The rise and fall of the Ruffe (*Gymnocephalus cernua*) empire in Lake Superior

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Dedication

I dedicate this dissertation to my husband and Baby Maggie. Thank you for your love and support throughout this endeavor.

Abstract

Invasive species are a global problem, impacting property, habitats, ecosystem function, and native species. Our ability to predict future habitat and spread of aquatic invasive species is limited because it is challenging to collect and integrate information regarding life history, movement, and habitat, especially across continents. Invasive Ruffe (*Gymnocephalus cernua*) has caused substantial ecological damage in North America, parts of Western Europe, Scandinavian countries, and the United Kingdom. Given the potential for ecological impacts, such as native fish declines, ongoing concern regarding the spread of Ruffe is warranted. But there are significant research gaps regarding life history, movement, and Ruffe distribution in the native and non-native range. Therefore, the overall goals of my dissertation were to acquire life stage-specific data for Ruffe, including dispersal, seasonal, and spawning movements, and characterize their life cycle, and to develop a lake-scale species distribution model for Ruffe at a 30-m resolution. First, I found that Ruffe exhibits plasticity with regard to chemical, physical, biological, and habitat requirements (Chapter One). Adult Ruffe has characteristics that allow it to adapt to a range of environments, including rapid maturation, relatively long life and large size, batch spawning, genotypic and phenotypic plasticity, tolerance to a wide range of environmental conditions, broad diet, and multiple dispersal periods. Notably, there is variability among these characteristics between the native, non-native North American, and European non-native populations. Second, I found that Ruffe populations in both the St. Louis River and Chequamegon Bay are at different invasion stages (Chapter Two). In the St. Louis River, the population

increased from the initial invasion in 1986 up to 1995 and has been in decline for the past two decades (1996-2015). In Chequamegon Bay, the overall population is increasing, but is doing so by oscillating every 5-7 years. I concluded that Ruffe populations in both systems partially conform to the typical “boom-bust” patterns seen with other invasive fish species. Third, carbon and nitrogen stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) revealed size-specific movements between coastal wetland and Lake Superior. I found significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between Ruffe captured in Lake Superior and those captured in the St. Louis River, but not among locations within the river (Chapter Three). I found size-based differences as well; medium-sized fish, 60-80 mm standard length (SL), had a $\delta^{13}C_{\text{lipid corrected}}$ of about -25‰ to -45‰, lower than either small (<60 mm SL) or large (80-148 mm SL) Ruffe (-38.2‰ to -14.2‰). Importantly, extremely ^{13}C-depleted fish (<-36‰ $\delta^{13}C$) indicate that some Ruffe captured within coastal wetlands were feeding in a methane-based trophic pathway. Finally, a variety of species distribution models constructed to predict Ruffe suitable habitat in Lake Superior based on environmental data resolved to a variety of scales all performed similarly but varied substantially in the area of habitat predicted (Chapter Four). Among the six distribution models (250-m, 500-m, 1000-m, 2000-m, and 2000-m selected model) constructed using catch and environmental data from various spatial resolutions, the best performing model used 500 m data and the worst performing model used 2000 m data. The important geographic discrepancies in potential habitat occurred around the Apostle Islands, WI, Isle Royale, MN, Grand Marais, MI, Whitefish Point, MI, and

Red Rock and Nipigon in Canada. Multiple models performed similarly according to the area under the curve (AUC) scores, but had different results with respect to the area and distribution of suitable habitat predicted. I further examined whether there were differences among species distribution models developed from cumulative time-series (cumulative decades) or discrete time stanzas (decades treated separately). The separate time-series models all performed similarly well, but the performance of the cumulative models declined as data were added to subsequent models. Despite relatively strong performance, the species distribution models indicated offshore habitat and exposed, rocky nearshore habitat were suitable habitat, which is not corroborated by my research on the habitat preference and movement ecology of Ruffe (Chapter 1, 2, 3). I conclude that, to interpret the outputs of the Ruffe species distribution models, both model performance and the ecology of Ruffe must be considered to better characterize its fundamental niche. Broadly, I demonstrate the importance of synthesizing the life stage-specific biology and distribution of an invasive species with species distribution models to advance our ability to predict the future habitat of an invasive species.

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Dissertation Introduction

Invasive species are a global problem, causing destruction of property, habitats, and threatening native species. Biological invasions can impact agriculture, forestry and health, all of which affect human economic wealth (Pimentel *et al.* 2001); invasions can further alter ecosystem function (Brooks *et al.* 2004) and threaten native biodiversity (Mack *et al.* 2000). In recent decades, the spread of species from their native ranges has increased dramatically, both in frequency and extent, due to the increase in global and international trade, as well as an increase in human movements (McNeely 2001; Thuiller *et al.* 2005). Once an introduced species has become established in a novel environment, it is nearly impossible to eradicate (Sindel and Michael 1992; Hastings 1996; Perrings *et al.* 2002; Peterson 2003). Preventing the introduction of potential invaders is the best, most cost-effective management strategy; however, when prevention is not possible, early detection tools can be used to help monitor new introductions and spread (Hoffman *et al.* 2016). One such tool is an ecological niche model (Peterson and Vieglais 2001).

The Laurentian Great Lakes have been severely impacted by aquatic invasive species (AIS) in the past two centuries (USEPA 2011). Owing to the severity of the invasion, a Great Lakes-wide aquatic invasive species (AIS) early detection and rapid response network is required under the Great Lakes Water Quality Agreement (GLWQA 2012). The goal of an early detection and rapid response network is to detect an invasive species at an early stage in its introduction when it is rare and geographically isolated (Hulme 2006). The success of eradication efforts, quarantines, and public education is increased during this early invasion stage before the invasive species becomes established, and these actions become much more costly (Gherardi and Angiolini 2004). To establish an effective network, locations of high risk for introduction of AIS need to be identified (Vander Zanden *et al.* 2010), and high-efficiency methods, including detection techniques that are more sensitive than traditional population monitoring need to be put in place (Trebitz *et al.* 2009; Vander Zanden *et al.* 2010; Hoffman *et al.* 2011).

Identifying locations of high risk for invasive species requires some understanding of vectors for spread, relative propagule pressure, and the suitability of the chemical, physical, and biological conditions (Colautti and MacIsaac 2004). Niche modeling is one way that has been shown to predict whether or not introduced species will be able to establish and spread throughout the landscape (Peterson 2003). Niche models are cost effective because they often use already existing data to model species' potential distributions, so there is no need for costly field efforts (Fielding and Bell 1997). However, these models have limitations based on how they are constructed. Typically, ecological niche models use global climate data as their ecological component and data from the native range of the organism. Often the prediction maps are at such a large scale that managers only have a vague idea (e.g., all of the Great Lakes) of where an invasive species might be able to establish a population. A model using data from the non-native range and environmental data that is at a resolution closer to the scale at which the animal lives may provide model outputs with finer geographic resolution to predict suitable habitat.

The overall goals of my dissertation were to acquire life stage-specific data for Ruffe, including dispersal, diet, seasonal, and spawning movements and characterize their life cycle and to develop a lake-scale species distribution model for Ruffe at a 30-m resolution. Ruffe is an invasive species that has caused ecological and economic damage in places it has invaded around the world (Maitland and East 1989; Adams and Tippett 1991; Selgeby and Edwards 1993; Adams 1994; Kalas 1995; Ogle *et al.* 1996; Selgeby 1998; Lorenzoni *et al.* 2009). By learning about its complete life history in the Laurentian Great Lakes and creating a lake-scale model of its suitable habitat, I have provided better information for targeted monitoring of Ruffe; further, these methods and this model can be used for other invasive species in Lake Superior.

I had three goals for Chapter One. First, I identified Ruffe's native and non-native range; second, I examined the chemical, physical, biological, and habitat requirements of Ruffe; and third, I characterized Ruffe's life cycle. For Chapter Two, my goal was to determine whether Ruffe populations in the St. Louis River and Chequamegon Bay conform to typical invasive species boom-bust patterns; moreover, as an exploratory analysis, I compared Ruffe abundance to potential predator and competitor abundance through time to identify species that might have strong interactions with Ruffe in the St. Louis River and Chequamegon Bay. For Chapter Three, I used carbon and nitrogen stable isotope ratios to identify trophic pathways supporting Ruffe in the St. Louis River, Chequamegon Bay, and Lake Superior. I measured carbon and nitrogen stable isotope ratios of Ruffe, used a stable isotope mixing model to estimate diet contributions from both Lake Superior (benthic periphyton) and wetland sources (including methane-oxidizing bacteria), and then characterized size-based movement between the wetland and Lake Superior based on the output of the mixing model. Finally, for Chapter Four, my goal was to apply lake-scale catch data and environmental variables to develop a Ruffe species distribution model (Maxent model) for Lake Superior. I evaluated the effects of resolving the data at a variety of spatial and temporal scales on the model output (i.e., the area within Lake Superior that is classified as suitable habitat). For the spatial analysis, I compared the model output among six different occurrence point distance buffers, including all points, 250-m, 500-m, 1000-m, 2000-m, and a 2000-m selected point removal procedure. In addition, I ran a cumulative and a separate time-series analysis on data from 1986, 1996, 2006, and 2014. To compare the model outputs, I determined the percent of suitable habitat for the lake for all models, as well as three zones—offshore, nearshore, and in-shore.

Ruffe can adapt to almost any aquatic environment (lakes, rivers, ponds, bays, brackish waters, tidal estuaries, non-tidal estuaries, and reservoirs (Hölker and Thiel 1998)). That adaptability is what makes it an effective invasive species (Adams and Tippett 1991; Ruffe Task Force 1992; Ogle *et al.* 1995, 1996; Mayo *et al.* 1998). Even though it is not a highly migratory fish, Ruffe has spread and established populations across continents (Matthey 1966; Maitland and East 1989; Adams 1991; Winfield 1992; Kalas 1995; Stepien *et al.* 1998; Eckmann 2004; Winfield *et al.* 2010, 2011, 2004; Lorenzoni *et al.* 2009; Volta *et al.* 2013). Also, Ruffe is highly competitive in low-light conditions and has the potential to alter population dynamics of prey (benthic invertebrates and zooplankton prey), competitors (forage fish), and fish predators (including through egg-consumption; (Mikkola *et al.* 1979; Sterligova and Pavlovskiy 1984; Pavlovskiy and Sterligova 1986; Adams and Tippett 1991; Kangur and Kangur 1996; Selgeby 1998; Kangur *et al.* 2000)). Notably, management actions to prevent the spread of Ruffe are critical because Ruffe matures rapidly and has high fecundity, and thus can quickly establish a population (Fedorova and Vetkasov 1974; Collette *et al.* 1977; Kolomin 1977; Lind 1977; Craig 1987; Neja 1988; Jamet and Lair 1991; Kovac 1998; Lappalainen and Kjellman 1998; Lorenzoni et al. 2009). In this dissertation, I present a detailed description of Ruffe life history and native and non-native range; a current and past description of its population dynamics and how that fits into invasion theory; detailed descriptions about its movements and trophic pathways based on stable isotope ratios; and a series of prediction maps showing suitable habitat of Ruffe for Lake Superior using 30-m-scale environmental variables.

Chapter 1: A review of Ruffe (*Gymnocephalus cernua*) life history in its native versus non-native range

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Abstract

Invasive Ruffe (*Gymnocephalus cernua*) has caused substantial ecological damage in North America, parts of Western Europe, Scandinavian countries, and the United Kingdom. The objectives of this review are to define Ruffe's native and non-native range, examine life history requirements, explore the life cycle, and differentiate between life stages. I compare data from its native and non-native ranges to determine if there are any differences in habitat, size, age, genotype, or seasonal migration. Literature from both the native and non-native ranges of Ruffe, with some rare, translated literature, is used. In each life stage, Ruffe exhibit plasticity with regard to chemical, physical, biological, and habitat requirements. Adult Ruffe has characteristics that allow them to adapt to a range of environments, including rapid maturation, relatively long life and large size (allowing them to reproduce many times in large batches), batch spawning, genotype and phenotype (having plasticity in their genetic expression), tolerance to a wide range of water quality, broad diet, and multiple dispersal periods. There is, however, variability among these characteristics between the native, non-native North American, and European non-native populations, which presents a challenge to managing populations based on life history characteristics. Monitoring and preventative strategies are important because, based on Ruffe's variable life history strategies and its recent range expansion, all of the Laurentian Great Lakes and many other water bodies in the U.K., Europe, and Norway are vulnerable to Ruffe establishment.

Introduction

Although Ruffe (*Gymnocephalus cernua*), a small freshwater fish, is an invasive species in Europe and North America, less than thirty years ago there was a commercial fishery for it along the coastal regions of the Baltic Sea. The Ruffe fishery dated back to 1886 in the Elbe River estuary, Germany. Historically, Ruffe fisheries were found in Denmark, Scandinavian countries, Holland, and the former USSR, including Estonia (Johnsen 1965; Hölker and Thiel 1998), harvesting up to 1759 tons per year (Johnsen 1965). Although once popular as a food fish, Ruffe is no longer commercially harvested. Rather, it has since been widely introduced outside of their native range, to water bodies in North America, the United Kingdom, Western Europe (defined for the purposes of this paper as Italy, Germany, France, Belgium, the Netherlands, Austria, Spain, Portugal, and Denmark), and Norway.

Once established, invasive Ruffe disrupts interactions among native organisms. It competes with native fishes for food resources due to niche overlap (Maitland and East 1989; Ruffe Task Force 1992; McLean 1993; Ogle *et al.* 1995). It also consumes fish eggs, especially those of *Coregonus* spp. (Mikkola *et al.* 1979; Sterligova and Pavlovskiy 1984; Pavlovskiy and Sterligova 1986; Adams and Tippett 1991; Kangur and Kangur 1996; Selgeby 1998; Kangur *et al.* 2000), and preys on young-of-the-year fish or small fishes (Kozlova and Panasenko 1977; Holker and Hammer 1994; Kangur and Kangur 1996). In the water bodies it has successfully invaded (i.e., established a reproducing population), Ruffe has outcompeted native fishes and evaded native piscivores (Ogle *et al.* 1995, 1996; Mayo *et al.* 1998).

In the 1980s, Ruffe was accidentally introduced to the Laurentian Great Lakes in North America via ballast water, and parts of Western Europe, Scandinavian countries, and the United Kingdom via canals, shipping, and bait bucket transfers. There are concerns about the adaptability of this fish to introduced water bodies due to their rapid and steady range expansion. To better understand its potential for further range expansion, it is important to characterize the chemical, physical, biological, and habitat requirements of Ruffe, as well as its interactions with other organisms. Substantial knowledge gaps remain regarding its habitat use and ecology. First, there is a lack of a complete description of Ruffe's native range, particularly in Asia, which is necessary to determine the extent of their native habitat. Second, seasonal movements and dispersal need to be characterized to fully describe the ecological niche of Ruffe.

The goals of this review are to (1) define Ruffe's native and non-native range; (2) examine the chemical, physical, biological, and habitat requirements of Ruffe; and (3) characterize Ruffe's life cycle. For this literature review, I conducted an exhaustive search of published literature and available reports from both the native and non-native range of Ruffe. Throughout, I examine differences with respect to habitat, size, age, genotype, or seasonal migration between populations from the native and non-native ranges.

Methods

To conduct the review, I searched for published literature using Google Scholar with key phrases, including "Ruffe habitat," "Ruffe life cycle," "Ruffe diets," and "Ruffe ecology." Historical literature, including unpublished reports, was identified using sources cited in primary literature and review articles. Most literature from the non-native range was published between 1980 and 2000, a period of rapid spread. Literature from the native range was from Russia, Denmark, Western Europe, Norway, and the former USSR, including Estonia, and was published between 1940 and 2000.

To describe the life cycle, I used four discrete stages—egg (embryonic), larva, juvenile, and adult. Ontogeny specific to Ruffe was based on Kovac (1994).

To describe the native range, location data came from any paper that mentioned Ruffe was present, even if Ruffe was not the topic of the paper (i.e., papers about parasites in Ruffe were common, as were papers examining the mechanisms of sensory organs in fish). The range map for their native distribution was based on literature descriptions; I associated Ruffe with the water bodies (i.e., rivers, lakes, and seas) surrounding the 229 native occurrence points, and below an elevation of 964 m above sea level (the highest elevation Ruffe are known to occur). For the range map, native and non-native occurrences were differentiated based on literature descriptions. England included both native and non-native occurrences; however, I was unable to find any occurrence coordinates for southern England although Ruffe is native to this region (Collette and Banarescu 1977; Kalas 1995; Winfield et al. 1998). Ruffe occurrences for southern England were interpreted from a UK map from the National Biodiversity Network (NBN Gateway 2013). For the marine coastal habitat, I applied a 15 km buffer from the shoreline because this is the furthest distance away from shore that Ruffe has been documented (Selgeby 1998).

Non-native populations of Ruffe usually were emphasized in specific articles, allowing us to identify native and non-native populations. For the non-native North American occurrence map, data (N=5,898 sampling events over a 29-year period) in the Laurentian Great Lakes was mostly provided by USGS, USFWS, and USEPA, including published and unpublished data.

FINDINGS

I discuss review findings, including the native and non-native ranges, life history requirements, Ruffe life cycle, and details of adult Ruffe.

NATIVE RANGE

Ruffe is native to a large part of Europe and Asia, ranging from the northeast of France (Berg 1965; Rösch *et al.* 1996) and southern England (Collette and Banarescu 1977; Kalas 1995; Winfield et al. 1998) to parts of Siberia and Russia (Berg 1949; McLean 1993; Mills *et al.* 1994; Gunderson *et al.* 1998; Mayo *et al.* 1998; Ogle 1998, 2009; Selgeby 1998; Ogle *et al.* 2004; Dawson *et al.* 2006) (Figure 1). Its range extends almost to the coast of the Arctic seas in eastern Scandinavia, including rivers entering the Baltic and White Seas at the northernmost part of its range (Holcik and Hensel 1974; Collette and Banarescu 1977; Kalas 1995; Popova *et al.* 1998; Brown *et al.* 1998; Lorenzoni *et al.* 2009). Ruffe exist throughout all of Siberia; it is present in the Kolyma River, but not in the Amur River (Holcik and Hensel 1974; Collette and Banarescu 1977; Kalas 1995; Brown *et al.* 1998; Lorenzoni *et al.* 2009). The Ob' and Nadym River in Russia comprise Ruffe's eastern border (Petlina 1967; Kolomin 1977; Matkovskiy 1987; Popova *et al.* 1998; Stepien *et al.* 1998). In

Slovakia, Ruffe is found throughout the Danube River, including the Little Danube and its side channels and tributaries in the lower parts of the river and on the Large Danube Island (Hensel 1979; Kovac 1998). The Danube River and Black and Caspian Seas form the southern border of Ruffe's native range (Popova *et al.* 1998).

NON-NATIVE RANGE

Ruffe has established populations in Lake Piediluco (Lorenzoni *et al.* 2009), Lake Ghirla, and Lake Mergozzo, Italy (Volta *et al.* 2013); Bassenthwaite Lake (Stepien *et al.* 1998; Winfield *et al.* 2004), Derwent Water, and Windermere, England (Winfield *et al.* 2010, 2011); Loch Lomond, Scotland (Maitland and East 1989; Adams 1991); Llyn Tegid (Bala Lake), Wales (Winfield 1992; Winfield et al. 1998; Winfield et al. 2011); Lake Constance, Germany, Austria, and Switzerland (Winfield et al. 1998; Eckmann 2004); Lake Geneva, Switzerland and France (Matthey 1966; Winfield et al. 1998); and Lake Mildevatn, Norway (Kalas 1995) (Figure 1).

In North America, Ruffe was introduced to the Laurentian Great Lakes in the 1980s via ballast water releases, establishing populations in both US and Canadian waters of Lake Superior, Lake Michigan, MI, and Lake Huron, MI. Propagule pressure (i.e., the abundance and frequency of Ruffe introduced) on the Great Lakes has been low (Kolar and Lodge 2001); genetic evidence suggests there was a single founding population from the Elbe River drainage region, Germany (Stepien *et al.* 2005). Among the Great Lakes, Ruffe is most abundant in Lake Superior (Figure 2); the highest densities have been observed in the St. Louis River, MN-WI (Figure 2A), and Chequamegon Bay, WI (Figure 2B).

LIFE HISTORY REQUIREMENTS: CHEMICAL

Ruffe tolerate a wide range of salinity (0-12 ppt) (Lind 1977) and pH (as eggs 6.5-10.5) (Kiyashko and Volodin 1978) (Table 1). It lives in waters ranging from oligotrophic to eutrophic but prefer eutrophic waters (Fedorova and Vetkasov 1974; Disler and Smimov 1977; Leach *et al.* 1977; Hansson 1985; Johansson and Persson 1986; Bergman 1988a, 1990, 1991; Bergman and Greenberg 1994; Rösch *et al.* 1996; Popova *et al.* 1998; Lehtonen *et al.* 1998; Brown *et al.* 1998). Ruffe may thrive in eutrophic waters for several reasons: it has a sophisticated lateral line system and sensory organs that aid mechanoreception in turbid waters (Disler and Smimov 1977; Johansson and Persson 1986; Bergman 1988a, 1990, 1991; Popova *et al.* 1998); Ruffe prefers to consume benthic invertebrates, and there may be an abundance of benthic organisms in eutrophic waters (Leach *et al.* 1977); and there may be less predation pressure and competition than in oligotrophic waters because its adaptations to low-light conditions aid avoidance of native piscivores and provide a foraging advantage compared to native demersal fishes (Bergman 1991; Lehtonen et al. 1998).

LIFE HISTORY REQUIREMENTS: PHYSICAL

Although Ruffe is considered a ‘temperature generalist,’ it is adapted for cold water rather than warm water (Bergman 1987; Hölker and Thiel 1998).

Adult Ruffe can feed at temperatures as low as 0.2°C (Lake Vortsjarv, Estonia) (Kangur *et al.* 1999) (Table 1) and is active and feeding at 4-6°C in other locations (Bergman 1987; Eckmann 2004; Tarvainen *et al.* 2008). In the Danube River, when the temperature is 16.2-23.0°C, Ruffe embryos hatch in 8 days and larvae transition to juveniles in 20 days (Kovac 1998) (Table 1). Hokanson (1977) stated that the optimal growth temperature for larval Ruffe is 25-30°C (Table 1). For juveniles, after an acclimation temperature of 20°C for 11 days, the upper incipient lethal temperature (i.e., the temperature at which 50% of individuals will die if exceeded) is 30.4°C (Alabaster and Downing 1966; Hokanson 1977); whereas, with an acclimation in the field with temperatures ranging from 24.1-25.7°C, the juveniles' critical thermal maximum (i.e., the temperature at which locomotory activity becomes disorganized) is 34.5°C (Horoszewicz 1973; Hokanson 1977) (Table 1). Based on a bioenergetics model, maximum consumption in laboratory conditions for adults occurs at 18-22°C (Tarvainen *et al.* 2008).

Ruffe spawns between 5-18°C in the non-native North American range (Brown *et al.* 1998). Notably, the minimum spawning temperature reported in the native range was 11.6°C, whereas the maximum reported was 18°C (Hokanson 1977).

Ruffe has been captured at depths of 0.25-85 m (Nilsson 1979; Van Densen and Hadderingh 1982; Sandlund *et al.* 1985) in its native range (Table 2). However, in Lake Superior, USA, Ruffe has been captured from 0.2-205 m (USGS, personal comm., 2014) (Table 2). In the eastern portion of their non-native range, Ruffe was caught as shallow as 4.9 m in Mildavetn, Norway (Kalas 1995) and as deep as 70 m in Lake Constance, Germany (Eckmann 2004) (Table 2).

LIFE HISTORY REQUIREMENTS: BIOLOGICAL- FEEDING HABITS AND BEHAVIORS

Adult Ruffe often lives in shoals (Kontsevaya and Frantova 1980; Popova *et al.* 1998). In North America, it competes for food resources with native fishes, such as Emerald Shiner (*Notropis atherinoides*), Yellow Perch (*Perca flavescens*), Trout-perch (*Percopsis omiscomaycus*), and other benthic planktivores (Ogle *et al.* 1995; Fullerton *et al.* 1998; MN Sea Grant 2013). Ruffe possesses a tapeta lucidum and sensitive lateral line systems, allowing it to forage in low-light conditions (Hölker and Thiel 1998). On each side of the head are three large lateral line canals (Jakubowski 1963; Wubbels 1991), inside of which are neuromasts that contain approximately 1000 hair cells and are innervated by about 100 afferent fibers (Wubbels *et al.* 1990). These canals provide directional sensitivity (especially to sound frequencies lower than 20 Hz (Gray and Best 1989)), allowing Ruffe to detect prey in low-light conditions when vision cannot be used (Wubbels 1991). In addition, it is speculated that Ruffe is fine-tuned to detect sound frequencies of their primary food item, chironomid larvae, which live in the surface of the mud on the bottom of a water body (Gray and Best 1989). This well-adapted foraging technique gives Ruffe a significant advantage over many fishes for feeding in deep, dark water, especially at night and during ice-cover (Eckmann 2004). Native fishes select against Ruffe; Mayo et al. (1998) found that native predators in Lake Superior, USA, including Northern Pike (*Esox lucius*), Smallmouth Bass (*Micropterus dolomieu*), Brown Bullhead (*Ameiurus nebulosus*), Walleye (*Sander vitreus*), and Yellow Perch, preferentially selected native fish species to eat even when Ruffe composed 71-88% of the available prey biomass in the environment.

LIFE HISTORY REQUIREMENTS: HABITAT

Adult Ruffe generally is demersal (Holcik and Mihalik 1968; Sandlund *et al.* 1985; Bergman 1988a) and prefer sandy, silty, well-aerated, slow-moving water with little or no vegetation (Kontsevaya and Frantova 1980; Popova *et al.* 1998; Ogle 1998) (Table 1). Ruffe inhabit lakes, rivers, ponds, bays, brackish waters, tidal estuaries, non-tidal estuaries, and reservoirs in its native range (Hölker and Thiel 1998). In non-native regions in North America, Ruffe is found in rivers, lakes, and coastal wetlands (Pratt 1988; Fairchild and McCormick 1996; Sierszen *et al.* 1996; Brown *et al.* 1998; Selgeby 1998; Stepien *et al.* 1998; Ogle *et al.* 2004; Ogle 2009; Peterson *et al.* 2011; USGS 2014); whereas, in other non-native regions, Ruffe is restricted to lakes and reservoirs (Wootten 1974; Maitland and East 1989; Duncan 1990; Kalas 1995; Eckmann 2004; Winfield *et al.* 2004; Lorenzoni *et al.* 2009; Volta *et al.* 2013) (Table 2).

Ruffe readily alters its behavior when introduced to a new water body. For example, Kalas (1995) demonstrated that Ruffe underwent a change in habitat use and prey consumption after introduction to Mildevatn, Norway, a lake that differs with respect to its fish and prey community structure from lakes in Ruffe's native range. Ruffe in Mildevatn fed primarily on zooplankton during June-

September. Further, it was mainly active during the day; 84% were caught during the day, significantly more compared to night capture (Kalas 1995) (Table 2). This finding is unusual, as Ruffe is typically nocturnal (Jamet and Lair 1991) or crepuscular (Westin and Aneer 1987).

EGGS

Ruffe can spawn multiple times per season (Fedorova and Vetkasov 1974; Kolomin 1977; Ogle 1998); spawning is intermittent and asynchronous (Hokanson 1977). Multiple studies report that Ruffe in its native range batch spawn (i.e., release multiple clutches of eggs throughout the spawning season) (Koshelev 1963; Fedorova and Vetkasov 1974; Hokanson 1977; Kolomin 1977) (Table 2). In Lake Glubokoe in the Moscow region of Russia, Ruffe spawned up to three batches in a two-month period (Koshelev 1963). Ruffe has the capacity to release up to three clutches of eggs (Lake Glubokoe, Russia (Koshelev 1963)); however, only two clutches typically are released in their native habitat (Fedorova and Vetkasov 1974; Hokanson 1977; Kolomin 1977) (Table 2). In the North American population, Brown et al. (1998) noted a prolonged spawning period, but they were unable to provide evidence for Ruffe laying multiple clutches of eggs (Table 2).

The first batch of eggs matures over winter (165 days (Hokanson 1977)) and is laid in the spring or early summer. The second batch, if there is one, matures during the summer (30 days (Hokanson 1977)) and is laid during the late summer (Koshelev 1963; Ogle 1998). During maturation, oocyte resorption of unspawned ova from a previous batch can occur without interfering with the growth of the current batch (Hokanson 1977).

Ruffe eggs are adhesive and laid on a variety of substrates (Balon *et al.* 1977; Collette *et al.* 1977) (Table 1, Figure 3A). A study conducted in the St. Louis River, USA, found the spawning period to last about 8 weeks, spanning April to June (depending on the year), during which temperatures ranged from 5-18°C (Brown *et al.* 1998) (Table 1). Hokanson (1977) stated that because of the fast rate of oocyte maturation, Ruffe requires relatively high temperatures (>11.6°C) (Bastl 1969) for spawning in their native range when compared with other percids, including Walleye, Eurasian Perch (*Perca fluviatilis*), Yellow Perch, and Pikeperch (*Sander lucioperca*), which all have lower spawning temperature limits (2-5°C). Ruffe embryos may require high dissolved oxygen concentrations because they lack a subintestinal-vitelline system and segmental vessels (Kovalev 1973; Kovac 1993); therefore, spawning grounds may need to be well-oxygenated (Table 1).

Fecundity is size-dependent and varies among water bodies (Kovac 1998). Neja (1988) found that absolute fecundity (total number of eggs per female) is less correlated to body length (r=0.752) than to body weight (r=0.801). In a study conducted in the side-arm of the Danube River in Baka, Slovakia (native range), the mean absolute fecundity for the first batch of a spawning female with a mean length of 96.3 mm was 23,731 eggs; the mean relative fecundity was 1,284 eggs/ gram of body weight (Bastl 1988; Kovac 1998). Fecundity estimates in the non-native range are limited. In Lake Piediluco, Italy (non-native) fecundity estimates were much smaller than those observed in most regions in the native range, although there was no information on batch spawning (Lorenzoni *et al.* 2009) (Table 2): the mean absolute fecundity was highly correlated with size—absolute fecundity ranged from 550 to 52,000 and the mean relative fecundity was 240 eggs/ g (Lorenzoni *et al.* 2009).

Absolute fecundity estimates for the first spawning batch range from 1,000 (Kovac 1998) to 200,000 eggs (Fedorova and Vetkasov 1974; Collette *et al.* 1977; Kolomin 1977; Neja 1988). Relative fecundities range from 585 to 1,540 eggs/ g (Neja 1988; Kovac 1998) in the native range but from 72 to 513 eggs/ g in the non-native range (Lorenzoni *et al.* 2009). The second batch was documented as being substantially smaller than the first batch in the native range: 352 – 6,012 eggs (Kolomin 1977). Kolomin (1977) determined that the first batch can be almost six times larger than the second batch.

Ruffe ovaries contain three types of eggs, only two of which are used during the spawning season (Neja 1988; Ogle 1998). The type that is not used is small, colorless, and glassy in appearance. The two that are used for spawning are in two different groups: 1) larger, opaque, whitish or light yellow to yellow or orange and 2) large, partly glassy, yellow or orange (Neja 1988; Ogle 1998). In the Danube River, Slovakia, Ruffe eggs were spherical and yellow (Kovac 1993, 1998).

Various ranges of egg diameter have been reported: 0.97-1.07 mm (Kovac 1998), 0.5-1 mm (Collette *et al.* 1977), 0.90-1.21 (Kolomin 1977), 0.71-1.59 mm (Lorenzoni *et al.* 2009), and 0.64-0.98 mm (Neja 1988) (Table 1). Ruffe in the Danube River and central and eastern Europe is thought to undergo saltatory ontogeny, described as seven embryonic stages and three larval stages prior to juvenile transition (Balon 1990). The embryonic period lasts approximately eight days when the water temperature is 16.2-23°C (Kovac 1998). The time to hatch is temperature-dependent. At 10^{-}15°C, Ruffe eggs hatch 5-12 days post-fertilization (Maitland 1977; Craig 1987); whereas eggs hatch 4-6 days after fertilization when temperatures range 16.2-23°C (Balon 1990; Kovac 1998) (Table 1).

LARVAE

Ruffe is 3.35-4.40 mm long at hatch (Fedorova and Vetkasov 1974; Kovac 1998) (Figure 3B, Table 1). It is stationary on the bottom of the water body for 3-7 days until they grow to 4.5-5.0 mm (Disler and Smimov 1977). Temperature for optimum growth in its native range is 25-30°C (Hokanson 1977) (Table 1). Approximately one week after hatch, larvae transition to exogenous feeding (French III and Edsall 1992) and remain demersal (Disler and Smimov 1977) (Table 1). At this stage, it is about 6-8 mm long and feeds primarily on zooplankton and small benthic invertebrates (Popova *et al.* 1998).

