OPTIMAL FORAGING OF THREE PREDATORY FISHES ON RED SWAMP CRAYFISH (PROCAMBARUS CLARKII)

By

Samantha DeAnne Strandmark

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ABSTRACT

Invasive species have detrimental effects on ecosystems around the world and are a driving factor behind the loss of biodiversity. Once established, many populations of invasive species are difficult to control or eradicate. Red Swamp Crayfish (*Procambarus clarkii*) is an extremely prolific invasive species that is established in more than 100 countries worldwide and is demonstrated to have negative effects on native ecosystems. Management of Red Swamp Crayfish is difficult and likely requires multiple approaches including biological control by fishes. However, little research exists to inform managers on which biological control agents are likely to be effective. Herein, I describe a foraging experiment to evaluate the predatory capacity of Largemouth Bass, Green Sunfish, and Bluegill Sunfish on Red Swamp Crayfish, all of which are likely biological control candidates. I used an optimal foraging framework to develop cost/benefit ratios based on crayfish size to determine the optimal range of crayfish sizes consumed by each predator species. I measured orientation, pursuit, and handling time to develop optimal foraging curves, while recording consumption of crayfish based on size, sex, and reproductive form. My results indicated that the optimal sizes of crayfish were 12-15mm CL for Bluegill, 17-22mm CL for Green Sunfish, and 20-40mm for Largemouth Bass. These results indicate that managers should consider supplementing existing predator populations with both Lepomis species and Largemouth Bass to ensure a broad range of crayfish are consumed.

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Invasive species are one of the primary factors behind the world's biodiversity loss (Clavero and Garcia-Berthou 2005), and are a prominent issue for management and freshwater conservation (Sala et al. 2000; Blackburn et al. 2014). Invasive species can damage human infrastructure (Galil and Zenetos 2002), and management of invasive species costs the US an estimated $128 billion annually (Pimentel et al. 2005). Freshwater ecosystems are particularly vulnerable to invasions. Invasive species in freshwater ecosystems possess a higher innate ability to disperse compared to those in terrestrial habitats (Sala et al. 2000; Gherardi 2007). While many invasive species can influence aquatic habitats, crayfish are commonly considered a keystone species (Momot et al. 1978; Hill and Lodge 1994) that can dramatically affect ecosystem structure and function.

Crayfish are critical organisms in many freshwater ecosystems. There are over 600 species of crayfish found worldwide with about 75% of species residing in North America (Lodge et al. 2000). Crayfish are some of the largest and longest-lived freshwater invertebrates and tend to live in higher densities than other freshwater invertebrate species (Lodge et al. 2000; Gherardi 2007). Crayfish are omnivores and consume diverse taxa including benthic invertebrates, periphyton, detritus, algae and macrophytes (Momot et al. 1978; Nyström et al. 1996; Whitledge and Rabeni 1997). Crayfish are also consumed by many fish species (Roell and Orth 1993; Blake and Hart 1995).

Crayfish are an essential part of freshwater ecosystems, and their introduction or removal from established habitats can affect ecosystem properties and function. Crayfish invasions can lead to drastic changes in recipient freshwater ecosystems (Holdich 1999; Lodge et al. 2000;

Rodríguez et al. 2005), and are demonstrated to have negative impacts on a number of abiotic and biotic properties. Invasive crayfish are a leading contributor to the loss of indigenous crayfish species (Hill and Lodge 1999; Holdich 1999), and can also can significantly reduce the biodiversity and biomass of macroinvertebrates (Lodge and Lorman 1987; Nyström and Strand 2003), macrophytes (Lodge and Lorman 1987; Rodríguez et al. 2005), fishes (Horns and Magnuson 1981; Savino and Miller 1991; James et al. 2015), and amphibians (Gamradt and Kats 1996; Gamradt et al. 1997; Cruz et al. 2008; Francesco Ficetola et al. 2011; Kats et al. 2013). Invasive crayfishes are also demonstrated to reduce water quality and increase erosion (Momot et al. 1978; Momot 1995; Nyström et al. 1996; Nyström and Strand 2003; McCarthy et al. 2006). Although several species of crayfish are successful at initial stages of invasion and subsequent dispersal (Kolar and Lodge 2001), certain species represent a greater risk than others. The Red Swamp Crayfish, *Procambarus clarkii*, is one such species.

BIOLOGY AND ECOLOGY OF RED SWAMP CRAYFISH

Red Swamp Crayfish are native to the Southern U.S and northeastern Mexico (Hobbs et al. 1989; Gherardi et al. 2002), yet account for over 40% of worldwide introductions of invasive crayfishes (Gherardi 2006). This species can tolerate a broad range of abiotic conditions including nutrient-rich ponds, lakes, and other waterbodies with low dissolved oxygen such as marshlands and rice paddies (Gherardi et al. 2000; Nyström 2002).

Red Swamp Crayfish possess a suite of biological and behavioral traits that allow them to establish invasive populations in new environments. Biological traits include rapid growth rates, early maturity, and high fecundity (Huner and Barr 1991; Barbaresi and Gherardi 2000; Gherardi 2006; Gherardi et al. 2011). For example, Red Swamp Crayfish can reach maturity in 18 months or less and produce between 325 and 600 eggs, depending on size (Huner and Barr 1984; Oluoch

1990; Payne 1996). High fecundity can aid Red Swamp Crayfish establishment by reducing the probability of population extirpation through environmental stochasticity or Allee effects (Sakai et al. 2001; Larson and Olden 2010). According to Huner and Barr (1984) Red Swamp Crayfish prefer to inhabit water with temperatures between 21°C and 30°C, but Peruzza et al. (2015) observed survival and successful reproduction at mean water temperatures as low as 13ºC. Together, rapid population growth paired with broad abiotic tolerances has allowed Red Swamp Crayfish to expand their range to six continents (Oficialdegui et al. 2019). Though biological traits of Red Swamp Crayfish help to establish populations in new locales, their behavioral attributes lead to the displacement of native species and ecosystem modification.

In general, Red Swamp Crayfish are both larger and more aggressive than many native species they encounter. Numerous studies demonstrate that invasive crayfish tend to dominate native species through size-based competitive or agonistic interactions (Butler and Stein 1985; Hill and Lodge 1999; Chucholl et al. 2008). The aggressive behavior displayed by invasive crayfish species such as Red Swamp Crayfish plays a large part in the competitive displacement of native crayfish (Figler et al. 2006). Size-based competition is tied to this behavior (Rabeni 1985; Keller and Moore 2000), with chela size acting as an important determinant of agonistic behavior outcomes in other crayfish species (Bovbjerg 1953; Garvey and Stein 1993). Not surprisingly, invasive Red Swamp Crayfish tend to dominate agonistic interactions with native species, even if no food or shelter resources are present (Gherardi and Astra 2004). In situations where shelter is present but limited, Red Swamp Crayfish are often able to exclude native species through aggression and size-based dominance. Competitive superiority for shelter can lead to rapid expansion of invading Red Swamp Crayfish populations (Figler et al. 2006). Laboratory studies demonstrate that male Red Swamp Crayfish rapidly displace individuals of sympatric *P.*

zonangulus established within shelters and maintain shelter occupation despite removal attempts (Blank and Figler 1996).

The burrowing behavior of the Red Swamp Crayfish is a key factor in its success and subsequent damage to aquatic habitats (Huner 1977). Burrow use increases as temperatures rise (Ilhéu et al. 2003), and high densities of Red Swamp Crayfish burrows can lead to bank erosion or soil collapse (Barbaresi et al. 2004; Arce and Diéguez-Uribeondo 2015). Soil collapse damages aquatic infrastructure such as dykes, rice irrigation structures, and riparian zones (Holdich 1999; Arce and Diéguez-Uribeondo 2015). The use of burrows also provides the ability to seek shelter during otherwise stressful environmental conditions such as drought (Gherardi et al. 2002). There is relatively little understood regarding how to mitigate these impacts, and how to manage this species in invaded systems (Gherardi et al. 2011).

RED SWAMP CRAYFISH IN MICHIGAN

Previous evidence suggests that invasive crayfish (including Red Swamp Crayfish) pose a serious threat to freshwater ecosystems (Lodge et al. 1998; Beisel 2001) and multiple species have the potential to spread throughout suitable habitats found in the Midwest and Laurentian Great Lakes region (Lodge et al. 2000; Pintor et al. 2008; Egly et al. 2019). Although Red Swamp Crayfish is considered a "warmwater" species, they can tolerate winter conditions typical in the Great Lakes region (Vesely et al. 2015), which is evident in established populations in the Chicago Area Waterway System and in Ohio's Sandusky Bay (Peters et al. 2014; O'shaughnessey 2019). The proximity of established populations to Michigan waterways was cause for concern for state managers prior to 2017 when the first populations were discovered in this state.

In 2013, the Michigan DNR received reports of live crayfish used by anglers and purchased as bait from food markets (MDNR 2013). Several Red Swamp Crayfish were also found dead at popular fishing areas around Lake Macatawa in southwest Michigan. A subsequent assessment of over 400 Michigan rivers and streams failed to detect any Red Swamp Crayfish (Smith et al. 2018), but a related risk assessment found potential pathways for Red Swamp Crayfish introductions into Michigan that included the live bait trade, classroom use, aquaculture, and the aquarium trade, all of which are documented sources of Red Swamp Crayfish introductions (Lodge et al. 2012; Drake and Mandrak 2014; Smith 2018). Managers decided to implement strategies to reduce the risk of continued spread of Red Swamp Crayfish in Michigan including an order that prohibits the possession of live Red Swamp Crayfish in the state. Despite these efforts to detect and reduce the risk of possible invasions of Red Swamp Crayfish, the MDNR received reports of live Red Swamp Crayfish at Sunset Lake in southwest Michigan on July 13th, 2017. A separate report several days later from Novi, MI indicated the presence of an infestation in a local retention pond. Subsequent investigation by MDNR staff confirmed the first established populations of Red Swamp Crayfish in Michigan.

To manage the infestation, the MDNR formed a response team to implement and evaluate adaptive management options for early detection, control, and possible eradication of Red Swamp Crayfish. This team consists of the MDNR in collaboration with Michigan State University (MSU), The United States Geological Survey (USGS), and Auburn University (AU). This team is currently investigating the potential of several management strategies which include combinations of trapping, eDNA collection, sound trials, chemical controls and lastly, the purpose of this study: the evaluation of biological control agents for the management of Red Swamp Crayfish.

BIOLOGICAL CONTROL

A broad definition of “biological control” or “biocontrol” is a management strategy that uses organisms to control populations of non-native or pest species, or more precisely, to use parasites, predators, or pathogens, to maintain populations of other organisms below what typically occurs in nature (De Bach 1964; Freeman et al. 2010). There are several ways to implement biological control methods used by managers. One method is "classical” biological control, which uses imported “exotic” natural enemies such as parasitoids, predators, and pathogens to control pest populations such as insects, weeds, and pathogens (Caltagirone 1981). The successes of classical biological control are thoroughly captured in literature over the years. However, there are limitations with this approach. There is a history of scholars that object to the use of exotic control agents, citing non-target species effects and instances where control agents become pests (Kiviat et al. 2019). In a review of trends in introduced insect biological agents within the BIOCAT10 database, Cock et al. (2016) found that out of 6,158 introduction, 36% lead to established populations of introduced agents and 10.1% lead to the successful management of pests. This method is mostly implemented for agri-environmental management, including terrestrial weeds and arthropod pests. (Brodeur et al. 2018)

Other biological control methods focus on the conservation or augmentation of native predators to accomplish population control objectives (Ehler 1998). The introduction or supplementation of native biological control agents can have fewer social constraints and may be viewed as a more acceptable management practice compared to classical control (Olszańska et al. 2016; Brodeur et al. 2017). Public perception is an important consideration for effective invasive species management practices to ensure successful implementation (Fischer and Young 2007). Conservation and/or supplementation of native predator populations into native waterbodies can also pose lower risks to ecosystems that become infested by non-native species and can be used in a variety of waterbodies where other control methods cannot be implemented or have proven to be unsuccessful over time. The implementation of native predators as biological–control agents is also a common tool managers use to mitigate the negative effects of aquatic invasive species (Blake and Hart 1995; Holdich 1999; Frutiger and Müller 2002; Holdich et al. 2017).

The use of native predators to control crayfish has advantages compared to other methods. For decades the primary technique used to manage invasive crayfish populations was trapping efforts, which resulted in various degrees of success (Gherardi et al. 2011; Hansen et al. 2013; Green et al. 2018; De Palma-Dow et al. 2020). Many trap designs are biased towards larger male crayfish (Brown and Brewis 1978; Price and Welch 2009; Larson and Olden 2016), which may reduce the potential for population decline by leaving breeding females in the population. Toxicants may be effective in some situations, but are not be feasible everywhere given the potential for undesired non-target impacts and other social factors (Morolli et al. 2006; Barbee and Stout 2009; Sandodden and Johnsen 2010; Lidova et al. 2019). Additionally, methods such as male sterilization may not be feasible for large waterbodies (Aquiloni et al. 2009), or result in long-term altered sexual behaviors (Johović et al. 2019).

A number of studies suggest that fish predators offer some promise to reduce the size of crayfish populations (Svardson 1972; Westman 1991; Gherardi et al. 2011). For example, Aquiloni et al. (2010) demonstrated that native European eels (*Anguilla rostrata*) are an effective biological control agent for Red Swamp Crayfish in ponds, and Hein et al.(2006) and Hansen et al. (2013) suggest that native predators consumed 51% of invasive rusty crayfish during a control experiment using intensive trapping in a northern Wisconsin lake. Rach and Bills (1989) conclude that Largemouth Bass (*Micropterus salmoides*) predation reduced crayfish populations by 98%, while Tetzlaff et al. (2011) and Roth et al. (2007) provide evidence that high densities of native *Lepomis* can control invasive *F. rusticus* crayfish populations. Although many fishes consume crayfish as part of their diet (Probst et al. 1984; Westman 1991; Garvey et al. 2003), few are likely to be an effective biocontrol agents for Red Swamp Crayfish due to environmental and geographical constraints imposed by invaded systems that limit the pool of viable species. An overview of biological control strategies by Freeman et al. (2010) highlights that fish species suitable for biological control efforts will vary significantly with the habitat type and waterbody conditions, a logical conclusion given inherent differences in abiotic and biotic tolerances among fish species.

