Erie and Ontario all show high variability, but fit a similar pattern of declining density/biomass in recent years, and may be approaching equilibrium levels in all four lakes due to predatory control by piscivores (Bunnell et al. 2015; Gorman and Weidel 2015; Roseman et al. 2015). Patterns of round goby abundance in the Great Lakes fit with observations from an increasing number of biological invasions where contraction of introduced population sizes follows an initial phase of population growth and spread (Simberloff and Gibbons 2004; Blackburn et al. 2011). Evidence

of predatory control of round goby extends into invaded streams as well (secondary invasions). Hempel et al. (2016) found a negative correlation between round goby abundance and that of a predator, zander (*Sander lucioperca*), in European brackish waters and concluded biological control of round goby abundance was likely occurring in areas of high predator abundance.

### *Synthesis of case studies*

The case studies included in this paper represent examples where native predatory fish play an important role in controlling invasive fish or aquatic invertebrates. In two cases (common carp and rusty crayfish) predatory control in combination with targeted removal (biocontrol by humans) resulted in control of the pest species allowing ecosystem services to recover. This is significant because control of invasive fish or aquatic invertebrates in natural systems using approaches other than system-wide poisoning or dewatering has been rare. Case studies presented here are also different than the control of sea lamprey, which is mainly based on toxin application (but see Twohey et al. 2003; Johnson et al. 2009).

The common carp and rusty crayfish studies have several commonalities. In both cases, predation targeted juvenile stages, while removal targeted the adults. In this way, multiple life stages were targeted to curb recruitment while increasing mortality of adults. In both cases, most common native fish (*Lepomis*) was the predator. Both were conducted in relatively isolated systems (lakes) that at least in one case were separated from other bodies of water using natural and artificial physical barriers (the carp study). Both the examples of carp and crayfish were rooted in a relatively thorough understanding of the life history of the pest within the geographic area. For example, for the carp, it was shown that this species thrived by employing spawning migrations to adjacent marshes that winterkilled and lacked bluegills. In case of the crayfish, it was shown that juveniles are susceptible to predation by *Lepomis*, except when they can find refuge. Both studies were preceded by several years of basic research. Notable differences include the fact that to affect physical removal, seasonal aggregations were targeted for carp, while the crayfish were removed by trapping throughout. The sustainability of carp and crayfish control remains to be seen. In both cases, it will largely depend on the ability to curb the recruitment.

The case study of the round goby is different in many significant ways. Most notably, it represents perhaps the best documented example (diet studies, bioenergetics) where a community of native predatory fish heavily utilized the pest species in their diets, which appeared to have resulted in a large-scale suppression of the pest. The predators targeted multiple life stages of the pest, including adult individuals, unlike in the case of carp or

rusty crayfish where predators controlled early life stages. Also, unlike the case study of carp and crayfish, the biocontrol of round goby occurred in a very large ecosystem, without any human intervention (e.g. no barriers, size limits etc.). The example of round goby in the Great Lakes shows that, at least in some cases, abundant and diverse populations of native predatory fish might be important for controlling the pest, which has implications for native fish conservation.

## Conclusions

Biocontrol of invasive fish and aquatic invertebrates remains rudimentary with only a few examples of success. It is still based primarily on physical removal by humans and predation by native species. Social behaviors or cognitive abilities are being exploited to increase efficacy of physical removal including the use of food, pheromones or other gustatory or olfactory cues to condition some pest to form aggregations or lure them into traps. Because physical removal strategies are becoming more sophisticated and more grounded within the pests' life history and population dynamics, physical removal should be considered a form of biocontrol by humans to distinguish it from more haphazard removal efforts. Invasivory, or harvest of pests for human consumption, is also increasing especially in the case of invasive fish. New approaches are on the horizon. For example, toxin that can be specifically delivered to common carp with food pellets might be only few years away (Poole et al. 2018). Genetic technologies are most advanced in case of the common carp and focus on sex-biasing technologies (daughterless, female lethality), but have not yet advanced to testing laboratory populations. Plans also exist to release pathogens to control common carp in Australia. Next decade is likely to bring several of these new technologies to a stage where they could be applied. Social, ethical and biological concerns will need to be weighed to allow the use of these technologies. Meanwhile, we urge scientists (and funding sources) to devote more attention to basic studies of the life history of the pests. Invasive species are invasive only in a fraction of locales to which they are introduced, meaning that natural processes regulate their abundance at most sites. It would be very valuable to understand what these limitations are and exploit them to design integrated pest management strategies based on natural processes.

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