Although Ruffe generally is demersal after yolk sac absorption, it may temporarily occupy pelagic habitats to feed on large zooplankton prey (Popova et al. (1998) (native), Kalas (1995) (non-native)). By the end of the larval stage (16-18 mm), its prey includes large zooplankton (e.g., cladocerans, large copepods), ostracods, and small chironomids (Johnsen 1965; Ogle *et al.* 1995; Kangur and

Kangur 1996; Werner *et al.* 1996; Popova *et al.* 1998). The larval stage is about 20 days when temperatures range from 16.2-23°C (Kovac 1998) (Table 1).

Larvae can undertake both horizontal (i.e., between inshore and offshore) and vertical movements. Because it is sensitive to hypoxia, larval Ruffe may leave shallow spawning sites (less than 5 m) for deeper, cooler, well-oxygenated areas (Popova *et al.* 1998) (Table 1). In the Al. Stamboliiski Reservoir, Bulgaria (south), and the Votkinskoe Reservoir, eastern Russia (temperate), diel vertical migration (DVM) was observed in which larvae were concentrated at the surface (0-1 m) at night and concentrated at the bottom (5-6 m) during the day (Popova *et al.* 1998). Despite this isolated example, Ruffe larvae typically do not typically undergo DVM (Johnsen 1965; Fedorova and Vetkasov 1974; Disler and Smimov 1977; Ogle 1998).

JUVENILES

After the embryonic (8 days) and larval stage (20 days), the juvenile stage begins about 28 days after hatching (Kovac 1998) (Figure 3C, Table 1). Juveniles forage during the day, dawn, and night, although, more so at dawn and night (Disler and Smimov 1977; French III and Edsall 1992). Unlike larvae, they typically live in shoals (Disler and Smimov 1977; French III and Edsall 1992) and will undergo DVM during the summer, occupying deep water at night and shallow inshore habitat at dawn (Kovac 1998; Peterson *et al.* 2011). Juveniles may migrate from upstream reservoirs to downstream water bodies (Kovac 1998). However, in a survey of 22 lakes and reservoirs in temperate and northern Russia (native range), downstream movement of Ruffe was only observed in

54% of cases, while movements by European Perch and Pikeperch were more frequent, 75% and 100%, respectively (Popova *et al.* 1998). In temperate regions, from about June to July, juvenile Ruffe has been found to move from littoral to profundal areas in lakes in the former USSR (native range) (Mikheev and Pavlov 1993; Popova *et al.* 1998) (Table 1).

Juveniles also make seasonal movements. For example, in Russia (native range), they move to the deepest part of the body of water in which they reside, regardless of whether it is a lake, river, reservoir, or estuary to overwinter (Kovac 1998) (Figure 3E-F, Table 2). In June and July, juvenile Ruffe (40-60 mm) in the St. Louis River, USA (non-native range), was collected to determine habitat use; based on stable isotope ratios, half of the sample demonstrated recent use of Lake Superior habitat, and the other half showed recent use of river habitat (Hoffman *et al.* 2010) (Table 1).

In both the native and non-native range, juvenile Ruffe primarily consumes benthic invertebrates (Popova *et al.* 1998; Hoffman *et al.* 2010) (Table 1). However, if there is high abundance of large zooplankton prey, adult and juvenile Ruffe will ascend to the pelagic zone to feed periodically (Popova *et al.* 1998) (Table 1).

ADULTS: AGE AND SIZE AT MATURITY

Age at maturity for Ruffe varies from 1-4 years (Fedorova and Vetkasov 1974; Craig 1987; Neja 1988; Jamet and Lair 1991) (Figure 3H, Table 2). At the northern range of their climate, Ruffe matures at 2-3 years of age (Lind 1977; Maitland 1977; Ogle 1998). Presumably due to the northern climate, Ruffe in

Finland reached maturity at the age of 2-3 (Lind 1977; Lappalainen and Kjellman 1998) (Table 2). In the Nadym River basin, Russia (northern portion of the native range), Ruffe mature as early as age 2 but usually at age 3 or 4; most spawning Ruffe were reported to be 3-7+ years, between 20-30 grams and 110-120 mm (Kolomin 1977) (Table 2). However, in the Baka system of the Danube River (southern border of the native range), females matured between 57-90 mm and males matured at 80+ mm (Bastl 1988) (Table 2). Early maturity could be caused by a response to high mortality rates at the population level (Lind 1977) or to warmer water at a physiological level (Fedorova and Vetkasov 1974; Craig 1987).

No studies have been conducted on the age and size at maturity of the North American population; however, Ogle (1998) reported estimates of 2-3 years of age and 110-120 mm, based on Lind's (1977) Finland study and Maitland's (1977) fish guide to Britain and Europe. In the non-native population in Lake Piediluco, Italy, the age of maturity for both sexes was age 1; however, size of maturity varied between sexes—females matured at 78.74 ± 0.83 mm while males matured smaller at 69.42 ± 1.91 mm (Lorenzoni *et al.* 2009) (Table 2). In Loch Lomond, Scotland (non-native range), female Ruffe matures at 11.67 g and males at 7.5 g (Devine *et al.* 2000) (Table 2).

ADULTS: MAXIMUM AGE AND SIZE

Reports from Ruffe's native range in Finland and parts of Europe and non-native range in Britain indicate females live up to 11 years and males up to 7 years of age (Lind 1977; Maitland 1977; Crosier and Molloy 2007) (Table 2).

Whereas, in the Ob’ River, Russia (native range), Ruffe was as old as 20 years of age (Popova *et al.* 1998) (Table 2). Popova et al. (1998) noted that there are regional age differences—in temperate water bodies, the maximum age is typically 10 years, but in southern water bodies, the maximum age is closer to 8 years (Table 2).

Maximum age in the North American population (non-native range) was extrapolated from the native range. Given that the majority of Ruffe occurrences are in the Great Lakes fall in the 30°N temperate zone, the maximum age should be about 10 years based on former USSR information from Popova et al. (1998) (Table 2). Similarly, in the non-native ranges in Europe, Britain, and Scandinavia, one can infer the maximum age to be 8-10 years (Popova *et al.* 1998) (Table 2) because the introduced populations span from temperate to the southern regions. In Lake Piediluco, Italy (non-native range), the maximum age is 6 years (Lorenzoni *et al.* 2009) (Table 2).

The most-cited maximum length (290 mm) reported for Ruffe was from the Elbe River estuary (as cited in Holker and Thiel 1998), where adult Ruffe average size is about 250 mm (Holker and Hammer 1994) (Table 2). According to Berg (1949), a 500 mm Ruffe was caught in Siberia; however, this report has never been confirmed (Sanjose 1984) (Table 2). In Finland, it was reported that Ruffe only reach 200 mm (Lind 1977) (Table 2). Ruffe often do not grow to a large size in freshwater habitats. In the non-native North American population, the maximum size recorded was 207 mm (Ogle and Winfield 2009) (Table 2). In European non-native populations, Eckmann (2004) state Ruffe obtains lengths of

124 mm (Lake Constance, Germany), and Lorenzoni et al. (2009) report that the maximum length in Lake Piediluco, Italy is 191 mm and maximum weight is 141 g (Table 2).

ADULTS: FEEDING HABITS

In their native range, adult Ruffe primarily feeds on benthic organisms, generally chironomid larvae or pupae (Johnsen 1965; Polivannaya 1974; Kozlova and Panasenko 1977; Boikova 1986; Nagy 1988; Jamet and Lair 1991; Kangur and Kangur 1996; Werner *et al.* 1996; Kangur *et al.* 2000). Ruffe also consumes *Chaoborus* (Glassworm) larvae, Perlodidae (Stonefly) larvae, Culicidae (Mosquito) pupae, Ceratopogonidae (Biting Midge) larvae, (Jamet and Lair 1991), Tricoptera (Caddisfly) larvae (Polivannaya 1974; Jamet and Lair 1991; Ogle *et al.* 1995; Kangur *et al.* 2000), Odonata (Dragonfly) larvae, and Ephemeroptera (Mayfly) larvae (Ogle et al., 1995; Polivannaya, 1974); crustaceans (Johnsen 1965; Kozlova and Panasenko 1977) – *Asellus* (isopods), Ostracoda (Johnsen 1965; Kangur and Kangur 1996; Kangur *et al.* 2000), mysids, and brown shrimp (Holker and Hammer 1994) – and, when large enough, juvenile fish, such as Yellow Perch (Kozlova and Panasenko 1977) or Rainbow Smelt (*Osmerus mordax*) (Kozlova and Panasenko 1977; Holker and Hammer 1994; Kangur and Kangur 1996). Adult Ruffe periodically feeds on zooplankton (Kozlova and Panasenko 1977; Kangur *et al.* 2000), including copepods (Johnsen 1965; Boikova 1986; Holker and Hammer 1994; Kangur and Kangur 1996; Werner *et al.* 1996), cladocerans (Johnsen 1965, Boikova 1986, Kangur and Kangur 1996, Werner et al. 1996), and adult *Chaoborus* (Boikova 1986; Werner *et al.* 1996).

Ruffe eats Vendace (*Coregonus albula*) and Powan (*Coregonus lavaretus*) eggs in their native and non-native range (Kangur and Kangur 1996; Selgeby 1998; Kangur *et al.* 2000), potentially impacting populations of these fishes in some invaded areas (Adams and Tippett 1991) (Table 2). Lab experiments have been conducted to determine predation effects on Whitefish (*Coregonus* spp.) eggs (Mikkola *et al.* 1979; Sterligova and Pavlovskiy 1984; Pavlovskiy and Sterligova 1986) and demonstrated that Ruffe will eat the eggs, especially if there is no other prey (Sterligova and Pavlovskiy 1984) or if the eggs are fertilized (Mikkola *et al.* 1979). When Ruffe establishes populations in new water bodies, however, its feeding habits can shift to acclimate to the local habitats.

Adult Ruffe primarily feeds in shallow, littoral habitats at night (Leszczynski 1963; Holcik and Mihalik 1968; Jamet and Lair 1991) or twilight (Westin and Aneer 1987) and move to deeper waters during the day (Holcik and Mihalik 1968; Ogle *et al.* 1995) (Figure 3J, Table 1). However, in the St. Louis River, USA (non-native), adult Ruffe fed during the day in deep water (Ogle *et al.* 1995).

ADULTS: MOVEMENTS

Ruffe populations undergo routine movements throughout their life cycle (Figure 3); these movements vary by season and life stage and influence their distribution among habitats. Some important abiotic factors that affect its distribution include current velocity (in rivers), temperature, oxygen concentration, and salinity (in estuaries); however, food availability is probably the most important factor influencing movements and distributions of Ruffe (Popova *et al.* 1998). On a daily basis, predation risk can also cause Ruffe to change habitats and activity patterns (Popova *et al.* 1998).

ADULTS: SEASONAL MOVEMENTS

Adult Ruffe moves seasonally from shallow water during summer months to deep water (up to 70 m) in the fall and during spring ice-out to overwinter (Johnsen 1965; Kolomin 1977; Sandlund *et al.* 1985; Kovac 1998; Popova *et al.* 1998; Brown *et al.* 1998; Selgeby 1998; Eckmann 2004) (Figure E-G). Factors influencing the timing and location of seasonal movements include refuge from water currents, dissolved oxygen, salinity, or food availability (Johnsen 1965; Sandlund *et al.* 1985; Kovac 1998; Popova *et al.* 1998).

In the native Nadym River basin, Russia, many of the flood-plain lakes experience extreme hypoxia and freezing conditions, persisting from February to March. As a result, Ruffe moves seasonally, descending into Ob' Bay in late October and early November to overwinter and returning to the Nadym River in the spring (Kolomin 1977).

In the non-native range in North America, Ruffe was observed several kilometers offshore during December in Lake Superior, USA, at a depth of 15-30 m where they fed on Mysis (*Mysis diluviana*) and Cisco (*Coregonus artedi*) eggs (Selgeby 1998). It is likely these Ruffe return to nearby tributaries, such as the St. Louis River, USA, to spawn in the spring (Figure G-J). Ruffe may also remains in tributaries during the winter but moves to deep, channel habitats. In deep channels in the St. Louis River, USA, Ruffe was more abundant at ice out than during the summer months and was observed returning to deep channels when winter returned (Brown *et al.* 1998).

Ruffe was captured at depths of 30-70 m in the winter in Lake Constance, Germany (non-native), which suggests it had moved offshore (Eckmann 2004). In another invaded lake, Loch Lomond, Scotland, gut contents analysis showed no difference between winter and summer diets, possibly indicating these Ruffe were not moving; however, there was no mention of where the fish were captured (Adams and Tippett 1991). In Lake Mildevatn, Norway (non-native), Ruffe stayed in deep water in the winter and moved to shallow water in the summer, possibly due to spawning, change in diet, or reduced oxygen concentration (Kalas 1995).

ADULTS: SPAWNING MOVEMENTS

Ruffe spawning habitat varies with respect to both water quality and substrate. Spawning occurs in shallow water, approximately three meters or less, with pH levels of 6.5-10.5 for normal egg development (Kiyashko and Volodin 1978) (Table 1). Temperatures need to range from 6-18°C (Kovalev 1973; Fedorova and Vetkasov 1974; Kolomin 1977; Willemsen 1977; Kiyashko and Volodin 1978; Neja 1988; Ogle 1998) (Table 1). Spawning substrate varies; Ruffe can deposit their eggs on submerged plants, branches, rocks, or logs (Balon *et al.* 1977) (Table 1). Collette et al. (1977) found that Ruffe lays their eggs on sand, clay, or gravel substrates (Table 1). Field studies have supported both of these findings (Kovalev 1973; Fedorova and Vetkasov 1974; Kolomin

1977), suggesting that Ruffe spawning substrate is either population- or environment-specific.

Prior to spawning, Ruffe moves in shoals from their deep, overwinter habitats toward shallow, nearshore habitats (Figure 3G-J). Ruffe moves along the shoreline and concentrate at the mouths of rivers in its native habitat in the former USSR, including Kursian Bay, Syam Lake, rivers Prut and Dniester basins, lakes of the Bolshezemelskaya Tundra, bays of Ob' and Taz, and Lake Zaisan (Kontsevaya and Frantova 1980; Popova *et al.* 1998). In the waters of Kazakhstan, Ruffe shoals appear under the ice in March prior to spawning (Popova *et al.* 1998). Further, in the lakes of the Bolshezemelskaya Tundra, spawning Ruffe was already in shoals near the shore during the break-up of ice. Females arrived two days after the males to the spawning grounds (Popova *et al.* 1998).

ADULTS: GENOTYPE AND MORPHOLOGY

There are genetic and phenotypic differences among native and non-native populations. Stepien et al. (1998) identified five mitochondrial DNA control region haplotypes: a North American (Laurentian Great Lakes, USA) and Danube River, Slovakia haplotype; a Bassenthwaite Lake, United Kingdom haplotype; a St. Petersburg, Russia, including the Neva River Embankment and Komsomolskoe Lake haplotype; and two haplotypes in the Ob' River at Novosibirsk, Siberia, Russia (Table 2).

Within these haplotypes, there are two distinct groups that are genetically and morphologically different: a North America-Danube-Elbe River group and a

Bassenthwaite Lake-St. Petersburg-Ob' River group. Between the two groups, there is a mean genetic distance of 0.010 ± 0.0035, which is close to the distance (0.016 ± 0.005) separating two species of *Gymnocephalus* that Stepien et al. (1998) also examined. Multiple Ruffe experts have stated that Ruffe in the Danube River (same as North American Ruffe) are morphologically different than Ruffe in any other European regions, and the Danube River Ruffe was previously classified as a distinct morphotype (Stepien *et al.* 1998), *G. cernuus* natio *danubica*. There are four significantly different morphological traits among the five haplotypes of Ruffe. These traits include the relative length of the caudal peduncle, the number of pre-opercular spines, the relative length of the anal fin, and the number of soft spines in the dorsal fin (Stepien *et al.* 1998).

Based on mitochondrial DNA, the North American population matches the Danube and Elbe River population (Stepien *et al.* 1998); Stepien et al. (2005) had similar findings based on mtDNA and found that the Elbe River population matched the North American population. However, based on nuclear DNA, Stepien et al. (2005) determined that the Great Lakes population was established by a single founding population from the Elbe River drainage. More recent results using 10 nuclear DNA microsatellite loci confirm that the North American Ruffe population genetically matches that from the Elbe River region (C. Stepien, personal comm.). Moreover, Ruffe in North America has remained genetically similar over 20 years, with no evidence of additional introduction events, indicating that spread throughout the northern Great Lakes stemmed from the original population that was established at Duluth, MN (an international maritime freshwater port) in the St. Louis River, a tributary to Lake Superior (C. Stepien, personal comm.).

Summary/ Conclusion

Ruffe has a wide tolerance for chemical, physical, and biological conditions. This tolerance reflects their wide geographic distribution and utilization of a broad range of aquatic habitat types, including lakes, rivers, ponds, bays, coastal wetlands, brackish waters, tidal estuaries, non-tidal estuaries, and reservoirs. Ruffe also demonstrates variable movement and feeding strategies that are responsive to local environmental conditions. These characteristics help to explain the ability of Ruffe to successfully invade a wide variety of lakes and reservoirs. Yet, I did find that non-native populations have more restricted habitat use compared to native populations. Further, I found differences among native, non-native North American, and European non-native populations with regard to life stage-specific characteristics (i.e., number of eggs, reproduction, feeding habits, movements, and size and age). Several key knowledge gaps include geographic discrepancies and lack of data with respect to the native range; lack of reproduction information for populations in the non-native range, specifically from North America; and an overall lack of overwintering studies in both the native and non-native ranges. These topics are specifically addressed in the discussion. I further discuss the ecological implications of variability in life history characteristics between the native and non-native range, as well as management implications for Ruffe spread and invasion.

UNCERTAINTIES IN NATIVE AND NON-NATIVE RANGE

Despite an exhaustive literature search, my proposed range is fragmented in some regions, indicating undocumented introduction or lack of occurrence data (i.e., I could not distinguish between the absence of studies citing Ruffe captures in specific areas and actual Ruffe absences). The largest of these gaps is between the Nadym River, Russia (East) and Volga River, Russia (West). Although water bodies connect these rivers, I found no known Ruffe occurrences in this area.

Further, the biogeographic information is lacking and ambiguous in some regions. For example, many literature sources state that southern England is part of the native Ruffe range, but I could not find specific occurrences by water body in this region. Stepien and Haponski (2015) indicate the range of Ruffe is somewhat more widespread than my range, especially in Russia and Asia, a region for which the range has been poorly described. I found few occurrences within Eurasia, and thus the range within Eurasia should be interpreted with due caution. Stepien and Haponski (2015) also include regions within Ukraine in the range, whereas I found no published occurrences for that region. As with Russian and Asia, the range description would benefit from additional occurrence data here. I also have more discontinuities throughout Norway than Stepien and Haponski (2015). This discrepancy is likely due to my elevation cut-off, which was based on the highest elevation native Ruffe has been found.

Further, Ruffe may have been introduced to more locations than we are presently aware. For example, in the southwest region of the map, there is a native population in Lake Aydat, France, that is not connected to the rest of the range. Nearby, there is a cluster of introduced populations in Italy and Germany. The population in Lake Aydat could be introduced but was not documented as such because Ruffe was already present when the study was conducted. The author of the study simply states, “These fishes are widely distributed in European waters” (Jamet and Lair 1991). Lake Vastra Kyrksundet on the Aland Islands in Finland is another example of a potentially undocumented introduction (Bonsdorff and Storberg 1990). Ocean surrounds the island on all sides (on the eastern side there is a series of islands), but a native Ruffe population exists in a lake in the middle of the island. In 1932, a small artificial canal was built connecting the lake to the Baltic Sea. This tributary was blocked by a dam in 1979 in an attempt to return the lake to its original hydrological and ecological conditions (Bonsdorff and Storberg 1990). It is unknown if Ruffe was in the lake prior to 1932, but Bonsdorff and Storberg (1990) suggest it was. Ruffe is native and present along the coasts of Sweden and Finland in the Baltic Sea, Gulf of Finland, and the Gulf of Bothnia, so it is feasible that Ruffe could have established there naturally.

KNOWLEDGE GAPS AND UNCERTAINTIES

I determined that there were several substantial knowledge gaps in the scientific literature, specifically, reproduction information from the non-native range and overwintering ecology. Based on my review, data on fecundity, age and size at maturity, and spawning movements are all lacking for populations in the non-native range, especially North America. Few studies have been conducted on overwintering ecology and movements, an important stage for temperate fishes because it potentially represents a “bottleneck” for population size due to poor habitat condition (Reimers 1963, Cunjak and Power 1987, Nickelson et al. 1992, Giannico and Hinch 2003). Overwintering is also a period during which Ruffe may disperse. There are a few studies addressing overwintering in native and non-native European ranges and only one in North America. Despite the difficulty of sampling during the winter, there need to be more studies to identify overwintering habitat, including location, environmental character (i.e., depth, temperature, food availability), and differences between adults and juveniles.

NATIVE VERSUS NON-NATIVE POPULATIONS

I found substantial differences in certain life history characteristics, including maturity, size and growth, and temperature, between the native and non-native range. I found age at maturity to be based on latitude—generally, Ruffe further north matures later than southern Ruffe populations. Also, maximum length of Ruffe is almost always greater in native ranges than non-native ranges, possibly because in the native range Ruffe inhabits highly productive brackish water that provides high amounts of food, whereas Ruffe solely lives in freshwater in the non-native range. In addition to food abundance, Hölker and Thiel (1998) proposed that Ruffe has higher growth rates in brackish water due to temperature or salinity (or both).

Finally, Ruffe demonstrates adaptability to temperature differences between native and non-native ranges. For example, Hokanson (1977) stated that the optimal growth temperature for larval Ruffe is 25-30^{o}C, a temperature range that is rarely reached in its non-native North American range. Similarly, in the non-native North American range, Ruffe begins spawning at temperatures as low as 5^{o}C (Brown *et al.* 1998), but Ruffe requires a higher temperature (>11.6^{o}C) for spawning in the native range (Hokanson 1977). Ruffe seems to be well-adapted to the cooler temperatures of some of its native and non-native habitats; however, this adaptation is not without consequence. Ruffe in colder climates at more northern latitudes generally is shorter in maximum length (Eckmann 2004; Hölker and Thiel 1998; Lind 1977; Lorenzoni et al. 2009; USFWS, personal comm. 2014), matures later (Lind 1977; Maitland 1977; Ogle 1998), is smaller at maturity (and therefore likely less fecund) (Kolomin 1977; Devine *et al.* 2000; Lorenzoni *et al.* 2009), and requires longer for eggs to hatch (Maitland 1977; Craig 1987), leaving it vulnerable to predators for a longer period of time.

IMPLICATIONS FOR SPREAD AND ESTABLISHMENT

Even though it is not a highly migratory fish, Ruffe has spread and established populations across continents. Ruffe is particularly able to disperse and spread during the larval stage and the overwintering period. During the larval stage when Ruffe is a few millimeters long, water currents can potentially disperse it long distances. Further, although larvae are generally demersal, they can move into open waters where they are vulnerable to entrainment in ballast water by commercial ships and subsequent inadvertent translocation (as with the introduction to North America). At this small stage, accidental, human-mediated transport by bait bucket is also possible (commonly implicated with introductions in England).

Juvenile and adult Ruffe can move long distances to overwintering grounds. In some cases, these grounds were greater than 15 kilometers away from the summer rearing grounds; however, the fidelity to a specific spawning location is not known. Characterizing movements between spawning grounds and overwintering grounds, as well as straying rates when returning to natal spawning grounds, is likely important to understand spread across large, hydrologically-connected landscapes. Spread may be limited by spawning habitat availability. Each year, mature Ruffe must find warm (5-18˚C) and shallow (<5 m) habitat to spawn. However, Ruffe overwinters at depths greater than 15 m, so individuals must move inshore to spawn. In aquatic landscapes where suitable spawning habitat is widely geographically separated, this could limit dispersal.

Multiple traits combine to facilitate the successful establishment of Ruffe in an introduced water body. Ruffe has a broad tolerance for environmental conditions, including salinity, pH, and trophic level, and thus are able to inhabit a broad array of aquatic habitat types and conditions. Ruffe rapidly matures and can reproduce annually thereafter. It has a high fecundity with the ability to batch spawn for a prolonged spawning period, which is a useful trait for successful reproduction in variable environments (Koshelev 1963; Fedorova and Vetkasov 1974; Hokanson 1977; Kolomin 1977). It has multiple defenses against predators, such as a large dorsal spine, sensitive lateral line, and strong night vision. Ruffe is also an effective competitor, especially in dark environments, due to their tapeta lucidum, and sensitive lateral line (making hunting for food easier). Further, Ruffe can change its diet preference to select for the most abundant prey, which is a useful trait when introduced to a new water body.

Based on Ruffe's life history strategies and occurrence patterns in its native and non-native ranges, all of the Laurentian Great Lakes and many water bodies, particularly lakes, in the U.K., Europe, and Scandinavian countries are vulnerable to a Ruffe invasion. However, my review suggests there may be broad constraints to the spread and ecological impact of Ruffe establishment. To date, the types of water bodies in which it has established have been limited to lakes and reservoirs. Because Ruffe prefers turbid (eutrophic) and cool systems, this habitat preference may further constrain their spread.

Given the potential for ecological impacts, ongoing concern regarding the spread of Ruffe is warranted. Notably, management actions to prevent the spread of Ruffe are critical because Ruffe matures rapidly and has high fecundity, and thus can quickly establish a population. Upon establishment, Ruffe populations can increase rapidly and exceed the local carrying capacity, but then subsequently decline (Ruffe Task Force 1992, Peterson et al. 2011). Thus, the ecological impact of Ruffe establishment may be diminished over time. However, in an introduced water body, native predators may initially be reluctant to prey on Ruffe (Mayo *et al.* 1998). Also, Ruffe is highly competitive in low-light conditions and has the potential to alter population dynamics of prey (benthic invertebrates and zooplankton prey), competitors (forage fish), and fish predators (including through egg-consumption). One particular area of concern are isolated, inland lakes, exemplified by invasions in Western Europe and the UK, including Lake Constance, Germany, Austria, and Switzerland (Matthey 1966; Winfield et al. 1998), Loch Lomond, Scotland (Maitland and East 1989; Adams 1991), Lake Bassinthwaite, England (Winfield *et al.* 2004), and Lake Mildevatn, Norway (Kalas 1995). These lakes possessed environmental conditions suitable for Ruffe, and because they are closed systems with relatively low biodiversity, Ruffe has had a substantial effect on the benthic invertebrate, zooplankton, and prey fish communities.

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Chapter 2: Population change of an invasive fish, Ruffe, thirty years post-introduction: boom or bust?

Abstract

Invasive species often show a period of rapid initial increase (boom) followed by a population crash (bust) before settling into a relatively stable equilibrium population size. The purpose of this study was to determine trends in abundance of Ruffe at two locations and how they relate to the typical "boom-bust" population invasion patterns. Further, to identify potential interactions with native fishes, I compared the Ruffe catch per unit effort (CPUE) time-series to the corresponding time-series for common prey and predatory fishes in both the St. Louis River, MN/ WI, USA, and Chequamegon Bay, WI, USA, from 1993-2015. These systems were invaded by Ruffe at different time periods, both have similar fish communities, and CPUE data has been collected in both locations since Ruffe invaded. I found that Ruffe populations in the two systems are at different stages of invasion. In the St. Louis River, overall the population decreased from 1993-2015; the population increased from the initial invasion up to 1995 and has been declining for two decades (1996-2015). In Chequamegon Bay, the overall population is increasing, but is oscillating every 5-7 years. I conclude that Ruffe populations in both systems partially conform to the typical "boom-bust" patterns seen with other invasive fish species.

Introduction

Invasive species threaten biodiversity globally, alter the ecological function of invaded ecosystems, and cause extensive economic damage (D'Antonio *et al.* 2001; Arim *et al.* 2006). Invasive species can impact native species through both direct interactions, such as competition, predation, mutualism, herbivory, and parasitism, and indirect interactions, such as habitat alteration, cascading trophic interactions, and apparent predation (Sakai *et al.* 2001). However, the severity of a particular invasion depends on the invasive species' competitive ability and how the species interacts with its new environment (Blossey and Kamil 1996).

The Laurentian Great Lakes are among the most invaded ecosystems in North America; they have been subject to biological invasions since at least the early 1800s, following settlement by Europeans (Mills *et al.* 1994). They are vulnerable to invasion because of high shipping traffic, particularly transoceanic cargo ships, ballast water discharge, and a history of pollution and ecological disturbance (Stepien *et al.* 2005). The economic and ecological costs of some invasive species have been immense (Pimentel *et al.* 2005).

The timeline of population growth and spread of an introduced species can be conceptualized as a series of invasion stages (Sakai *et al.* 2001; Colautti and MacIsaac 2004; Simberloff and Gibbons 2004). In stage 0, propagules of the introduced species are in the donor region; in stage 1, the introduced species is transported outside of its current range; in stage 2, individuals are released and introduced into a new region. In stage 3, the species becomes established, distributed in a small area and is numerically rare. In stage 4, the species' population is either spatially widespread but numerically rare, or localized but abundant. Finally, in stage 5, organisms are widespread and dominant (Colautti and MacIsaac 2004). Often with invasive species, there is a lag time between stage 3 and stage 4 or 5, after which there is exponential growth (Sakai *et al.* 2001). Another common feature seen in invasive populations is a "boom-bust" cycle. A population crash ("bust") is often seen following the exponential growth ("boom") in some invasive populations (Simberloff and Gibbons 2004; Cooling and Hoffmann 2015). Lags and "boom-bust" cycles are thought to exist because of adaptive evolution as a part of the colonization and establishment process. During colonization there may be genetic constraints on the probability of successful invasion (Sakai *et al.* 2001). Once the population overcomes these genetic constraints, it has the ability to "boom" or grow very rapidly. This boom can result in dense local population or rapid range expansion (Sakai *et al.* 2001). At some point, these populations crash (Simberloff and Gibbons 2004). Studying these post-boom population declines may help us to understand the timeline and pattern of introductions.

The focus of this study is Ruffe (*Gymnocephalus cernua*: Percidae), a small-bodied, demersal fish native to Europe and Asia; specifically, its native range is from parts of Siberia and Russia to northeast France and southern England (Berg 1965; Kalas 1995; Rösch *et al.* 1996; Winfield *et al.* 1998b; Ogle 1998; Dawson *et al.* 2006; Gutsch and Hoffman 2016). Ruffe is invasive in parts of both Europe and North America (Gutsch and Hoffman 2016). In North America, Ruffe was first introduced to the Lake Superior basin, presumably via ballast water from transoceanic commercial vessels (Pratt *et al.* 1992a). Ruffe was first discovered in the Duluth-Superior harbor (the Great Lakes largest commercial shipping port), which is located at the far western end of Lake Superior in the St. Louis River (SLR), in 1986 (Bowen and Keppner 2013). It subsequently spread eastward, likely by dispersal along the southern shore of Lake Superior (MN Sea Grant 2016), and by 1993, Ruffe established in Chequamegon Bay (CB), a large embayment about 110 km east of Duluth-Superior harbor (MN Sea Grant 2016). Ruffe continued to spread along the south shore of Lake Superior, eventually reaching Whitefish Bay in the far east end of the lake in 2006. It was found in Lake Huron in 1995, and Lake Michigan in 2002 (Bowen and Keppner 2013). By 1998, Ruffe inhabited 16 tributaries on the south shore of the western arm of Lake Superior (Mayo *et al.* 1998). Bronte et al. (1998) concluded the increase in Ruffe was due to recruitment of large year classes in 1990, 1994, and 1995.

Ruffe can potentially reduce native fish diversity and abundance (Gutsch and Hoffman 2016). After it was first detected in Lake Superior, there was substantial concern that Ruffe would compete with native species (Ruffe Task Force 1992; Selgeby 1994; Evrard *et al.* 1998; Czypinski *et al.* 2002). During the early 1990s, when the Ruffe population size was rapidly increasing in the St. Louis River, the abundance of many native species were declining, including Yellow Perch (*Perca flavescens*), Emerald Shiner (*Notropis atherinoides*), Spottail Shiner (*Notropis hudsonius*), Trout Perch (*Percopsis omiscomaycus*), and Johnny Darter (*Etheostoma nigrum*) (Selgeby and Edwards 1993; Bronte *et al.* 1998). At that time, Mayo et al. (1998) conducted a diet study of native piscivores including Northern Pike (*Esox lucius*), Walleye (*Sander vitreus*), Smallmouth Bass (*Micropterus dolomieu*), large Brown Bullhead (*Ameiurus nebulosu*), and large Yellow Perch, and found that Northern Pike were the only predator that consumed a substantial biomass of Ruffe, but all predators consumed some Ruffe (Mayo *et al.* 1998). Notably, comparisons between the St. Louis River and Chequamegon Bay were useful to diagnose the effects of Ruffe by examining common trends in fish abundance; based on a set of comparisons between these two systems, Bronte et al. (1998) concluded that Ruffe was not causing declines in native fishes.