In Michigan, the aquatic environments invaded by Red Swamp Crayfish are generally small (<5ha), shallow (<3m deep) ponds in urban and suburban areas. This constrains the selection of effective species for control because predator species are often sensitive to biotic and abiotic conditions that vary across aquatic ecosystems (Howick and O'Brien 1983; Probst et al. 1984). In classical biological control, researchers suggest that effective control agents are those that can become established, have reproductive success, and have high dispersal rates (DeBach and Rosen 1991). However, this suggestion is primarily based on evidence from studies of crop management and the use of introduced insects, predators and pathogens that have specific hosts (Symondson et al. 2002). Characteristics of specialists are not always desired when trying to utilize populations of natural predators. Generalist predators are able to survive on alternative prey species when the target of biological control is reduced (Settle et al. 1996; Blaustein and Chase 2007; Bhattacharjee et al. 2009; Taylor and Snyder 2021). The plasticity of life history and foraging behaviors of Red Swamp Crayfish could warrant consideration of generalist predators as control species. Ideally, a biological control agent should consume large enough quantities of prey to severely reduce population size or consume life stages that maximizes the population's vulnerability to collapse (Musseau et al. 2015), but survive subsequent periods of low target species abundance to ensure the maintenance of high predation pressure. Candidate species should also be easy to implement, manage, and monitor while minimizing non-target impacts in infested waterbodies. *Lepomis spp.* (Werner and Mittelbach 1981) and Largemouth Bass (Rach and Bills 1989), are generalist predators that readily switch prey species based on prey abundance, predation risk, habitat and life stage of fish (Mullan and Applegate 1970; Hodgson and Kitchell 1987; Rabeni 1992; Hickley et al. 1994; Schindler et al. 1997; Taylor et al. 2007). Further, multiple *Lepomis* species (e.g. Bluegill (*L. macrochirus*) and Green Sunfish (*L. cyanellus*)) and Largemouth Bass are both native and common in Michigan, thus maximizing the ability to easily implement predator augmentation in invaded ponds. However, while much is known regarding the foraging patterns of these species more generally (Lewis and Helms 1964; Mullan and Applegate 1970; Werner 1974; Werner and Hall 1974; Mittelbach 1981; Ringler 1983; Hodgson and Kitchell 1987; Ehlinger 1989; Hickley et al. 1994), less is known regarding how these species forage on crayfish specifically.

Fishes are size-selective predators, and size selection can vary between fish species. Predator mouth morphology, placement, and gape act to limit the type and size of prey fish can consume. There are several other factors can influence what prey predator select, such as prey aggression, which can alter prey choice and reduce the maximum size of prey consumed by predators (Crowl 1989). Fish seek to forage optimally, and alter prey selection based on species, size, and life stage in addition to prey abundance (Stein 1977; Werner and Hall 1988). Similar rules apply to fish selection for crayfish (Stein 1977). Fish species vary in their consumption of crayfish (Pintor et al. 2008), where smaller and less aggressive crayfish are consumed more readily than larger individuals. At a species level this propensity has implications for invasions where less aggressive and smaller crayfish species are consumed disproportionately to their abundance (DiDonato and Lodge 1993; Lodge 1993; Roth and Kitchell 2005). Together with constraints that limit the pool of predatory species available for biological control, logic indicates that predator introduction or supplementation would best be served by native predator species that are documented to consume crayfish and are already found in areas proximal to, and that can thrive in, abiotic conditions where Red Swamp Crayfish are established.

The ability to predict outcomes of interactions between crayfish and predators can help identify species that are more likely to be effective biological control agents of Red Swamp Crayfish in Michigan. The evaluation of candidate biological control agents prior to large-scale conservation or supplementation can ensure a higher probability of successful control and avoid failed efforts that could leave Red Swamp Crayfish populations unregulated. One theoretical framework that could be used to evaluate the effectiveness of candidate biological control agents is optimal foraging theory.

The development of optimal foraging theory originated with Emlen (1966) and MacArthur and Pianka (1966), and is based on the study of feeding behaviors and food preference of predators. Optimal foraging theory suggests that animals attempt to maximize energy gain of prey they consume relative to the costs incurred while foraging. The theory is used in ways that hypothesize animal foraging behaviors by means of mathematical models (i.e., optimal foraging models). These models are often measured by choosing a “currency” (Schoener 1971), variables that a predator should maximize or minimize. Cost/benefit models are a derivation of optimal foraging and are commonly used to reflect variables associated with foraging. Within this framework, the costs (i.e., variables) associated with these models are often the time spent foraging for optimal prey, including the time to search, pursue, handle, and consume prey. Benefits are the energy intake from prey, which can be measured in calories or joules, or simply prey weight for comparisons within a single or similar prey species. The quantification of these variables in the context of cost/benefits model can then be used to predict the breadth of diets that animals prefer to consume. The determination of these variables is heavily researched in relation to the optimal foraging theory and cost/benefit analysis (Emlen 1966; MacArthur and Pianka 1966; Werner 1974; Stein 1977; Griffiths 1980; Mittelbach 1983). For example, Stein (1977) evaluated size selective foraging by Smallmouth Bass (*Micropterus dolomieu*) on Northern Clearwater Crayfish (*Faxonius propinquus),* calculating the cost/benefit ratio using pursuit and handling as costs, and the consumed crayfish mass as the benefit. Werner (1974) created cost/benefit curves to not only determine the optimal prey size for different size and species of predators, but also to compare diet breadths among bluegill and other predator species. Both studies reflect that prey with minimal handling time to mass ratios should be consumed first and then in increasing order of the cost/benefit ratio (Stein et al. 1984; Hodgson and Kitchell 1987). Therefore, the development of optimal foraging (cost/benefit) curves for candidate biocontrol species represents a useful framework to evaluate and compare their relative effectiveness in controlling various sizes of Red Swamp Crayfish.

There is an ongoing need to explore and quantify the effectiveness of fish predators as control agents for Red Swamp Crayfish. While the studies and theories mentioned above provide key insights for invasive species management and fish foraging, information on the foraging behaviors of fish predators consuming Red Swamp Crayfish is lacking. This study aims to evaluate the potential of three fish species native to invaded waterbodies to act as biological control of Red Swamp Crayfish: Largemouth Bass, Bluegill and Green Sunfish hybrids. These three species are logical candidates for biological control of Red Swamp Crayfish for several reasons aligned with goals of biological control outlined above: 1) all are found proximal to invaded sites, 2) all can thrive in abiotic conditions where Red Swamp Crayfish are established, and 3) all are demonstrated to consume crayfish. I use cost/benefit ratio calculations similar to Stein (1977) and Werner (1974), ultimately creating cost/benefit (optimal foraging) curves to quantify the predatory capacity of each predator species to consume Red Swamp Crayfish. I use an experimental framework to address four questions: 1) Does predator species affect size-specific handling time of crayfish? 2) Does crayfish sex affect the handling time of predators? 3) What crayfish sizes might we expect each predator species to consume? and 4) Do predators differ in size-specific consumption rate across species? To answer these questions, I conducted laboratory feeding experiments where I analyzed the number, size, weight, and sex of Red Swamp Crayfish consumed by these candidate species. Results of this study will help guide recommendations for predator augmentation and conservation in locations where Red Swamp Crayfish are already established, and other methods of control cannot be used.

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CHAPTER 2: LABORATORY EVALUATION OF SIZE-BASED OPTIMAL FORAGING BY THREE FISH PREDATORS ON RED SWAMP CRAYFISH (*PROCAMBARUS CLARKII*)

INTRODUCTION

Invasive species are a global issue with adverse effects documented worldwide (Dueñas et al. 2018). Invasive species can significantly alter ecosystems and can lead to significant environmental damage and economic losses amounting to billions of dollars annually (Pimentel et al. 2005). The introduction of non-native species is also a primary cause of global decline in biodiversity (Sala et al. 2000; Rodríguez et al. 2005). Freshwater ecosystems are particularly vulnerable to invasions due to the interconnectivity of inland waters and their frequent use by humans for commerce and recreation (Rodríguez et al. 2005; Gherardi 2007; Gherardi 2010). Crayfish invasions in particular are notorious for their negative impacts on recipient ecosystems, including on aquatic biodiversity (Hobbs et al. 1989; Taylor et al. 1996; Lodge et al. 2012). There are over 640 species of freshwater crayfish worldwide (Crandall and Buhay 2008), but few pose significant threats to freshwater habitats through invasions. One such species is the Red Swamp Crayfish (*Procambarus clarkii*), which is the most widely distributed crayfish worldwide (Lodge et al. 2012; Oficialdegui et al. 2020).

The adverse effects of Red Swamp Crayfish on ecosystem functions are due to the combination of their large size, foraging habits, and the ability to attain high abundances. Red Swamp Crayfish exhibit many classic characteristics of successful invasive species (Simberloff and Stiling 1996; Kolar and Lodge 2001), including high fecundity, rapid growth, fast maturity, emigratory behavior, and transport by humans through commercial trade (Larson and Olden 2010; Lodge et al. 2012; Souty-Grosset et al. 2016; Thomas et al. 2019). Introductions of Red Swamp Crayfish outside of their native range have led to documented negative effects on freshwater biodiversity, including fish, amphibians (i.e. consumption of eggs), macroinvertebrates, macrophytes, and other crayfish species (Gamradt and Kats 1996; Rodríguez et al. 2005; Francesco Ficetola et al. 2011; Reynolds 2011). The foraging and burrowing behavior of Red Swamp Crayfish can lead to erosion of the littoral and riparian zone, and have direct and indirect effects on benthic food webs and nutrient cycling (Angeler et al. 2001). Red Swamp Crayfish burrowing behavior can also damage human infrastructure and managed wetlands (Souty-Grosset et al. 2014; Arce and Diéguez-Uribeondo 2015; Faller et al. 2016). For example, Red Swamp Crayfish burrows account for 30% of documented damage to irrigation canals in Italy (Souty-Grosset et al. 2016).

Management of invasive crayfish can be challenging. Red Swamp Crayfish in particular are common in the aquaculture and aquarium trade, resulting in global movements (Lodge et al. 2000; Oficialdegui et al. 2019; Oficialdegui et al. 2020). Management through legislative regulation can reduce the risk of introductions, though restricting possession conflicts with stakeholder interests including the aquarium and live food market trades (Manfrin et al. 2019). Prohibitions on possession or import are likely effective to reduce the probability of new introductions (Hulme 2006), but Red Swamp Crayfish are already established in over 100 countries (Oficialdegui et al. 2019). For more established populations, there is an urgent need for effective control methodologies to control or eradicate *P clarkii* infestations (Hulme 2006).

Several methods can be implemented for the management of invasive crayfish. The most common methods fall under three categories: mechanical (e.g. manual removal, netting, trapping), physical (i.e., habitat destruction, drainage), and use of chemicals and pathogens (Hein et al. 2007; Gherardi et al. 2011; Holdich et al. 2017). However, these methods may not be desirable or feasible for areas infested with Red Swamp Crayfish. The introduction of toxicants or pathogens is often not desirable or feasible due to potential negative impacts on non-target species and negative perceptions by the public (Laurent 1995; Roqueplo et al. 1995). Physical removal or habitat alteration requires extensive effort that may be too expensive or deemed socially intractable (Holdich and Reeve 1991)). Trapping alone may suppress populations temporarily, but long-term population control is likely to require additional sources of crayfish mortality (Bills and Marking 1988; Hansen et al. 2013; Holdich et al. 2017). Trapping combined with increased fish predation may be a more effective means to achieve long-term suppression (Rach and Bills 1989; Hein et al. 2006). Some evidence exists that predatory fishes can reduce the abundance of invasive crayfish species, including Red Swamp Crayfish (Neveu 2001; Aquiloni et al. 2010). Thus, fish as biological control is one potential option to maintain Red Swamp Crayfish at low population abundances.

Although various species have the potential to be effective biological control agents for Red Swamp Crayfish (Westman 1991), native predatory fishes are worth further investigation to avoid potential unintended consequences of introducing a non-native species into a novel ecosystem (Elvira et al. 1996; Hein et al. 2006; Hein et al. 2007; Tetzlaff et al. 2011; Tyser and Douthwaite 2014). Rigorous evaluation will maximize the chance of success and minimize adverse outcomes such as failed introductions of biocontrol species and unsuccessful control (Messing and Wright 2006). Aquarium studies of predator-prey interactions are commonly used to gather valuable information on the capacity of a predator to consume target species prior to introducing biocontrol agents (Su Sin 2006). Therefore, research on interactions between invasive crayfish and native predators is important to develop a successful strategy for reducing Red Swamp Crayfish populations through biological control.

Optimal foraging theory represents a useful framework to evaluate the capacity of predators to consume prey. Optimal foraging theory is based on the idea that predators seek to maximize the amount of energy they consume, often while minimizing the time and energy they spend in the search, pursuit, and handling of their food (Emlen 1966; Emlen 1968; Werner and Hall 1974; Stein 1977). Measurements of foraging costs associated with prey capture, in addition to benefits returned through consumption, can then be used in models that help determine optimal prey species or prey size.

Fish predators are size-selective consumers (Brooks and Dodson 1965; Wootton 1990). Selectivity based on prey size can be evaluated through cost/benefit ratios, where optimal prey should represent the nadir of a curve that spans potential prey sizes (Werner and Hall 1974; Stein 1977). Prey vulnerability to predation can vary during specific life stages (e.g., pre-reproductive juvenile vs reproductive adult) (Werner and Hall 1988), and therefore predators of varying sizes may be beneficial in managing Red Swamp Crayfish (Simberloff and Stiling 1996). The construction of predictive models by mapping cost to benefit ratios can help identify prey sizes that are optimal for a given predator species.

In Michigan, there is a need to evaluate local predator species as biological control agents. Red Swamp Crayfish were first discovered in Michigan in 2017 in several suburban ponds and a single natural lake. Since their discovery, most Red Swamp Crayfish populations have been subjected to intensive response that includes manual trapping and/or chemical control. However, these methods are either infeasible (due to waterbody size, environmental regulations, or access) or undesirable (due to potential secondary impacts on non-target taxa) in some locations. Biological control through predator augmentation such as stocking or restrictive angling regulations provides an alternative control methodology that can mitigate many of these concerns and could provide auxiliary benefits in terms of an improved fishery. A large-scale predator augmentation effort would benefit from the evaluation of species that are broadly applicable in invaded ecosystems.

For this study, I conducted feeding trials to quantify size selectivity of three native predatory fish species on Red Swamp Crayfish. The purpose is to evaluate consumption of Red Swamp Crayfish among candidate species for biocontrol: Largemouth bass (*Micropterus salmoides*), Green Sunfish (*Lepomis cyanellus*), and Bluegill Sunfish (*L. macrochirus*). These three species are commonly found in or nearby invaded waterbodies (Budnick et al. 2022) and represent likely candidates for predator augmentation of ecosystems invaded by Red Swamp Crayfish. I quantify the costs and benefits associated with foraging based primarily on crayfish size, but include an additional analysis of the influence of crayfish sex and male reproductive form on foraging based on the understanding that crayfish size and sex are correlated in most Cambarid crayfishes (Taylor et al. 1996). I used several research questions to determine which species or combination of species should be prioritized for predator augmentation: 1) Does size-specific handling time of crayfish differ among predator species? 2) How does crayfish sex affect the handling time of predators? 3) What crayfish sizes might we expect predators to consume in nature? and 4) How do predators differ in size-specific consumption rate across species? To answer these questions, I conducted laboratory feeding experiments where I analyzed the number, size, weight, and sex of crayfish consumed by each species and individuals within each species. Results of this study will help inform predator augmentation decisions in the future.

METHODS

My goal was to identify how crayfish size and sex affect foraging by common predatory fish species Largemouth Bass, Green Sunfish, Bluegill Sunfish and Channel Catfish (*Ictalurus* *punctatus*). I executed laboratory feeding trials within a randomized design to quantify parameters associated with optimal foraging calculations. These parameters include costs associated with the predatory sequence (orientation, pursuit, and handling times) and benefits (wet weight crayfish mass). I used mass as a functional equivalent to energy gain, similar to Stein (1977).

Crayfish Collection

Crayfish for experimental trials were collected from several invaded ponds in SE Michigan. Crayfish were collected using minnow traps modified to have an enlarged (approximately 45 mm) opening and baited with approximately 100g of dry dog food, or extracted from burrows. Following capture, crayfish were transported back to the laboratory at Michigan State University and sorted into 3mm carapace-length bins for use in feeding trials (e.g. 4mm-7mm, 8mm-11mm…etc.). Altogether, I captured crayfish ranging from 4mm to 51mm, for a total of 12 bins. Crayfish that were not selected for experimental trials were euthanized. Crayfish were fed algae wafers and bloodworms until the initiation of trials.

Crayfish were also reared in lab when field sampling was not possible to increase the supply of juvenile crayfish for feeding trials. Form I and II male crayfish and females previously collected from the field were placed together until mating occurred, and females were berried. All berried females (both from the field and those bred in lab) were placed in isolation until juveniles were released from their abdomen. Juveniles were then separated from the female and held in separate aquaria until trials began.

Predator fish collection

I initially attempted to collect four predatory fish species for this study including Largemouth Bass, Channel Catfish, Bluegill, and Green Sunfish. Individuals of Largemouth

Bass, Bluegill, Green Sunfish, and Green Sunfish hybrids were captured from local ponds or lakes by angling. Captured fish were placed in coolers with battery operated air pumps for transport back to lab. The parentage of the hybrid Green Sunfish is unknown. However, all specimens for laboratory tests had the outward appearance of F2 backcrosses of Green Sunfish and are therefore grouped together as Green Sunfish. All attempts to capture wild Channel Catfish failed. I also attempted to raise Channel Catfish from individuals purchased from a hatchery, but these individuals expressed significant reticence to consume crayfish during preliminary trials and were thus removed from further trials.

I deliberately limited the size range of each predator species as an attempt to minimize the influence of intraspecific gape size variation on results (Stein 1977; Mittelbach 1983; Dorn et al. 1999). Bluegill and Green Sunfish ranged between 150-200 mm total length (TL), while Largemouth Bass were between 250- 300 mm TL. Fish for this study were similarly sized to other experiments of predators foraging on crayfish (Stein 1977; Mittelbach 1983; Anderson 1984), but I acknowledge that the restriction on predator size limits the inference of this study for wild fish populations. Fish were kept in closed system tanks at ambient laboratory temperatures (20-23°C) and allowed to acclimate to aquaria for a minimum of three weeks prior to the initiation of feeding trials. Fish acclimation occurred in 75-gallon (110cm x 53cm x 46.7cm) aquaria, with additional fish housed in individual 76cmx30.48cmx30.48cm holding tanks until trial acclimation. During the holding and acclimation period, all specimens were fed live crayfish and frozen shrimp to prepare for feeding trials.

Feeding Trials

Predator fish were removed from holding tanks and placed at random into trial tanks. Trial predators were allowed to acclimate to the trial aquaria 1-5 days before the start of the trial.

An individual predator remained in the trial aquaria until they were twice introduced to all size categories (see above) of crayfish available at the time of the trial. Predators were not fed for 24 hours prior to each crayfish introduction. Although fully independent trials of unique predator and prey are desired, they were not feasible given the difficulty of capturing adequate numbers of predators, limitations on laboratory space to hold the number of predators that would be required for full independence, and restrictions on laboratory use during the COVID-19 shutdowns. After a series of trials was completed, fish were removed from trial tanks and euthanized using MS-222. Trial tanks were then siphoned, drained, and refilled to prepare for the next fish predator.

I desired to establish relationships between crayfish size (carapace length) and sex with variables associated with optimal foraging calculations, including orientation, pursuit, handling time, and consumption (i.e. the predation sequence). I also desired to understand how crayfish size affects the probability of consumption across our predator species. Thus, I attempted to present each individual predator a range of crayfish carapace lengths up to sizes where crayfish were no longer consumed.

I introduced both female and male crayfish over a range of carapace lengths to predator tanks to estimate consumption rate along with orientation, pursuit, and handling time of predatory fishes. Crayfish sizes and sexes were selected at random for introduction. Before each introduction, I recorded the sex, carapace length (mm), chela length (mm) and weight (g).

I introduced crayfish to predators via one of six opaque pipes (selected at random) placed at each corner and at the midpoints of the long axis of the aquaria. The purpose of this method of introduction was to minimize the probability of predators learning cues to indicate feeding. The pipes extended from 5cm above the waterline to 5cm above the substrate. Crayfish could only be observed by the predator after it emerged from the pipe within the aquarium. Preliminary observation during predator acclimation indicated that crayfish that emerged from corner pipes were consumed as readily as those introduced from pipes along the aquarium sides.

I measured orientation, pursuit, and handling times with a stopwatch. Orientation time was defined as the time from when the crayfish emerged from the presentation pipe to when the predator turned its body and head towards and in line with the crayfish. Pursuit time was defined as the period between the end of orientation and initial capture. Occasionally crayfish would be captured, spit out, and immediately recaptured. I stopped measuring pursuit at the time of first capture. I defined successful capture as an event where the crayfish entered and remained in the mouth of the predator. Handling time was measured as the time between successful crayfish capture and the resumption of normal opercular movement associated with respiration (Werner 1974; Stein 1977). If the crayfish was attacked (either captured or not) and rejected (and not immediately attacked again), the watch was stopped, and the crayfish was removed from the aquarium. I then restarted the presentation with the same crayfish in the same tube and recorded whether the crayfish was consumed on the first introduction, second introduction, or not at all. Presentations of each crayfish would end if the crayfish was either consumed, attacked and rejected, or once the time for the presentation expired (5 minutes for crayfish 4-11mm CL, 10 minutes for 12-51mm CL crayfish), following Stein 1977. If the crayfish was not consumed during the two presentations, the trial was terminated, following methods outlined in Stein (1977).

This procedure was repeated for each crayfish size bin within the range of crayfish sizes fed to each predator species. Based on preliminary trials crayfish size ranges introduced to each predator species were 4-31mm CL for Bluegill, 4-39mm CL for Green Sunfish, and 4-51mm CL for Largemouth Bass. The full suite of crayfish sizes, defined above, were presented to each individual predator twice, after which the individual predator was retired from trials. In total, 12 suites of crayfish sizes were presented to 13 individual predators of the three species, representing 459 crayfish introductions. The COVID-19 crisis prevented crayfish collection and laboratory feeding trials over much of the study period, and therefore the study design was unbalanced and not fully randomized. See Table 1 for a complete description of samples sizes.

Data Analysis

Species-Specific Pursuit, Handling, and Total Cost

I desired to quantify relationships between crayfish size and pursuit time, handling time, and total cost (pursuit time plus handling time) specific to each predator species and to individuals used in each run. For this set of analyses, I only used data from trials where crayfish were successfully consumed. Initial plots of the relationship between crayfish carapace length and handling time, pursuit time and total cost indicated a log transformation was appropriate for linear analysis. Subsequent Box-Cox tests provided Lambda values between -0.5 and 0.5, supporting this decision. All ANCOVA analysis occurred with these response variables log transformed.

I first conducted one way analysis of variance tests for each predator species (Bluegill, Green Sunfish, and Largemouth Bass) to determine if carapace length influenced the outcome of handling, pursuit and cost. I recognize that there is the potential for individual predators within a given species to demonstrate unique relationships between crayfish carapace length and handling, pursuit, and total cost. To account for this difference, I then ran ANCOVA models with individuals as a factor and carapace length as the covariate for each predator species. Significant differences in the slope and intercept were found for individual Largemouth Bass and Bluegill but not for Green Sunfish for handling, pursuit, and total cost (all $p>0.2$).

I used ANCOVA to detect differences across species in the relationships between handling time, pursuit time, and total cost (handling plus pursuit times) using the covariate of carapace length. Analysis was conducted in RStudio version 2023.09.1+494 (Posit Team 2023) using the package "stats". Because my study was unbalanced (i.e., I had incomplete sampling of crayfish sizes for individuals within and across species), I expected interactions of main effects (carapace length: species). Linear ANCOVA models included the interaction term with predator species as a factor and carapace length as a continuous variable. I then executed analysis using the Anova function in the "car" package (Fox and Weisber 2019) to provide summary output. If an ANCOVA yielded a significant interaction term, I ran individual linear regression models for each species to evaluate species-specific relationships between carapace length and handling time, pursuit time, or total cost. If the interaction term was not significant the interaction was dropped, and new analysis was conducted with only the main effects included.

Sex Specific Differences

I included sex along with size and predator species in regression models of handling time to investigate whether optimal foraging costs differed between female and male crayfish for each predator species. Juvenile crayfish were removed from this analysis due to the difficulty of accurately determining sex. Crayfish sex and predator species were set as factor variables and carapace length as a covariate. I then compared the variables and the covariate with type Anova III (Fox and Weisber 2019) analysis. If any of the model interaction terms were not significant, the interaction term in the model would be dropped, and new analysis was conducted without the interaction term.

Differences in the consumption rate and handling time between sexes could be the result of dimorphism associated with chela size, which is an important determinant of fish-crayfish predation (Stein 1977). Further, crayfish males exhibit two reproductive forms, where sexually active Form I individuals possess larger chelae than sexually inactive Form II individuals. Preliminary analysis showed that male Form II Red Swamp Crayfish had similar chelae lengths to females, but male Form I crayfish had significantly larger chelae lengths than both (ANCOVA, $p<0.001$). However, only Largemouth Bass consumed both male forms. Thus, while the bulk of my analysis was conducted relative to carapace length, chelae size likely holds some explanatory power for observed results, particularly for Largemouth Bass.

Cost/Benefit curves

I fit cost/benefit curves to identify qualitative species-specific differences in curve shape and location of the nadir, which indicates optimal feeding. The cost/benefit ratio was calculated as the sum of handling and pursuit time(s) divided by total wet weight of crayfish (g).
I used successful consumption attempts to plot the cost/benefit ratio against crayfish carapace length overlapped with unsuccessful attempts. I used the Loess smooth function from the ggplot2 package (Wickham 2016) to fit cost/benefit curves equation. I then overlayed unsuccessful captures on top of the curves generated from successful captures to visually identify crayfish size cutoffs where a size refugia is likely to exist.

Consumption probability

To determine the effect of crayfish size on the probability of consumption by different fish species, I ran logistic regression using the glm (generalized linear model) function from the “stats” package. This analysis used the full data set that included both the first and second attempts by each predator species to determine binary outcomes (consumed vs rejected). I created two models. In the first model, predator species and carapace length were included as main effects only to isolate species-specific consumption curves. For the second model, I allowed the interaction between species and carapace length. I then compared the Akaike Information Criterion (AIC) outputs of both models to determine which model had a better balance of parsimony. The model with the lowest AIC value was selected as the model of best fit.

RESULTS

Pursuit time

Analysis of variance for pursuit time indicated that carapace length was a significant predictor of pursuit time for Green Sunfish only ($F_{1,90} = 16.54$, $p < 0.001$). However, the adjusted r squared value (Adj-r^2 =0.1459) indicated that the fit was relatively weak (Figure 2) (Table 2).

Analysis of pursuit time across all predator species indicated that the main effects of predator species and carapace length had no significant effect on pursuit time (both $p>0.1$). However, the interaction between carapace length and predator species was significant (ANCOVA, $F_{2,275} = 6.3681$, $p < 0.01$) on pursuit time, confounding any differences in pursuit time across predators (Table 6, Figure 2).

Pursuit time demonstrated relatively consistent, weak relationships with increasing carapace length for each individual within a predator species (Figure 2a-c). Only Largemouth Bass individuals had a significant effect on pursuit time when carapace length was held constant ($F_{3,134} =5.68$, $p<0.001$; Table 4). However, crayfish carapace length was a significant predictor of pursuit time for Largemouth Bass (ANCOVA, $p< 0.05$) and Green Sunfish (ANCOVA, $p< 0.001$; Table 4).

Handling Time

Handling time increased with increasing carapace length of crayfish for all predator species I evaluated (Figure 3). For each predator species, carapace length had a significant effect on handling time (ANOVA, All $p<0.001$) (Table 5). In general, Largemouth Bass had shorter handling times than either Bluegill or Green Sunfish, particularly at large crayfish sizes. Handling time for crayfish less than 14 mm CL was always shorter than 3 seconds for all species, but by 30mm CL handling time exceeded one minute for Green Sunfish and Bluegill. Handling time remained short (<150 sec) for Largemouth Bass until a size of approximately 40 mm CL. By 50mm CL, the average handling time for Largemouth Bass exceeded 5 minutes.

Handling time increased inconsistently across species. There was significant interaction between the effect of species and carapace length on handling time (ANCOVA, $F_{2,275} = 15.63$, $p<0.00$; Table 6), indicating that the slopes for handling time were different across species. This difference was most apparent at crayfish sizes greater than 10mm CL, where Bluegill and Green Sunfish consistently had a longer handling times than Largemouth Bass (Table 6, Figure 4).

Analysis of ANCOVA indicated unique differences in how individuals within each species handle crayfish of varying sizes. Individuals within each species largely shared similar relationships between handling time and carapace length, with single individuals deviating from the rest for Bluegill and Largemouth Bass (Figure 5a and c). ANCOVA analysis indicated that the main effects of carapace length and individual had significant effects on the handling time for Bluegill ($F_{1,46} =107.41$, $p<0.001$ and $F_{2,46} =13.95$, $p<0.001$, respectively), likely due to individual number 3 which appeared to have a flatter slope over a smaller range of crayfish sizes compared to the other two Bluegill. For Green Sunfish, only the covariate of carapace length had a significant effect on handling time ($F_{1,86} = 121.75$, $p<0.001$). In contrast, I found a significant effect of individual, carapace length, and their interaction on handling time for Largemouth Bass individuals (ANCOVA, $F_{3,131} = 12.59$, $p<0.001$; Table 7). This result was likely driven primarily by individual number 4, which demonstrated a somewhat longer handling time than the other three individuals at larger crayfish sizes (Figure 5c). As stated previously, I proceeded with analysis with individuals lumped by species given the consistency among most individuals of all species.