Despite an intense, regional focus on Ruffe during this time period, and the subsequent spread of this fish to other US Great Lakes, we know little of how its abundance has since changed in either the St. Louis River (SLR) or Chequamegon Bay (CB) over the past two decades. The objective of this study was to determine whether Ruffe populations in SLR and CB conform to typical invasive species boom-bust patterns. The boom-bust pattern is defined by an exponential increase followed by an exponential decrease to some equilibrium. Further, as an exploratory analysis, I compared Ruffe abundance to potential predator and competitor abundance through time to identify species that might have strong interactions with Ruffe in SLR and CB. For this study, my main hypothesis was that Ruffe populations conform to initial exponential growth and subsequent exponential decline (i.e., a boom-bust pattern). I tested the hypothesis separately for populations in the St. Louis River, WI/ MN, USA, and Chequamegon Bay, WI, USA.

Methods

STUDY AREA

The St. Louis River (SLR) is located in the western arm of Lake Superior (Figure 4, A). Its lower 30 km is classified as a drowned river mouth coastal wetland, also known as a “freshwater estuary,” which extends from Fond du Lac, MN, to the mouth at Lake Superior, and has a surface area of about 44 square km. The Port of Duluth-Superior is located where the river enters Lake Superior, and is afforded protection by a 16 km long barrier beach. The thalweg has a maximum depth of 16 m in the harbor and 8 m at the upper end of the river (Angradi *et al.* 2015). The river is mesotrophic (Bellinger *et al.* 2016), unlike Lake Superior, which is oligotrophic (Bronte *et al.* 1998). The turbidity is generally high with total suspended solids between the harbor, bay, and the river ranging from 10.2-13.0 mg/L (Bellinger *et al.* 2016). Mean dissolved oxygen in June and July is 7.82 mg/L (2.78-10.30 mg/L) (Bellinger *et al.* 2016). The maximum temperature is about 29^{o}C (G. Peterson, personal comm.). As of 2014, there were 52 documented fish species in SLR, most of which were cool or cold-water species (Peterson *et al.* 2011; Hoffman *et al.* 2016).

Chequamegon Bay (CB), WI, is located in southwestern Lake Superior (Figure 4, B). The surface area of CB is about 160 square km. It has a maximum depth of 23 meters and a mean depth of 9 meters. The bay is also mesotrophic (Bronte *et al.* 1998). Typically, total suspended solids range from non-detect to 3 or 4 mg/L (R. Lehr and M. Hudson, Northland College, personal comm.). The maximum temperature is 23^{o}C, and the average dissolved oxygen concentration is 10.5 mg/L (8.5-14.3 mg/L) between April and August (R. Lehr and M. Hudson, Northland College, personal comm.). It has 53 known fish species, 41 of them in common with SLR as of 2014 (USGS, personal comm.). Chequamegon Bay is a useful location for comparison to the St. Louis River because Ruffe established in CB shortly after the SLR population began to increase rapidly, and because the two systems have a similar fish assemblage, are part of the same drainage, are at the same latitude, and have been compared in previous studies (Bronte *et al.* 1998).

COMPETITOR AND PREDATOR SPECIES

For the St. Louis River, Ruffe and competitor catch data came from bottom trawl surveys conducted by US Fish and Wildlife Service (USFWS), 1854 Treaty Authority, US Environmental Protection Agency (USEPA), and US Geological Survey (USGS) (Table 3); predator capture data were from the Minnesota Department of Natural Resources (MN DNR) gill net survey. For Chequamegon Bay, Ruffe and competitor catch data came from bottom trawl surveys conducted by USFWS and USGS; predator catch data were from a Wisconsin DNR creel survey. Annual data were available for both systems from 1993-2015. During this time period, USFWS, USEPA, and 1854 Treaty Authority all used the same equipment and methods for bottom trawling; however, the methods used by the USGS varied slightly (Table 3).

I standardized trawl catch data for area swept catch per unit effort (CPUE; number of fish/ hectare) based on trawl width, tow duration, and vessel speed, assuming that the vessel type and speed did not affect trawl performance (Table 3). I calculated CPUE using the following equations:

$$\frac{\#\ of\ fish\ caught}{Tow\ time\ (min)} \times \frac{60\ min}{hour} = \#\ of\ fish/hour$$

Eq. 1

$$\frac{\#\ of\ fish/hour}{\#\ of\ hectares/hour} = \#\ of\ fish/hectare$$

Eq. 2

A notable concern is that different vessels were used for different time stanzas, that bottom trawl CPUE is density-dependent (i.e., the number of fish ahead of the bottom trawl affects catchability) (Godø *et al.* 1999) and influenced by environmental factors such as water clarity (Buijse *et al.* 1992) and substrate, and the St. Louis River in particular has undergone substantial ecological change over the course of the time-series (Bellinger *et al.* 2016). However, species-specific catches within the same system from vessel to vessel are generally consistent with regard to spatio-temporal effects (Benoit and Swain 2003). As such, I present the data throughout with due caution.

For the MN DNR gill net survey (76.2 m length, 1.83 m height, 5- 15.24 m panels with corresponding mesh sizes of 19.05 mm, 25.4 mm, 31.75 mm, 38.1 mm, and 50.8 mm), I calculated CPUE by dividing the mean summed total by the total number of net sets in a given year. I also analyzed gear selectivity to determine if the gill net was catching predator fish that were large enough to consume Ruffe (Figures A-1-4). I determined that the majority of predator fish caught in the gill nets were large enough (>300 mm) to consume adult Ruffe because most fish this size have a gape large enough to consume a fish that is an average of 70-120 mm (Scharf *et al.* 2000).

To calculate creel survey CPUE, I divided the annual sum of fish caught each year reported by anglers by the number of angling hours. This estimate is my least reliable relative measure of fish abundance, but is the only annual measure of game fish for Chequamegon Bay.

ANALYSIS

I estimated average Ruffe CPUE for sampling dates and sites and vessels per year for each system (SLR and CB). I used this same method for all competitors (Round Goby, Trout Perch, Yellow Perch, Spottail Shiner, Emerald Shiner, and Johnny Darter) and predators (Walleye, Northern Pike, Smallmouth Bass, and Muskellunge) of interest, as well. I chose the competitor species because they were the main fish affected by the Ruffe invasion back in the 1980s (Ruffe Task Force 1992); whereas, I chose the predator species because they were found to eat Ruffe (Mayo *et al.* 1998) or are large enough to eat Ruffe. Each species had a column of CPUE data and each row represented an average year of sampling. I standardized the samples to a common level of effort, and the level of effort used was one year. Some species had missing values for several years (Table A-1-4); I used a cubic spline method to impute data for those species (R package CRAN). The cubic spline method achieves a smooth interpolating function by creating a formula in which the first and second derivative are continuous and minimize error (Brumback and Rice 1998; Junninen *et al.* 2004). Columns of fish CPUE with too many (more than three) missing values together were removed from the analysis because the data were insufficient to support imputation. I analyzed SLR and CB data separately. The SLR dataset had 10 species: four predator and six competitor species. The CB dataset had 7 species: two predator species and five competitor species.

To test my hypothesis that Ruffe exhibited exponential growth ("boom") or decay ("bust"), I used an exponential growth model to estimate r using $N(t)= N(0)e^{rt}$, assuming N(0) and t_0 are population size and time at first detection, respectively, where r= relative growth rate, t= time, and N(t)= population after a time t has passed. I fit a linear model to the plot of ln(Ruffe CPUE + 1) vs Year for my dataset from 1993-2015. I conducted this analysis separately for SLR and CB, which allowed for comparisons. In addition, I expanded my analysis to include data from Pratt (1988), Ruffe Task Force (1992), and USGS from 1985-1992 in SLR to determine boom-bust cycles from the beginning of the Ruffe invasion. This addition allowed me to view the entire invasion period of Ruffe in SLR from 1985-2015. This data pre-1993 was not calculated by me, but CPUE was estimated using the same methods as data post-1993, and the data was collected using similar methods, so I considered it comparable. For this second analysis, I fit two linear models to the data: one from 1985-1995 (introduction to the maximum CPUE) and one from 1996-2015 (decline following maximum CPUE).

To test for a monotonic change in competitor or predator CPUE through time, I used the Mann-Kendall (MK) test (Mann 1945; Kendall 1975; Gilbert 1987), using the Kendall package in R (Hirsch *et al.* 1982). To determine which species were correlated with one another and with Ruffe, I analyzed each dataset using a Pearson correlation matrix and used the Pearson r value scale to classify the correlation strength: 0.00-0.19 = “very weak,” 0.20-0.39 = “weak,” 0.40-0.59 = “moderate,” 0.60-0.79 = “strong,” and 0.80-1.00 = “very strong” (Evans 1996).

To determine which species had the strongest statistical effect on Ruffe CPUE, I used univariate generalized linear models (GLMs) with Gaussian distributions for each of the variables in each of the systems (independent variables: competitor or predator species CPUE; dependent variable: Ruffe CPUE). I compared separate univariate models rather than multivariate GLMs due to model assumption violations and variable correlations. I natural log-transformed all catch data (i.e., (ln(CPUE +1)). For SLR, I had 11 models, and for CB, I had 8 models, including each competitor or predator species and intercept only model. I used Akaike Information Criterion (AIC) for model selection, correcting for small sample size (AIC_c). All analyses were conducted using R.

I ran an additional preliminary analysis examining fish lengths of Yellow Perch, Trout Perch, and Ruffe between the two systems to try to determine a condition factor between the populations. In SLR, I examined years 1989, 1995, and 2016. In CB, I examined 1998, 2011, and 2015. I chose these years because the first year was just after the Ruffe invasion, the second year was the peak of the Ruffe invasion so far, and the third year was the most recent data I had in that system. SLR and CB Ruffe, Yellow Perch, and Trout Perch lengths were collected from USGS and USFWS catch data. I averaged all recorded lengths for the three species for the specified dates. To compare ratios of total Yellow Perch, Trout Perch, and Ruffe in each system to one another, I multiplied average length by CPUE as a surrogate for biomass.

Results

Ruffe in SLR exponentially declined significantly from 1993-2015 (ln(Ruffe CPUE+1) = -0.113(Year) + 231.942, adj. $R^2 = 0.59$, $p<0.001$) (Figure 5). Incorporating the additional data for SLR, I found that the Ruffe population significantly increased from 1985-1995 (ln(Ruffe CPUE+1) = 0.634(Year) – 1256, adj. $R^2 = 0.88$, $p<0.001$) in the ten years immediately following its first detection, and declined from 1996-2015 (ln(Ruffe CPUE+1) = -0.147(Year) + 301.227, adj. R2 = 0.725, $p<0.001$) (Pratt 1988; Ruffe Task Force 1992, USGS, personal comm.) (Figure 6 and 7). In contrast, the Ruffe population in CB has undergone a significant exponential increase (ln(Ruffe CPUE+1) = 0.196(Year) -390.398, adj. $R^2 = 0.50$, $p<0.001$; Figure 8) since its first detection, but with apparent oscillations (Figure 6).

Based on the Mann-Kendall test, Ruffe CPUE in SLR has decreased overall from 1993-2015 ($p<0.001$, tau=0.66). In SLR, the CPUE of several fishes did change significantly over time. The CPUE of Northern Pike ($p=0.0013$, tau=0.488) and Yellow Perch ($p=0.02$, tau=0.352) both decreased, whereas the CPUE of Trout Perch ($p<0.001$, tau= 0.589), Round Goby ($p<0.001$, tau=0.544), and Emerald Shiner ($p=0.035$, tau=0.32) increased over time. Spottail Shiner, Johnny Darter, Muskellunge, Smallmouth Bass, and Walleye CPUE did not change over time (Figures 9 and 10). Ruffe CPUE in CB increased overall since its introduction from 1993-2015 (p<0.001, tau=0.561). According to the MK test, no other fish CPUE changed significantly over time in CB (Figure 11 and 12), recognizing that the predator CPUE data are from a creel survey. However, based on the plots in CB, Yellow Perch, Emerald Shiners, Spottail Shiners, and Johnny Darters all showed similar trends. They had a relatively high CPUE between 1993-2000, then decreased from 2001-2008, and increased again from 2009-2015 (Figure 11).

Based on the Pearson correlation matrices, I found that Ruffe and Trout Perch CPUE were strongly, negatively correlated and that Ruffe and Yellow Perch CPUE were strongly, positively correlated in SLR (Table 4). Ruffe CPUE was also moderately, negatively correlated with Emerald Shiner, and moderately, positively correlated with Northern Pike. Further, Northern Pike and Yellow Perch CPUE were strongly, positively correlated and Walleye and Spottail Shiner CPUE were also strongly, positively correlated (Table 4).

In CB, Ruffe CPUE had very weak to weak (Evans 1996) correlations with all other fish CPUE. Among the other fishes, Spottail Shiner and Emerald Shiner CPUE were very strongly, positively correlated (Table 5). Spottail Shiner CPUE was also strongly, positively correlated with Johnny Darter and Yellow Perch CPUE. Yellow Perch and Johnny Darter CPUE, too, were strongly, positively correlated. Emerald Shiner CPUE was moderately, positively correlated with Johnny Darter and Yellow Perch CPUE (Table 5).

Based on the generalized linear models, four univariate models make up 99% of the model weight for SLR (Table 6). As Ruffe CPUE decreased, so did

Yellow Perch and Northern Pike CPUE, while Trout Perch and Emerald Shiner CPUEs increased (Figure 13). The best model was the Yellow Perch model (62% of the AIC_c weight), followed by the Trout Perch model (24%), the Northern Pike model (7%), and the Emerald Shiner model (5%). Three of the four top models were competitors, and the proportion of model weight in the top 99% associated with competitors was about 93% (Table 6). All of the variables in the top four models were significant (their 95% confidence limits did not encompass zero); parameter estimates for Yellow Perch and Northern Pike were both positive, whereas parameter estimates for Trout Perch and Emerald Shiner were both negative (Table 7). Trout Perch and Emerald Shiner have been the most abundant fish in SLR recently, with the highest abundances of all time in 2013.

For CB, the generalized linear model was inconclusive. All of the models were within two AIC_c points of each other (Table 8). The two models with the most weight were the null model (intercept only) and the Northern Pike model, each of which made up 18% of the model weight (Table 8). That is, none of the species were significantly related to the increase of Ruffe in CB. Yellow Perch is the most abundant fish in CB, with the highest recorded abundances in 1998 and 2013.

In SLR, since the Ruffe invasion, average Yellow Perch lengths have decreased by about 20 mm and have not changed in CB (Figure 14). In both systems, Trout Perch lengths have not changed. In SLR, Ruffe lengths have stayed approximately the same and in CB they have increased by about 30 mm (Figure 14). The carrying capacity of the native fishes (Yellow Perch and Trout

Perch) in SLR seems to be about 4 times that of the carrying capacity in CB (Figure 15).

Discussion

I found that Ruffe CPUE in SLR significantly decreased overall, and Ruffe CPUE significantly increased from 1985-1995 and subsequently decreased from 1996-2015. In SLR, the Ruffe population conforms to the typical invasion theory “boom-bust” model and is currently in the “bust” phase. I also found that Ruffe CPUE in SLR is related to the CPUE of numerous potential competitors. Ruffe CPUE in CB significantly increased from 1993-2015. In CB, the Ruffe population partially conforms to the “boom-bust” model and is in the “boom” phase. CPUE in CB is not related to the CPUE of any potential competitor or predator species examined. Here, I discuss the CPUE patterns of Ruffe in SLR and CB and whether they conform to a boom-bust cycle, the weight of evidence for interactions with respect to both potential competitors and predators, and different factors responsible for fish population dynamics in SLR and CB.

CPUE PATTERNS OF RUFFE AND INVASION THEORY

By my analysis, the Ruffe population in the St. Louis River has been declining for two decades and was in the “bust” phase of the invasion at the time of the study. In 1995, the Ruffe CPUE reached a maximum, possibly indicating the population had reached or exceeded its carrying capacity, and then slowly declined. In the initial analysis, there was a modest rate of decline in CPUE from 1993-2015 (r=-0.113). In the additional analysis, I found a similarly modest rate of decline from 1996-2015 (r=-0.147), which contrasted strongly with a much greater rate of increase from 1985-1995 (r=0.634; Figure 6). Overall, the Ruffe population in SLR is at or past invasion stage 5 (Colautti and MacIsaac 2004) because it has been established for at least 30 years. Being in this stage should mean Ruffe is everywhere and regularly found within the ecosystem, not just captured in the original "hotspot" areas.

I found exponential growth in CB after 1993 but no evidence of recent long-term decline. Overall, there was a significant increase in Ruffe CPUE in CB, but the rate of increase is relatively small (r=0.196), much smaller than the rate of increase in SLR and similar to the rate of decline in SLR. It does not completely match the typical "boom" of most invasive species in a new environment, which usually has a very high rate of change after a lag period (Ruffe Task Force 1992; Simberloff and Gibbons 2004; Branstrator *et al.* 2017). That is, in SLR, in the first ten years of being established, the population boomed to over 1808 fish/ hectare; whereas in CB, in the first ten years of establishment, the captured population size was only about 7 fish/ hectare (Figure 6). The Ruffe population in CB either was slow to establish since it was first discovered in 1993, or agencies had difficulties catching it, because there was nearly 0 CPUE for the first five years of its invasion. This lag time in population growth is similar to the lag time that was described by Sakai et al. (2001) and Branstrator et al. (2017) commonly found in aquatic invasive populations between stage 3 and stage 4 or 5. In CB, Ruffe is at an earlier stage of invasion than in SLR and is in the "boom" phase of the invasion, indicated by the exponential population increase since 1993. In CB, the invasion stage is likely at a 4 (Colautti and MacIsaac 2004). The distinct pattern observed in CB CPUE is that every 5-7 years the population oscillates, underlying the overall increase in abundance (Figure 8). The cause of these oscillations are not known, but they could be due to an unreliable food source or inter- or intraspecific competition (Ruffe Task Force 1992).

Comparing these two systems, which include the two largest populations of Ruffe in the North America (Gutsch and Hoffman 2016), Ruffe partially conforms to the typical “boom-bust” invasion population patterns, but they are at different stages (Figure 6) (Simberloff and Gibbons 2004; Cooling and Hoffmann 2015). The “bust” in SLR has been slow (21 years), and the “boom” in CB is gradual and is in the 23rd year of the invasion. The “boom” in CB (r=0.196) is very different from the “boom” in SLR (r=0.634) after the Ruffe’s first detection (Figure 6). However, it is possible that Ruffe was present long before its first detection in SLR.

EXPLORATORY ANALYSIS OF COMPETITORS AND PREDATORS

The strong correlations between Ruffe CPUE and competitor CPUE in SLR suggests that competition for food, space, or other resources may be contributing to the Ruffe decline. As Ruffe populations decrease, Trout Perch and Emerald Shiner may be outcompeting Ruffe and Yellow Perch. However, based on many sources, I could not find a mechanistic explanation for the Ruffe decline. The two lines of evidence I examine are spawning habitats (Beard and Carline 1991) and diet (Chapman 1966) because these factors are the most common causes of competition that may cause a population to decline.

Ruffe and Trout Perch may compete for spawning habitat. Trout Perch and Ruffe spawn at similar times (starting in early spring and continuing through the summer) (Muncy 1962; Magnuson and Smith 1963) and depths (less than 1.524 m) (Muncy 1962; Magnuson and Smith 1963; Gutsch and Hoffman 2016). Trout Perch spawns on silt or boulder bottoms at 4-10^{o}C (Lawler 1954). Ruffe spawns on almost any substrate at 5-18^{o}C (Gutsch and Hoffman 2016). Yellow Perch, however, spawns in submerged vegetation and brush at 36-44^{o}C (Muncy 1962). This is a feasible hypothesis, but more evidence is needed to claim that this is the reason for the Ruffe decline.

According to Ogle et al. (1995), Ruffe and Yellow Perch have similar diets, as do Trout Perch (Wells 1980), suggesting competition for food resources. Adult Ruffe eats midges, macrobenthos, burrowing mayflies, and caddisflies (Ogle *et al.* 1995). Adult Yellow Perch eats amphipods, fish eggs, Mysis (which are not in the river), and crayfish (Wells 1980), as well as small fish. Muncy (1962) found that Yellow Perch eats small crustaceans and insects, especially chironomids, one of the Ruffe's preferred food items (Gutsch and Hoffman 2016). Trout Perch eats amphipods, immature midges, and zooplankton (Wells 1980). Thus, the three species could compete for food resources owing to diet overlap. However, Hoffman et al. (2010) found that Ruffe and Yellow Perch in SLR are more isotopically similar to each other than Trout Perch, not suggesting competition for food resources. They found that Trout Perch had higher $\delta^{15}N$ values than Yellow Perch or Ruffe, suggesting they are feeding at different trophic levels. Moreover, Yellow Perch and Trout Perch are typically inactive at night (except during spawning) and feed during the day (Muncy 1962; Magnuson and Smith 1963); whereas, Ruffe is often most active at night, feeding in the shallow areas in the darkness (Ogle *et al.* 1995). Also, it uses different habitats (Peterson *et al.* 2011). Ruffe is primarily in the thalweg (highest CPUE in trawls), whereas Yellow Perch tends to be in littoral habitat (highest CPUE in fyke nets and electrofishing) (Peterson *et al.* 2011). So, while it is possible these fishes are depleting the same resources, the competition may not overlap temporally or spatially. Based on stable isotope evidence and likely diel habitat partitioning, it is unlikely that there is diet competition with Ruffe and Yellow Perch.

FACTORS THAT AFFECT FISH POPULATION DYNAMICS

My findings suggest a recent divergence between SLR and CB. Bronte et al. (1998) found similar trends between SLR and CB among many fish species in the years 1989-1996; whereas I found Ruffe CPUE trends were quite different between the two systems. I found both positive and negative associations between Ruffe and other fishes in SLR, but no significant associations between Ruffe and other fishes in CB. The CPUE data indicate that the population dynamics of Ruffe, and possibly other fishes in CB and SLR are highly variable and are likely not influenced by the same variables. The data included in this study (CPUE of competitor and predator fishes) was not able to account for the observed oscillations of Ruffe CPUE in CB. There was possibly a divergence of these two systems since Bronte et al. (1998), and this topic is worthy of further investigation.

In CB, I found no indication that other fish populations have declined due to the invasion of Ruffe. Because CB is at an earlier invasion stage, it is possible the ecological effects of Ruffe has not yet been realized (i.e., Ruffe densities are too low or catch efficiency is too low); therefore, interactions with other fishes would not be measurable yet. The overall population size of Ruffe in CB since its introduction has been substantially less than the population size of Ruffe in SLR in the corresponding year of invasion (Figure 6). It is possible that CB is not as suitable of an environment for Ruffe. If that is the case, there may not be significant ecological changes to CB due to the invasion of Ruffe. Future research should examine and map Ruffe range expansion and contraction, which could provide new insights regarding changes from “boom” to “bust” and time-dependent patterns of invasion of a particularly prolific invasive species. Understanding these boom-bust cycles in invasive species is important to recognize for formulation of management decisions relating to invasive species control.

Chapter 3: Using stable isotopes to characterize Ruffe (*Gymnocephalus cernua*) trophic pathways and movements in the St. Louis River and Chequamegon Bay, USA

Abstract

Food webs have been altered by invasive species in ecosystems throughout the globe. Stable isotope ratios are commonly used to trace trophic pathways and study complex landscape inputs, and thereby understand how food webs are structured. The goals of this study were to identify energy sources contributing to Ruffe production and use habitat-specific stable isotope ratios to study life stage-specific movements. I measured Ruffe $\delta^{13}C$ and $\delta^{15}N$ values in the St. Louis River and Chequamegon Bay and estimated the diet contributions from various habitat-specific organic matter (OM) sources, including Lake Superior benthic periphyton, coastal wetland benthic periphyton, riverine matter derived from a mix of phytoplankton and terrestrial OM, and river sediment methane using a mass-balance mixing model. Further, I identified size-based or stage-based movements between Lake Superior and inshore habitats based on Ruffe $\delta^{13}C$ and $\delta^{15}N$ values. I found significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between Ruffe captured in Lake Superior and those captured in the St. Louis River, but not among locations within the river. I found size-based differences, as well; medium-sized fish, 65-85 mm standard length (SL), had $\delta^{13}C_{\text{lipid corrected}}$ values of about -40‰ to -16‰, a spread of 24‰. However, small fish (<65 mm SL) had $\delta^{13}C_{\text{lipid corrected}}$ values of -50‰ to -24‰, shifted -10‰ with a spread of 26‰; and large fish (80-148 mm SL) had $\delta^{13}C_{\text{lipid corrected}}$ values of -54‰ to -14‰, which is a spread of 40‰, spanning the range of values measured in this study. Extremely depleted ^{13}C values (<-36‰ $\delta^{13}C$) indicate that some fish captured within coastal wetlands were feeding in a methane-based trophic pathway. The high $\delta^{13}C$ values of both small and large Ruffe indicate these fish were both swimming and

feeding in Lake Superior; the higher values of medium size Ruffe indicate coastal wetland dependence during the spawning period. The broad range in $\delta^{13}C$ values of large Ruffe indicate routine occupancy of both lake and wetland habitats; 59.7% of individuals were predominantly feeding in a wetland-dominated trophic pathway, whereas 40.3% were feeding in a lake-dominated trophic pathway. This observation is the first of wetland fish obtaining substantial energy from a methane-based food web, as well as the first observation of distinct, size-based diet shifts and movements among coastal habitats in Ruffe. This indicates Ruffe has the ability to occupy a novel trophic niche within coastal wetlands and is an obligate user of wetland habitat during spawning but otherwise facultative user of lake and wetland habitat.

Introduction

Great Lakes coastal wetlands support many ecological, economic, and cultural ecosystem services (Sierszen *et al.* 2012). Coastal wetlands provide plant and animal habitat, hydrologic retention, nutrient cycling, shoreline protection, and sediment trapping, providing an important role in the Great Lakes ecosystem. They support a great biodiversity that drives the Great Lakes food web with up to one-third of the primary production originating in coastal wetlands (Brazner *et al.* 2000). Characterizing the food web of a coastal wetland is challenging because the organic matter supporting consumers comes from a variety of sources within the ecosystem (Hoffman *et al.* 2015). The landscape mosaic of a Great Lakes coastal wetland generally is composed of three ecosystems: terrestrial, coastal wetland (river and wetland), and lake. Within the aquatic ecosystems are littoral, benthic, and pelagic habitats, each supported by distinct energy sources.

Positioned between the land and the lake, coastal wetland food webs are fueled both by high photosynthetic production (i.e., autochthonous energy sources) and by inputs of energy and nutrients from these adjacent ecosystems (i.e., allochthonous inputs; (Hoffman *et al.* 2010)). Another potential source of energy to the food web is chemosynthetic production of methane within river sediments, which can contribute to higher trophic levels when primary consumers graze on a mix of particles and methane-oxidizing bacteria (MOB) in stratified sediments (Bastviken *et al.* 2004; Jones and Grey 2011). At the base of most food webs is phytoplankton. The autochthonous carbon from phytoplankton can be limited by nutrient availability, light, resident time, phytoplankton growth rate, and dissolved CO_2 (DIC) concentration and may be used by organisms like zooplankton and benthic macroinvertebrates (O'Leary 1981; Farquhar *et al.* 1982; Hoffman and Bronk 2006; Hoffman *et al.* 2010). Primary consumers, including zooplankton, benthic invertebrates, and fish, may also consume allochthonous organic matter, such as particulate organic matter derived from riparian or upland vegetation, which can potentially enhance overall productivity (Wallace *et al.* 1997; Cole and Caraco 2001; Hoffman *et al.* 2008, 2010). These allochthonous carbon and energy subsidies can supplement autochthonous primary production in both pelagic and benthic food webs (Jansson *et al.* 2007; Reynolds 2008; Jones and Grey 2011; Hoffman *et al.* 2015).

These same allochthonous carbon inputs can be processed by heterotrophic bacteria under oxic conditions, providing biomass for zooplankton grazers (Jones and Grey 2011). However, in anoxic conditions, which are common in the hypolimnion of stratified lakes and in aquatic sediments, carbon may originate by different microbial metabolic pathways, especially methanogenesis. Lake sediments are known for their high methane production and their significant contribution to the global methane budget (Bastviken *et al.* 2004). Some of this methane is available to methane-oxidizing bacteria (MOB), which oxidize it once it reaches an oxygenated sediment layer or water column (Rudd and Taylor 1980; Bastviken *et al.* 2003, 2004; Whalen 2005; Juutinen *et al.* 2009; Jones and Grey 2011). Not only does methane get added to the biogeochemistry of the lake, but it also becomes an important source of carbon and energy in freshwater trophic pathways, where it is readily available to benthic invertebrates (Bastviken *et al.* 2003; Jones and Grey 2011).

Across the globe, aquatic food webs have been greatly impacted by invasive species (Gurevitch and Padilla 2004). These food web impacts can have detrimental ecosystem-level effects, including modified habitat coupling, nutrient cycling, and ecosystem resilience (Eby *et al.* 2006; Britton *et al.* 2010; Pilger *et al.* 2010; Walsworth *et al.* 2013). Invasive species can have strong impacts on aquatic food webs owing to the competitive advantage invasive fish have over native fish (Cox and Lima 2006; Walsworth *et al.* 2013). Although it is challenging to detect or predict the impacts of invasive species on aquatic food webs, some of these interactions are still measureable (Polis 1991; Lodge 1993; Polis and Strong 1996). This is an even greater challenge at the landscape-scale because it requires consideration of inputs from multiple aquatic habitats and also adjacent ecosystems (Hoffman *et al.* 2015).

Stable isotopes of light elements such as hydrogen, carbon, nitrogen and sulfur are useful for tracing both autochthonous and allochthonous trophic pathways in coastal food webs (Hoffman 2016). For example, because there is little isotopic fractionation of carbon between a consumer and its diet (about 0.4‰) (Vander Zanden and Rasmussen 2001), carbon stable isotopes can be used to trace consumer diets, identify predator-prey relationships, and elucidate trophic pathways (i.e., the connection between a carbon source such as phytoplankton and a high-level consumer). In particular, where organic matter sources that are potentially contributing to a coastal food web have distinct carbon stable isotope ratios (i.e., $\delta^{13}C$ values), aquatic food webs can be reconstructed and major trophic pathways identified (Hecky and Hesslein 1995; Vander Zanden and Rasmussen 2001). Further, nitrogen stable isotope ratios can be used to estimate consumer trophic position because consumers exhibit a consistent and measurable enrichment in ^{15}N with each successive trophic level (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999, 2001). Typically, consumer $\delta^{15}N$ values are enriched by 3.4‰ on average above that of their prey (Vander Zanden and Rasmussen 2001; McCutchan *et al.* 2003). If both carbon and nitrogen stable isotope ratios are measured, trophic position, omnivory, energy sources and flows, and food chain length can be determined (Vander Zanden and Rasmussen 2001). Carbon and nitrogen stable isotopes have been shown to be particularly helpful in studying Great Lakes coastal wetland food webs because many of the available organic matter sources (e.g., phytoplankton, epiphytic periphyton, emergent vegetation, benthic periphyton, etc.) have distinct isotopic ratios (Keough *et al.* 1996; Hoffman *et al.* 2015).

I studied the trophic ecology of Ruffe, an invasive fish, in Lake Superior coastal wetlands. Ruffe is native to Europe and Asia and was accidentally introduced to the US through ballast water discharge (Simon and Vondruska 1991; Pratt *et al.* 1992b). Ruffe is a small, demersal percid that consumes benthic invertebrates and has been found to compete with other small forage fishes native to Lake Superior (Ruffe Task Force 1992; Evrard *et al.* 1998; Czypinski *et al.* 2002). In 1986, Ruffe was first discovered in the St. Louis River (SLR), a drowned river mouth coastal wetland in far western Lake Superior, and subsequently spread across the upper Laurentian Great Lakes (Bowen and Keppner 2013). Ruffe inhabits coastal wetlands throughout the year, but also inhabits Lake Superior waters up to 205 m depth (Gutsch and Hoffman 2016). The effects of Ruffe on Lake Superior coastal wetland food webs were studied in the mid-1990s during a period when Ruffe had become relatively abundant (Czypinski *et al.* 2002; Bowen and Keppner 2013) but not since. Over the past twenty years, these wetlands have undergone substantial change with respect to fish assemblages and environmental conditions (Angradi *et al.* 2015; Bellinger *et al.* 2016). My objectives for this study were to identify trophic pathways between basal energy sources and Ruffe using carbon and nitrogen stable isotope ratios (i.e., $\delta^{13}C$ and $\delta^{15}N$ values) and to use habitat-specific stable isotope ratios to trace movements of Ruffe between coastal wetlands and Lake Superior. First I measured $\delta^{13}C$ and $\delta^{15}N$ values in Ruffe in two large, coastal ecosystems in Lake Superior – St. Louis River and Chequamegon Bay. I used dual-isotope mixing models to estimate the contribution of both photosynthetic and chemosynthetic carbon sources to the food web. The photosynthetic sources included coastal wetland benthic periphyton, Lake Superior benthic periphyton, and riverine organic matter (itself a mix of freshwater phytoplankton and terrestrial-derived organic matter). The chemosynthetic source was methane from river sediments. I further identified movements of Ruffe based on mis-matches between where the individual fish was captured (i.e., Lake Superior or coastal wetland) and the fish's trophic pathway based on its $\delta^{13}C$ and $\delta^{15}N$ values.