Total cost

The total cost of foraging (in seconds) increased linearly with carapace length for each predator species with R^2 values ranging from 0.56 to 0.68 (Figure 6). All species demonstrated a significant relationship between total cost and crayfish carapace length (ANOVA all $p< 0.001$, Table 8) but comparisons across species showed a significant interaction effect between predator species and carapace length (ANCOVA, $F_{2,275} = 13.79$, $p<0.001$) (Table 9). As a result, slopes varied by predator species, where the total cost of foraging increased at a faster rate for Bluegill and Green Sunfish compared to Largemouth Bass (Figure 6, Table 17). For Bluegill, the cost of foraging was consistently greater than either Green Sunfish or Largemouth Bass as the size of crayfish increased. I also observed similar relationships in slopes as I did for handling time between total cost and carapace length for individuals within species, indicating that the addition of pursuit time had little influence on total cost calculations (Table 10, Figure 7).

Handling Time Differences Between Female and Male Crayfish Across Predator Species

I sought to determine if crayfish sex influenced handling time. However, previous analysis indicated the carapace length was a dominant influence on handling time. Therefore, I constructed a regression model containing sex, carapace length, and species to control for the effect of carapace length on results. This model along with their interactions was significant (F

$_{6,201}$=50.14, p<.001), but the main effect of sex was not (p>0.2). ANCOVA results did indicate significant interactions between carapace length and predator species (ANCOVA, (F $_{2,201}$ =7.82, p< 0.001. Figure 8; Table 11), consistent with previous analyses.

Handling time differences between Male form (I and II) for largemouth bass

Only Largemouth Bass consumed both male reproductive forms, and therefore Green Sunfish and Bluegill were excluded from the analysis. The regression model containing crayfish male form, carapace length, and their interaction was statistically significant, but the interaction term was not significant. A new model containing only the main effects of male form and carapace length was also significant ($F_{2,74}$ = 131.1, p <0.001). Both the main effects of male form and carapace length significantly affected handling time (both p <0.001) with handling time for male Form I generally exceeding that for Form II (Figure 9).

ANCOVA analysis determined that male form significantly affected handling time when carapace length is held constant (ANCOVA, $F_{1,74}$ = 29.241, p<0.001). Additionally, carapace length was also significantly related to the handling time ($F_{1,74}$ = 91.045, p<0.001; Table 12).

Cost Benefit Curves

Cost/benefit analysis was investigated qualitatively as a fitted loess curve to identify crayfish sizes that represent optimal prey for each species. The nadir of each curve represents the optimal size of crayfish each species consumes. Results indicate the optimal foraging size of crayfish for Bluegill, Green Sunfish and Largemouth Bass are 13.8mm, 20.9mm 18.6mm, respectively (Figure 10).

Probability of Consumption

Results from logistic regression demonstrate a significant decrease in consumption rate as crayfish carapace length increases for all predator species. The model that included the interaction between species and crayfish carapace length was statistically significant ($p<0.01$, AIC= 446.5). The logistic regression slopes were statistically significant (interaction term was significant, $p<0.001$) indicating that the rate of decrease varied among species (Figure 11). Bluegill possessed the fastest decline with carapace size. The predicted probability of Bluegill consuming crayfish with carapace length < 15 mm was consistently above 75% but begins to decline rapidly to near 0% around 30mm (Bluegill consumed crayfish up to 22.2 mm CL). The average probability of consumption for Green Sunfish was lower than that of Bluegill for crayfish smaller than 16 mm, with consumption rates between 65-90%. The consumption rate fell below 50% consumption rate at approximately 20mm CL. The largest crayfish consumed by Green Sunfish was 32.4 mm. Largemouth Bass possessed the highest probability of consuming crayfish across all carapace lengths, which did not drop below 50% until ~45 mm carapace length (Figure 11).

I was unable to determine the effect of male reproductive form on consumption rate. The only predator species that successfully consumed male Form I crayfish was Largemouth Bass. Although the consumption rate for male Form I crayfish decreased with increasing carapace length (Figure 12), Largemouth Bass consumed every Form II crayfish presented to them, which prohibits further analysis due the lack of contrast in response between Form I and Form II crayfish.

DISCUSSION

Invasive crayfishes represent a substantial threat to native biodiversity in aquatic ecosystems. The ability to manage established populations of invasive crayfishes is limited, and few studies have demonstrated successful attempts to control or eradicate established populations (Hein et al. 2006; Freeman et al. 2010; Hansen et al. 2013; Manfrin et al. 2019). Fish predators are documented in some instances to control crayfish (Hein et al. 2006; Tetzlaff et al. 2011; Hansen et al. 2013), but further research is required to construct prescriptive recommendations given the diversity of systems Red Swamp Crayfish have invaded.

This study documents a comparison of three predatory fish species foraging on Red Swamp Crayfish. Previous studies have either only evaluated the consumption patterns of individual fish species (e.g. (Stein 1977)), or documented the general consumption of crayfish in the wild by either a single or multiple species (Applegate 1966; Mullan and Applegate 1970; Probst et al. 1984; Rach and Bills 1989; Roth and Kitchell 2005; Hein et al. 2006). In addition, no study has identified optimal sizes of Red Swamp Crayfish for any of the three fish species I tested. Thus, this study can inform management of invasive Red Swamp Crayfish in locations where Largemouth Bass, Green Sunfish, and Bluegill represent viable options for predator enhancement or augmentation.

In laboratory trials, Largemouth Bass generally handled crayfish faster than either Green Sunfish or Bluegill. Largemouth Bass handling times were on average twice as fast as Green Sunfish at 20mm CL, and five times faster than Bluegill at this crayfish size (~13s, ~29s, and ~78s for Largemouth Bass, Green Sunfish, and Bluegill, respectively). The difference in handling time among the three species only increased as crayfish size increased. The observed difference in handling time is likely a product of gape size and perhaps to a lesser degree, the ratio of prey length to predator length (Juanes 1994; Mihalitsis and Bellwood 2017; Fernando et al. 2018). Although I did not measure gape, Largemouth Bass of the size I used in my trials have gape widths approximately 66% and 250% larger than either Green Sunfish or Bluegill, respectively (Fernando et al. 2018). Hoyle and Keast (1987) indicate that Largemouth Bass can readily consume crayfish less than 20% of their body length, with handling time rapidly increasing at higher percentages. In my study, the 20% threshold corresponds to a carapace length between 50-60mm, where Largemouth Bass handling time exceeded 5 mins. Observations of increased handling time of larger crayfish for Largemouth Bass was similar to Hoyle and Keast (1987), who noted that Largemouth Bass would capture and then drop crayfish prior to consumption which acts to lengthen handling time. Bluegill and Green Sunfish had substantial difficulty handling crayfish larger than 20mm and 24mm CL, respectively (Figure 4). Previous studies demonstrate the optimal prey diameter for Bluegill at approximately 60% of gape, after which handling time increases exponentially (Werner 1974). Although the diameter of crayfish consumed by Bluegill in these trials is unknown, there was a clear increase in handling time for Bluegill at sizes larger than approximately 15mm CL.

My results indicate that crayfish sex (Male vs Female), had little effect on handling, pursuit, or consumption rate for all three predator species, but there was a significant relationship between male reproductive form. Further, every Form II crayfish (max size = 42.9mm CL) fed to Largemouth Bass was consumed in our trials, whereas the probability of consumption decreased rapidly with carapace length for Form I males at sizes above 40mm CL. These results are similar to the findings of Stein (1977) for *F. propinquus* fed to Smallmouth Bass (*Micropterus dolomieu*) and concurs with our understanding of agonistic interactions between crayfish and fish predators (DiDonato and Lodge 1993; Garvey et al. 1994; Hill and Lodge 1994; Roth and

Kitchell 2005). This body of research demonstrates that in addition to carapace length, chela size is also a prominent determinant of predator-prey outcomes. The Form I males used in my experiments attained a larger body size and had comparatively larger chelae compared to Form II crayfish relative to body size (Stein 1977, Garvey et al. 2003). Crayfish chelae plays an important role in defense against predation (Bovbjerg 1953; Stein 1976; Stein 1977; Garvey and Stein 1993), and both male (collective) and female crayfish had similar chela length and carapace size in my trials. This result contradicts numerous studies that demonstrate that male Cambarid crayfish tend to have larger chelae than females (Weagle and Ozburn 1970; Stein 1976; Garvey and Stein 1993; Dörr et al. 2006) including Red Swamp Crayfish (Wang et al. 2011). Further, male reproductive crayfish (Form I) have larger chelae than non-reproductive males (Form II) (Garvey and Stein 1993). Only 39% of male crayfish fed to fishes in my study were Form I, and 71% of these Form I individuals were fed to Largemouth Bass. This is a byproduct of the inherent relationship between crayfish size and maturity. I fed Largemouth Bass larger crayfish than either Bluegill or Green Sunfish to quantify the maximum crayfish size consumed by this species. Additional evaluation of differences in predation between male reproductive form should also consider the size of Form I and II chela to separate the influences of both chela length and width as determinants of consumption.

Pursuit time had negligible effects in cost calculations for all three predator species. Pursuit time rarely exceeded 30s for all species and crayfish sizes (Figure 3). Werner (1977) demonstrated negligible pursuit times for Largemouth Bass and Green Sunfish across a range of prey sizes, but a substantial increase in pursuit times for Bluegill as the ratio of prey size to predator size increased, surpassing 20s at 1% of Bluegill mass and one minute at 2% of Bluegill mass. This contrasts with my findings, where Bluegill pursuit times for nearly all crayfish sizes were less than 20s (two crayfish exceeded 20s). Although my analysis focused on crayfish lengths, I also recorded crayfish masses, and crayfish commonly exceeded 1% of bluegill mass at carapace lengths greater than ~16mm. Thus, whereas the handling time of crayfish increased for Bluegill at these sizes, they eagerly pursued crayfish of all lengths.

In optimal foraging frameworks, costs typically included into analyses are handling time and a combination of search time or search area. There are many ways to incorporate various costs in optimal foraging calculations, and authors evaluating costs have used search, pursuit, attack, handling times, or some combination of these factors (Werner 1974; Werner and Hall 1974; Pyke et al. 1977; Stein 1977; Griffiths 1980; Janssen 1982; O'Brien et al. 1989). I opted to include only pursuit and handling time to isolate the effect of crayfish size, given the uniformity of the search area (aquaria). Future studies could use alternative approaches to further parse all predatory sequence stages in more natural settings to further clarify the impact of habitat complexity on the predation sequence. These studies could then highlight differences in predators' foraging strategies, which influence their ability to detect and effectively pursue crayfish prey in more complex habitats (O'Brien et al. 1989; Simberloff and Stiling 1996).

My analysis of cost-benefit curves demonstrated that each predator species has an optimal crayfish size for consumption as represented by the nadir of the cost-benefit curves. Results indicate that the nadir is approximately 13.80mm CL for Bluegill, 20.92mm CL for Green Sunfish and 18.64 mm CL for Largemouth Bass. The cost-benefit curves for Bluegill increased steeply at sizes larger than 17mm, whereas both Green Sunfish and Largemouth Bass both had broad basins in the cost/benefit ratio. This indicates that Bluegill have a distinct foraging optimum, but the other two species are likely to demonstrate selectivity for crayfishes larger than approximately 17mm CL up to the incline in their cost/benefit ratio.

Few studies have documented cost/benefit relationships of fish predators foraging on crayfish in the field (but see Stein 1977). Although my investigation of crayfish foraging was limited to a laboratory setting, other field investigations corroborate these findings to a limited degree. For example, (Tetzlaff et al. 2011) indicates that the mean size of rusty crayfish consumed by *Lepomis* spp. (predominantly Bluegill) was 10mm CL +/- 2.3mm. These observations overlap with, but are slightly below, my predicted nadir of the cost-benefit curve. For Largemouth Bass, I found several studies that provide evidence that crayfish are important prey for this species (Taub 1972; Scalet 1977; Hickley et al. 1994), but few report the size of crayfish consumed. Similarly, I could find no field observations of crayfish size in Green Sunfish diets. Clearly, more field research is needed to corroborate my laboratory results.

High predation rates on juvenile crayfish could improve the probability of successful Red Swamp Crayfish control. My evidence suggests that *Lepomis* species are viable candidates for augmentation towards this end, but success is likely dependent on the availability of Red Swamp Crayfish juveniles to *Lepomis* predators. Tetzlaff et al (2011) found that *Lepomis* species could consume an entire year-class of juvenile rusty crayfish in some Northern Wisconsin lakes, which likely contributes to the maintenance of low crayfish densities in lakes with high *Lepomis* populations. However, I remain uncertain whether Lepomis could achieve similar results on Red Swamp Crayfish in Michigan. In their native range, the period of Red Swamp Crayfish vulnerability to *Lepomis* predators is likely short (Mullan and Applegate 1970) as Red Swamp Crayfish can attain 30mm CL in a single year in Louisiana (Penn 1943). In Louisiana, free-swimming juveniles peak from August to November (Penn 1943) but can be found throughout the wet period (Huner and Barr 1991). Thus, there appears to be at least some availability of juvenile crayfish to *Lepomis* in the native range of Red Swamp Crayfish. Availability could be magnified in Michigan, where slower Red Swamp Crayfish growth and reproduction may yield extended periods of vulnerability to *Lepomis* predators (Sousa et al. 2013). I could find few other studies that address *Lepomis* consumption of crayfish (see Applegate (1966)). The relative scarcity of studies that evaluate *Lepomis* species as crayfish predators is perplexing given that Tetzlaff et al. (2011) found that up to 11% of bluegill diets is comprised of crayfish, and Green Sunfish diets were up to 20% crayfish in Beaver Reservoir, Arkansas (Mullan and Applegate 1970). Both species readily consumed crayfish in my laboratory study. Bluegill and Green Sunfish are generally considered opportunistic predators of benthic invertebrates and (less so for Green Sunfish) zooplankton (Ehlinger 1989). Few researchers have focused on *Lepomis*-crayfish interactions, and there is uncertainty in most *Lepomis* diet studies whether crayfish exist as a prey item, or whether categories of low resolution taxonomic (e.g. Crustacea) includes crayfish. Alternatively, there could be a specific suite of abiotic and biotic conditions that are necessary for *Lepomis* to engage in crayfish predation. For example, crayfish consumption could be limited by the size structure of *Lepomis*. Ontogenetic changes in *Lepomis* diets could limit the number of individuals in each population capable of consuming crayfish, but this idea has yet to be tested rigorously. My study used relatively large *Lepomis* (160-180mm) compared to other diet studies (Applegate 1966; Mullan and Applegate 1970; Janssen 1982), which limits the ability to evaluate whether *Lepomis* size influences consumption of crayfish. Clearly, further field and laboratory investigation is needed to highlight *Lepomis* consumption of crayfish and potential impacts on crayfish populations, and potentially identify habitat and population conditions that influence *Lepomis* consumption of crayfishes.

The utilization of Largemouth Bass to consume crayfish within infested systems is important. Both Smallmouth and Largemouth Bass eagerly consume crayfish (Swingle and

Smith 1942; Bennett 1951; Lewis and Helms 1964). Studies such as (Lewis et al. 1961), indicate that while Largemouth Bass demonstrate a preference for foraging on fish in a pond setting, they demonstrate an increased propensity to consume crayfish at sizes >200mm (Rach and Bills 1989; Hickley et al. 1994; Wheeler and Allen 2003). Rickett (1974) indicates that Largemouth Bass larger than 100mm TL will readily integrate crayfish into their diet.

Management implications

One goal of this research is to provide recommendations for managers seeking to manage Red Swamp Crayfish invasions with biological control. My research provides a quantitative framework for evaluating how three native predator species consume invasive Red Swamp Crayfish. The laboratory-based nature of the study limits my ability to translate these results into natural settings. Natural ecosystems are likely to have higher habitat complexity and are subject to variation in climate and population abundance not found in laboratory studies. However, other laboratory evaluations of predation on crayfish (Stein 1977; Aquiloni et al. 2010) were corroborated in the field suggesting that laboratory studies on this topic are relevant to management.

My study provides evidence that all three predator species I evaluated likely have some utility as biological control agents. Largemouth Bass are well-adapted to consuming medium and large crayfish (including Male Form I crayfish), whereas both *Lepomis* species are well-adapted to consuming much smaller individuals. Thus, an approach that incorporates Largemouth Bass to consume mature adults, and *Lepomis* species to consume juveniles could be a powerful approach for biological control. However, several caveats must be addressed. First, the ponds in Michigan where Red Swamp Crayfish are established (Budnick et al. 2022) already sustain some combination of *Lepomis* and Largemouth Bass. However, *Lepomis* in these ponds are severely stunted (*Personal observation*), which is common in Michigan lakes and elsewhere (Murnyak et al. 1984; Schindler et al. 1997; Hurt 2007). Our laboratory study used relatively large individuals of both Green Sunfish and Bluegill. Thus, I recommend any biological control strategy that uses *Lepomis* to control crayfish should seek to sustain populations of large individuals. Although Largemouth Bass are present in these ponds, they are uncommon. My research does not address the abundance of predators required to control crayfish (but see Tetzlaff et al. 2014), yet this represents a critical uncertainty towards effective management of Red Swamp Crayfish through biological control. Logic suggests that sustaining an abundant adult Largemouth Bass population through some combination of natural reproduction, multiple stocking events, and/or restrictive angling regulations would be beneficial not only for crayfish consumption, but also to help maintain adequate *Lepomis* size structure (Otis et al. 1998). An important factor that leads to stunting is high juvenile *Lepomis* survivorship, and Largemouth Bass are commonly used to help control abundant juvenile *Lepomis* (Swingle and Smith 1942; Otis et al. 1998), although the effectiveness of this approach is debated. Further mitigation and population maintenance may be needed if *Lepomis* demonstrate signs of stunting (e.g. reduced growth rate of large year-classes), including restrictive angling regulations that allow large sunfish to survive (Schindler et al. 1997; Rypel 2015).

In conclusion, there is a need to explore alternative methods managers can use to manage invasive species. The use of native predatory fish is considered a good way to reduce juvenile crayfish and complements trapping, which removes reproducing adults (Elvira et al. 1996; Dorn et al. 1999). Implementation of biological control of Red Swamp Crayfish within an adapted management framework will be important to manage ecosystems invaded by crayfish to iteratively reduce uncertainty through experimentation. This project provides new insight into how multiple fish predators can be implemented to manage the world's most prolific invasive crayfish and offers an initial starting point for related management strategies.

TABLES

Table 1. Sample Sizes of Predator Species and Red Swamp Crayfish.

Trial Organism		Crayfish		
Species	Individuals	Fed	Consumed	Rejected
M. salmoides	4	188	139	49
L. macrochirus	3	99	50	49
L. macrochirus x cyanellus	5	172	92	80
Total	12	459	281	178

Table 2. Analysis of Variance of effect of carapace length on Log pursuit time for Green Sunfish predators.

Predictor	Type I SS	*df*	MS	*F*	*p*
Carapace Length	18.69	1	18.69	16.54	**<0.001**
Error	101.69	90	1.13		

Table 3. ANCOVA results for log pursuit time as a function of crayfish carapace length (mm) and predator species.

Predictor	Type III SS	*df*	*MS*	*F*	*p*
(Intercept)	0.66	1	0.66	0.44	0.506
Carapace Length	0.93	1	0.93	0.63	0.429
Species	1.96	2	0.98	0.66	0.518
Carapace Length x Species	18.98	2	9.49	6.37	**0.002**
Error	409.91	275	1.49		

Table 4. ANCOVA results for log pursuit time as a function of crayfish carapace length (mm) and individuals within species.

	Bluegill			**Green Sunfish**			**Largemouth Bass**		
Predictor	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
(Intercept)	1	0.45	0.507	1	0.16	0.688	1	3.63	0.059
Individuals	2	0.04	0.958	4	0.62	0.649	3	5.68	**<0.001**
Carapace Length	1	0.41	0.523	1	14.42	**<0.001**	1	5.33	**0.023**
Error	46			86			134		

Table 5. Analysis of Variance effects of carapace length on log handling time for each predator species.

	Bluegill		**Green Sunfish**		**Largemouth Bass**	
Predictor	*F*	*p*	*F*	*p*	*F*	*p*
Carapace Length	87.09	**<0.001**	114.75	**<0.001**	441.72	**<0.001**
Error	48		90		137	

Table 6. ANCOVA results for log handling time as a function of crayfish carapace length (mm) and predator species.

	Bluegill			**Green Sunfish**			**Largemouth Bass**		
Predictor	*df*	*F*	*p*	df	*F*	*p*	*df*	*F*	*p*
(Intercept)	1	17.71	**<0.001**	1	26.3	**>0.001**	1	67.13	**<.001**
Individuals	2	13.95	**<0.001**	4	1.85	.127	3	5.72	**0.001**
Carapace Length	1	107.41	**<0.001**	1	121.7	**>0.001**	1	71.99	**<.001**
Individuals x Carapace Length			*			*	3	12.59	**<.001**
Error	46			86			131		

Table 7. ANCOVA results for log handling time as a function of crayfish carapace length (mm) and individuals within each predator species.

Predictor	Type III SS	*df*	MS	*F*	*p*
(Intercept)	1.96	1	1.96	4.44	**0.036**
Species	0.92	2	0.46	1.04	0.354
Carapace Length (mm)	48.27	1	48.27	109.17	**<.001**
Species x Carapace Length	13.82	2	6.91	15.63	**<.001**
Error	121.6	275	0.44		

*Bluegill and Green Sunfish equations the interaction term was nonsignificant. The models were rerun without the interaction term.

Table 8. Analysis of Variance results log cost (pursuit + handling) for predator species.

	Bluegill		**Green Sunfish**		**Largemouth Bass**	
Predictor	*F*	*p*	*F*	*p*	*F*	*p*
Carapace Length	64.91	**<0.001**	121.75	**<0.001**	303.03	**<0.001**
Error	48		90		137	

Table 9. ANCOVA results for log cost (pursuit+ handling) as a function of crayfish carapace length (mm) and across predator species.

Predictor	Type III SS	*df*	MS	*F*	*p*
(Intercept)	8.78	1	8.78	21.69	**<0.001**
Species	0.4	2	0.2	0.5	0.607
Carapace Length	34.67	1	34.67	85.68	**<0.001**
Species x Carapace Length	11.16	2	5.58	13.79	**<0.001**
Error	111.27	275	0.4		

Table 10. ANCOVA results for log cost (Pursuit + Handling) as a function of crayfish carapace length (mm) and individuals within species.

	Bluegill		**Green Sunfish**		**Largemouth Bass**	
Predictor	*F*	*p*	*F*	*p*	*F*	*p*
(Intercept)	33.71	**<0.001**	68.26	**<0.001**	118.07	<**0.001**
Individuals	8.22	**<0.001**	1.75	0.145	1.65	0.18
Carapace Length	68.32	**<0.001**	127.84	**<0.001**	44.81	<**0.001**
Individuals x Carapace Length		*		*	7.9	**<0.001**

*Interaction terms were not significant for *Lepomis* predators.

Table 11. ANCOVA Handling Time Between Male and Female Crayfish Across Species.

Predictor	Type III SS	*df*	MS	*F*	*p*
(Intercept)	0.16	1	0.16	0.31	.577
Sex	0.00	1	0.00	0.01	.932
Carapace Length	21.51	1	21.51	43.22	**<0.000**
Species	1.60	2	0.80	1.60	0.204
Carapace Length x Species	7.79	2	3.90	7.82	**<0.001**
Error	100.05	201	0.50		

Table 12. ANCOVA Handling Time for Male Crayfish Forms by Largemouth Bass.

Predictor	Type III SS	*df*	MS	*F*	*p*
(Intercept)	8.1	1	8.1	34.75	**<0.001**
Carapace Length	21.21	1	21.21	91.05	**<0.001**
Male Form	6.81	1	6.81	29.24	**<0.001**
Error	17.24	74	0.23		

Table 13. Regression Models- Log Pursuit Time Across Predator Species.

	Largemouth Bass			**Bluegill**			**Green Sunfish**		
Predictors	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
(Intercept)	0.61	0.26	**0.023**	0.31	0.51	0.541	0.15	0.28	0.591
Carapace Length	-0.01	0.01	0.419	0.03	0.04	0.468	0.06	0.02	**<0.001**
F-stats	$F_{1,137}=0.656$			$F_{1,48}=0.536$			$F_{1,90}=16.54$		
R^2 / R^2 adjusted	0.005 / -0.002			0.011 / -0.010			0.155 / 0.146		

Table 14. Regression Models- Pursuit Time for Predator Individuals.

	Largemouth Bass			**Bluegill**			**Green Sunfish**		
Predictors	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
Intercept	0.50	0.27	0.059	0.38	0.57	0.507	0.12	0.30	0.688
Individual 2	0.39	0.31	0.201	-0.10	0.45	0.829	-0.38	0.42	0.373
Individual 3	0.93	0.30	**0.002**	-0.16	0.66	0.815	0.14	0.57	0.809
Individual 4	1.06	0.28	**<0.001**				0.28	0.30	0.345
Individual 5							0.06	0.02	**<0.001**
Carapace Length	-0.02	0.01	**0.023**	0.02	0.04	0.523	0.15	0.29	0.593
F-Stats	$F_{4,134}$ =4.42			$F_{3,46}$=0.20			$F_{5,86}$ =3.75		
R^2 / R^2 adjusted	0.117 / 0.091			0.013 / -0.051			0.179 / 0.131		

Table 15. Regression Models- Log Transformed Handling Time of Crayfish by Predator Species.

	Largemouth Bass			**Bluegill**			**Green Sunfish**		
Predictors	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
(Intercept)	0.76	0.12	**<0.001**	0.54	0.29	0.066	0.97	0.20	**<0.001**
Carapace Length	0.09	0.00	**<0.001**	0.19	0.02	**<0.001**	0.12	0.01	**<0.001**
F-stats	$F_{1,137}$=441.7			$F_{1,48}$=87.1			$F_{1,90}$=114.7		
R^2 / R^2 adjusted	0.763 / 0.762			0.645 / 0.637			0.560 / 0.556		

Table 16. Regression Models- Log Handling Time for Species Individuals.

	Largemouth Bass			**Bluegill**			**Green Sunfish**		
Predictors	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
(Intercept)	1.23	0.15	**<0.001**	1.06	0.25	**<0.001**	1.07	0.21	**<0.001**
Individual 2	0.08	0.28	0.782	-0.88	0.20	**<0.001**	-0.12	0.29	0.693
Individual 3	-0.72	0.29	**0.014**	-1.13	0.30	**<0.001**	0.53	0.39	0.180
Individual 4	-1.01	0.30	**0.001**				-0.29	0.21	0.167
Individual 5							-0.37	0.20	0.072
Carapace Length	0.06	0.01	**<0.001**	0.18	0.02	**<0.001**	0.12	0.01	**<0.001**
Individual 2 x Carapace Length	0.02	0.01	0.186						
Individual 3 x Carapace Length	0.05	0.01	**<0.001**						
Individual 4 x Carapace Length	0.06	0.01	**<0.001**						
F-stats	$F_{7,131}$=98.07			$F_{3,46}$=53.99			$F_{5,86}$= 29.29		
R^2 / R^2 adjusted	0.840 / 0.831			0.779 / 0.764			0.595 / 0.572		

Table 17. Regression Models- Log Cost of Crayfish by Predator Species.

	Largemouth Bass			**Bluegill**			**Green Sunfish**		
Predictors	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
Intercept	1.29	0.12	**<0.001**	1.14	0.28	**<0.001**	1.43	0.18	**<0.001**
Carapace Length	0.08	0.00	**<0.001**	0.16	0.02	**<0.001**	0.11	0.01	**<0.001**
F-stats	$F_{(1,137)} = 303$			$F_{(1,48)} = 64.91$			$F_{(1,90)} = 121.7$		
R^2 / R^2 adjusted	0.689 / 0.686			0.575 / 0.566			0.575 / 0.570		

Table 18. Regression Models- Log Cost of Crayfish by Individual Predators.

	Largemouth Bass			**Bluegill**			**Green Sunfish**		
Predictors	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
(Intercept)	1.64	0.15	**<0.001**	1.57	0.27	**<0.001**	1.52	0.18	**<0.001**
Individual 2	0.17	0.29	0.561	-0.73	0.22	**0.001**	-0.25	0.26	0.329
Individual 3	-0.44	0.29	0.132	-0.90	0.32	**0.007**	0.46	0.35	0.193
Individual 4	-0.41	0.30	0.172				-0.25	0.18	0.179
Individual 5							-0.30	0.18	0.092
Carapace Length	0.05	0.01	**<0.001**	0.15	0.02	**<0.001**	0.11	0.01	**<0.001**
Individual 2 x Carapace Length	0.01	0.01	0.244						
Individual 3 x Carapace Length	0.04	0.01	**<0.001**						
Individual 4 x Carapace Length	0.04	0.01	**<0.001**						
F-Stats	$F_{7,131}$=73.34			$F_{3,46}$=33.63			$F_{5,86}$= 26.57		
R^2 / R^2 adjusted	0.797 / 0.786			0.687 / 0.666			0.607 / 0.584		

FIGURES

Figure 1. Opaque Pipes used in feeding trials. Other side of tank had same array of pipes.