Methods

STUDY SITE

In this study, I examined coastal wetland and lake ecosystems and benthic habitats in the landscape mosaic. My primary study sites were two Great Lakes coastal systems: St. Louis River, MN and WI, a drowned river mouth coastal wetland located in the western arm of Lake Superior, and Chequamegon Bay, WI, a large coastal embayment located in the southwestern part of Lake Superior (Figure 16). Both areas are biogeochemical mixing zones and are suitable for stable isotope food web studies because the variety of organic matter source inputs (i.e., Lake Superior phytoplankton or benthic periphyton, coastal wetland phytoplankton or periphyton, coastal wetland vegetation, terrestrial-derived organic matter) have distinct $\delta^{13}C$ and $\delta^{15}N$ values (Hoffman *et al.* 2015). Coastal wetlands in the Great Lakes are good examples of “transition zones,” where one geochemically distinct water source flows into another, even though all the water is freshwater (as opposed to a marine estuary) (Hoffman *et al.* 2010). These geochemical transition zones are important for conducting stable isotope studies because they provide the basis for food webs along the transition zones to have distinct isotopic compositions owing to isotopic mixing. The St. Louis River is 288 km long, and the watershed has an area of 9,412 km^2 (Hoffman *et al.* 2010). The estuary is about 50 km^2 and lies between Minnesota and Wisconsin (Angradi *et al.* 2015). Water height varies daily by about 13 cm due to weak semi-diurnal tides and periodic seiche flows of about 8 hour duration (Trebitz 2006). There are several ecologically distinct regions within the St. Louis

River, including two turbid, clay-influenced bays (Allouez Bay, Pokegama Bay), two large lake influenced bays (Superior Bay, St. Louis Bay), a large river-influenced bay (Spirit Lake) and an upper section that, although bi-directional in flow, has a confined channel and for which the water chemistry is not influenced by lake exchanges (Figure 16). Water clarity is relatively low throughout the river owing to both high dissolved organic carbon concentrations and occasionally high suspended solids concentrations (Bellinger *et al.* 2016). The average depth is 3.0 m (maximum depth 16 m; (Angradi *et al.* 2015; Bellinger *et al.* 2016)).

Chequamegon Bay has a surface area of about 160 km^2. Water quality in Chequamegon Bay is much more lake-influenced than in the St. Louis River; influence of tributary waters is largely limited to the south end, at the mouth of Fish Creek, which is the largest tributary to Chequamegon Bay (Hoffman et al. 2012). The mean depth is about 9 m (maximum 23 m). Water clarity throughout Chequamegon Bay is generally higher than in the St. Louis River.

FISH COLLECTIONS

Fish were collected in the summer and fall of 2014, winter of 2014-2015, spring of 2015, and summer of 2015 using a mix of approaches, including by otter trawl, fyke net, or anglers ice fishing (Table 9, Figure 17). Once collected, Ruffe were placed in a clean, plastic bag, and then stored on ice to be transported back to the US EPA Mid-Continent Ecology Division, Duluth, MN, laboratory where they were frozen at -20° C until they were processed.

LABORATORY METHODS

Ruffe were thawed, measured (standard, fork, and total length ±1 mm), and weighed (± 0.1 g wet weight). Using a sterilized scalpel, I obtained a muscle sample from the dorsal side of each fish and removed the skin from the tissue sample. I rinsed the sample thoroughly with DI water, dried the tissue at 45^oC for 24 hours, and ground the tissue into a powder. I used a Costec 4010 EA and Therma Delta Plus XP isotope ratio mass spectrometer to analyze the fish tissue (US EPA Mid-Continent Ecology Division, Duluth, MN). Stable isotope ratios are reported in δ notation, $\delta X{:}\delta X = (R_{sample}/R_{standard} - 1) \times 10^3$, where X is the C or N stable isotope, R is the ratio of heavy to light stable isotopes, and Pee Dee Belemnite and air are the standards for $\delta^{13}C$ and $\delta^{15}N$, respectively. I normalized $\delta^{13}C$ value for lipid content using an arithmetic mass balance correction based on bulk C:N ($C{:}N_{bulk}$) values, with $C{:}N_{lipid\ free}$ of 3.5 (SD±0.3) and lipid isotopic discrimination of -6.5‰ (SD±0.4‰; (Hoffman *et al.* 2015)).

ANALYTICAL METHODS

To test whether there were significant differences in either $\delta^{13}C_{lipid\ corrected}$ or $\delta^{15}N$ values among capture areas (upper estuary, lower estuary, and Lake Superior), I used a Kruskal-Wallis One-Way Analysis of Variance on Ranks. The Upper estuary area included the St. Louis River and Spirit Lake; the lower estuary area included St. Louis Bay, Superior Bay, and Allouez Bay; and the Lake Superior area included both open waters and embayments (e.g., Cheqaumegon Bay).

I used Ruffe $\delta^{13}C$ and $\delta^{15}N$ data to build a dual isotope, three-source mixing model (Phillips and Gregg 2001) to quantify source contributions from

Lake Superior benthic periphyton, a mix of benthic and pelagic organic matter from lower estuary (the “bentho-pelagic” food web, which is mix of phytoplankton and river sediment that is isotopically difficult to separate; (Hoffman *et al.* 2010)), and a mix of phytoplankton and river sediment from the upper estuary. For the mixing model, the proportional contribution to the fish’s isotopic composition from each source must sum to 1 (Phillips and Gregg 2001). Following Blazer et al. (2014), I selectively fit δ^{15}N and $\delta^{13}C_{\text{lipid corrected}}$ values when either or both value fell outside the convex hull of the polygon defined by the δ^{13}C and δ^{15}N values of the three sources. The model fit was iterative, adjusting the δ^{15}N (or δ^{13}C) until all source contributions were between 0 and 1. This is necessary because the model does accommodate variability in source stable isotope ratios. I preferentially adjusted the δ^{15}N value because small changes in the trophic level have a much larger effect on the fish’s δ^{15}N value than its δ^{13}C value. I had to adjust 133 (out of 220 fish) δ^{15}N values and 21 $\delta^{13}C_{\text{lipid corrected}}$ values to fit the fish to the model. The mean adjustment was 0.64‰ (range: 0‰ to 5.2‰) for δ^{15}N values and 1.0‰ (range: 0‰ to 1.9‰) for $\delta^{13}C_{\text{lipid corrected}}$ values.

I used available fish and invertebrate data to define the sources for the mixing model. These sources were used to represent spatially distinct trophic pathways within Lake Superior and coastal wetlands to facilitate the interpretation of the stable isotope data with respect to both diet and movements. The Lake Superior trophic pathway is based on benthic periphyton, which is an important carbon source in the nearshore of the lake (Keough *et al.* 1996; Sierszen *et al.* 1996). To define the source value, I used Ruffe captured in Lake

Superior that had an isotopic composition consistent with consuming nearshore benthic invertebrates ($\delta^{13}C$ <<-20‰; (Hoffman *et al.* 2015)): mean $\delta^{13}C_{\text{lipid corrected Lake Superior}}$ = -16.3‰, SD±2.17‰, and mean $\delta^{15}N_{\text{Lake Superior}}$ = 5.38‰, SD±0.78‰, N=74. The two estuarine trophic pathways are both based on a mix of river sediment and phytoplankton, but are distinguishable by location (upper estuary versus lower estuary) due to the longitudinal mixing of river and lake waters, which enriches the ^{13}C content of the food web at the river mouth (Hoffman *et al.* 2010), as well as the contribution of waste water treatment effluent, which enriches the ^{15}N content of the food web at the river mouth (Hoffman *et al.* 2012). To define the upper estuary source value, I used the mean $\delta^{13}C_{\text{lipid corrected}}$ and $\delta^{15}N$ values of White Sucker (*Catostomus commersonii*) captured in the river above Spirit Lake (i.e., associated with my upper estuary locations) from Blazer et al. (2016): mean $\delta^{13}C_{\text{lipid corrected upper estuary}}$= -34.0‰. SD±1.9‰, mean $\delta^{15}N_{\text{upper estuary}}$= 8.6‰, SD±1.3‰ (N=104). I used these values because White Sucker, like Ruffe, is a demersal fish that primarily consumes benthic invertebrates (Blazer *et al.* 2014; Gutsch and Hoffman 2016). The water near the Western Lake Superior Sanitary District (WLSSD) effluent, near the city of Duluth in the lower estuary, is typically ^{15}N-enriched (Hoffman *et al.* 2012). To define the lower estuary source value, I used the mean $\delta^{13}C_{\text{lipid corrected}}$ and $\delta^{15}N$ values of two highly ^{15}N-enriched benthic invertebrate samples taken adjacent to the effluent outfall of the WLSSD waste water treatment plant: $\delta^{13}C_{\text{lipid corrected lower estuary}}$= -30.2‰, SD±1.10‰, $\delta^{15}N_{\text{lower estuary}}$= 12.8‰, SD±0.33‰, N=2. This data was aquatic Mayfly data from Roesler (2016), processed using the methods described above.

A subset of the fish had substantially lower $\delta^{13}C$ and $\delta^{15}N$ values than my upper estuary source (i.e., Ruffe had $\delta^{13}C < -35‰$ and $\delta^{15}N < 7‰$), implying they were feeding in a trophic pathway based on an organic matter source not included in the three source model. To address this issue, I created a four source model. Because the solution of the four source model is mathematically underdetermined (i.e., two stable isotope ratios and four sources), I used an IsoSource model to estimate source contributions (IsoSource version 1.3). IsoSource is a Microsoft Visual Basic software package which iteratively calculates ranges and means of source proportional contributions to a mixture on stable isotope analyses when the number of sources is too large to permit a unique solution. The four sources I included in the model were upper estuary, lower estuary, Lake Superior, and methane contribution. I took a conservative approach with respect to this fourth source, assuming only fish with relatively low $\delta^{13}C$ values were obtaining some diet contribution from the source. I therefore only include Ruffe in the model that had a $\delta^{13}C_{\text{lipid corrected}}$ value less than -36‰. I chose this value because, based on the current literature, there are no fish ever recorded in SLR with a lower $\delta^{13}C_{\text{lipid corrected}}$ value (-36.6‰) (Sierszen *et al.* 1996; Hoffman *et al.* 2015). Very low $\delta^{13}C$ values in aquatic food webs occur when methane contributes to the food web (Bastviken *et al.* 2003; Ravinet *et al.* 2010; Jones and Grey 2011); methane $\delta^{13}C$ values typically range from -50‰ to -60‰ (Whiticar 1999). A small number of burrowing trichopterans had been sampled previously from the St. Louis River with very low $\delta^{13}C$ values, indicating the potential for a methane-based trophic pathway to contribute to production of higher-order consumers (J. Hoffman, unpublished data). To define the source value for the methane-based trophic pathway, I used the mean of five trichopterans samples with very low $\delta^{13}C$ values that were obtained from the upper estuary and correcting for the trophic enrichment factor (+0.4‰ $\delta^{13}C$, +3.4‰ $\delta^{15}N$; (Vander Zanden and Rasmussen 2001; McCutchan *et al.* 2003)): $\delta^{13}C_{\text{lipid corrected methane}}$= -72.0‰, SD±22.7‰, $\delta^{15}N_{\text{methane}}$= -3.1‰, SD±5.4‰.

Results

I analyzed a total of 205 Ruffe captured in the St. Louis River, 2 captured in Lake Superior, 74 captured in Chequamegon Bay, and 16 captured from unknown (regions identifiable) locations (Table 10). The $\delta^{13}C_{\text{lipid corrected}}$ and $\delta^{15}N$ values were significantly different among the Ruffe captured in Lake Superior (including fish captured in Chequamegon Bay) compared to those captured in the upper estuary (ANOVA, df=2, Q<0.001, p<0.001) and lower estuary (ANOVA, df=2, Q<0.001, p<0.001), but there was no difference among the $\delta^{13}C_{\text{lipid corrected}}$ values (ANOVA, df=2, Q=1.481, p=0.416) or $\delta^{15}N$ values (ANOVA, df=2, Q=2.145, p=0.096) between Ruffe captured in the upper and lower estuary. Ruffe captured in Chequamegon Bay and Lake Superior were isotopically similar (Figure 18), though the two fish caught in Lake Superior are slightly more ^{15}N-enriched than the fish caught in Chequamegon Bay. Two Ruffe in Chequamegon Bay had $^{13}C_{\text{lipid corrected}}$ values indicating recent use of wetland habitat ($\delta^{13}C$ -29.81‰, $\delta^{15}N$ 7.68‰, and $\delta^{13}C$ -28.03‰, $\delta^{15}N$ 5.57‰) (Figure 18), which was unusual for Ruffe in Chequamegon Bay. Within the St. Louis River, some of the Ruffe captured had stable isotope ratios similar to either the upper estuary or lower estuary sources values, implying these fish were likely exclusively feeding in these areas. Ruffe were also captured with $\delta^{13}C$ and $\delta^{15}N$ values intermediate between these source values, implying these fish were likely feeding throughout the lower and upper estuary (Figure 18). Among fish caught in the lower estuary, there were two fish that are noticeably ^{15}N-enriched ($\delta^{13}C$ -28.29‰, $\delta^{15}N$ 15.87‰) and ($\delta^{13}C$ -26.74‰, $\delta^{15}N$ 16.14‰). About half of the fish caught in the upper estuary and a quarter of the fish caught in the lower estuary had a $\delta^{13}C_{\text{lipid corrected}}$ value of -36‰ or less (Figure 18).

There were size differences associated with capture location and stable isotope ratios. Ruffe captured in Chequamegon Bay were the smallest among the capture locations (mean=59.53 mm, SD=25.04), but did not have either the smallest or the largest individual Ruffe (range: 33-117 mm) (Figure 19). This small mean size can be attributed to the abundance of juvenile Ruffe captured in Chequamegon Bay during summer of 2015 (Table 9). In the St. Louis River, fish size varied by capture location. The Ruffe captured in the lower estuary were an intermediate size (mean=70.70 mm, SD=17.21), but did include young-of-year (YOY; 25 mm total length). The Ruffe captured in the lower estuary ranged in size from 25-133 mm, which encompasses the larval, juvenile, and adult stages (Gutsch and Hoffman 2016). The Ruffe captured in Lake Superior also included YOY Ruffe. The Ruffe captured in the upper estuary included the majority of large, adult Ruffe (mean=88.57 mm and 83.1 mm, SD=16.47 and 16.27, respectively) (Figure 19). Moreover, among Ruffe captured within the estuary, those with a $\delta^{13}C$ <-36‰ included large adults (mean=83.1 mm, SD=16.27, range=37-119). Ruffe from unknown locations, which were all caught in the winter, were the largest fish captured (mean=113.75 mm, SD=18.01, range: 82-148 mm) (Figure 19).

Ruffe had an unprecedented range in $\delta^{13}C$ values: -52.2‰ to -14.2‰. Ruffe exhibited a remarkable size-based shift with respect to $\delta^{13}C_{\text{lipid corrected}}$ values (Figure 20a). Small Ruffe (<60 mm SL) generally had a $\delta^{13}C_{\text{lipid corrected}}$ value of about -20‰ to -35‰, indicating these fish have trophic pathways based in a mix of Lake Superior and estuarine organic matter sources. At lengths ranging from 60-80 mm, most Ruffe had a $\delta^{13}C_{\text{lipid corrected}}$ value of -25‰ to -45‰, indicating a marked shift away from Lake Superior habitat and towards a greater variety of estuarine organic matter sources, including the methane-based trophic pathway. The largest fish sampled, which ranged from 80-148 mm, had the largest range of $\delta^{13}C_{\text{lipid corrected}}$ values: -54‰ to -14‰ (Figure 20a). The range in $\delta^{15}N$ values was substantially less than the range in $\delta^{13}C$ values, generally 3‰ to 13‰ across the range of lengths. Two fish were ^{15}N-enriched, with $\delta^{15}N$ values of about 16‰ (corresponding to fish of 45 mm and 95 mm total length; Figure 20b).

Upon closer examination, an interesting pattern is apparent (Figure 21). Ruffe less than 65 mm rely on both lake- and wetland-dominated trophic pathways. For fish that are 25-65 mm, the majority of the fish with higher than 50% lake-dominated trophic pathways are from Chequamegon Bay and Lake Superior and the ones with less than 50% are from everywhere else. There is a size-based shift after fish get larger than 65 mm. One hundred percent of fish 65-85 mm have a wetland-dominated trophic pathway. Then, once the fish are greater than 85 mm, they disperse again, almost equally, with 59.7% with a wetland-dominated trophic pathway and 40.3% with a lake-dominated trophic pathway (Figure 21).

Consistent with the wide range of stable isotope ratios observed, all three sources contributed to Ruffe nutrition (Figure 22). Among Ruffe captured in Chequamegon Bay, Lake Superior benthic periphyton was the dominant organic matter source (69 or 74 fish had >75% contribution from this Lake Superior trophic pathway). However, among Ruffe captured in the St. Louis River, many of the fish relied on upper estuary organic matter sources: 51 of the 205 fish had >75% contribution from the upper estuary source. In contrast, only 9 Ruffe had >75% contribution from the lower estuary source. There is also a notable break in the distribution of stable isotope ratios between the Ruffe caught in the estuary and the fish caught in Lake Superior (Figure 23). The remainder of the 76 fish relied on a mix of sources; 57 derived 25-75% of their nutrition from Lake Superior, 67 derived 25-75% of their nutrition from the lower estuary, and 71 derived 25-75% their trophic nutrition from the upper estuary. The standard deviations (SD) associated with the contribution estimates were source-dependent. For contributions <5% from the upper estuary source, the mean SD was 34%, and for contributions >95%, the mean SD was 27%. For the lower estuary source, contributions <5% had a mean SD of 22%; there were no contributions greater than 95%. Contributions <5% from the Lake Superior source had a mean SD of 9% and contributions >95% had a mean SD of 33%.

Based on the four-source IsoSource model, the chemosynthetic trophic pathway based on MOB contributed an average of 23% (SD=10%, range= 13-53%) of nutrition to the subset of Ruffe captured in the St. Louis River with a $\delta^{13}C_{\text{lipid corrected}}$ <-36‰ (Figure 24a). Among these same Ruffe, the upper estuary trophic pathway contributed an average of 48% (SD=35%, range= 0-101%) to their nutrition, whereas the Lake Superior trophic pathway only contributed an average of 26% (SD=29%, range= 0-100%) (Figure 24a). In contrast, among the Ruffe captured in Chequamegon Bay, the Lake Superior trophic pathway contributed an average of 79% (SD=11%, range= 23-96%) to their nutrition, whereas the lower estuary trophic pathway (physically associated with the Fish Creek mouth and south end of Chequamegon Bay) contributed an average of 6% (SD=6%, range= 0-22%) (Figure 24b).

Discussion

The flow of energy and nutrients among adjacent habitats and ecosystems is a defining character of coastal food webs (Hoffman *et al.* 2015). Evidence for both routine and episodic energy exchanges between coastal wetlands and riparian ecosystems, rivers and the adjacent open coast, and benthic and pelagic habitats is widespread (Vander Zanden and Vadeboncoeur 2002; Carpenter *et al.* 2005; Hoffman *et al.* 2015). The results of this study stand apart because I found evidence for a novel source of energy to a coastal wetland food web: chemosynthetic methane-oxidizing bacteria. The data are remarkable in part because of the unusually large range in $\delta^{13}C$ values in Ruffe, but also because the very low $\delta^{13}C$ values indicate reliance on a methane-based trophic pathway. The data are also remarkable because they indicate a distinct, size-based shift in trophic pathways that are consistent with movements between coastal wetlands and the nearshore waters of Lake Superior. As such, the data indicate Ruffe – an invasive species - occupies a unique trophic niche within the Great Lakes. By occupying a unique niche, it allows Ruffe to reduce potential competition, and may also facilitate establishment of new wetland habitats. Within the context of the food web in an invaded coastal wetland, it also facilitates the emergence of novel trophic pathways. Here I discuss the role of MOB in the food web; limitations of the data and mixing models; and then habitat-specific, life cycle-based movements of Ruffe and implications for spread.

METHANE CONTRIBUTION

Ruffe were captured throughout St. Louis River and Chequamegon Bay, but Spirit Lake, a particular area within the St. Louis River, had a surprisingly high number of Ruffe (27) that were highly ^{13}C-depleted. Sixty-two Ruffe had very low $\delta^{13}C$ values (>36‰); Ruffe captured in Spirit Lake composed nearly half of the ^{13}C-depleted Ruffe. The lowest previously recorded $\delta^{13}C$ value for Ruffe is -43.6‰; the fish was captured in a temperate lake in Finland at a depth > 12 m, and it was estimated that within the lake methane contributed between 12% and 17% to Ruffe biomass (Ravinet *et al.* 2010). Those Ruffe were primarily consuming chironomid larvae (Ravinet *et al.* 2010). Sierszen et al. (1996) measured Ruffe that were ^{13}C-depleted ($\delta^{13}C$ -36.6‰), which is the lowest $\delta^{13}C$ value previously recorded in the St. Louis River; the authors concluded that Ruffe was utilizing a carbon source not previously characterized in the river. Hoffman et al. (2010) measured Ruffe in the St. Louis River that was relatively ^{13}C-enriched; the lowest $\delta^{13}C$ value was about -26‰ and the highest $\delta^{13}C$ value was -15‰. The Ruffe measured in this study is much more ^{13}C-depleted than prior studies, with $\delta^{13}C$ values as low as -52.5‰. The highest $\delta^{13}C$ value for Ruffe was -14.2‰. The data show a remarkably wide range of stable isotope values, with a span of ^{13}C of 38.3‰ from the highest to lowest measured $\delta^{13}C$ value. Additionally, trichopterans captured in the St. Louis River had $\delta^{13}C$ values as low as -77.5‰.

To my knowledge, this is the first discovery of a higher consumer (Ruffe) having an extremely ^{13}C-depleted signature in a coastal wetland. The carbon stable isotope ratio of the fish indicates it is feeding in a chemosynthetic trophic pathway, most likely based on methane production in anoxic sediment at the bottom of the river (Ravinet *et al.* 2010; Jones and Grey 2011). Trichopterans and chironomids most likely assimilate methane carbon by consuming methane-oxidizing bacteria (MOB). MOB are the source of extremely depleted ^{13}C because biogenic methane $\delta^{13}C$ values typically range from -60‰ to -50‰ (Whiticar 1999). MOB use of methane can result in further ^{13}C depletion with isotopic fractionation up to 20‰ (Summons *et al.* 1994; Jones and Grey 2011). Although chironomid larvae that are highly ^{13}C-depleted can be consumed by higher consumers (Jones and Grey 2011), few studies have attempted to evaluate this (Harrod and Grey 2006; Ravinet *et al.* 2010), and there is little evidence for methane-derived carbon in higher consumers. Deines and Grey

(2006) found that demersal fish do not consume ^{13}C-depleted chironomid larvae because they do not feed in oxygen-depleted water layers where the larvae are abundant. In the St. Louis River, only burrowing trichopterans captured in benthic dredge samples have been found to be sufficiently ^{13}C-depleted to indicate feeding in a methane-based trophic pathway. It is not known how methane carbon is assimilated by these trichopterans. Presumably, their burrow intersects anoxic sediment within stratified sediment, and the overlying water has sufficient oxygen for these trichopterans to survive. It is plausible that the trichopterans are directly consuming MOB (i.e., feeding in the microbial food web) within their burrow, or consuming a mix of sediment and MOB. Little is known about this trophic pathway, and future research is needed.

Methane is an allochthonous carbon source, likely produced from terrestrial-derived organic matter, such a decaying litter and soil. The methane-influenced food web is a donor system to the overall St. Louis River food web (recipient) through benthic invertebrates (trichopterans). Methane is transferred to bacteria, and in turn the energy is transferred up several trophic levels and consumed by Ruffe. Because trichopterans are intolerant to hypoxia, it is likely that the top layer of sediment is well-oxygenated, and their tubes are colonized by MOB at a depth within the sediment corresponding to a strong redox gradient. I found no methane fish outside of the St. Louis River, suggesting that Lake Superior is not a recipient of the methane-influenced food web.

The existence of a methane-based tropic pathway has not previously been demonstrated in a coastal wetland ecosystem. These trichopterans are the only other organisms measured in SLR to have such a ^{13}C-depleted stable isotope signal (Hoffman, personal comm., Gutsch, unpublished data). Both Bastviken *et al.* (2003) and Jones and Grey (2011) found chironomid larvae and zooplankton with depleted ^{13}C in other freshwater ecosystems, but these invertebrates have been analyzed in the St. Louis River and none has yet been measured with any unusually low δ^{13}C values (Keough *et al.* 1996; Sierszen *et al.* 1996; Hoffman *et al.* 2010; Blazer *et al.* 2014). Ruffe has the ability to feed in hypoxic environments at great depths (Bergman 1988b; Hölker and Thiel 1998), perhaps allowing it to forage in places other fish cannot (Jones and Grey 2011). Ruffe has been found previously to feed on chironomids in a methanogenic food web (Ravinet *et al.* 2010).

SIZE-BASED HABITAT USAGE

I found size-based habitat usage of Ruffe that corroborated the proposed Ruffe life-cycle from Gutsch and Hoffman (2016). Small fish have high $\delta^{13}C_{\text{lipid corrected}}$ values, medium-size fish have low $\delta^{13}C_{\text{lipid corrected}}$ values, and large-size fish have a wide range of $\delta^{13}C_{\text{lipid corrected}}$ values. The size-based patterns indicate a distinct connection between movement and life history. At small sizes, Ruffe disperses from wetland habitat and uses both the lake and the wetland as rearing habitat. At 65-85 mm, it is mature and moves into wetlands to spawn (Gutsch and Hoffman 2016). The associated shift in the stable isotope composition is noteworthy, as other migratory fishes are known to spawn and not feed, allowing researchers to use the stable isotope composition to track their origin (Groot and Margolis 1991). The shift implies either that the fish is moving into the wetland to feed prior to spawning (i.e., staging), or that it feeds in the wetland during the spawning period. After spawning, in mid- to late-summer it disperses again, moving into the lake or else remaining in the coastal wetland.

LAKE SUPERIOR VS WETLAND USAGE

Although Ruffe is commonly found in wetlands, my results demonstrate it uses Lake Superior at multiple life stages. Its life-history is comparable to the native percid, Yellow Perch (*Perca flavescens*). Ruffe lays its eggs in the spring or early summer in a wetland, similar to Yellow Perch, which also lays its eggs in the spring (Schoen *et al.* 2016). Ruffe exclusively spawns in coastal wetlands but not Yellow Perch (Robillard and Marsden 2001). Ruffe spawns in shallow (<3 m) and relatively warm water (5-18^{o}C;Kiyashko and Volodin 1978; Brown *et al.* 1998; Gutsch and Hoffman 2016). Yellow Perch can spawn in deeper (14 m), cooler water (Huff *et al.* 2004) than Ruffe. As larvae, Ruffe is demersal and remains on the spawning grounds in the wetland (Disler and Smimov 1977; Gutsch and Hoffman 2016). In contrast, Yellow Perch larvae have a 40-day pelagic phase post-hatch to evade predation and begin feeding, after which they return to littoral vegetation (Whiteside *et al.* 1985). As Ruffe transitions to the juvenile stage, it moves into lake and coastal wetlands, as shown by the stable isotope ratio data. Juveniles and adults move freely from wetland to lake to access resources and overwinter (Gutsch and Hoffman 2016). Its use of the coastal wetland and lake is similar to Yellow Perch. Yellow Perch in the Great Lakes has a variety of life history strategies, including annual use of wetland habitat, bi-annual or year-round use of wetland habitat, and wetland habitat use as juveniles and movement to nearshore as adults, suggesting it can spawn in nearshore habitat (Schoen *et al.* 2016). In contrast, Ruffe migrates to and from the lake and wetland throughout the different stages of its life (some may stay in the wetland their whole life), but it only spawns in coastal wetlands (Gutsch and Hoffman 2016). As such, spawning habitat is a limiting factor for Ruffe (Gutsch and Hoffman 2016).

STABLE ISOTOPE AND MIXING MODEL OUTPUT UNCERTAINTY

An important consideration for interpretation of stable isotope ratios of fish is the isotopic turnover, which has an allometric relationship to the size of the fish (Vander Zanden *et al.* 2015). Based on the allometric relationship (Vander Zanden et al. 2015, Eq. 2: constant 0.16, intercept 3.28), for all Ruffe (average weight 13.66 g) the estimated half-life is 40.4 days. For small Ruffe (25-60 mm), the half-life is 31.2 days, for medium Ruffe (60-85 mm), the half-life is 37.5 days, and for large Ruffe (85-148 mm) the half-life is 45.7 days. The ecological implication of these half-life estimates is that stable isotope ratios reflect diet and movement integrated over seasons in large fish, whereas they reflect within-season diet and movement in small fish. These long half-lives for large fish prevent a direct interpretation with respect to life history because seasonal movements are common (Gutsch and Hoffman 2016). However, these are still relatively short half-lives, less than a year, compared to other fish.

For mixing models, the error in source contribution is related to the isotopic differences among sources. For the mixing model, the methane and lake source δ^{13}C and δ^{15}N values are well-separated; however, the upper and lower estuary sources values were much more isotopically similar to each other. This similarity reduces the certainty attributing upper and lower estuary sources to fish production relative to lake and methane sources.

Second, among the Ruffe I sampled, a few had unusually high $\delta^{15}N$ values, the source of which is likely nitrogen in Western Lake Superior Sanitary District (WLSSD) effluent (Hoffman *et al.* 2012). It is likely that these Ruffe were feeding in the effluent near this facility, the outflow of which is located in the north corner of St. Louis Bay (Figure 16).

Finally, many of the Ruffe sampled had $\delta^{13}C$ and $\delta^{15}N$ values that were intermediate between the sources (Figure 22). This movement behavior of these fishes is difficult to interpret because the fish can either be moving between locations to feed, feeding in a location with an intermediate isotopic value associated with the food web, or feeding in a region but occasionally intercepting prey drifting from the other location. The model output cannot discern among these alternatives. The question arises as to whether the evidence for lake habitat could be acquired without feeding in Lake Superior. While it is possible that some lake signal could be acquired by consuming the eggs of potomadromous fishes, these fish generally spawn in a part of the river that is poor habitat for Ruffe, at the top of the estuary where there is gravel and cobble substrate and fast current. Alternatively, Ruffe feeding at the river mouth near the edge of transition zone may have a lake-influenced isotopic composition, but the river discharge is generally sufficient that the isotopic composition of the food web at the river mouth is more similar to the wetland than Lake Superior (Hoffman *et al.* 2010; Bellinger *et al.* 2016).

CONCLUSIONS

My goals were to identify movements linked to life-history and to identify trophic pathways supporting Ruffe in the St. Louis River. I found that Ruffe exhibit remarkable size-based movements throughout its life cycle, and it is dependent on coastal wetlands and demonstrates facultative use of Lake Superior. The landscape mosaic in this study included three ecosystems: river bottom, coastal wetland, and lake. The ecosystems are connected by a mixture of autochthonous and allochthonous inputs, including a chemosynthetic pathway. The stable isotope analysis revealed that some Ruffe were feeding in a methane-based trophic pathway, possibly reducing resource competition. No other study has found use of this trophic pathway in coastal wetlands. The role of methane in coastal wetlands merits further investigation because, based on this study, it potentially has important implications with respect to both carrying capacity and invasive species resource competition.

Chapter 4: Lake Superior-scale species distribution modeling of Ruffe (*Gymnocephalus cernua*)

Abstract

Species distribution modeling is an innovative way to predict suitable habitat of invasive species. My goal was to understand how using environmental data resolved to relatively fine spatial scales (i.e., 100m to 1000 m), as well as using different species occurrence data of varying temporal windows, would affect model performance with respect to predicting potential habitat of an invasive fish, Ruffe (*Gymnocephalus cernua*). I used 30-m-scale environmental variables to develop a Maxent species distribution model. To examine the effect of spatial data resolution, I developed and compared competing models at different spatial scales: 250-m, 500-m, 1000-m, 2000-m, and 2000-m selected model. In addition, I conducted two time-series analyses, comparing models developed from occurrence data broken into decade time blocks (1986-1996, 1997-2006, 2007-2014) and analyzed separately or cumulatively. I calculated percent suitable habitat for all of the models. I predicted that there would be an optimal spatial scale to model Ruffe—that very low and very high spatial scale models would not perform well, but a model at intermediate spatial scales would be the best model. Among the models constructed using environmental data from various spatial resolutions, the best performing model used 500-m data and the worst performing model used 2000-m data. The important geographic discrepancies in potential habitat occurred around the Apostle Islands, WI, Isle Royale, MN, Grand Marais, MI, Whitefish Point, MI, and Red Rock and Nipigon in Canada. I showed multiple models that performed similarly, according to area under the curve (AUC) scores but had different physical results with the suitable habitat prediction maps and percent area predicted. Differences in grid sizes of

100s of meters resulted in differences of thousands of square kilometers of predicted suitable habitat. The Maxent model results from the separate and cumulative time-series analyses were similar. I found minor differences in the environmental variable outputs. However, I found substantial differences in the AUC scores for the time-series analyses. The separate time-series models all performed similarly well, but the performance of the cumulative models declined as data were added to subsequent models. A 30-m-scale species distribution model for Ruffe in Lake Superior can be used for showing areas that are suitable habitat for them. Maxent can be a powerful tool to model invasive species, using the precautions outlined in my methods.