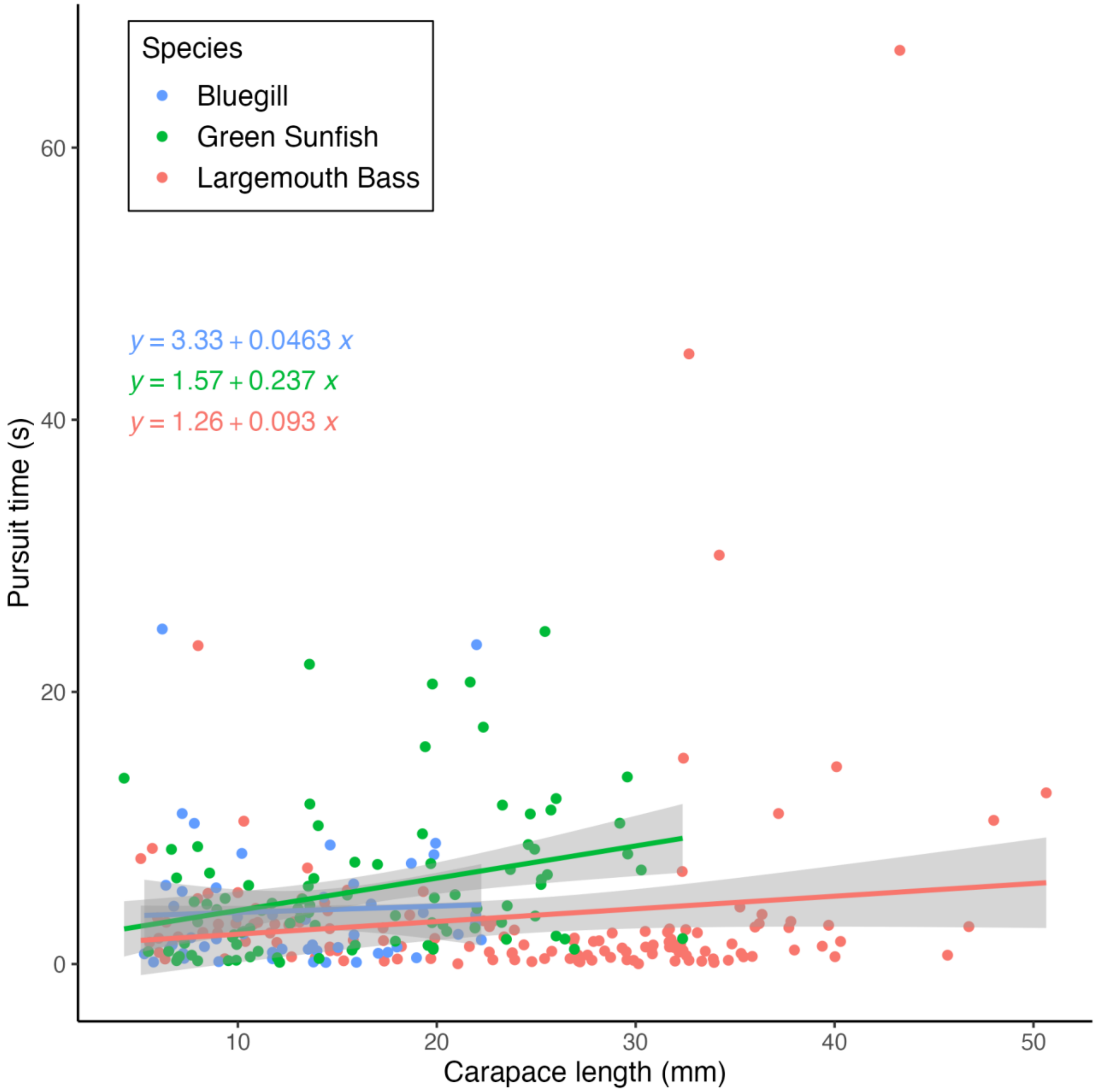

Figure 2. Pursuit time by Bluegill, Green Sunfish and Largemouth Bass for various crayfish size (mm) (sex and male form combined). Regression equations for each line are included in the figure. See Table 13 for regression statistics.

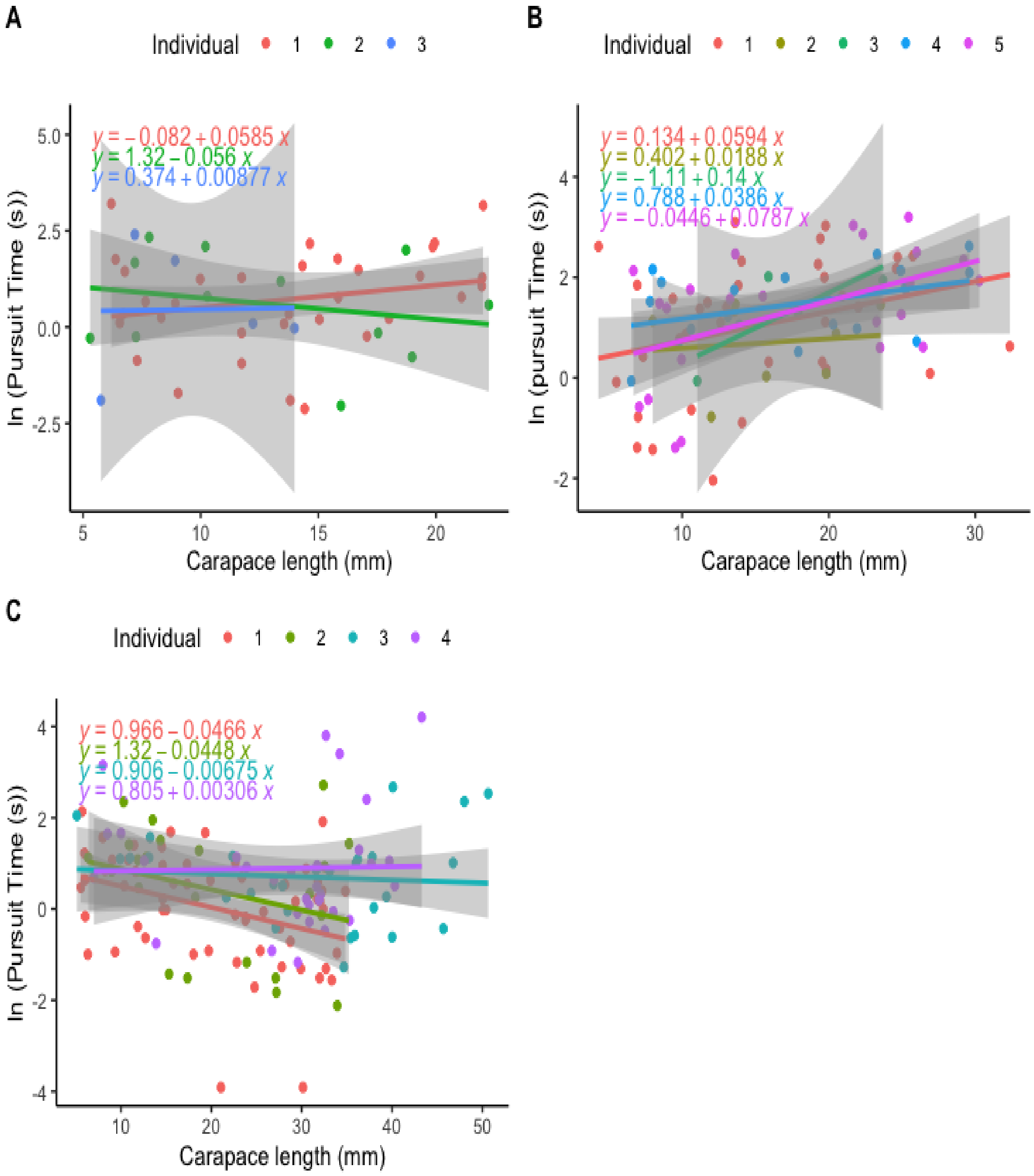

Figure 3. Log pursuit time by Bluegill (a), Green Sunfish (b) and Largemouth Bass (c) individuals for various sizes of crayfish (mm) (sex and male form combined). See Table 14 for regression statistics.

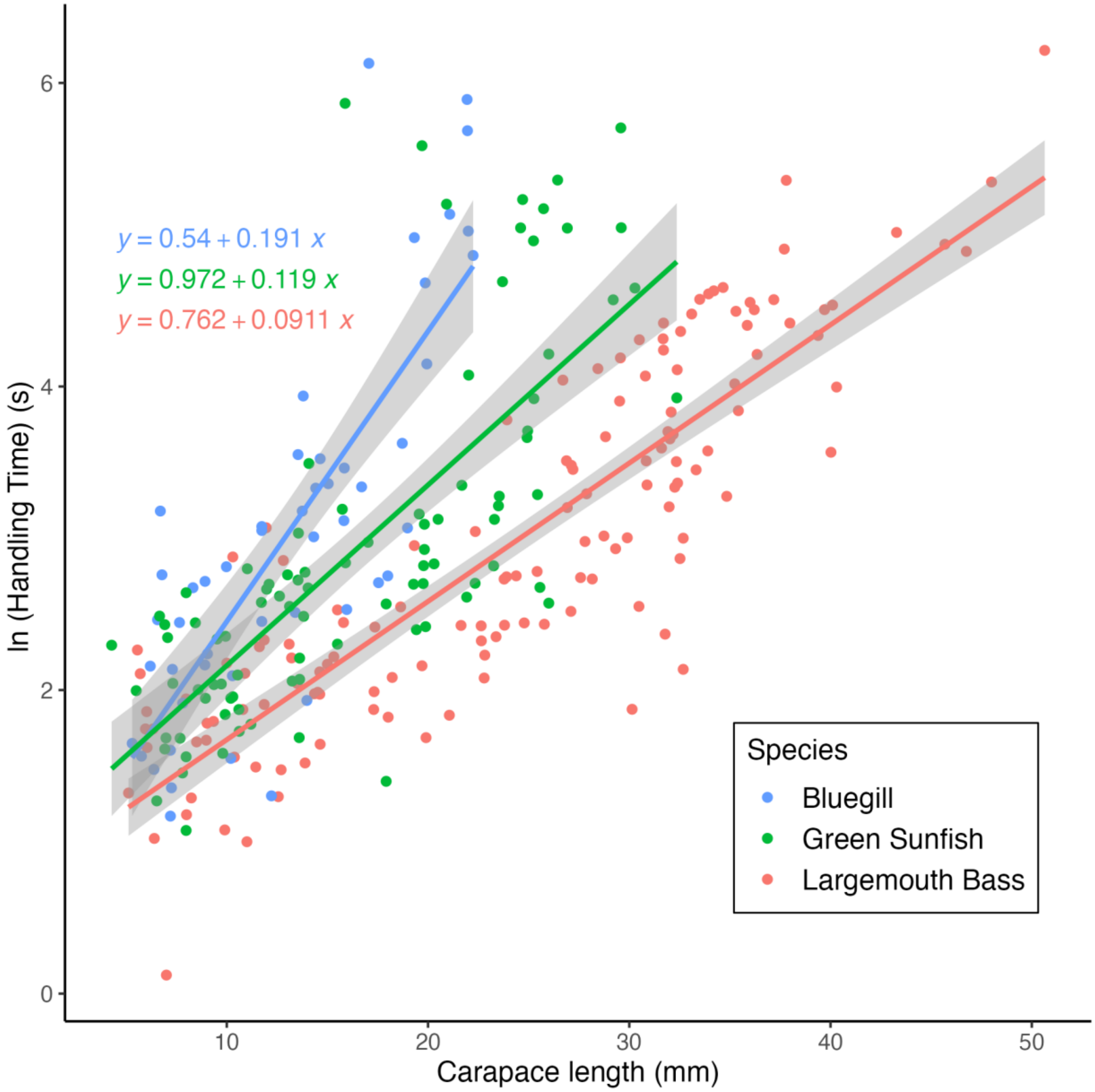

Figure 4. Log handling time for Bluegill, Green Sunfish, and Largemouth Bass for various sizes of crayfish carapace (mm), sex and male form are combined. Regression equations for each line are included in the figure. See Table 15 for regression statistics.

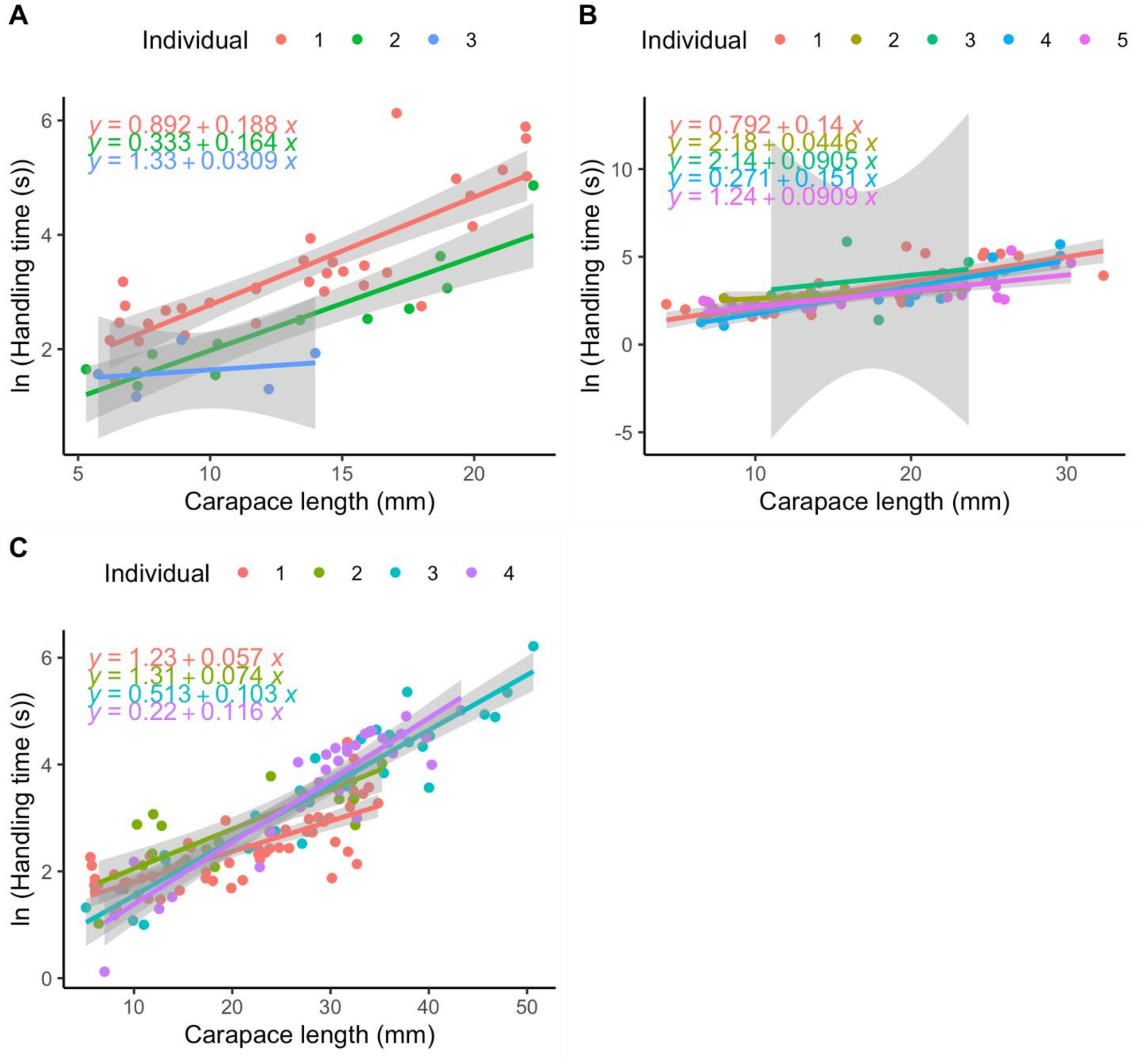

Figure 5. Log handling time by Bluegill (a), Green Sunfish (b) and Largemouth Bass (c) individuals used in feeding trials on crayfish of various carapace sizes (mm) (sex and male form combined). See Table 16 for regression statistics.

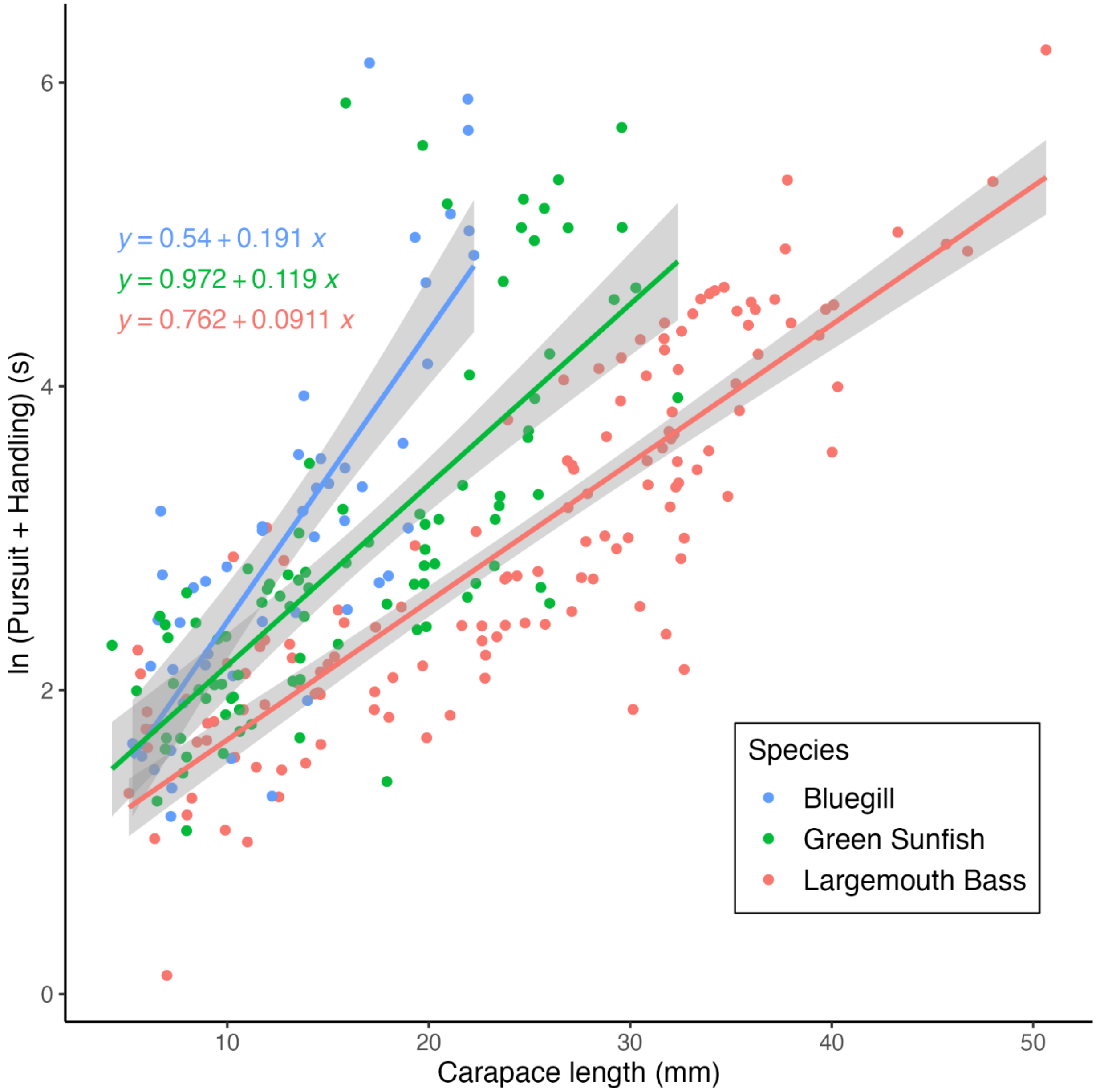

Figure 6. Log total cost versus carapace length (mm) for each bluegill, green sunfish, and largemouth bass in feeding trials. refer to table 17 for regression statistics for each species.

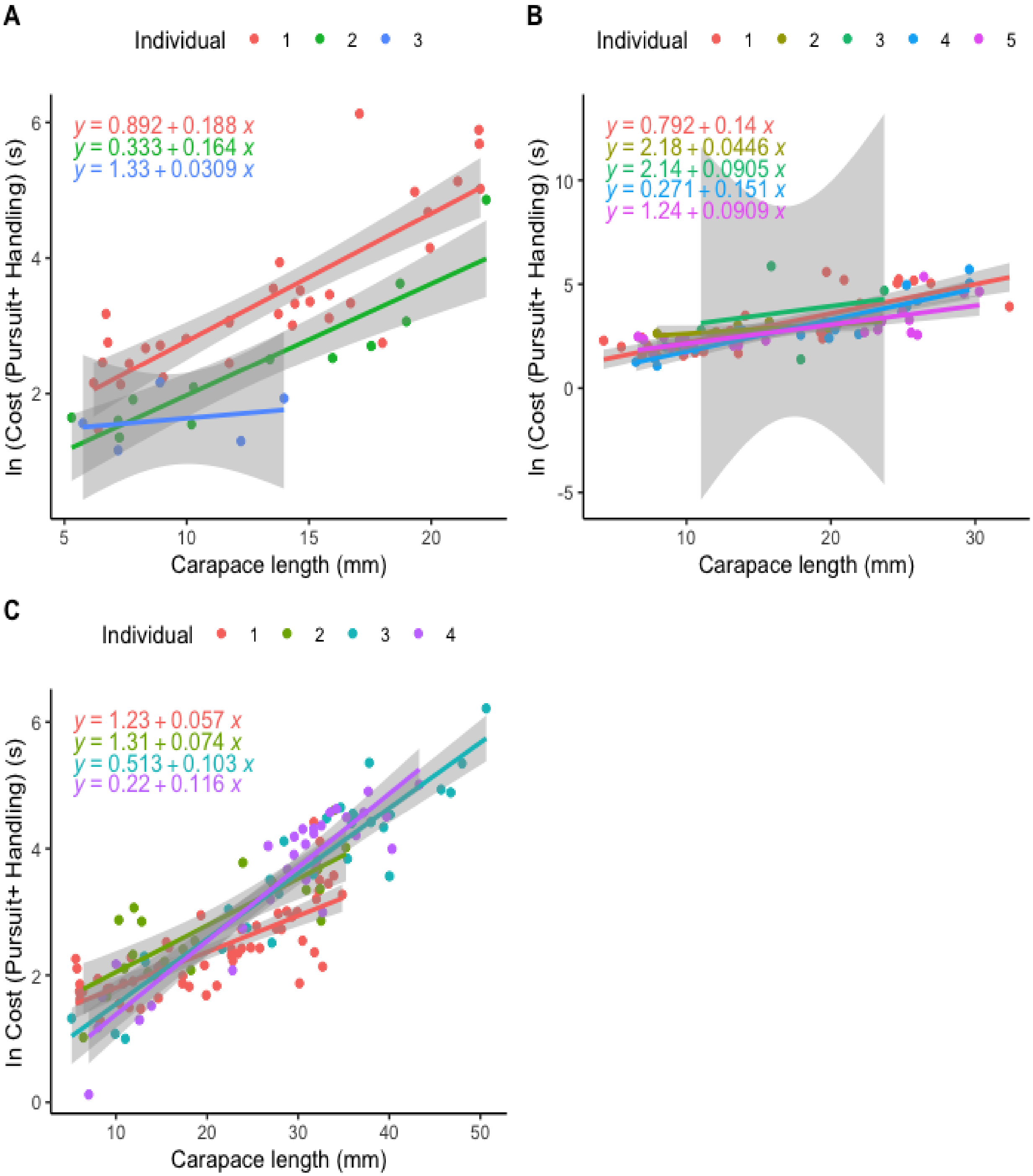

Figure 7. Log cost (handling(s) + pursuit time (s)) for Bluegill (a), Green Sunfish (b) and Largemouth Bass (c) individual versus crayfish carapace length (mm) (sex and male form combined). See Table 18 for regression statistics.

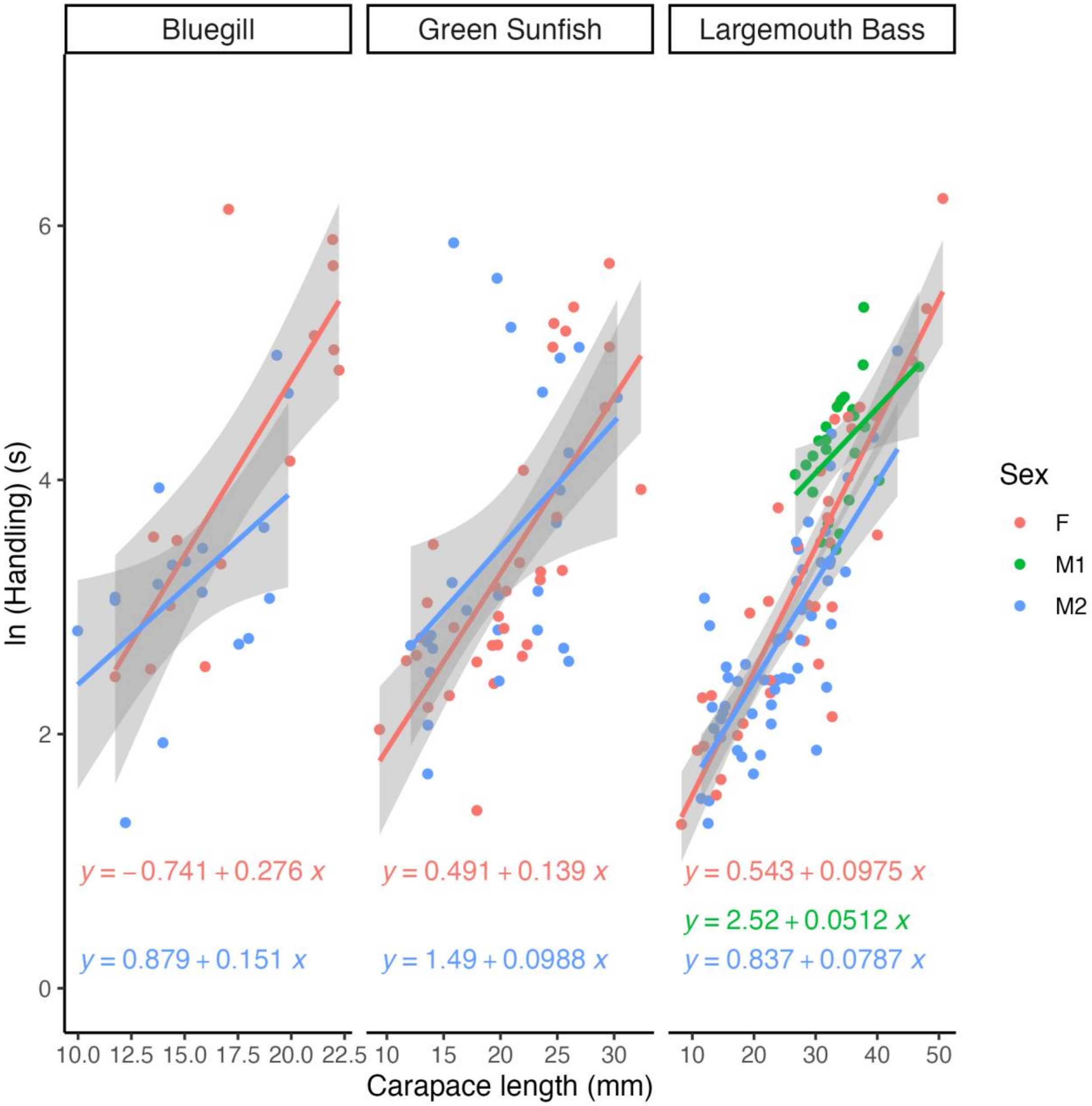

Figure 8. Log handling time(s) across predator species versus crayfish carapace length of male and female crayfish. Juvenile crayfish excluded.