Introduction

There have been recent advances in the ability to model a species' geographic distribution based on their ecological niche (Elith 2002; Elith *et al.* 2006, 2010, 2013; Phillips and Dudík 2008; Khanum *et al.* 2013; VanDerWal *et al.* 2013; Yang *et al.* 2013; Guillera-Arroita *et al.* 2014; Matyukhina *et al.* 2014; Yi *et al.* 2016), an idea first introduced by Joseph Grinnell (Grinnell 1924; Guisan and Zimmerman 2000; Pearson and Dawson 2003; Peterson 2003, 2006; Soberon and Peterson 2004). Grinnell (1924) focused on an individual species' geographical confinement by its biotic and abiotic ecological needs and posited that understanding an organism's niche would better help us understand the evolution of that organism. Elton (1927) later expanded the niche concept to include a species' interaction within its community, not only its geographic location. Elton (1927) observed that organisms can have almost identical niches, such as a specific type of carnivory, in different communities even when they are geographically separated. Hutchinson (1957) later postulated that the niche could be conceived as a n-dimensional hypervolume, wherein the hypervolume is defined by all biotic and abiotic factors that affect the species in the community and represents the multi-dimensional space in which an organism can exist based on all of these factors. Hutchinson (1957) called the hypervolume an organism's fundamental niche. MacArthur (1972) quantified and integrated the two concepts of the individual and community ecological niches. According to Peterson (2003), the niche defined by Grinnell and MacArthur is: "the quantity [any ecological requirement] that limits geographic distributions of species." The fundamental niche is defined by all of the variables in which the organism can exist long-term. In contrast, the realized niche is usually within the fundamental niche and is the subset where it actually occupies (Hutchinson 1957; Phillips *et al.* 2006).

Species distribution models (SDMs) are used to predict suitable habitat (or fundamental niches) for species across a particular landscape. In the context of non-native species, they have been applied to identify likely places where non-native species could successfully establish if introduced, as well as locations to which they could spread (Peterson and Vieglais 2001; Peterson and Robins 2003; Thuiller *et al.* 2005; Chen *et al.* 2007; Ficetola *et al.* 2007; Broennimann *et al.* 2007; Jeschke and Strayer 2008; Jiménez-Valverde *et al.* 2011). For example, Drake and Lodge (2006) created a SDM that predicted suitable habitat for Rainbow Smelt (*Osmerus mordax*) and Ruffe (*Gymnocephalus cernua*) within North America; based on the model, Ruffe was likely to invade the Midwestern and Northeastern United States. However, because the model output had a relatively coarse geospatial resolution of 0.1 degree decimals, it had low predictive power at the "local" level.

Identifying locations at high risk for invasion requires some understanding of vectors for spread, relative propagule pressure, and the suitability of the chemical, physical, and biological conditions (Colautti and MacIsaac 2004). Species distribution modeling is used to predict whether or not chemical or physical (or both) conditions are suitable for an introduced species to establish and spread throughout a particular landscape (Peterson 2003). SDMs are cost effective because they can use existing data (Fielding and Bell 1997). However, these models have limitations based on how they are constructed. Typically, SDMs use global climate data, such as annual cloud cover, annual frost frequency, annual vapor pressure, annual precipitation, mean annual temperature, slope, etc., as their environmental component and occurrence data from the native range of the organism (Peterson and Vieglais 2001; Peterson *et al.* 2003; Phillips *et al.* 2006). Often the prediction maps are at such a large scale that the output gives only a vague idea (e.g., all of the Great Lakes) of where an invasive organism might be able to establish a population.

Within Lake Superior, Ruffe is an ideal model invasive species for constructing a SDM. It first invaded the St. Louis River estuary, MN, (Figure 25A) in 1986; there was a steady population increase until 1995, and then the population sharply declined, indicative of the typical “boom-bust” cycle of most invasive species (Chapter 2). Ruffe spread to Thunder Bay Harbor, Ontario, Canada, by 1991, Lake Huron by 1995, and Lake Michigan by 2002, most likely by inter-lake spread when eggs or larvae were introduced in ballast water from commercial ships (Ricciardi and MacIsaac 2000). Ruffe is a habitat generalist, spawns multiple times throughout the spawning season, and it has high fecundity (Gutsch and Hoffman 2016). Ruffe is highly competitive with native, benthic fishes (Ogle 1998). Despite these characteristics, Ruffe has yet to spread extensively through the upper Great Lakes (USEPA 2008; USGS 2014). Because it has not spread everywhere in Lake Superior, the opportunity exists to use available presence data within the Laurentian Great Lakes to model potential suitable habitat elsewhere in Lake Superior.

I developed a SDM using Ruffe as a model species. My lake-scale environmental variables were at a 30-m-scale instead of a global scale. To examine the effect of spatial data resolution, I developed and compared competing models at different spatial scales: 250-m, 500-m, 1000-m, 2000-m, and 2000-m selected model. In addition, I conducted two time-series analyses, comparing models developed from occurrence data broken into decade time blocks (1986-1996, 1997-2006, 2007-2014) and analyzed them separately and cumulatively. I predicted the area of suitable habitat within the buffer and Lake Superior for each model and for three habitat zones—offshore, nearshore, and in-shore. I predicted that there would be an optimal spatial scale to model Ruffe—that very fine and coarse spatial scaled models would not perform well, but a model with intermediate spatial scale would be the best model.

Methods

STUDY AREA

My study area was Lake Superior, USA (Figure 25). The lake has a surface area of 82,097 km^2 (maximum length 563 km, maximum width 257 km), and a shoreline length of 4,393 km (including islands). Its volume is 12,232 km^3 (maximum depth 406 m, average depth 149 m), with a retention time of 173 years (GLERL and NOAA 2000).

RUFFE OCCURRENCE DATA AND ENVIRONMENTAL DATA

For my model, I used adult and juvenile Ruffe occurrence data (i.e., presence only, absences were excluded) from multiple sources (Table 11). I had a total of 362 occurrences (Figure 26). Most occurrences were within Lake Superior, but a few occurred in inland lakes or streams connected to Lake Superior for which I lacked corresponding environmental data. Assuming these fish at some time occupied the connecting water body, I associated the points with the nearest, connected shoreline location using shoreline data from the Great Lakes Aquatic Habitat Framework (GLAHF 2017). I found substantial clustering of occurrences in two locations, the St. Louis River (194 points) and Chequamegon Bay (74 points), which accounted for 74% of the total occurrences (Figure 26). Based on the variogram, the occurrence data were autocorrelated at a relatively fine spatial scale (range = 77.43 km, nugget = 13.22 km, sill = 13219.14) due to this clustering in Chequamegon Bay and St. Louis River. Model iterations to address this autocorrelation are described below.

I limited the spatial domain of the model using the occurrence data by setting a buffer around the Lake Superior shoreline (Figure 26). The limit of the buffer was set to either the maximum depth (205 m) or distance from shore (15 km) that Ruffe has been captured in Lake Superior, assuming these bounds represent a limit on suitable habitat. Several areas along the north shore on the US side that were excluded from the model because the bottom depth was too great (Figure 26).

The environmental data I included in all of the models were turbidity, depth, substrate type, wave height, and distance to the nearest wetland (Table 12). Light extinction is one of the most important variables to Ruffe. Ruffe lives in dark or turbid areas and is adapted to low-light conditions. It possesses both a tapeta lucidum and well-developed lateral line (Gutsch and Hoffman 2016). Ruffe is also often found in deep, dark water. However, it requires shallow water habitat, whether turbid or clear, for spawning (Gutsch and Hoffman 2016). Ruffe do not exhibit strong preferences for specific substrates and has been found in almost every kind of substrate. However, it may prefer mud or clay due to the turbid qualities (Gutsch and Hoffman 2016). Wave height was used a proxy for both depth and exposure. For example, in a deep, offshore, exposed location, waves are typically higher than in a shallow, inshore, protected location. Finally, distance to wetland was chosen because Ruffe is wetland-dependent. It is routinely captured in and requires coastal wetlands for spawning (Chapter 3). All data layers were resampled to a 30-m resolution.

Turbidity data came from the Michigan Tech Research Institute (http://www.mtri.org/). Turbidity was determined using MODIS imagery from NOAA and NASA at K490, which is the diffuse attenuation coefficient at 490 nm (Wang *et al.* 2009) (Figure 27). In essence, it measures the rate at which light at wavelength 490 nm is attenuated with depth. I retrieved turbidity data only for the summer months (June, July, and August) for 2010-2013 and averaged those images. June, July and August were chosen because they include both stratified (July and August) and unstratified (June) conditions and are ice-free months. I had a total of 12 images, 1 image for each month, 3 images for each year. Michigan Tech averaged the values of MODIS images of cloud-free pixels and provided the monthly averages, from which I estimated the annual averages. The original resolution for turbidity was 1 km x 1 km, but I resampled it to 30 m x

30 m so I could use it in the model. The range of turbidity within the model spatial domain was 0-12.7 nm (mean 0.16 nm, and one standard deviation [SD] 0.31 nm).

Depth, substrate type, wave height, and distance to wetland all came from the Great Lakes Aquatic Habitat Framework (GLAHF) data set (https://www.glahf.org/). Depths within the model domain ranged from 0-205 m, with an average of 85.9 m ± SD of 59 m (Figure 27). Available substrate types included mud, sand, hard, and clay (Figure 27). The percentage of each of these within my buffer varied: mud (21.0%), sand (9.3%), hard (43.2%), and clay (26.6%). Substrate types for the offshore (>100 m) were digitized from observations published in peer-reviewed publications, and in the coastal and nearshore areas (<100 m) were described by the Army Corp of Engineers (2012) and confirmed by researchers across the Great Lakes (GLAHF 2017). I calculated distance from occurrence points to coastal wetlands using Euclidean distance (mean 32,555 m ± SD 37,717 m, range 0 to 146,456 m). The coastal wetlands dataset published by GLAHF came from the Great Lakes Coastal Wetland Consortium (GLCWC) (GLAHF 2017). Wave height was retrieved from the GLAHF wave action section, developed by U. S. Army Corps of Engineers (USACEs) Wave Information Studies (Figure 27). WISWAVE is a model used to calculate wave height. WISWAVE is a discrete spectral wave model (Engineers 2010) that models wind wave generation and propagation and helps determine spatial and temporal changes in wave field as a function of wind (Dhanak and Xiros 2016). I derived wave height from GLAFH; I interpolated it using ArcGIS software. Within my model domain, wave height averaged 0.324 m ± SD 0.009 m and ranged from 0.0985 to 0.530 m. I used Pearson's coefficient to examine whether the environmental variables were correlated; correlations were generally weak (Table 13).

SDM Model

For my SDMs, I used a maximum entropy algorithm and the Maxent software (Maxent, version 3.3.3k) (Phillips *et al.* 2006). Maxent is a maximum entropy based machine learning program. It is becoming increasingly popular to use for species distribution modeling due to its high performance (Elith *et al.* 2006; Hernández *et al.* 2006). Maxent uses presence-only occurrence data and environmental data (continuous or categorical) in ArcGIS. It uses environmental constraints to estimate the probability distribution for a species' occurrence (Phillips *et al.* 2006). Maxent uses the equation:

$$\Pr(y = 1|\, z) = f_1(z)\Pr(y = 1)\,/f(z),$$

that shows if I know the conditional density of the covariates at the presence sites ($f_1(z)$) and the unconditional density of the covariates across the study area, f(z), I then need to know the prevalence Pr(y=1) to calculate the conditional probability of occurrence. Maxent first estimates the ratio $f_1(z)/f(z)$, which is the raw output and then estimates the logistic output: $\log(f_1(z)/f(z))$ (Elith *et al.* 2011). The output of Maxent is a relative probability estimate of presence of the species from 0 to 1, with 0 being low probability and 1 being high probability. The prediction map shows suitable habitat. For each of my models, I used the default settings in Maxent, which is standard practice. Thirty percent of the occurrence data were kept out as test data; the other seventy percent were used as training data.

Ruffe occurrence data together with background data were used to determine the Maxent distribution. Background data are a random sample of points from the landscape (that may or may not be occupied by Ruffe). I created 6 different models for comparison and 5 additional models for the time series analysis. Different numbers of occurrences were assigned to test, training, and background data for each of the six models (Table 14).

For each model, I calculated percent suitable habitat using a logistic threshold at maximum test sensitivity plus specificity within my buffer and for Lake Superior. This was a value I used from the output as a cutoff to determine the percentage of suitable habitat; everything above that value was suitable and everything below the value was not suitable. To evaluate the ecological significance, I calculated the percent of suitable area within the model domain found within each of three depth zones (in-shore (<30 m), nearshore (<100 m), and offshore (>100 m)) commonly used for Lake Superior management plans (Figure 28). I used an ESRI Zonal statistics tool to calculate the suitable area and percent per zone. The 30 x 30-meter raster was then converted to meters squared to determine the final area that was occupied by each model and zone within the buffer and Lake Superior. All raw data and calculations are reported in Table A-3.

MODEL VARIATIONS

Because non-native species in the Great Lakes have generally been found most commonly in and around urban areas and shipping ports, spatial clustering of species presence data around urban areas and ports is typical (O’Malia *et al., in review*). I found substantial clustering in the St. Louis River and Chequamegon Bay, with significant autocorrelation as indicated by the associated variogram. Because of this autocorrelation, I created 6 different SDMs, each with a different distance buffering surrounding the occurrence points (focal point) to remove clustering. These buffers included 250-m, 500-m, 1000-m, 2000-m, 2000-m selected removal, and no point removal (all data). The buffering distances were chosen by analyzing variograms of all the data to identify the sill, and then choosing several distances surrounding the sill distance. The buffers were created in ArcGIS. Each point was buffered at 250-m, 500-m, 1000-m, and 2000-m and presence was recalculated at the specified buffer scale. For the 2000-m selected model, only points in St. Louis River and Chequamegon Bay were removed at 2000-meter distances and all the other points were left alone. The 250-m, 500-m, all data, and 2000-m selected models still had some autocorrelation. The autocorrelation effects the model covariates, but not the model outputs.

In addition, I conducted a time-series analysis on all of the Ruffe data from 1986-2014. I broke the data into approximate ten-year increments: 1986-1996, 1997-2006, and 2007-2014. First, I examined a cumulative time series analysis (i.e., sequentially adding the data by decade). Second, I examined a discrete time-series analysis (i.e., treating each decadal data set separately). My goal was to determine whether examining the time-series cumulatively would yield different results than the discrete analysis. The cumulative time-series analysis mimics the tracking of Ruffe movements through time, whereas the discrete analysis maintains the evolution of distribution through time. For the cumulative time-series analysis, I developed three Maxent models using all of the occurrence points in Lake Superior within the following calendar years: 1986-1996, 1986-2006 and 1986-2014. For the separate time-series analysis, I created separate Maxent models for each ten-year time frame: 1986-1996, 1997-2006, and 2007-2014. I compared models within each type of time-series analysis using area under the curve (AUC), and I compared the environmental variables of each model using several Maxent outputs: response curves (variable vs logistic output), percent contribution (percent the variable contributed to the model), and jackknife of the test gain (determines maximum likelihood with the variable in the model alone or without the variable in the model). I also produced a map of the predicted suitable habitat within Chequamegon Bay to illustrate differences among the models. Chequamegon Bay was of particular interest because Ruffe established there many years after first introduction into the lake and because it has diverse habitat.

I used the area under the receiver operating characteristic (ROC) curve AUC test statistic to evaluate model performance (Phillips and Dudík 2008). Phillips and Dudik (2008) described the AUC as the probability that a randomly chosen presence site will be ranked above a randomly chosen absence site. AUC on average is 0.5 and 1.0 is perfect; 0.75 is considered “potentially useful”

(Elith 2002). Without absence data, background or pseudo-absence data is used, as with my study, to perform the test. In this case, the AUC is described as being the probability that a randomly chosen presence site is ranked above a random background site (Phillips *et al.* 2006). I also compared models qualitatively using map outputs (i.e., prediction maps). I qualitatively compared environmental variables within each of the models using Maxent output response curves. Then I compared the variables in the models using two Maxent outputs - percent contribution and jackknife of test gain. The jackknife refers to the method of removing one variable at a time and rerunning the model without it. It allows the testing of the influence of the variable on "gain" which is basically a likelihood statistic that maximizes the probability of the presences in relation to the background data.

Results and Discussion

COMPARISON OF SDMS VARYING SPATIAL RESOLUTION

All of the Maxent models showed high predictive power (AUC > 0.9). However, the best model, based on the AUC score using test data, was the 500-m model, with an AUC score of 0.977 (Figure 29). The model with all the data and the 2000-m selected model had AUC scores similar to the 500 m model (Figure 29). The 250-m and the 1000-m models had about the same AUC score, and the-2000 m model had the lowest AUC score using test data. However, all of the models were greater than 90% accurate based on their AUC scores, and all but one was greater than 95% accurate (Figure 29).

As the distance buffer increased, clustering decreased, and the AUC increased to its maximum (500-m model) and then began to decrease again (Figure 30). However, the 2000-m selected model, where I only removed points at a distance of 2000-m from the very clustered areas (Chequamegon Bay and St. Louis River), performed very well, almost as well as the best distance buffer model (Figure 29). But the 2000-m selected model also had the most spatial autocorrelation due to clustering at other locations.

The Maxent models showed similar habitat suitability among spatial variations of buffer distances. The all-data model and the 500-m model had very similar habitat suitability (Figure 31). The 2000-m selected model had the most predicted suitable habitat (Figure 31, Table 14). As expected, all models predicted that the St. Louis River and Chequamegon Bay were highly suitable (Figure 31). Similarly, all models predicted high habitat suitability for Ruffe along the south shore of the western arm of Lake Superior, across the central south shore, from L'Anse, MI, to Au Train, MI, along the southeast corner of the lake from Whitefish Bay to Sault Ste. Marie, MI, and by Hurkett and Thunder Bay in Canada. There were some notable differences as well, described here in counterclockwise order about the lake, starting at the Apostle Islands. Habitat suitability around the Apostle Islands is high in all models except the 250-m model (Figure 31). There is high habitat suitability for Ruffe around the Keweenaw Peninsula and through Portage Lake in all of the models except the 250-m model. There is high habitat suitability around Grand Marais, MI, and Whitefish Point, MI in the model with all data, 500-m, and 2000-m selected models (Figure 31). There is some suitable habitat in those locations in the other models as well. The 1000-m and 2000-m model show some suitable habitat for Ruffe near Red Rock and Nipigon in Canada (Figure 31). There is some unexpected prediction of suitable habitat for Ruffe along the north side of Isle Royale for the 500-m, 1000-m, 2000-m and 2000-m selected models; for the 500-m and the 2000-m selected models, the entire island was deemed suitable habitat. This is surprising because there is substantial angler effort and multiple fisheries-independent surveys in the nearshore habitat of Isle Royale, yet only one Ruffe has ever been captured and reported there (Figure 31). All models were in agreement that there is a lack of suitable habitat along the north shore of Lake Superior (Figure 31). This finding is likely due to the geomorphology of the areas. The north shores of Lake Superior are steep and rocky with very few wetlands, low turbidity, and high exposure. In addition, Ruffe requires wetlands at some point during its life cycle to reproduce (Gutsch and Hoffman 2016).

The percent area predicted to be suitable habitat within the buffer increased from the 250-m model to the 1000-m model, but then decreased slightly for the 2000-m model (Table 15). The model with the most predicted area was the 2000-m selected model. Whereas, the model with all the data had an intermediate percentage (Table 15). The same trends are true for prediction of suitable habitat in Lake Superior. The observation that the maximum suitable area was associated with the 1000-m and 2000-m models can potentially be explained by the methodology. By expanding the buffers to reduce autocorrelation, the proportion of habitat assigned to be suitable for Ruffe was increased. Plausibly, this is because as the buffer distance increases, the buffer extends farther into Lake Superior and includes both suitable and unsuitable conditions (turbidity, depth, wave height). This process causes the model to associate a presence with habitat that is less turbid, deeper, or with greater wave height than where the fish was actually captured because the shallow, turbid, protected nearshore composes a very small amount of habitat area in Lake Superior.

The predicted distribution of habitat within the inshore, nearshore, and offshore depths varied widely among models. For inshore habitat, there is an increase from the 250-m model (~6%) to the 1000-m model (~16%), then the percentage decreases again for the 2000-m model (15.5%). The model with all the data is intermediate. For the nearshore habitat, I found the same relative ranking. For the offshore habitat, however, there is no suitable area for the 250-m model, almost 0% for the 500-m and the 2000-m models, less than 1% for the all-data model and the 1000-m model, and almost 3% for the 2000-m selected model (Table 14).

The 500-m model and the 2000-m selected model have almost identical AUC scores, and yet the percent of suitable area predicted for the 2000-m selected model is almost three times that of the 500-m model (Table 14). Further, there is 6 times more offshore habitat predicted for the 2000-m selected model than the 500-m model, despite having the same accuracy. The 2000-m selected model was highly spatially autocorrelated, but the 1000-m model, with an AUC just below the two best models and no autocorrelation, also predicts almost 3 times the amount of suitable habitat for Ruffe than the 500-m model and about the same amount of offshore suitable habitat as the 2000-m selected model (Table 15). Similar issues arise when comparing the in-shore habitat among models. The 500-m model predicts about half as much suitable habitat than the 1000-m and the 2000-m selected models (Table 15).

It is important to examine model performance versus the model outputs from a management perspective. If a natural resource manager were to choose to use the 500-m model, he or she might greatly under-predict the amount of area to be monitored for Ruffe and might subsequently fail to detect the fish. However, if he or she used the 2000-m selected model, they might greatly over-predict the amount of area to be monitored for Ruffe and subsequently waste resources and lower the overall probability of detection. Ruffe is known to occupy in-shore habitats and some nearshore habitats, but less commonly known is that that it occupies so much offshore habitat (Chapter 1). Ruffe occupies deep waters of Lake Superior, but the ecological role of deep water habitat for Ruffe remains unknown. Both larvae and adults are captured in Lake Superior (Chapter 3).

Overall, the response curves (environmental variables vs. logistic output) are consistent across all models, except for one difference. For every model, when other environmental variables are held at their average value all categories (mud, sand, clay, and hard) are important; when substrate is by itself in the model, sand is most important. Overall, all environmental variables have high logistic output at low values and decrease as the values of the variables increase.

Based on percent contribution, depth and wave height were generally the most important variables in the model. Depth was the most important environmental variable for all models except the all-data and 250-m models, for which it was second most important next to wave height (Table 16). In all of the other models, wave height was second most important, except for the 2000-m selected model, whereas distance to wetland was the second most important variable. Substrate type was least important for the model with all data, 250-m, 500-m, and 1000-m models, whereas turbidity was least important for the 2000-m and the 2000-m selected model (Table 16).

Based on the jackknife of the test gain results, wave height was the best variable alone in all of the models, except for the 2000-m model, in which distance to wetlands was best by itself (Figure 32). It is unknown why these results are not wholly consistent with the previous results (i.e., depth generally was most important when all variables were considered together). In the all-data model, the likelihood of the model decreased if depth, turbidity, or wave height were removed (Figure 32). In the 250-m model, the likelihood of the model decreased when removing wave height and distance to wetland. In the 500-m model, wave height and depth decreased the likelihood of the model. For the 1000-m model and 2000-m selected model, wave height and turbidity decreased the likelihood of the model. In the 2000-m model, turbidity decreased the likelihood of the model (Figure 32).

As a whole, the results indicate that among the environmental variables considered, depth, wave height, and turbidity can explain much of the variation in Ruffe distribution in Lake Superior. Depth and wave height possibly have a high magnitude of change (or large range) and are spread across a large gradient, and so might be better predictors than substrate, distance to wetland, and turbidity. This is apparent in the jackknife analysis; turbidity was an important variable on its own, but not in combination with the other variables. However, when all of the variables are included in the model, depth and wave height have a higher percent contribution than turbidity. It is also possible that individual variable importance is affected by spatial autocorrelation. Note that for the 2000-m selected model, in which spatial autocorrelation was removed from the St. Louis River and Chequamegon Bay, no single variable contributes strongly to the model outcome, and there is little, if any, effect on the likelihood of the model when any single variable is removed from the model (Figure 32). That turbidity and depth were important model factors is consistent with Ruffe biology. Ruffe is a demersal species that prefers low light conditions of either turbid or deep waters (Gutsch and Hoffman 2016). To some extent, depth and wave height may be confounded in the models because depth and wave height are related (Pearson correlation coefficient = 0.418, p=0). In contrast, high turbidity generally only occurs in shallow waters. Given that Ruffe requires wetlands for spawning, it was surprising that distance to wetlands was only best alone in the 2000-m model. This is plausibly because at this large grid size (2000 m), there is loss of depth and turbidity resolution such that Ruffe that are in shallow and turbid locations near the shoreline are assigned to a greater depth and lower turbidity because the cell in which they are located includes more nearshore and less inshore habitat compared to the smaller grid sizes. In contrast, distance to wetlands becomes more important because the distances (generally >2000 m) are relatively unaffected by this scaling exercise.

TIME SERIES ANALYSIS

For the separate time-series analysis, the AUC scores and response curves were similar among models (Figure 33). Wave height had the greatest percent contribution in all three models. For 1986-1996, turbidity had the second highest percent contribution, whereas for 1997-2006 and 2007-2014, depth had the second highest percent contribution. In the jackknife analysis, for the 1986-1996 model, wave height and turbidity were most important when alone in the model, and there was only a small effect when any variable was removed from the model. For the other two stanzas, wave height was the most important variable when alone in the model. For the 1997-2006 model, there was only a small effect when any variable was removed from the model. For the 2007-2014 model, model likelihood was decreased the most by removing depth, turbidity, and wave height. The maps of Chequamegon Bay indicate an increase in suitable habitat as the time frames progress. By the 2007-2014 times, almost all of Chequamegon Bay is predicted to be suitable habitat (Figure 34). This result indicates that the model prediction of suitability of a given place (i.e., Chequamegon Bay) depends on the time-dependent habitat information provided as Ruffe spreads along the lake’s southern shore.

For the cumulative time-series model, the AUC scores decreased as data were added for each time period; 1986-1996 had the highest AUC score (0.979), and 1986-2014 had the lowest AUC score (0.954) (Figure 35). The response curves are similar among the three models, and, as in the separate time-series analysis, wave height had the highest percent contribution for all the models. For 1986-1996, turbidity had the next highest percent contribution, and for 1986-2006 and 1986-2014, depth had the next highest percent contribution, similar to the separate time-series analysis. In the jackknife analysis for 1986-1996, wave height and turbidity are about equally most important when alone in the model, and there is little change when any variable is removed from the model. For the 1986-2006 model, wave height is most important when alone in the model, and depth causes a decrease in likelihood when removed. For the 1986-2014 model, wave height is most important again, and wave height and depth cause a decrease in likelihood when removed. Overall, the results from the separate and cumulative time-series analyses were similar, with only minor differences in the relative rankings of the environmental variables. However, there were substantial differences in the AUC scores among the models (Figure 33 and 35). The separate time-series models all performed very well, but the cumulative models decreased in performance as data were added to subsequent models. One explanation for this finding is that as Ruffe spreads from west to east through time, it started to inhabit new locations that were deeper, with larger waves, and less turbid (Table 17), and the variability in the conditions increased, causing the AUC to decrease. For example, early in the invasion, perhaps it inhabited a drastically reduced subset of the current locations in terms of the overall distribution, thus also reducing the variability in the covariate needed to explain their habitat association. Through time, Ruffe has become widely distributed and has been captured in a wide array of locations (whether suitable habitat or not), increasing the variability in covariates and reducing the precision of the model.

Conclusion

Overall, this study demonstrates the strong potential to apply Maxent at spatial scales that could be used in ecological risk assessment or monitoring design. I used lake-scale environmental and geographical data to produce a high-resolution (30 x 30 m grid) predictive distribution map for Ruffe in Lake Superior. However, my results demonstrate that there are some important considerations when developing a SDM at a lake-scale. I found multiple models performed similarly according to AUC scores but had ecologically different suitable habitat prediction maps. Indeed, relatively small differences in buffers (±100s of meters) resulted in differences of billions of square meters predicted. To identify the degree to which data aggregation effect model results, using multiple buffers is necessary. Additionally, with the time-series analysis, the AUC scores decreased as more data was added to the models through time; this suggests that the ability to predict suitable declines as an invasion progresses if presence data are combined through time. If only one data aggregation method is chosen or all of the data is used and autocorrelation is ignored, there is potential for substantial over- or under-prediction of suitable habitat in the model (Table 15).

Dissertation Summary

Chapter 1 summary

Invasive Ruffe (*Gymnocephalus cernua*) has caused substantial ecological damage in North America, parts of Western Europe, Scandinavian countries, and the United Kingdom (Maitland and East 1989; Adams and Tippett 1991; Selgeby and Edwards 1993; Adams 1994; Kalas 1995; Ogle *et al.* 1996; Selgeby 1998; Lorenzoni *et al.* 2009). Once it invades a new waterbody, it is nearly impossible to eradicate, in part, due to its adaptability. In each life stage, Ruffe exhibits plasticity with regard to chemical, physical, biological, and habitat requirements. Adult Ruffe has characteristics that allow it to adapt to a range of environments, including rapid maturation, relatively long life and large size (allowing it to reproduce many times in large batches), batch spawning, genotype and phenotype (having plasticity in their genetic expression), tolerance to a wide range of water quality, broad diet, and multiple dispersal periods. There is, however, variability among these characteristics between the native, non-native North American, and European non-native populations, which presents a challenge to managing populations based on life history characteristics. Monitoring and spread prevention strategies are important because, based on Ruffe's variable life history strategies and its recent range expansion, all of the Laurentian Great Lakes and many other water bodies in the UK, Europe, and Norway are vulnerable to Ruffe establishment.

Chapter 2 summary

Invasive species often show a period of rapid initial increase (boom) followed by a population crash (bust) before achieving a relatively stable, equilibrium population size. My study was located in St. Louis River, MN/ WI, and Chequamegon Bay, WI. I used these two systems to compare because they were invaded by Ruffe at different time periods, and they have similar fish communities. The timeline of population growth and spread of an introduced species can be conceptualized as a series of invasion stages (Sakai *et al.* 2001; Colautti and MacIsaac 2004; Simberloff and Gibbons 2004). In stage 0, propagules of the introduced species are in the donor region; in stage 1, the introduced species is transported outside of its current range; in stage 2, individuals are released and introduced into a new region. In stage 3, the species becomes established, distributed in a small area and is numerically rare. In stage 4, the species' population is either spatially widespread but numerically rare, or localized but abundant. Finally, in stage 5, organisms are widespread and dominant (Colautti and MacIsaac 2004). Stage 4-5 is typically when the population "booms," and following stage 5, there is often a population crash that is referred to as the "bust."

I found that Ruffe populations in both the St. Louis River and Chequamegon Bay are at different invasion stages. In the St. Louis River, the population increased from the initial invasion in 1986 up to 1995 and has been in decline for the past two decades (1996-2015). In Chequamegon Bay, the overall population is increasing, but is doing so by oscillating every 5-7 years. I conclude that Ruffe populations in both systems partially conform to the typical "boom-bust" patterns seen with other invasive fish species. I also found many differences in the fish population trends, in addition to Ruffe, between the St. Louis River and Chequamegon Bay. Understanding patterns of invasive species can be helpful to natural resource managers who are interested in population trends of invasive species.

Chapter 3 summary

Food webs have been greatly impacted by invasive species in ecosystems across the globe. My goal was to study the role of Ruffe in the St. Louis River food web, using carbon and nitrogen stable isotope analysis to characterize its associated trophic pathways (i.e., the various organic matter sources and associated habitats supporting Ruffe's diet). I found significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between Ruffe captured in Lake Superior and those captured in the St. Louis River but not among locations within the river. I found size-based differences as well; medium-sized fish, 60-80 mm total length (SL), had a $\delta^{13}C_{\text{lipid corrected}}$ of about -25‰ to -45‰, lower than either small (<60 mm SL) or large (80-148 mm SL) Ruffe (-38.2‰ to -14.2‰). Extremely depleted ^{13}C values (<-36‰ $\delta^{13}C$) indicate that some fish captured within coastal wetlands were feeding in a methane-based trophic pathway. The high $\delta^{13}C$ values of both small and large Ruffe indicate these fish were both swimming and feeding in Lake Superior; the higher values of medium size Ruffe suggest coastal wetland dependence during the spawning period. The broad range in $\delta^{13}C$ values of large Ruffe indicate routine occupancy of both lake and wetland habitats; 59.7% of individuals were predominantly feeding in a wetland-dominated trophic pathway, whereas 40.3% were feeding in a lake-dominated trophic pathway. This is the first observation of wetland fish obtaining substantial energy from a methane-based food web, as well as the first observation of distinct, size-based diet shifts and movements among coastal habitats in Ruffe. This indicates Ruffe has the ability to occupy a unique trophic niche within coastal wetlands, and it is an obligate user of wetland habitat during spawning but otherwise a facultative user of lake and wetland habitat.