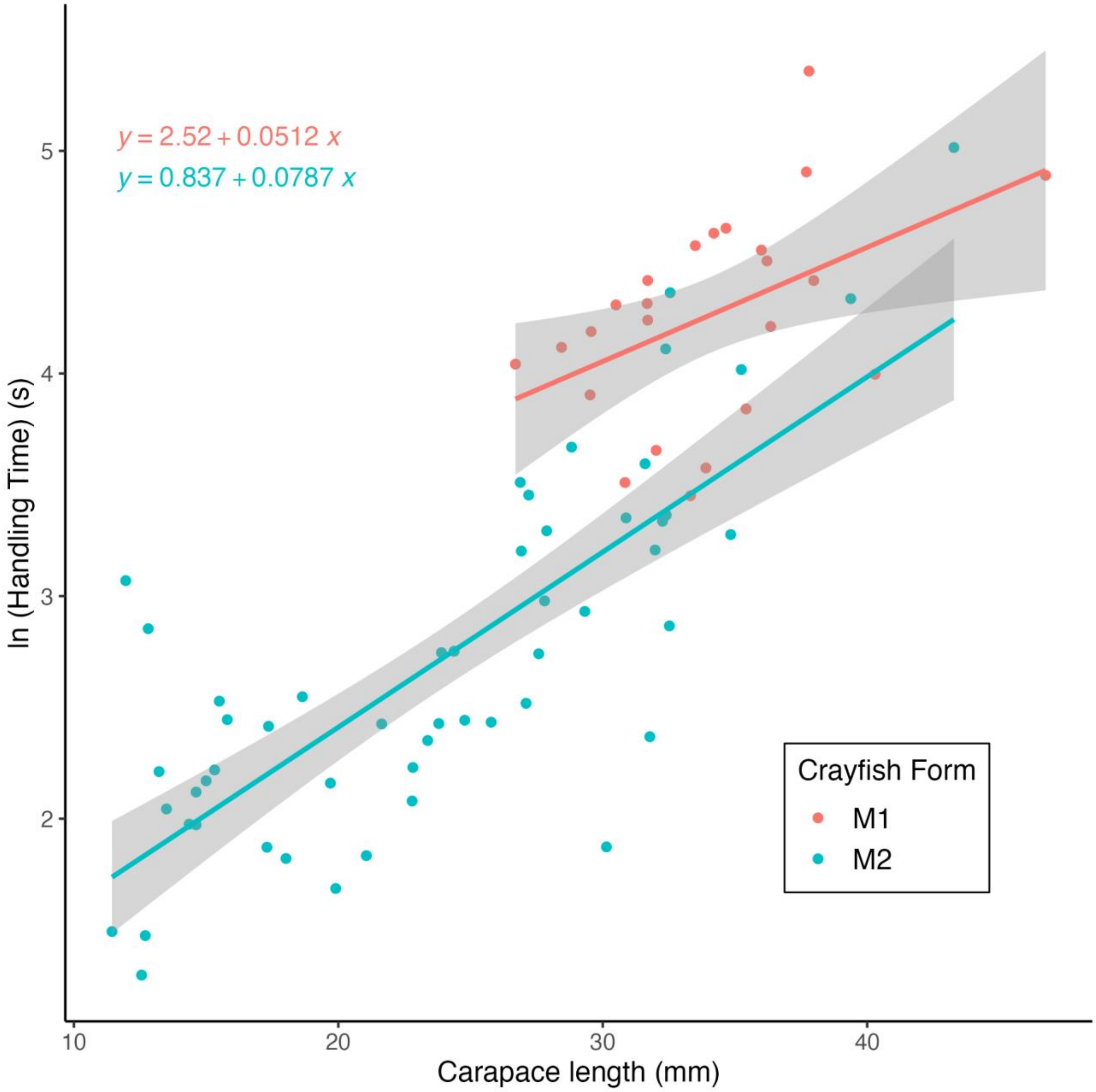

Figure 9. Largemouth Bass handling time between Male form I and II crayfish.

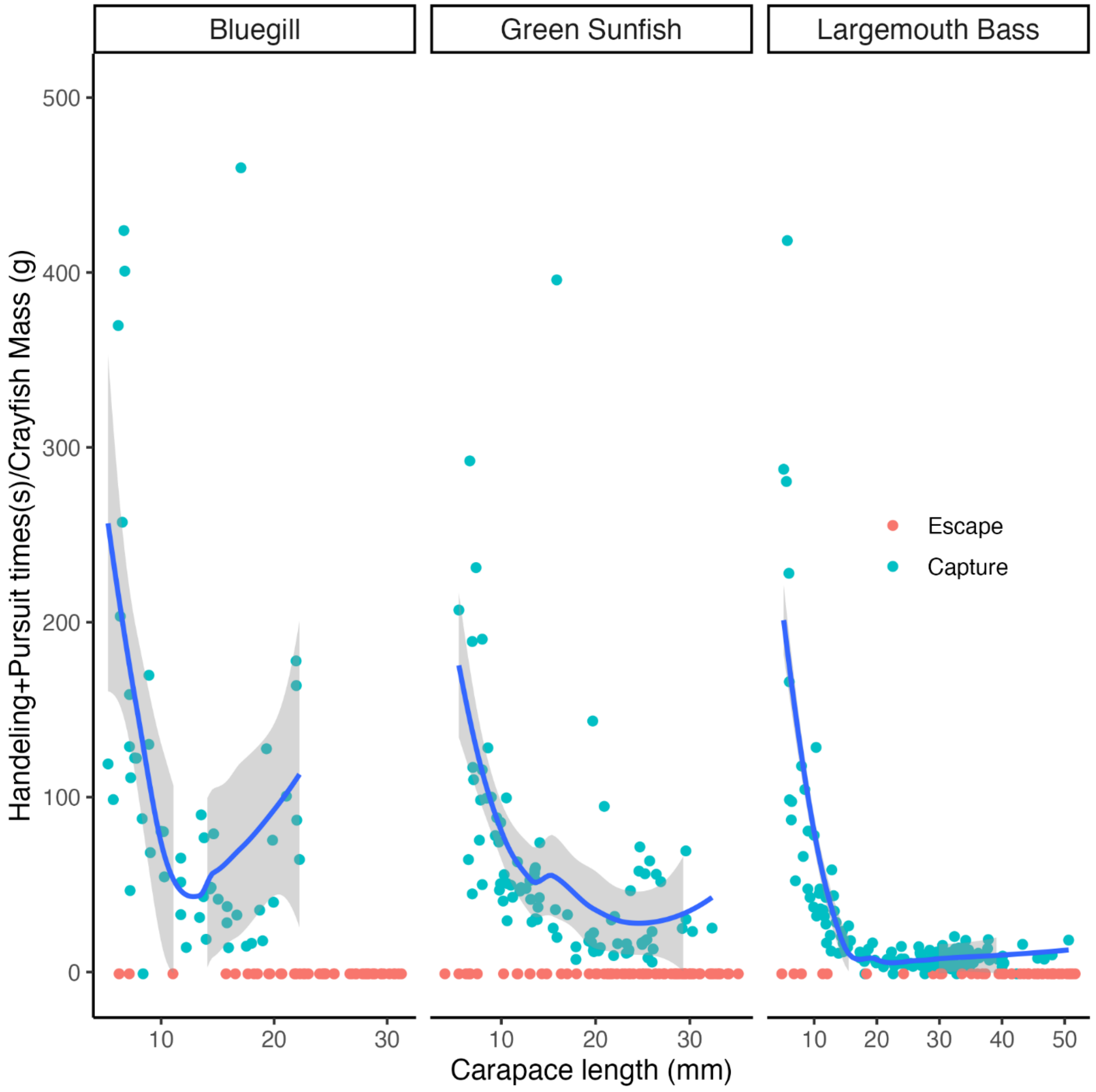

Figure 10. Handling time(s) plus handling time (s) by Bluegill, Green Sunfish, and Largemouth Bass of successful captures and escaped crayfish divided by crayfish mass (g) (H t + Pt / O) versus crayfish carapace length (mm). Curves were fitted by Loess smoothing (y ~ x). Sex, male form and juvenile combined.

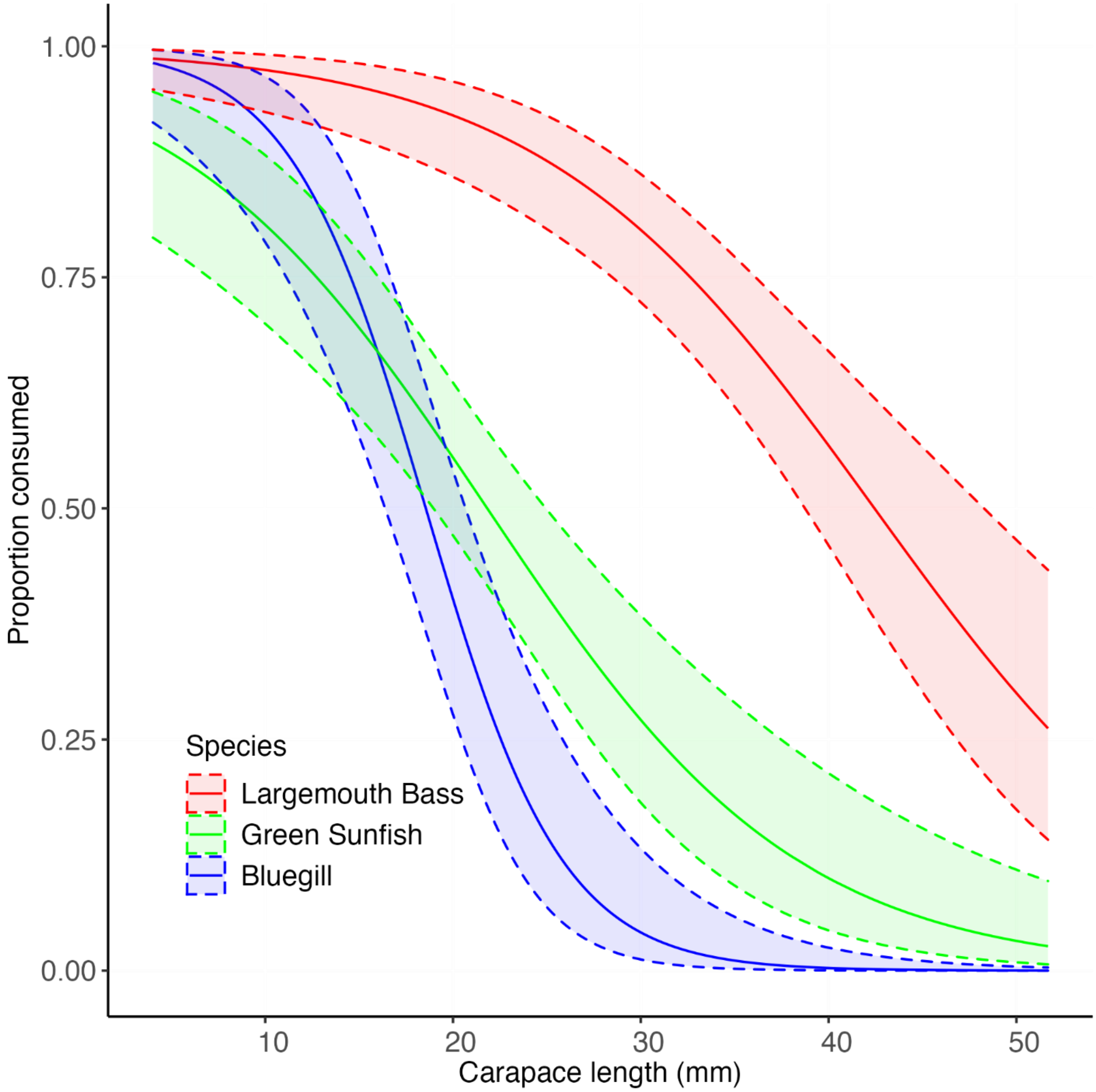

Figure 11. Predicted crayfish consumption by Bluegill, Green Sunfish, and Largemouth Bass predators versus crayfish carapace length.

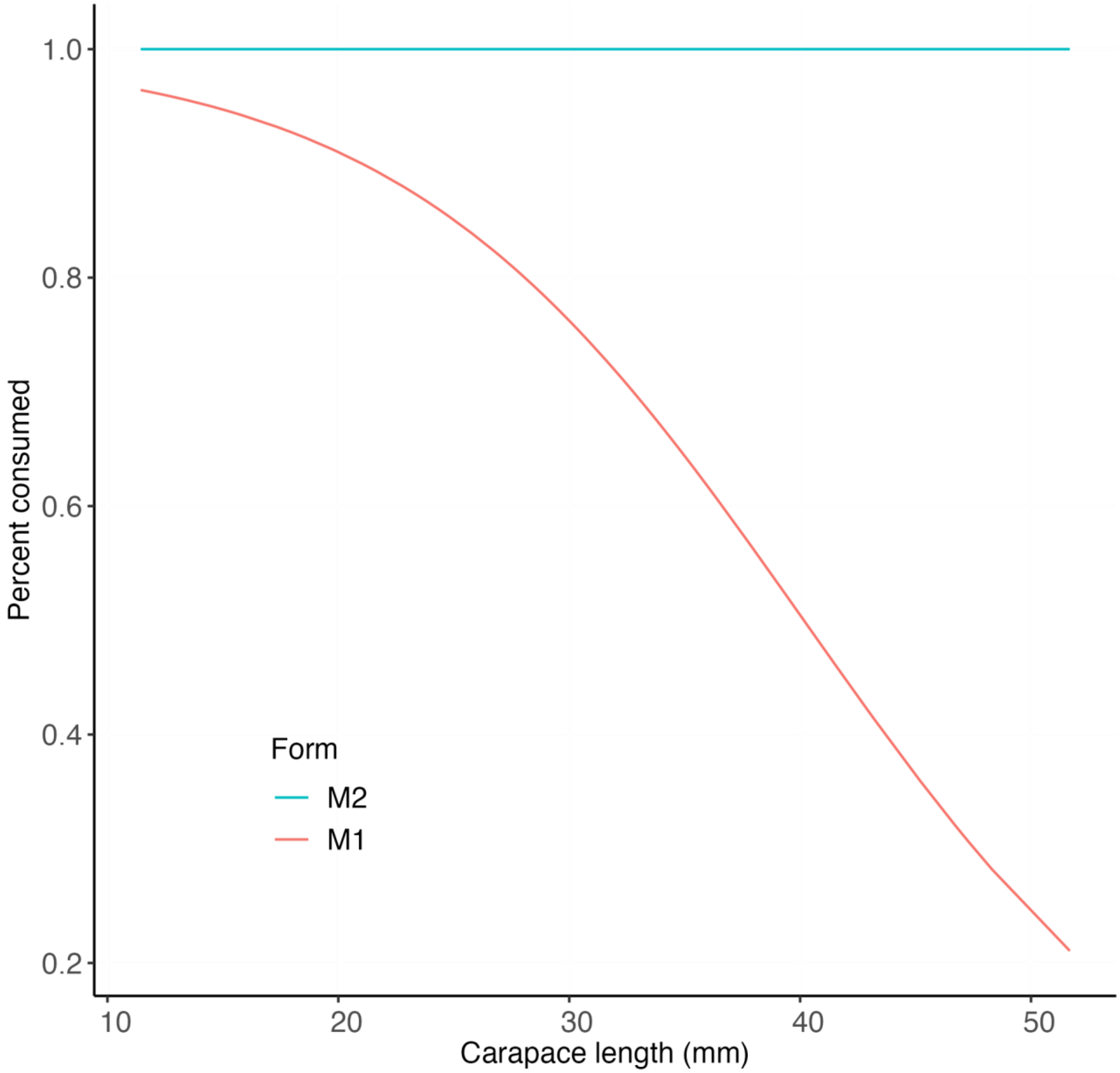

Figure 12. Predictive Consumption of Male Form Crayfish by Largemouth Bass.

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