Chapter 4 summary

My goal was to understand how using environmental data resolved to relatively fine spatial scales (i.e., 100m to 1000 m), as well as using different species occurrence data of varying temporal windows, would affect species distribution model performance with respect to predicting potential habitat of an invasive fish, Ruffe. I used Lake Superior catch data and environmental variables to develop a Maxent species distribution model. To examine the effect of spatial data resolution, I developed and compared competing models at different spatial scales: 250-m, 500-m, 1000-m, 2000-m, and 2000-m selected model. In addition, I conducted two time-series analyses, comparing models developed from occurrence data broken into decade time blocks (1986-1996, 1997-2006, 2007-2014) and analyzed separately or cumulatively. I calculated percent suitable habitat for all of the models. I predicted that there would be an optimal spatial scale to model Ruffe—that very low- and very high-spatial scale models would not perform well, but an intermediate model would be the best. Among the models constructed using catch and environmental data from various spatial resolutions, the best performing model used 500 m data and the worst performing model used 2000 m data. The important geographic discrepancies in potential habitat occurred around the Apostle Islands, WI, Isle Royale, MN, Grand Marais, MI, Whitefish Point, MI, and Red Rock and Nipigon in Canada. I showed multiple models that performed similarly according to the area under the curve (AUC) scores, but had different results with respect to the area and distribution of suitable habitat predicted. The Maxent model results from the separate and cumulative time-series analyses were similar. I found minor differences in the environmental variable outputs. However, I found substantial differences in the AUC scores. The separate time series models all performed similarly well, but the performance of the cumulative models declined as data were added to subsequent models. Maxent can be a powerful tool to model invasive species, using the precautions I provide.

Synthesis

Species distribution models produce a variety of maps with varying accuracy. Statistically, these maps are “accurate” and illustrate “suitable” habitat based on occurrence and environmental data. However, it is worthwhile to critically evaluate the model output from a biological perspective. For example, some of the models predicted suitable habitat around the entire Isle Royale, a large island in the northwest corner of Lake Superior about 38.9 km from the Minnesota shore. Isle Royale is a rocky island with a few small wetlands. It has very little sheltered habitat. The question arises as to whether the habitat is suitable based on the biology and ecology of Ruffe.

Based on the results presented in Chapter 1, Ruffe has specific life-history requirements that might prevent it from establishing a population on Isle Royale. Isle Royale is in the north shore of Lake Superior. It is very rocky, and conditions can be harsh. It has 19 embayments surrounding the island adjacent to Lake Superior (Gorman *et al.* 2008). Average depth in the embayment is highly variable, but the mean is 1.28 m (Gorman *et al.* 2008). In Lake Superior, Ruffe has been captured from 0.2-205 m (USGS, personal comm., 2014), but they prefer deep, dark habitats (Gutsch and Hoffman 2016). Substrate is between silty sand and bedrock but predominantly bedrock (Gorman *et al.* 2008). Ruffe prefers sandy, silty, well-aerated, slow-moving water with little or no vegetation (Kontsevaya and Frantova 1980; Popova *et al.* 1998; Ogle 1998). There is very little organic matter, only 5%. Of the existing organic matter, 60% of it is woody debris (Gorman *et al.* 2008). Organic matter is very important for Ruffe because it provides nutrient-rich food for invertebrates (Pinder 1995), so Ruffe can feed on them (Ogle *et al.* 1995). Very little of the shoreline is protected by wave action and ice scouring, which is why there is so little organic matter. The wave action has also caused there to be a lack of overhead shade, logs, and emergent vegetation (Gorman *et al.* 2008). Ruffe requires protected, slow-moving water in which to reside (Gutsch and Hoffman 2016). It lives in waters ranging from oligotrophic to eutrophic but prefer eutrophic waters (Fedorova and Vetkasov 1974; Disler and Smimov 1977; Leach *et al.* 1977; Hansson 1985; Johansson and Persson 1986; Bergman 1988a, 1990, 1991; Bergman and Greenberg 1994; Rösch *et al.* 1996; Popova *et al.* 1998; Lehtonen *et al.* 1998; Brown *et al.* 1998). Although some of the embayments and wetlands on Isle Royale might be eutrophic, most of them are likely lake influenced so they are probably more oligotrophic. It prefers turbid, dark conditions because Ruffe possesses a tapeta lucidum and sensitive lateral line systems, allowing it to forage in low-light conditions (Hölker and Thiel 1998).

In addition to the life history characteristics being a barrier to establishing a population on Isle Royale, there are also movement barriers (Chapter 3). Based on stable isotope findings, when Ruffe is small (25-65 mm), it uses both the lake and the wetland to feed, but when it is 65-85 mm, it is restricted to the wetland. Thus, there is limited opportunity to complete its life cycle on or around Isle Royale, which only has a few, small coastal wetlands. Once the fish is greater than 85 mm, it disperses again to lake and wetland. Although Ruffe could go out to Isle Royale, as the SDM predicts, based on what I know about movements and biology, it is very unlikely that Ruffe would establish a population out there.

Other inconsistencies between the ecology of Ruffe and the SDM model outputs arose. Notably, the SDM predicted that the St. Louis River is a suitable Ruffe habitat; however, based on the population dynamics modeling (Chapter 2), the Ruffe population is exponentially decreasing in the St. Louis River and has been since 1995. Given the population is declining, this could indicate the habitat is not suitable for Ruffe though Ruffe remain abundant, despite the significant decline of Ruffe in the St. Louis River. At present, the St. Louis River catch per unit effort (CPUE) is comparable to Ruffe CPUE in Chequamegon Bay. Given their known life history characteristics and habitat preferences (i.e., turbid, deep, cool, organic, sandy, silty substrate, slow-moving water, and shelter). Based on the scientific literature, the St. Louis River is high-quality habitat for Ruffe (Chapter 1).

Further, the SDM indicates that both Chequamegon Bay and the St. Louis River are equally suitable habitats for Ruffe, though there are ecologically-relevant differences in habitat quality. Coastal wetlands are less extensive in Chequamegon Bay than in the St. Louis River, the open water is turbid (30.6 NTU (16.8 SD)), cool (23^{o}C) (Hoffman *et al.* 2015), deep (maximum depth = 23 m) (Bronte *et al.* 1998), and the bottom is mostly clay, sand, and silt. Because of the substrate and the cold water, the abundance of benthic invertebrates is lower than in coastal wetlands (DUAN *et al.* 2009). The Ruffe caught in Chequamegon Bay are small to medium in size (<100 mm). The water in the St. Louis River is also turbid (67.8 (30.1 SD)), warmer (29^{o}C) (Hoffman *et al.* 2015), shallower (maximum depth = 16 m) (Angradi *et al.* 2015), and the bottom is mostly organic matter because it is a drowned river mouth. Because of the warmer water and the productive organic matter substrate, benthic invertebrates are abundant in the St. Louis River (DUAN *et al.* 2009). As a result, there is high-quality foraging fish habitat. A SDM that incorporates this more extensive habitat quality data could possibly distinguish the suitability of these two systems but georeferenced data to support such a SDM are not available, and these two systems are among the most well-studied in Lake Superior.

Species distribution models can produce maps of suitable habitat for invasive species to help predict introduction, spread, and movement. However, when using finely-scaled (i.e., lake scale) environmental variables, one must use caution when examining the results, both from a management and a biological perspective. I found a variety of inconsistencies between the SDM model output and the biological traits of Ruffe. From this study, I conclude that biological data (e.g., habitat preference, environmental tolerance, life history) are needed along with model performance statistics to evaluate model success from plausibility. Such evaluation should be ongoing and iterative, because as new detections of an invasive species arise, both the predicted suitability will and the SDM accuracy will change. This challenge highlights the fundamental challenge to predicting invasive species habitat – that both the species and its new environment will change through time, yielding a dynamic understanding of suitable habitat. In this context, it is necessary to continually study an invasive species habitat preferences and distribution to obtain the most accurate depiction of the animal's suitable habitat or fundamental niche.

Illustrations

Tables

Table 1. Life history traits of Ruffe (Gymnocephalus cernua) throughout each main life stage. 1. (Collette *et al.* 1977); 2. (Balon *et al.* 1977); 3. (Kolomin 1977); 4. (Lorenzoni *et al.* 2009); 5. (Neja 1988); 6. (Kovac 1998); 7. (Maitland 1977); 8. (Craig 1987); 9. (Kiyashko and Volodin 1978); 10. (Brown et al. 1998); 11. Fedorova and Vetkasov, 1974; 12. (Popova *et al.* 1998); 13. (French and Edsall 1992); 14. (Disler and Smimov 1977); 15. (Hokanson 1977); 17. (Eckmann 2004); 18. (Selgeby 1998); 19. (Kangur *et al.* 1999); 20. (Jamet and Lair 1991); 21. (Ogle *et al.* 1995); 22. (Lind 1977); 23. (Van Densen and Hadderingh 1982); 24. (Nilsson 1979); 25. (Sandlund et al. 1985); 26. (USGS, personal comm. 2014); 27. (Volta *et al.* 2013); 28. (Kalas 1995); 29. (Bastl 1988).

Stage	Habitat	Size (mm)	Duration	Diet	Movements	Depth (m)	Temperature (ºC)	Special Requirements
Egg	On bottom attached to sand, gravel, clay[1], plants, branches, rocks, or logs[2]	0.50-1.0[1]; 0.90-1.213; 0.71-1.59[4]; 0.64–0.98[5]; 0.97-1.07[6]	5-12 days[,7,8], 4-6 days[2,6]	Yolk	Stationary	≤ 5[9]	5 – 18[10]	pH=6.5-10.5[9]
Larvae	On bottom at spawning grounds[14]	3.35-4.40 at hatch[6,11], 6-8 one week after hatch[12], 16-18 end of larval stage[12]	20 days[6]	Yolk sac, exogenous[13]	Stationary[14], passive drift	0.5-5[10]	16.2 to 23[6], growth optimum: 25-30[15]	
Juvenile	Benthic littoral[6,10]	14-110[6,8]	28 days post-hatch[6]	Mainly benthic invertebrates [10,12]	Diel feeding, possibly migrating to overwintering grounds[17,18]	0-15+[18]	≥0.2[19], thermal max: 34.5[15]	Apparently feeds at overwintering habitat[18]
Adult	Benthic, sandy, silty areas[12,20,21]	57-90[29], 110+[22]	2-3 years (some systems	Mainly benthic invertebrates,	Diel feeding, migration to spawning	0.2-205.0[17,23,24,25,26,27,28],	≥0.2[19], spawning	Apparently feeds at

	Ruffe can mature in 1 year)[22]	some zooplankton	grounds, migration to overwintering grounds[17,18]	spawning grounds < 3[9], overwintering grounds 15+[17,18]	grounds are 5-18[10]	overwintering habitat[18]

Table 2. Differences between native, non-native North American, and other non-native Ruffe (*Gymnocephalus cernua*) populations with respect to habitat usage, depths inhabited, feeding habits, age and size at maturity, maximum age and length acquired, and reproduction (if batch spawning occurs). 1. (Hölker and Thiel 1998); 2. (Pratt 1988); 3. (Sierszen *et al.* 1996); 4. (Fairchild and McCormick 1996); 5. (Brown *et al.* 1998); 6. (Stepien *et al.* 1998); 7. (Selgeby 1998); 8. (Ogle *et al.* 2004); 9. (Ogle 2009); 10. (Peterson *et al.* 2011); 11. (USGS 2014); 12. (USEPA, personal comm. 2006-2007); 13. (USFWS, personal comm. 2014); 14. (USGS, personal comm. 2014); 15. (Maitland and East 1989), 16. (Eckmann 2004); 17. (Volta *et al.* 2013); 18. (Wootten 1974); 19. (Winfield *et al.* 2004); 20. (Kalas 1995); 21. (Lorenzoni *et al.* 2009); 22. (Duncan 1990); 23. (Nilsson 1979); 24. (Van Densen and Hadderingh 1982); 25. (Sandlund *et al.* 1985); 26. (Johnsen 1965); 27. (Polivannaya 1974); 28. (Kozlova and Panasenko 1977); 29. (Boikova 1986); 30. (Nagy 1988); 31. (Jamet and Lair 1991); 32. (Kangur and Kangur 1996); 33. (Werner *et al.* 1996); 34. (Kangur *et al.* 2000); 35. (Ogle *et al.* 1995); 36. (Adams and Tippett 1991); 37. (Neja 1988); 38. (Fedorova and Vetkasov 1974); 39. (Craig 1987); 40. (Lappalainen and Kjellman 1998); 41. (Lind 1977); 42. (Ogle 1998); 43. (Maitland 1977).44. (Bastl 1988); 45. (Kolomin 1977); 46. (Devine *et al.* 2000); 47. (Crosier and Molloy 2007); 48. (Popova *et al.* 1998); 49. (Berg 1949); 50. (Sanjose 1984); 51. (Koshelev 1963); 52. (Hokanson 1977).

	Native	**Non-native North America**	**Non-native Europe**
Habitats	Lakes, rivers, ponds, bays, brackish waters, tidal coastal wetlands, non-tidal coastal wetlands, and reservoirs[1]	Lakes, rivers, non-tidal coastal wetlands[2,3,4,5,6,7,8,9,10,11,12,13,14]	Lakes, reservoirs[15,16,17,18,19,20,21,22]
Depths	0.25 - 85 m[23,24,25]	0.2 - 205 m[14]	4.9[20] - 50 m[17], 30 - 70 m[16]
Feeding Habits	Primarily chironomid larvae or pupae[26,27,28,29,30,31,32,33,34]	Zooplankton (age-0); caddisflies and burrowing mayflies (>12 cm Ruffe)[35]; *Mysis* shrimp and Cisco eggs (winter diet)[7]	Loch Lomond, Scotland- Powan ova and caddisflies[36]; Lake Mildevatn, Norway- zooplankton[20]
Age at maturity	1-4 years[31,37,38,39]; Finland- <1[40,41]; Nadym basin- mainly 3-4[444]	2-3 years[42]	2-3 years[42,43];Lake Piediluco, Italy- age 1 for both sexes[21]
Size at maturity	Females: 57-90 mm, Males: 80+ mm[44]; Nadym basin- 20-30 g and 110-120 mm[45]	110-120 mm[42]	Loch Lochmond, Scotland- ~11.67 g/ ~7.5 g[46]; Britain/ Europe- 110-120 mm[42,52]; Lake Piediluco, Italy- females: 78.74±0.83 mm, males: 69.42±1.91 mm[21]
Maximum age	Females: 11 yrs, males: 7 yrs[41,47,43]; Bay of Ob' River, Russia- 20 yrs.[48]; 8-10[48]	10 years	8-10[47]; 6 years [21]

Maximum length	290 mm[1]; Siberia- 500 mm[49] (unconfirmed)[50], 200 mm[41] in Finland	184 mm[13]	Lake Constance, Germany- 124 mm[16]; Lake Piediluco, Italy – 191 mm, 141 g[21]
Reproduction	Multiple clutches of eggs throughout spawning season[38,45,51,52]	Prolonged spawning season but no evidence of multiple clutches[5]	Lake Piediluco, Italy- no information about batch spawning but small relative and absolute fecundities[21]

Table 3. Data comparison by location and vessel for the St. Louis River (SLR), WI/ MN, USA, and Chequamegon Bay (CB), WI, USA, for 1993-2015. Game fish are potential predators: Walleye, Smallmouth Bass, Muskellunge, and Northern Pike. Forage fish include Ruffe, as well as Emerald Shiner, Round Goby, Spottail Shiner, Johnny Darter, Trout Perch, and Yellow Perch.

Date	Data Type	Location	Survey Type	Vessel/Gear	Vessel Sweep (hec/hr)	Agency
1993-2015	Game Fish	SLR	Gill net	NA	NA	MN DNR
1993-2015	Game Fish	CB	Creel survey	NA	NA	WI DNR
2006, 2007, 2010-2015	Forage Fish	SLR	Bottom trawl	4.9 m otter trawl	0.7964	USWFS, USEPA, 1854 Treaty Authority
1993-1999	Forage Fish	CB/ SLR	Bottom trawl	R/V *Kiy*i or R/V *Grayling*- 11.9 m trawl	2.05	USGS, USFWS
1993-2004	Forage Fish	CB/ SLR	Bottom trawl	USGS *R/V* Coaster- 4.9 m trawl	0.785	USGS, USFWS

Table 4. Pearson correlation matrix for fish in the St. Louis River, MN/ WI, USA, from 1993-2015. Above the shaded region are the r values and below the shaded region are the p values. The bolded r values are classified “strong” or “very strong” correlations according to Evans (1996). The bolded p values are those considered significant (<0.05). Fish species are abbreviated as follows: RUF = Ruffe, EMS = Emerald Shiner, JOD = Johnny Darter, ROG = Round Goby, SPS = Spottail Shiner, TRP = Trout Perch, YEP = Yellow Perch, MUS = Muskellunge, SMB = Smallmouth Bass, NOP = Northern Pike, WAL = Walleye.

	RUF	EMS	JOD	ROG	SPS	TRP	YEP	MUS	SMB	NOP	WAL
RUF		-0.517	0.277	-0.255	0.269	**-0.604**	**0.644**	0.014	0.380	0.540	-0.033
EMS	**0.012**		-0.369	0.019	0.046	0.427	-0.466	0.136	-0.130	-0.078	0.294
JOD	0.201	0.083		0.597	0.455	0.200	-0.042	-0.082	0.243	-0.342	0.017
ROG	0.240	0.930	**0.003**		0.496	0.490	-0.433	-0.103	0.365	-0.483	0.478
SPS	0.215	0.834	**0.029**	**0.016**		0.229	0.046	0.195	0.203	0.085	**0.617**
TRP	**0.002**	**0.042**	0.361	**0.018**	0.293		-0.326	0.048	-0.359	-0.522	0.166
YEP	**0.001**	**0.025**	0.851	**0.039**	0.835	0.129		0.177	0.076	**0.603**	-0.289
MUS	0.948	0.537	0.708	0.639	0.374	0.829	0.419		-0.267	0.189	0.254
SMB	0.074	0.556	0.264	0.087	0.352	0.093	0.731	0.218		0.121	0.221
NOP	**0.008**	0.722	0.110	**0.020**	0.699	**0.011**	**0.002**	0.387	0.581		0.040
WAL	0.881	0.173	0.939	**0.021**	**0.002**	0.448	0.182	0.242	0.311	0.855	

Table 5. Pearson correlation matrix for fish in Chequamegon Bay, WI, USA, from 1993-2015. Above the shaded region are the r values and below the shaded region are the p values. The bolded r values are those classified as “strong” or “very strong” correlations according to Evans (1996). The bolded p values are those considered significant (below 0.05). Fish species abbreviations follow Table 4.

	RUF	EMS	JOD	SPS	TRP	YEP	NOP	WAL
RUF		0.272	0.283	0.239	0.130	0.275	-0.312	-0.016
EMS	0.209		0.551	**0.829**	0.419	0.517	-0.018	0.237
JOD	0.190	**0.006**		**0.650**	0.047	**0.749**	-0.358	-0.112
SPS	0.273	**0.000**	**0.001**		0.504	**0.635**	-0.205	0.050
TRP	0.555	**0.047**	0.830	**0.014**		0.053	0.068	0.180
YEP	0.205	**0.011**	**0.000**	**0.001**	0.809		-0.544	-0.270
NOP	0.147	0.934	0.094	0.348	0.759	**0.007**		0.564
WAL	0.942	0.276	0.612	0.819	0.410	0.213	**0.005**	

Table 6. Univariate linear models of Ruffe (*Gymnocephalus cernua*) CPUE over 23 years in the St. Louis River, MN/ WI, USA, from 1993-2015 ranked by Akaike Information Criteria (AIC). For each model, ln(Ruffe CPUE + 1) is the response variable, k is the number of estimable parameters, including the intercept, and the parameter listed is the predictor variable. Corrected AIC (AIC_c) was used to account for my small sample size. Δ AIC_c is the difference in AIC_c from the smallest AIC_c (0.00 is the smallest). AIC_c weight represents conditional probabilities for each model.

Models	**k**	**Log-likelihood**	**AIC_c**	**ΔAIC_c**	**AIC_c weight (w_i)**	**Interaction**
Yellow Perch	2	-25.45883	57.52	0.00	0.62	Competitor
Trout Perch	2	-26.41271	59.43	1.91	0.24	Competitor
Northern Pike	2	-27.65816	61.92	4.40	0.07	Predator
Emerald Shiner	2	-28.04333	62.69	5.17	0.05	Competitor
Smallmouth Bass	2	-29.82926	66.26	8.74	0.01	Predator
Null (intercept only)	1	-31.62196	67.43	10.33	0.00	NA
Johnny Darter	2	-30.70602	68.01	10.49	0.00	Competitor
Spottail Shiner	2	-30.75934	68.12	10.60	0.00	Competitor
Round Goby	2	-30.84895	68.30	10.78	0.00	Competitor
Walleye	2	-31.60948	69.82	12.30	0.00	Predator
Muskellunge	2	-31.61955	69.84	12.32	0.00	Predator

Table 7. Parameter estimates for the top four models that explain 99% of the model weights for predicting Ruffe (*Gymnocephalus cernua*) densities in the St. Louis River, MN/ WI, USA, from 1993-2015 (CI = confidence interval). Parameter estimates with intercepts can be found in the supplemental tables.

Parameter or Variable	**Lower 95% CI**	**Parameter Estimate**	**Upper 95% CI**	**P value**
Yellow Perch	0.320	0.650	0.979	0.001
Trout Perch	-0.920	-0.588	-0.256	0.002
Northern Pike	0.550	1.649	2.749	0.010
Emerald Shiner	-0.862	-0.505	-0.147	0.010

Table 8. Univariate linear models of Ruffe (*Gymnocephalus cernua*) CPUE over 23 years in Chequamegon Bay, WI, USA, from 1993-2015 ranked by Akaike Information Criteria (AIC). For every model, ln(Ruffe CPUE + 1) is the response variable, k is the number of estimable parameters, including the intercept, and each parameter listed is the predictor variable. Each predictor variable for all models was natural log transformed. Corrected AIC (AIC_c) was used to account for my small sample size. Δ AIC_c is the difference in AIC_c from the smallest AIC_c (0.00 is the smallest). AIC_c weight represents conditional probabilities for each model. There were no significant variables—all of them encompass zero.

Models	**k**	**Log-likelihood**	**AIC_c**	**ΔAIC_c**	**AIC_c weight (w_i)**	**Interaction**
Null (intercept only)	1	-46.07433	96.34	0.00	0.18	NA
Northern Pike	2	-44.89592	96.39	0.05	0.18	Predator
Johnny Darter	2	-45.11274	96.83	0.49	0.14	Competitor
Yellow Perch	2	-45.17265	96.95	0.61	0.13	Competitor
Emerald Shiner	2	-45.19094	96.98	0.64	0.13	Competitor
Spottail Shiner	2	-45.39926	97.40	1.06	0.11	Competitor
Trout Perch	2	-45.87891	98.36	2.02	0.07	Competitor
Walleye	2	-46.07135	98.74	2.40	0.05	Predator

Table 9. Summarized sampling methods for Ruffe (*Gymnocephalus cernua*) from 2014-2015. Sampling was completed from Summer 2014 – Summer 2015 by various methods of capture.

Season of Sampling	**Year of Sampling**	**Survey Gear and Specs**	**Vessel**	**Method of Capture**	**Survey Design**	**Number of Fish Captured**
Summer	2014	18'-otter trawl, 5 minutes	FWS small trawling boat	Bottom trawl	1854 Treaty Authority: random three strata (depth ranges that cover dredged, original river channels, shallow/ floodplains), 40/ yr. USFWS: (Stevens, L and Olsen 1999; Stevens and Olsen 2004), 10 SLR, 15 Cheq. Bay/ yr.	221
Fall	2014	18'-otter trawl, 5 minutes in SLR, 10 min in Lake Superior	R/V Blue Heron	Bottom trawl	Random 9 SLR and 5 Lake Superior based on Selgeby (1998)	26
Winter	2014-2015	Angler fishing	N/A	Fishing pole	Opportunistic citizen science fish collection project to collect Ruffe in the SLR and Cheq. Bay from ice anglers, anglers instructed to collect Ruffe and place them in the bag and mark on the map where they caught them	34
Spring	2015	Fyke nets (4.76 mm mesh, front opening 0.9m x 1.2m, lead-to-lead length 15 m), 12 hr overnight set	Mudlark (small EPA vessel)	Fyke nets	Non-randomly chose 4 locations in Superior Bay, St. Louis Bay, and Allouez Bay during spring spawning, set paired fyke nets parallel to shore	0
Summer	2015	18'-otter trawl, Fyke nets, Windermere traps	FWS small trawling	Bottom trawl, fyke nets,	Non-random; selected habitat that was gear-appropriate in Amnicon River, Brule River, Flag River	51 (bottom trawling), 0 fyke and Windermere

	(length 1.22 m, width 0.71 m, diameter 0.60 m, conical entrances 50.8 mm	boat, Mudlark	Windermere traps	complex, Bark Bay Slough using 8 paired fyke nets and 4 baited Windermere traps

Table 10. Summary of stable isotope data. Data was collected and analyzed between the summer of 2014 and the summer of 2015. We used $\delta^{13}C_{lipidcorrected}$ values. SL is standard length. SD is standard deviation. 25 and 75 quartiles are the 25th and 75th percentile, respectively.

Year	Area	Location	Mean (SD) $\delta^{13}C$ lipid corr	Range $\delta^{13}C$ lipid corr	Median (25th -75th Quartiles) $\delta^{13}C$ lipid corr	Mean (SD) $\delta^{15}N$	Range $\delta^{15}N$	Median (25th -75th Quartiles) $\delta^{15}N$	Mean SL (mm)	Mean Weight (g)	Range C:N	Sample Size
2014	Cheq. Bay	Cheq. Bay	-21.0 (3.1)	-28.0 - -17.2	-20.5 (-22.6 - -18.4)	4.9 (0.9)	4.0 – 7.0	4.6 (4.2 - 5.7)	63.9	8.9	3.7 – 4.2	10
2015	Cheq. Bay	Cheq. Bay	-19.8 (1.8)	-29.8 - -16.8	-19.8 (-20.5 - -18.9)	6.3 (0.5)	5.2 – 7.7	6.3 (6.0 – 6.6)	48.4	2.6	3.6 – 6.5	53
2014-2015	Cheq. Bay	Cheq. Bay	-18.8 (2.4)	-22.8 - -14.2	-18.8 (-19.6 - -17.4)	6.1 (0.4)	5.5 – 6.9	6.1 (5.8 – 6.4)	108.4	29.6	3.7 – 4.2	11
2014	Lake Superior	Lake Superior	-19.8 (0.2)	-19.9 - -19.7	-19.8	8.0 (0.02)	8.0 – 8.0	8.0	29	0.4	3.8 – 4.3	2
2014-2015	Lake Superior	Lake Superior	-18.1	NA	NA	6.6	NA	NA	127	49.1	4.0	1
2014	Lower	Lower St. Louis Bay	-32.5 (5.1)	-45.0 - -23.9	-32.3 (-36.7 - -28.5)	8.9 (1.3)	5.8 – 12.2	8.9 (8.0 – 9.7)	83.1	16.6	3.5 – 4.6	75
2014	Lower	Pokegama Bay	-35.0 (2.5)	-37.7 - -31.6	-35.3 (-37.1 - -32.5)	7.4 (0.7)	6.5 – 7.9	7.6 (6.7 – 7.9)	43	1.9	3.6 – 3.8	4

2014	Lower	Superior Bay	-31.5 (4.2)	-48.0 - -22.3	-31.2 (-33.9 - -28.6)	9.9 (2.0)	4.0 – 16.1	9.8 (9.0 – 11.2)	67.7	8.7	3.7 – 4.3	72
2014	Lower	Upper St. Louis Bay	-32.4 (6.6)	-40.3 - -24.4	-32.0 (-39.7 - -26.0)	8.1 (1.4)	6.7 – 10.6	7.7 (7.2 – 9.1)	78	11.3	3.7 – 3.8	6
2014-2015	Lower	SLR Winter	-32.5 (4.8)	-36.7 - -26.4	-35.2 (-36.4 - -27.3)	9.3 (2.0)	7.3 – 12.3	9.1 (7.5 – 11.2)	104.2	28.7	3.7 – 4.2	5
2014-2015	Unspec. SLR	Unspec. SLR	-20.1 (4.0)	-31.8 - -16.3	-18.7 (-21.6 - -17.5)	5.8 (0.7)	4.1 – 6.8	5.9 (5.4 – 6.3)	113.8	39.4	3.6 – 4.3	16
2014	Upper	Spirit Lake	-38.0 (6.3)	-52.4 - -25.8	-37.4 (-41.7 - -33.8)	7.3 (1.8)	2.8 – 9.8	7.7 (6.4 – 8.5)	88.6	17.4	3.5 – 5.6	43

Table 11. Description of occurrence data for Maxent model. Data ranged from 2005-2015 and came from literature or agencies. Data was collected a variety of ways (Gear).

Organization/ Source	Years	Design	Gear	Habitat	Location Sampled	Number of Occurrence Points
Peterson et al. 2011, Lindgren et al. 2006	2007	Total catch	Fyke net, electrofish, trawl, seine	Coastal wetland	Lower St. Louis River, MN	1
USEPA 2006-2007	2006-2007	Total catch	Fyke net, electrofish, trawl, seine	Coastal wetland	St. Louis River estuary, MN	109
USFWS, personal comm. 2014-2015	2005-2014	Total catch	Bottom trawl, fyke net	Rivers and coastal wetlands	Amnicon River, Flag River, Iron River, Marquette Lower Harbor, Ontonogon river, Pike Bay, Grand Marais, Keeweenaw Lower Entry, Portage Lake, St. Louis River, Chequamegon Bay, Thunder Bay	180
USFWS/ USEPA 2008	2008	Total catch	Bottom trawl, fyke net	Coastal wetland	St. Louis River estuary, MN	23
USGS 2014	2005-2011	Total catch/ sightings	NA	NA	Amnicon River, WI, Beartrap-Nemadji, WI, Kaministiquia River, Ontario, Canada, West bay at Grand Marais, MI, Little Lake, MI, Misery River, Keweenaw Peninsula, MI, Sturgeon River Slough, Keweenaw Peninsula, MI, Squaw Bay, Beartrap-Nemadji, WI, St. Louis River/ Estuary/ Bay/ Harbor, MN/ WI, Chequamegon Bay, WI, near Tahquamenon Bay, MI, north of Whitefish Point, MI	11
USGS, personal comm. 2014-2015	2005-2014	Total catch	Bottom trawl	Lakes, wetlands, rivers	Chequamegon Bay, Preq I Bay- Stockton Isl, Bear Island, Superior Entry, Apostles inshore, E. Madeline Island, Is Royale (Lk. Desor Reef), Mawikwe (Squaw) Pt., Port Wing, Duluth-Superior grid 1402,	64

Tahquaenon Is, Whitefish Pt., Basswood Island, NE Herbster (Bark Point), Raspberry Island (PT.DET), Lake Superior, MN, USA/ Canada

Table 12. Description of environmental data for Maxent model. There are five environmental layers, four came from the Great Lakes Aquatic Habitat Framework (GLAHF). Data was collected and analyzed a variety of ways. For the best description of the data, see the metadata on the GLAHF and MIT websites.

Data	**Source**	**Resolution, as obtained**	**Years/ Seasons/ Dates**	**Link to data**	**Link to meta data**
Turbidity	Michigan Tech Research Institute	1 km x 1 km	2010-2013/ June-August	http://www.mtri.org/	http://spatial.mtri.org/static/greatlakeswaterquality/
Depth	GLAHF	30 m x 30 m	See metadata	https://www.glahf.org/	Metadata is in the link to data
Substrate	GLAHF	30 m x 30 m	1968-present	https://www.glahf.org/	Metadata is in the link to data
Wave height	GLAHF	30 m x 30 m	Hourly time step, 1979-2012	https://www.glahf.org/	Derived from GLAHF- interpolated using Arc software
Distance to wetland	GLAHF	30 m x 30 m	See metadata	https://www.glahf.org/	Calculated using the GLAHF “Coastal Wetlands” data- metadata within

Table 13. Number of points for Maxent modeling for all six models. We applied distance buffers to remove clustering of occurrences points. This tables shows the number of points that resulted from the cluster-removal and ended up in each of the six models, as well as the resulting background points assigned by the Maxent program.

	# occurrences	# training data	# test data	# points used to determine Maxent distribution (background and presence points)	# points in CB	# points in SLR
All data	362	254	108	10249	74	194
250 m	233	164	69	10162	53	127
500 m	168	118	50	10117	44	76
1000 m	109	77	32	10075	34	36
2000 m	69	49	20	10047	19	15
2000 m selected removal	129	91	38	10089	20	15

Table 14. Percent area predicted from buffer and from Lake Superior, as well as for different zones from the Maxent model for all six models using a logistic threshold at maximum test sensitivity plus specificity. Maximum test sensitivity plus specificity is an output from Maxent used as a threshold so everything above it was suitable habitat and everything below it was unsuitable habitat. I calculated percentages from the Maxent output predictive maps.

	Percent area predicted from buffer	Percent area predicted from Lake Superior	Depth (m)					
			In-shore <30		Nearshore <100		Offshore >100	
			Percent of Buffer	Area (km^2)	Percent of Buffer	Area (km^2)	Percent of Buffer	Area (km^2)
Full adult model	14%	5.76%	13.22%	4330	1.00%	329	0.21%	68.7
250 m	6%	2.38%	5.93%	1940	0.020%	6.50		
500 m	8%	3.45%	8.49%	2780	0.16%	51.8	2.75e-6%	0.0009
1000 m	20%	8.17%	16.38%	5370	3.50%	1150	0.58%	191
2000 m	17%	7.03%	15.51%	5080	2.11%	692	1.18e-4%	0.0387
2000 m selected removal	22%	8.70%	15.46%	5070	3.38%	1110	2.96%	969

Table 15. Percent contribution of environmental variables for all six models. Percent contribution is a Maxent output that explains how much the environmental variables contribute to the prediction of suitable habitat.

	Depth	**Wave Height**	**Distance to Wetland**	**Turbidity**	**Substrate**
Full model (all data)	31.5	36.2	16.8	13.5	2.1
250 m	38.7	40.1	5.4	13.6	2.2
500 m	33.3	31.1	16.8	15.6	3.1
1000 m	49.2	36.7	4.6	5.1	4.4
2000 m	55	28.6	5.2	5	6.2
2000 m selected model	48.5	14.5	29.9	2.6	4.6

Table 16. Pearson correlation r and p values of environmental variables from the Maxent models. The p values are shaded, r values are in white. A rho value of 0.65 or higher is typically considered correlated.

	Depth	Wave Height	Turbidity	Substrate Type	Distance to Wetland
Depth		0	8.19E-10	0	4.70E-06
Wave Height	0.418		0	2.61E-09	0.244
Turbidity	-0.264	-0.481		0.007	4.44E-16
Substrate Type	0.496	0.256	-0.117		0
Distance to Wetland	0.198	0.051	-0.343	0.155	

Table 17. Average value of environmental variables for the Maxent model east and west of the Keweenaw Peninsula (longitude -88.51). Ruffe (*Gymnocephalus cernua*) reached the Keweenaw Peninsula in 2002 and continued to spread east from there.

	East of Keweenaw	**West of Keweenaw**
Turbidity	0.222	0.404
Depth	35.259	5.153
Wave Height	0.219	0.149
Substrate	3	3
Distance to Wetland	3980.374	4068.116

Figures

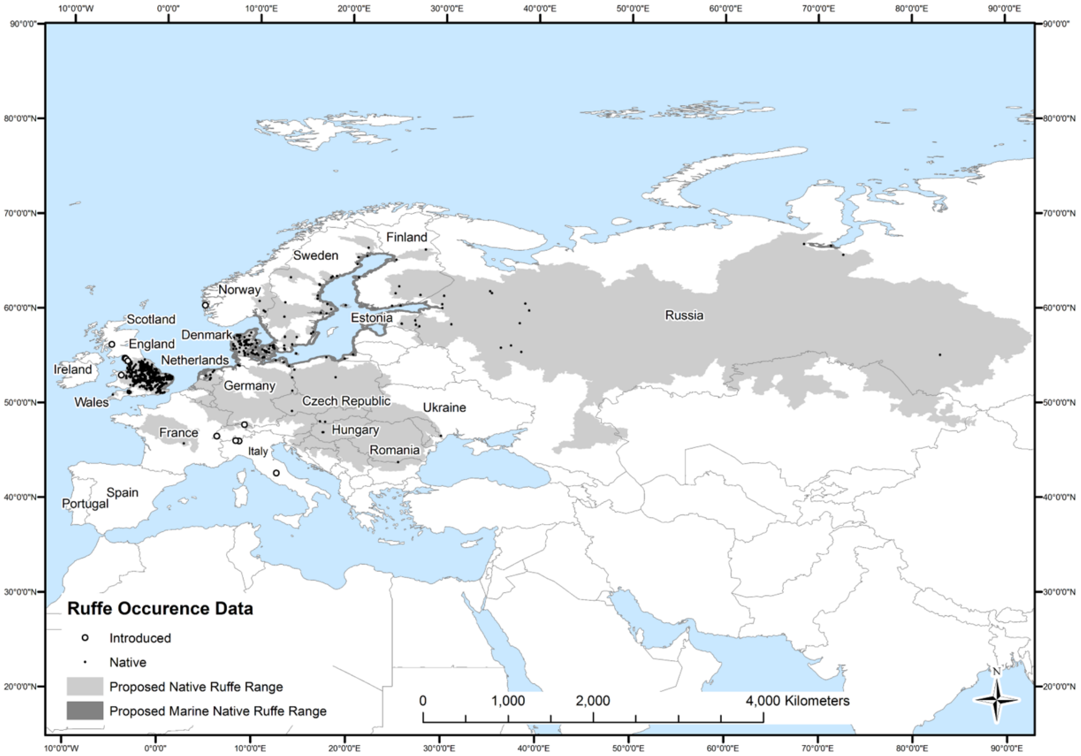

Figure 1. Proposed range map for Ruffe (*Gymnocephalus cernua*). Points include both native (N=229) and non-native (N=16) populations. Occurrence points were plotted in ArcGIS using latitudes and longitudes from Ruffe data in the literature (Johnsen 1965; Nygren *et al.* 1968; Travkina 1971; Wootten 1974; Nyman 1975; Kolomin 1977; Kozlova and Panasenko 1977; Willemsen 1977; Biro 1977; Dykova and Lom 1978; Doornbos 1979; Neuman 1979; Nilsson 1979; Pihu and Maemets 1982; Van Densen and Hadderingh 1982; Logvinenko *et al.* 1983; Hansson 1984, 1987; Sterligova and Pavlovskiy 1984; Bagge and Hakkari 1985; Sandlund *et al.* 1985; Vollestad *et al.* 1986; Boikova 1986; Bakanov *et al.* 1987; Matkovskiy 1987; Mayr *et al.* 1987; Peters *et al.* 1987; Boron and Kuklinska 1987; Bastl 1988; Nagy 1988; Neuman and Karas 1988; Bergman 1988a; Parmanne 1988; Bergman 1991; Eklov and Hamrin 1989; Maitland and East 1989; Neja 1989; Appelberg 1990; Duncan 1990; Lindesjoo and Thulin 1990; Tellervo Valtonen *et al.* 1990; Urho *et al.* 1990; Bonsdorff and Storberg 1990; Jamet and Lair 1991; Jokela *et al.* 1991; Mattila 1992; Kalas 1995; Werner *et al.* 1996; Popova *et al.* 1998; Hölker and Thiel 1998; Lehtonen *et al.* 1998; Stepien *et al.* 1998; Pietrock *et al.* 1999; Kangur 2000; Kangur *et al.* 2000, 2003; Lilja *et al.* 2003; Winfield *et al.* 2004; Lorenzoni *et al.* 2009; Peterson *et al.* 2011; Volta *et al.* 2013).

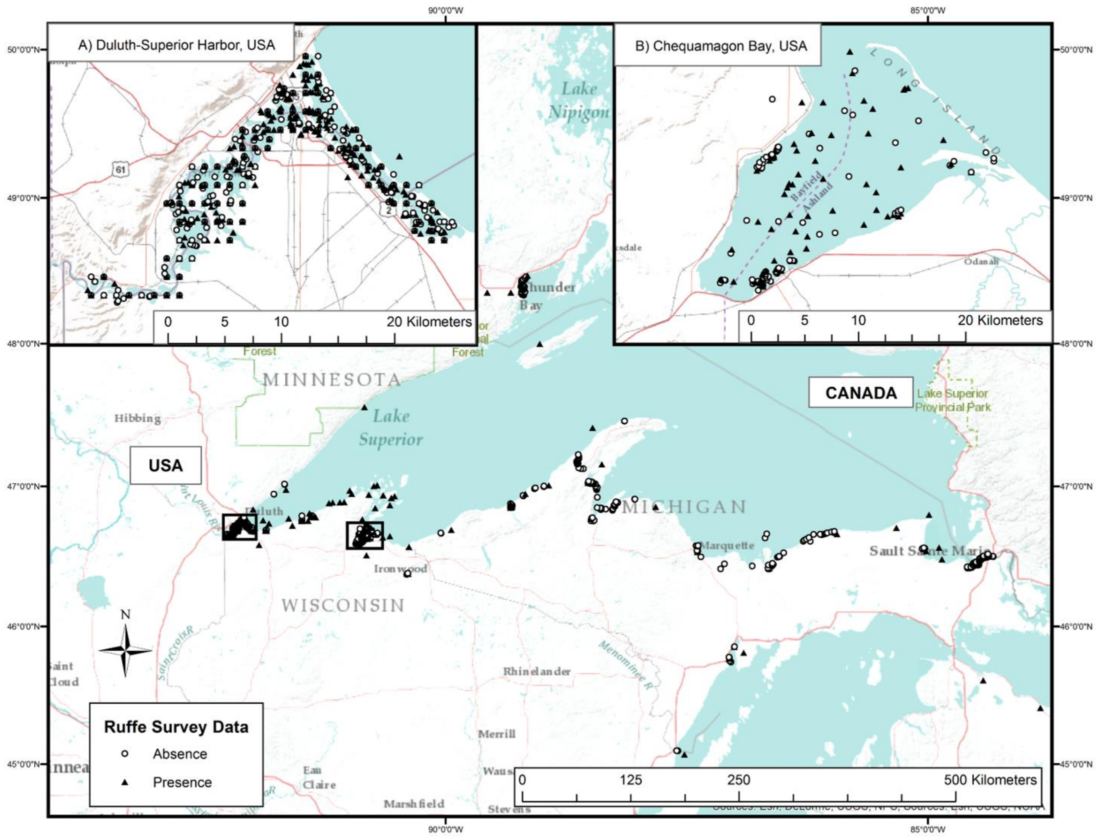

Figure 2. Occurrence data of Ruffe (*Gymnocephalus cernua*) in the Laurentian Great Lakes, North America. Points (N=5,898) include surveyed areas for Ruffe, monitoring presence (solid triangles) and absence (open circles) near the invaded regions in the Great Lakes (Brown et al., 1998; Eckmann, 2004; Fairchild and Howard McCormick, 1996; Lorenzoni et al., 2009; Maitland and East, 1989; Ogle, 2009; Ogle et al., 2004; Peterson et al., 2011; Pratt, 1988; Selgeby, 1998; Sierszen et al., 1996; Stepien et al., 1998; Volta et al., 2013) and from personal communication with several agencies, including United States Geological Survey- Lake Superior Biological Station, United States Fish and Wildlife Service- Ashland FWCO, and Environmental Protection Agency-MED.

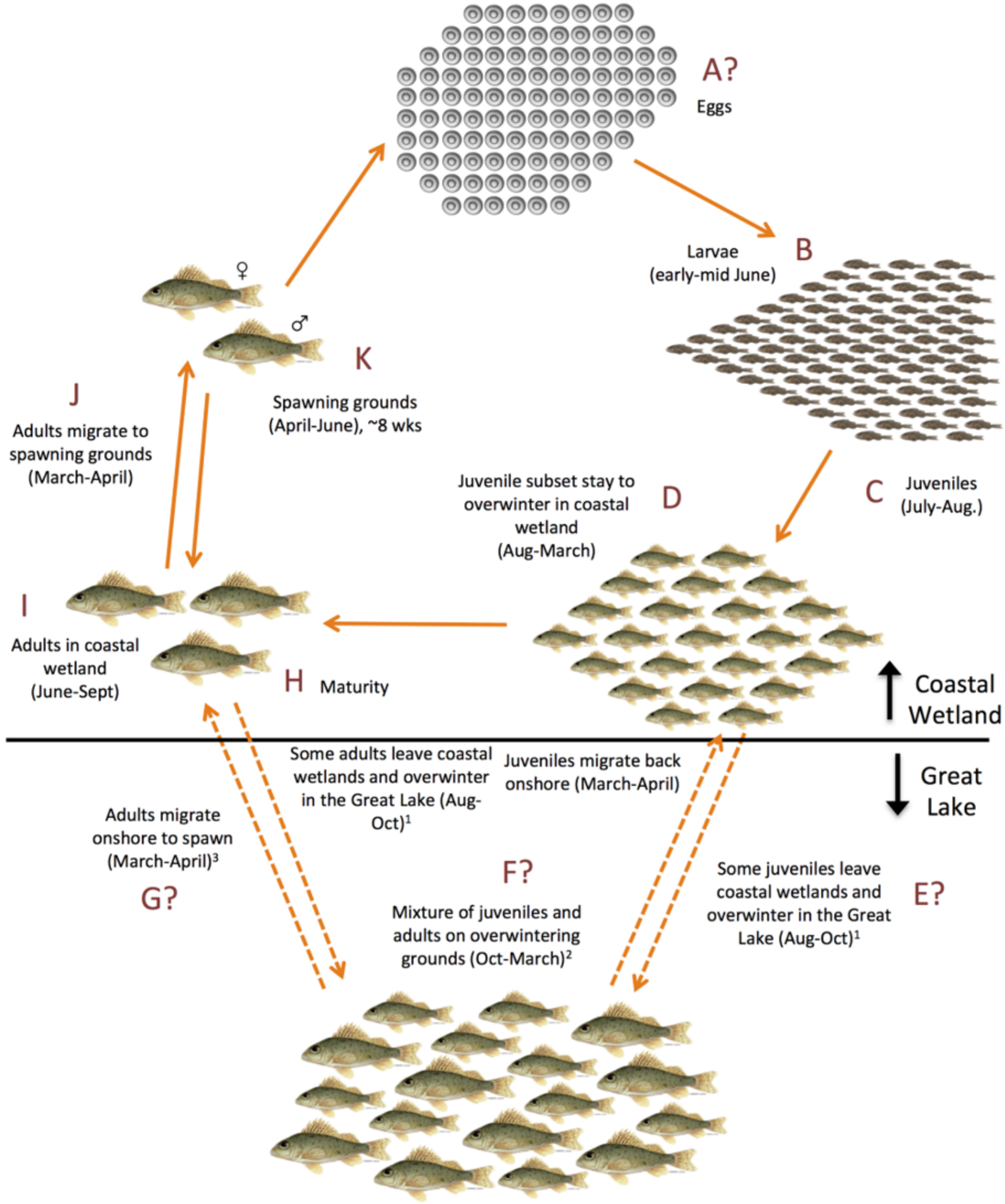

Figure 3. Proposed Ruffe (*Gymnocephalus cernua*) life cycle in the Laurentian Great Lakes. Letters with question marks indicate stages with some incomplete information; letters without question marks indicate there is a thorough understanding of that life stage in the literature. Solid lines between stages indicate a known life stage path; dotted line indicates a hypothesized life stage path. The lettering increases in order from egg to spawning pair in a clockwise fashion. Relative fish abundances at any stage are for illustration purposes only. 1. (Eckmann 2004); 2. (Selgeby 1998); 3. (Popova *et al.* 1998).

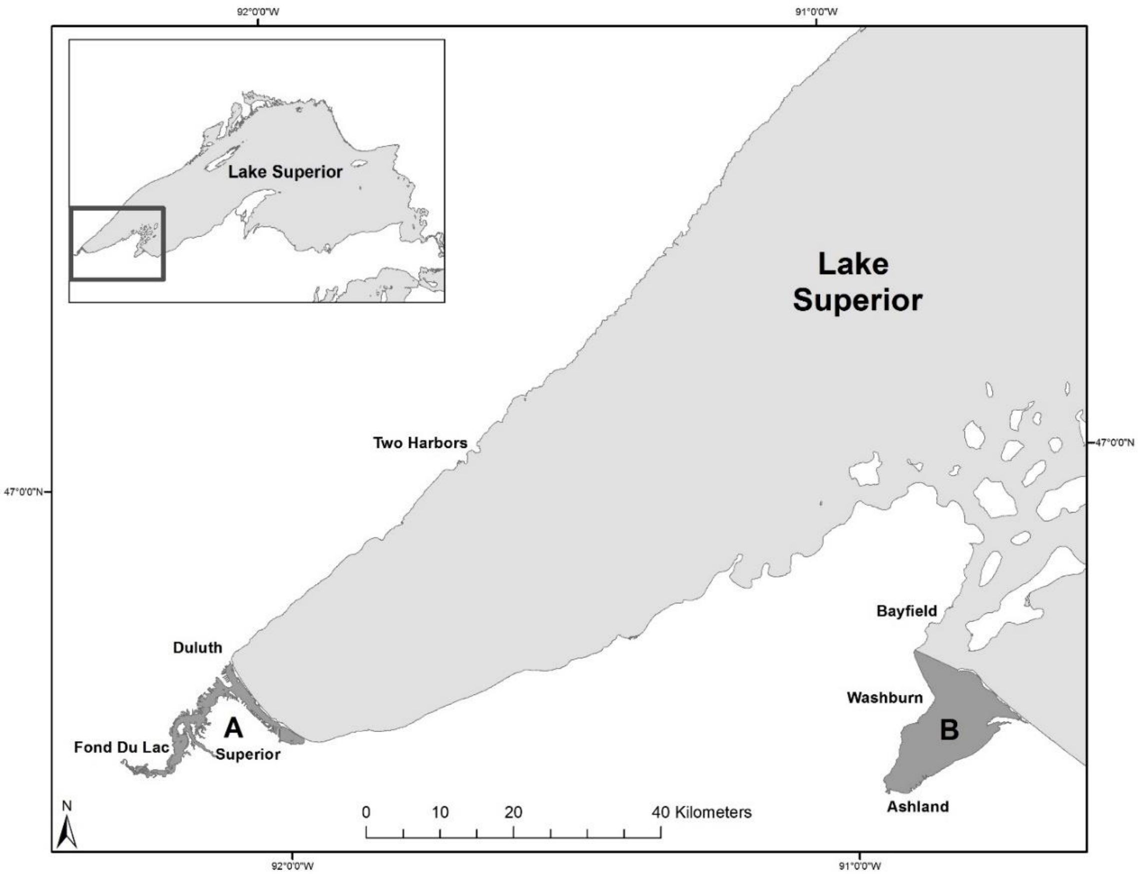

Figure 4. Map of western Lake Superior with study sites St. Louis River, MN/ WI, USA (A) and Chequamegon Bay, WI, USA (B).

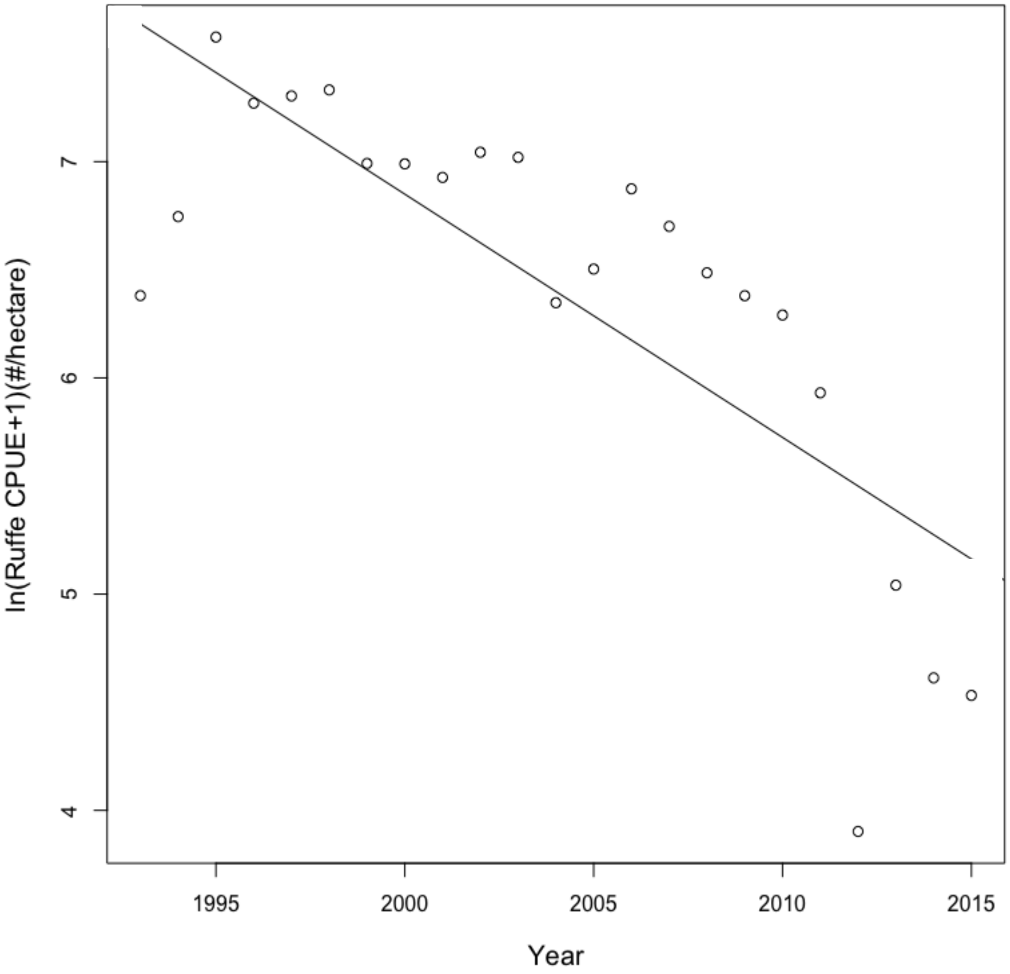

Figure 5. Ruffe (*Gymnocephalus cernua*) catch per unit effort (CPUE) in the St. Louis River, MN/ WI from 1993-2015. CPUE is represented in ln(Ruffe CPUE +1) in #/hectare. The points are annual mean CPUE, and the line is the linear model fit.

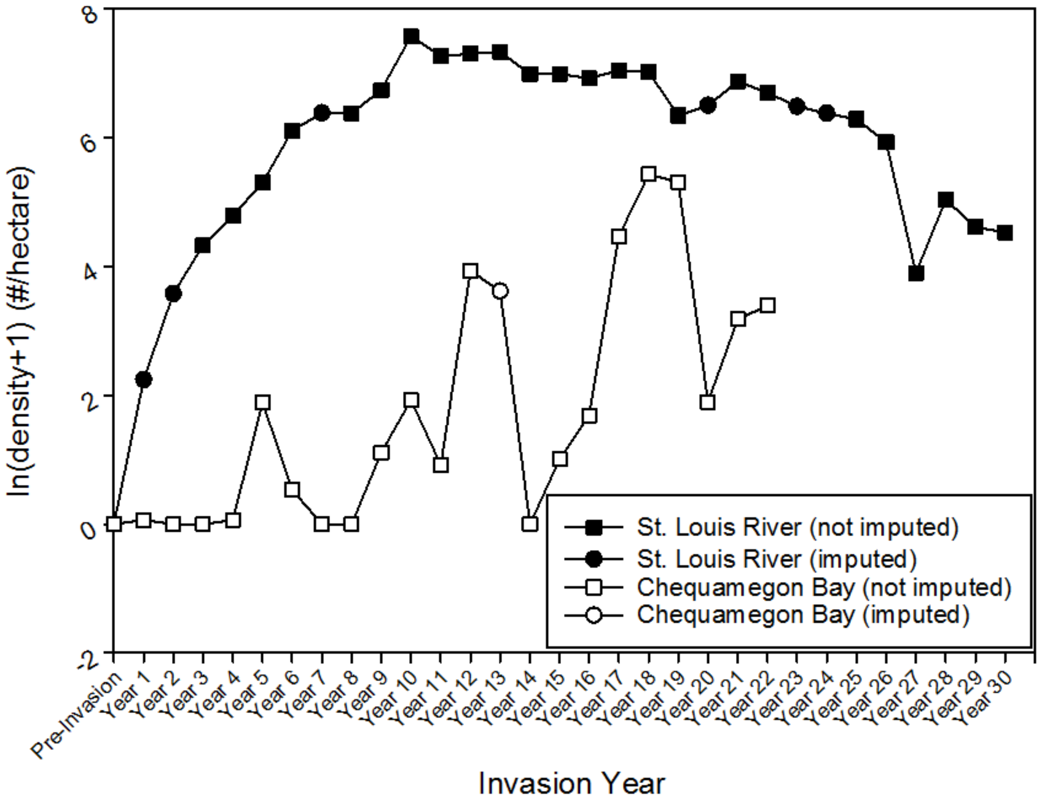

Figure 6. Annual mean catch per unit effort (CPUE) of Ruffe (*Gymnocephalus cernua*) in the St. Louis River, MN/WI and Chequamegon Bay, WI beginning from one year prior to the first Ruffe detection in each system (St. Louis River: 1985; Chequamegon Bay: 1993) to 2015. St. Louis River data from 1985-1992 was borrowed from Pratt (1988), Ruffe Task Force (1992), and USGS and missing data (St. Louis River: 2005, 2008, 2009; Chequamegon Bay: 2006) were imputed using the same spline curve technique described in the methods. The circles are the imputed values, and the squares are the known values.

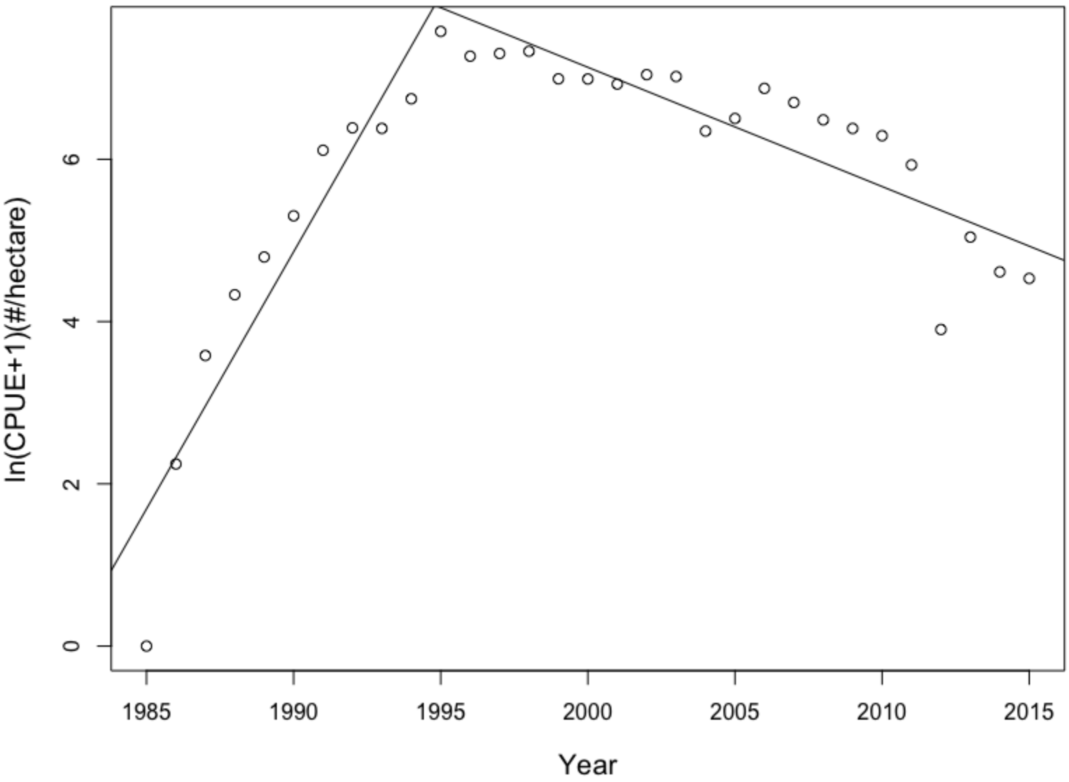

Figure 7. Annual mean catch per unit effort (CPUE) of Ruffe (*Gymnocephalus cernua*) in the St. Louis River, MN/WI from 1985-2015. Data from 1985-1993 was extrapolated from Ruffe Task Force literature and missing data (2005, 2008, 2009) were imputed using the same spline curve technique described in the methods (Ruffe Task Force 1992). Two linear models were fit: 1983-1995, and 1996-2015.

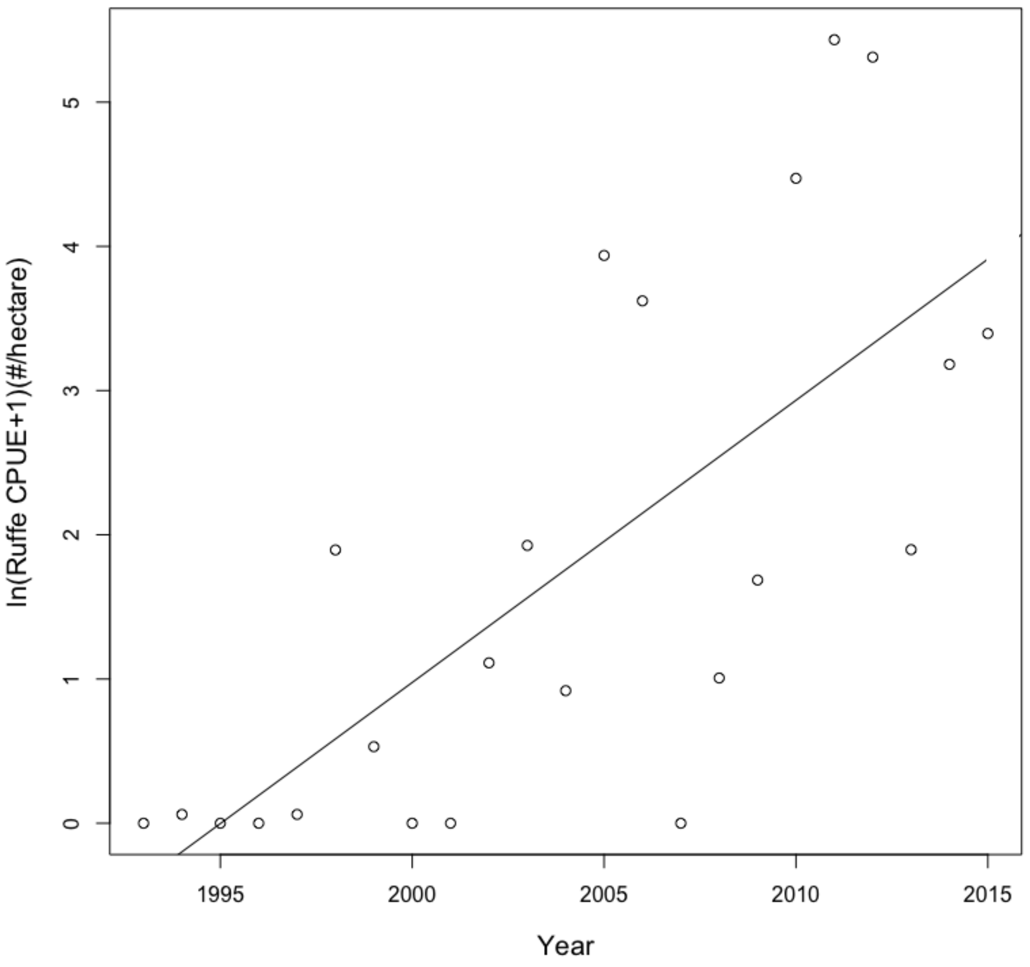

Figure 8. Ruffe (*Gymnocephalus cernua*) catch per unit effort (CPUE) in Chequamegon Bay, WI from 1993-2015. CPUE is represented in ln(Ruffe CPUE +1) in #/hectare. The points are the annual mean CPUE, and the line is the linear model fit.

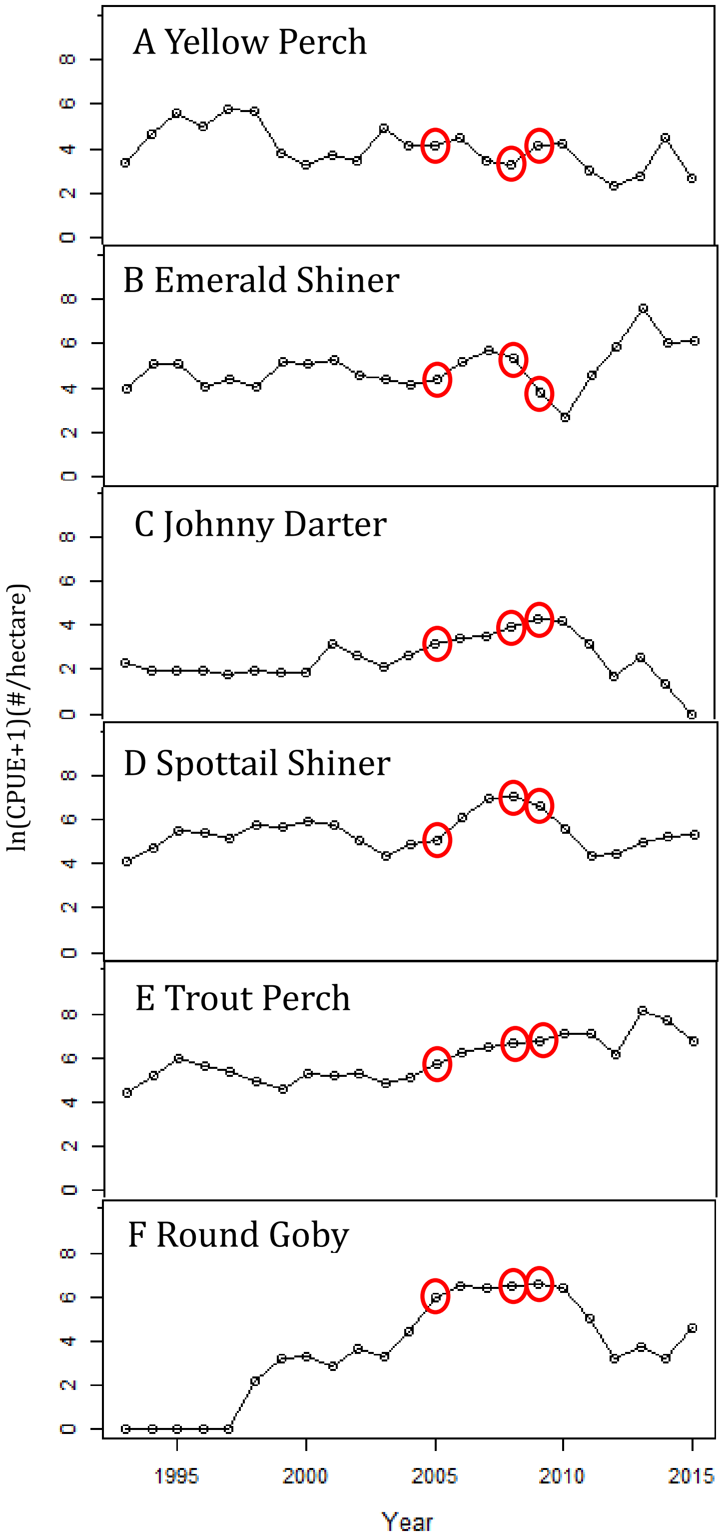

Figure 9. Annual mean catch per unit effort (CPUE) of potential Ruffe (*Gymnocephalus cernua*) competitors, including a) Yellow Perch (*Perca flavescens*), b) Emerald Shiner (*Notropis atherinoides*), c) Johnny Darter (*Etheostoma nigrum*), d) Spottail Shiner

(*Notropis hudsonius*), e) Trout Perch (*Percopsis omiscomaycus*), and f) Round Goby (*Neogobius melanostomus*) in the St. Louis River, MN/ WI from 1993-2015. The points circled are the imputed values.

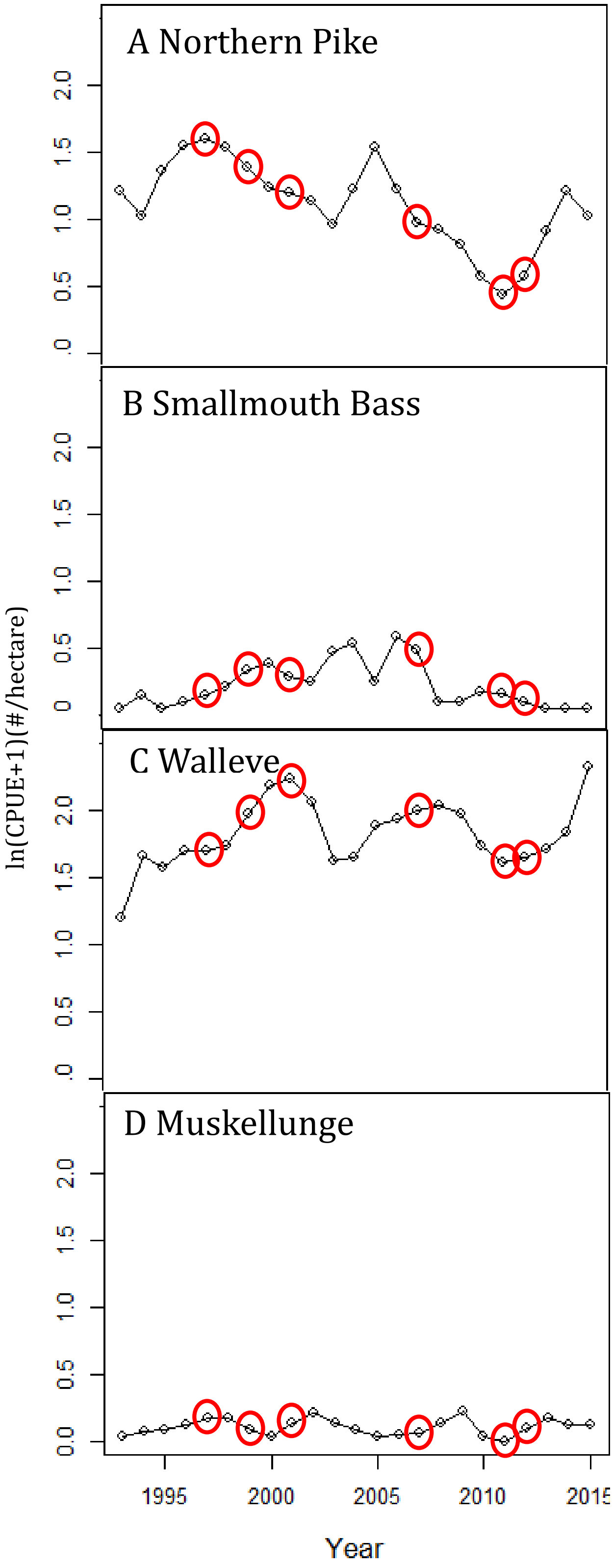
A Northern Pike
B Smallmouth Bass
C Walleye
D Muskellunge
ln(CPUE+1)(#/hectare)
0.0
0.5
1.0
1.5
2.0
1995
2000
2005
2010
2015
Year

Figure 10. Annual mean catch per unit effort (CPUE) of potential Ruffe (*Gymnocephalus cernua*) predators, including a) Northern Pike (*Esox lucius*), b) Smallmouth Bass (*Micropterus dolomieu*), c) Walleye (*Sander vitreus*), and d) Muskellunge (*Esox masquinongy*) in the St. Louis River, MN/ WI from 1993-2015. The points circled are the imputed values.

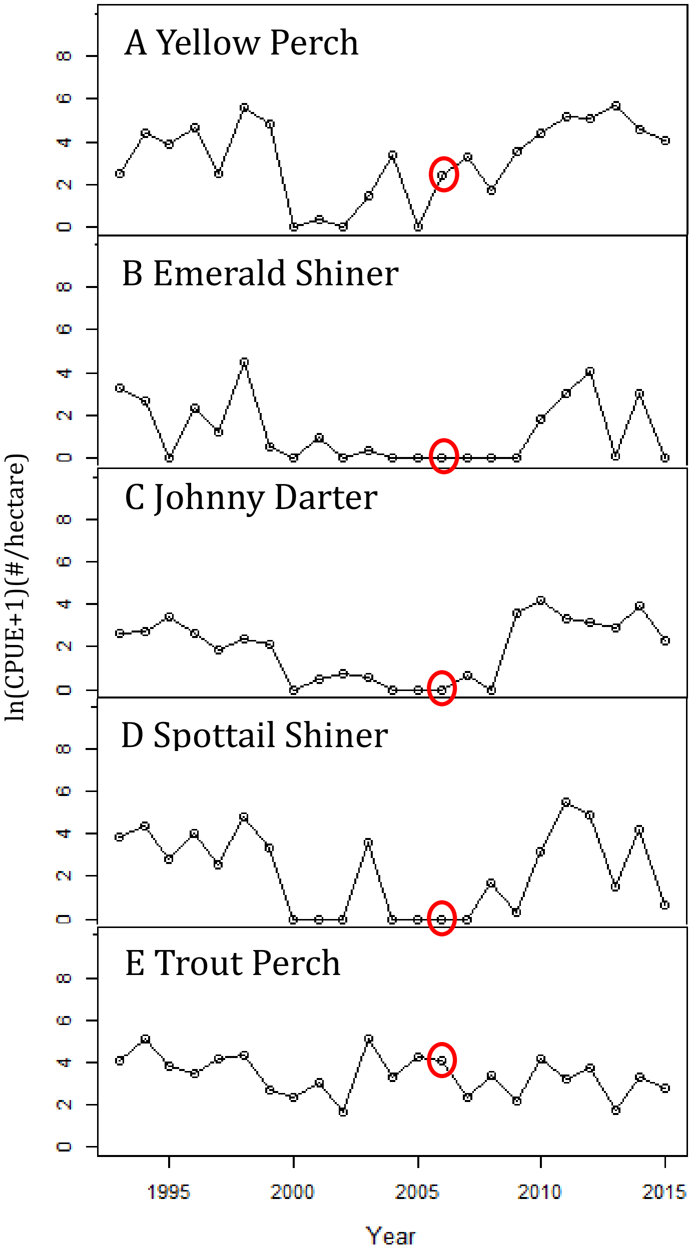

Figure 11. Annual mean catch per unit effort (CPUE) of potential Ruffe (*Gymnocephalus cernua*) competitors, including a) Yellow Perch (*Perca flavescens*), b) Emerald Shiner (*Notropis atherinoides*), c) Johnny Darter (*Etheostoma nigrum*), d) Spottail Shiner (*Notropis hudsonius*), and e) Trout Perch (*Percopsis omiscomaycus*) in Chequamegon Bay, WI from 1993-2015. The points circled are the imputed values.

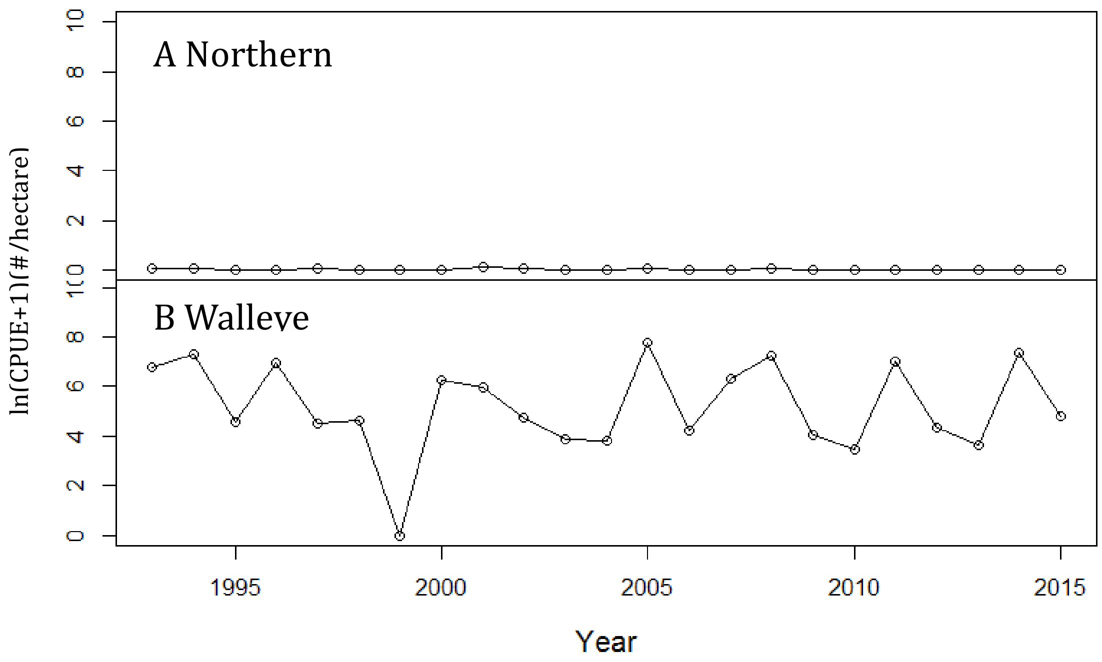

Figure 12. Annual mean catch per unit effort (CPUE) of potential Ruffe (*Gymnocephalus cernua*) predators, including a) Northern Pike (*Esox lucius*) and b) Walleye (*Sander vitreus*) in Chequamegon Bay, WI from 1993-2015. The points circled are the imputed values.

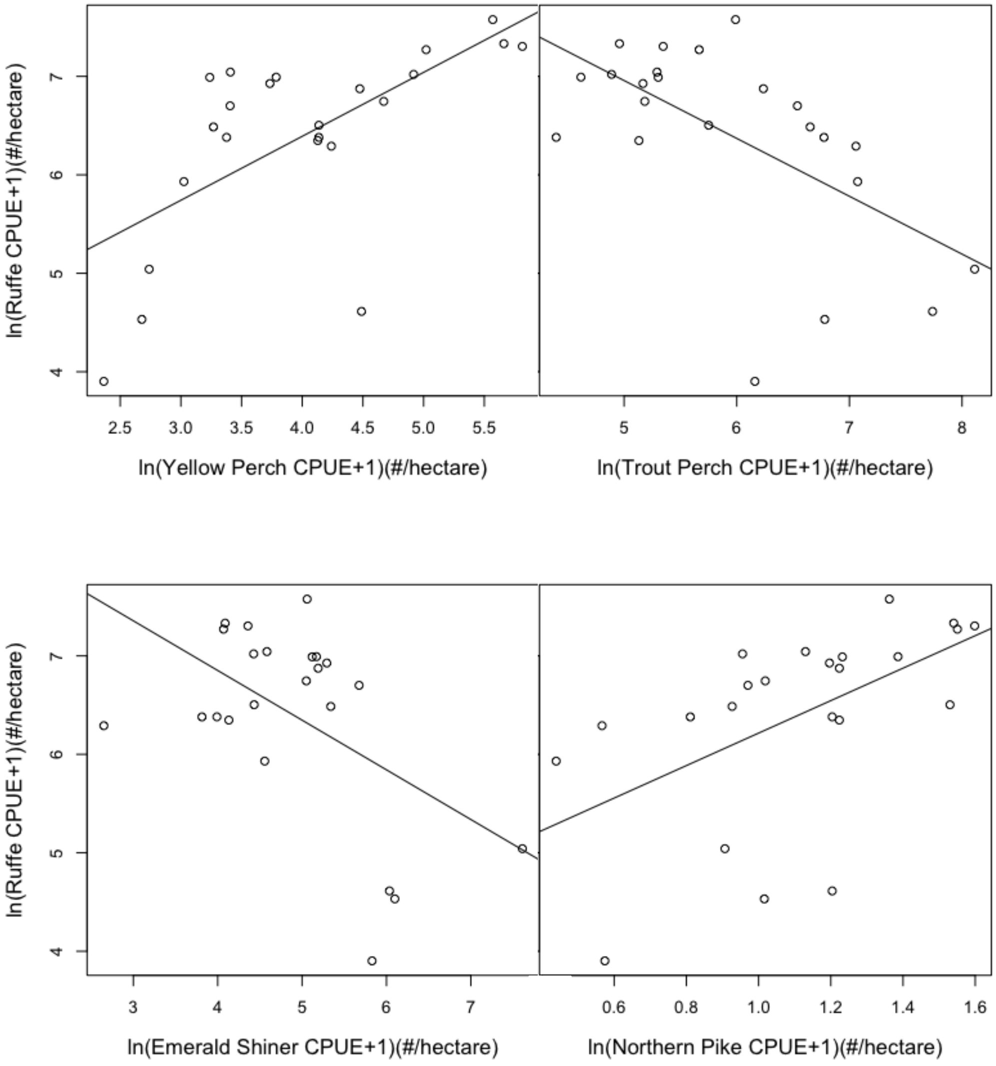

Figure 13. Best fit models of Ruffe (*Gymnocephalus cernua*) catch per unit effort (CPUE) in the St. Louis River, MN/ WI. These four models contain 99% of the model weight.

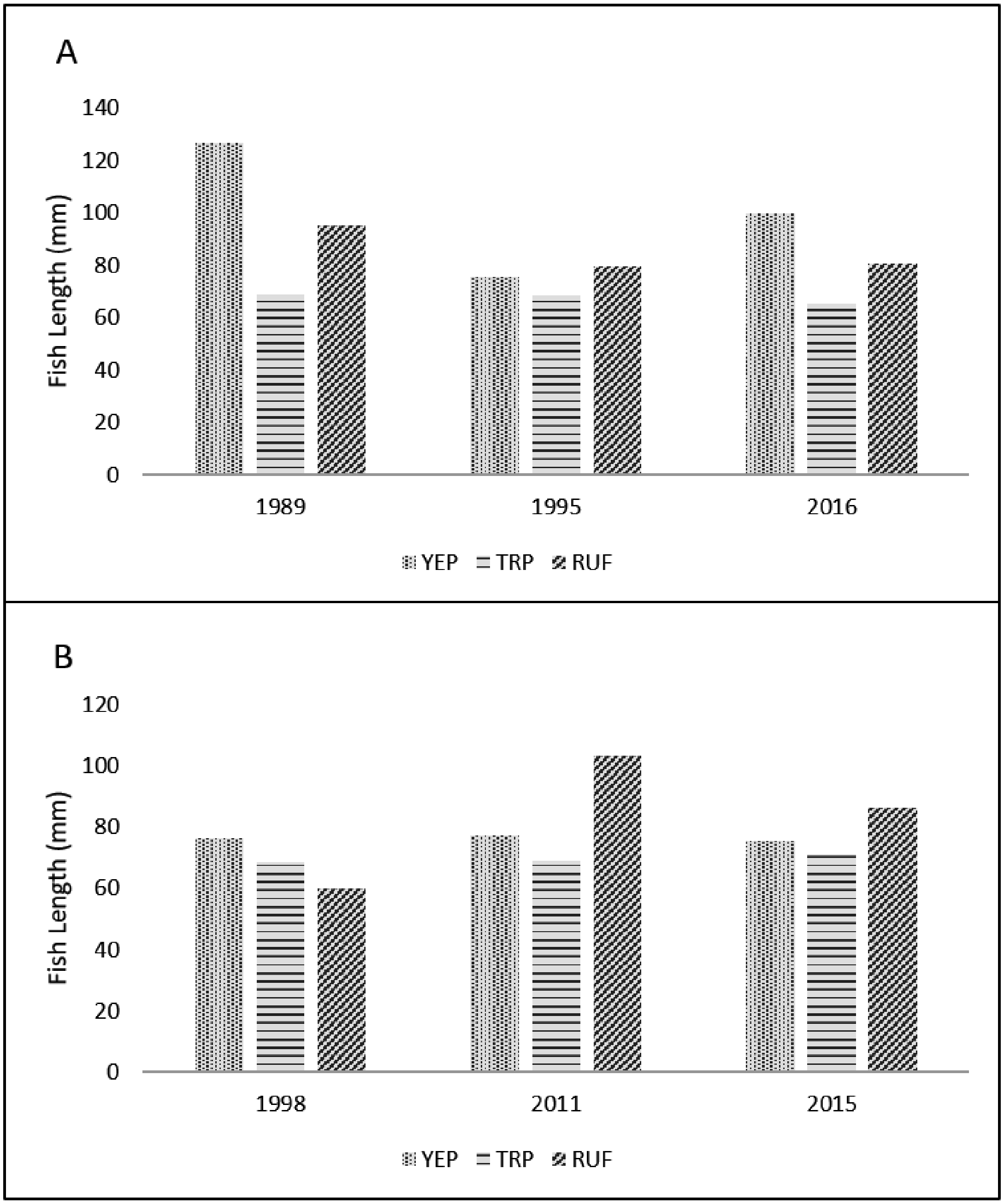

Figure 14. Fish lengths between systems (A) St. Louis River and (B) Chequamegon Bay for Yellow Perch (YEP), Trout Perch (TRP), and Ruffe (RUF). Years chosen represent a year close to initial Ruffe invasion, the year of peak Ruffe CPUE so far, and the most current data year we have.

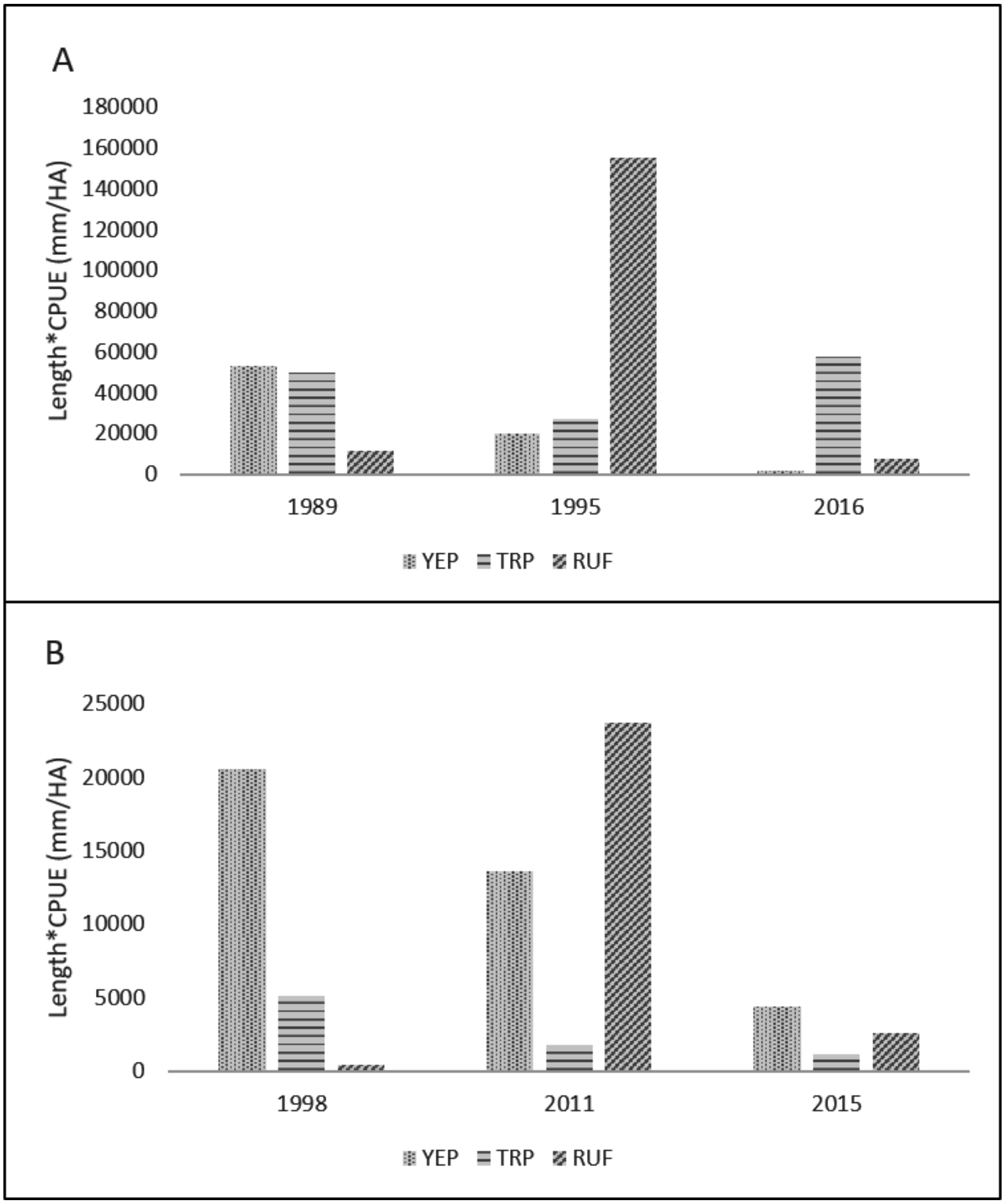

Figure 15. Fish length*CPUE, a surrogate for biomass, in each system (A) St. Louis River and (B) Chequamegon Bay for Yellow Perch (YEP), Trout Perch (TRP), and Ruffe (RUF). Years chosen represent a year close to initial Ruffe invasion, the year of peak Ruffe CPUE so far, and the most current data year we have.

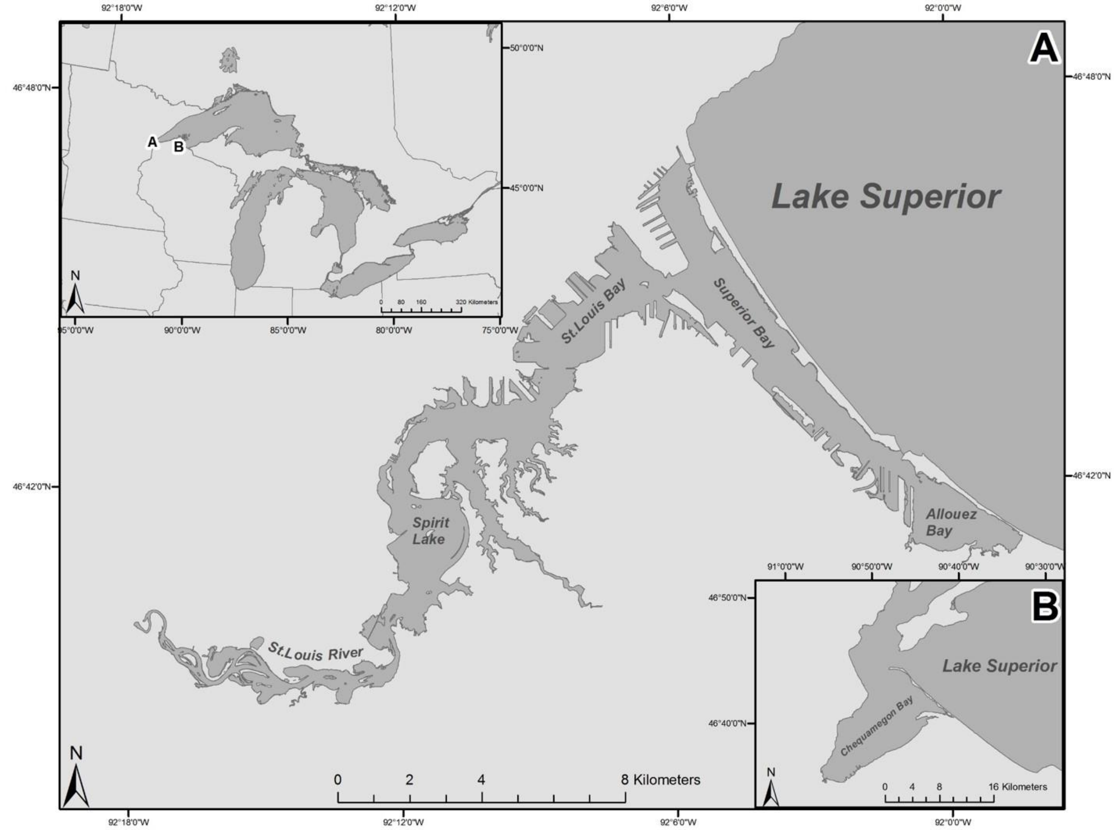

Figure 16. Map of primary study sites for stable isotopes study. **A** is the St. Louis River watershed, MN/WI, and **B** is Chequamegon Bay, WI.

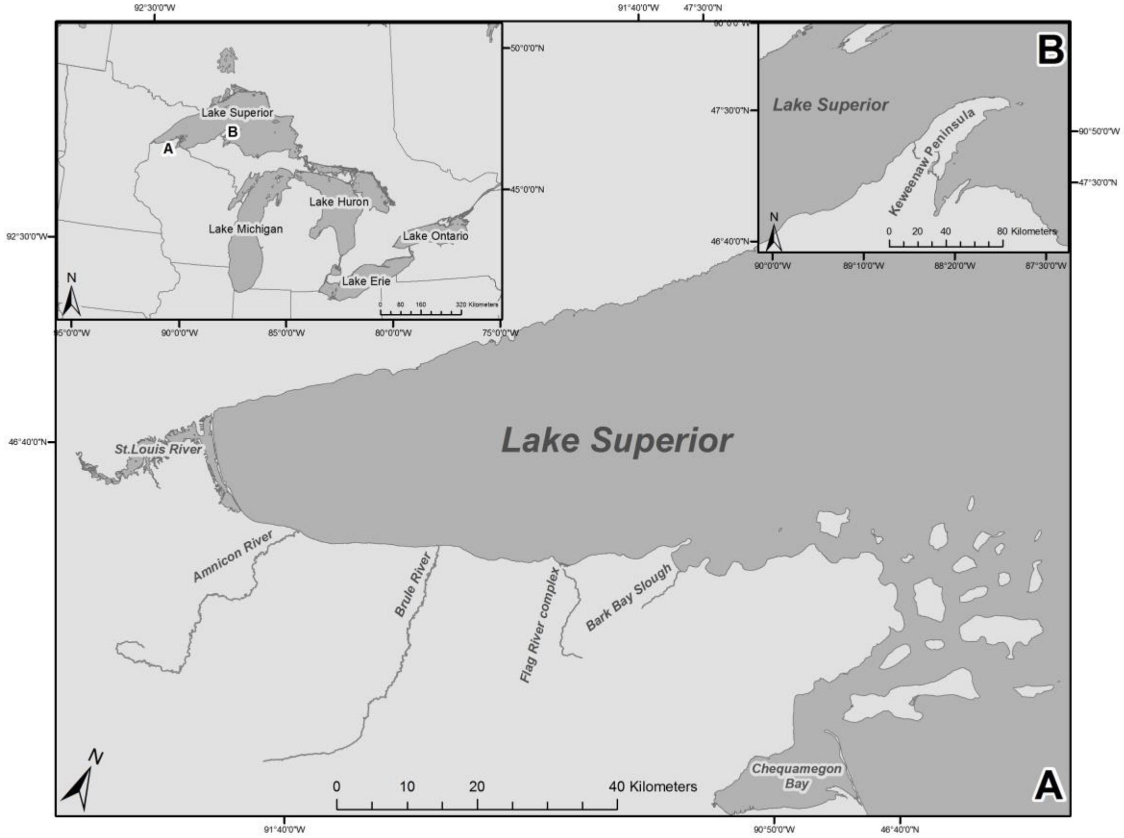

Figure 17. Map of south shore and over-winter study sites. **A** includes Amnicon River, Brule River, Flag River complex, and Bark Bay slough, WI. **B** includes Keweenaw Peninsula, MI.

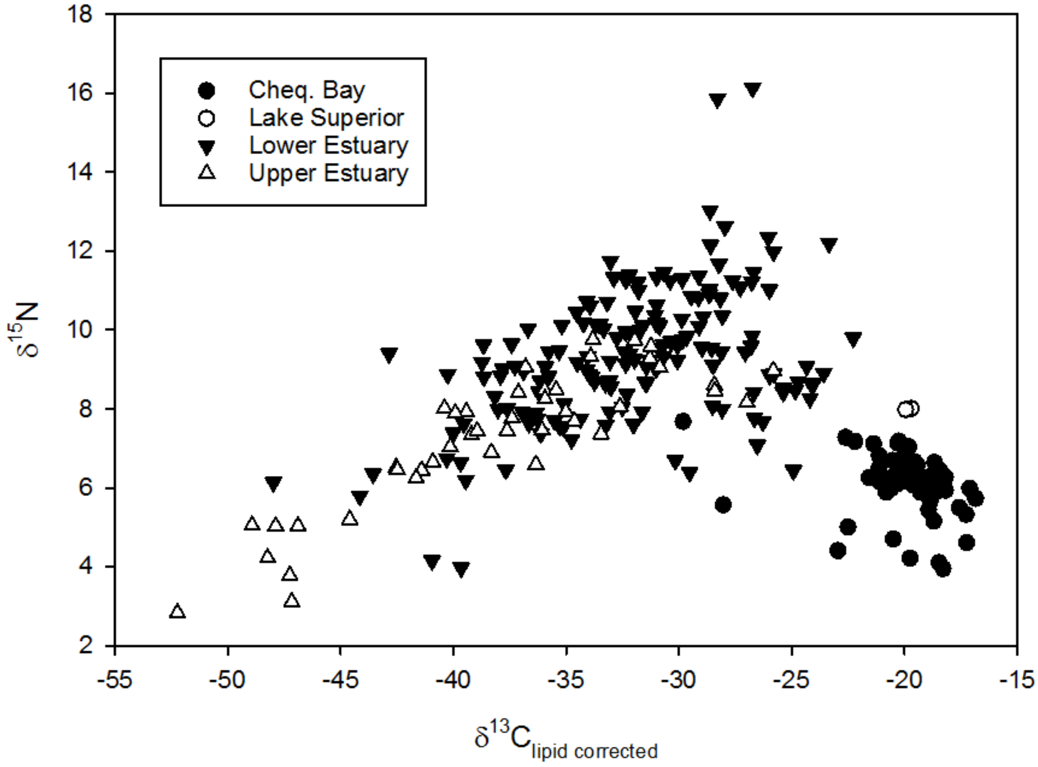

Figure 18. δ^{13}Clipid corrected and δ^{15}N values by capture location. Points represent individual fish in different locations based on stable isotope composition.

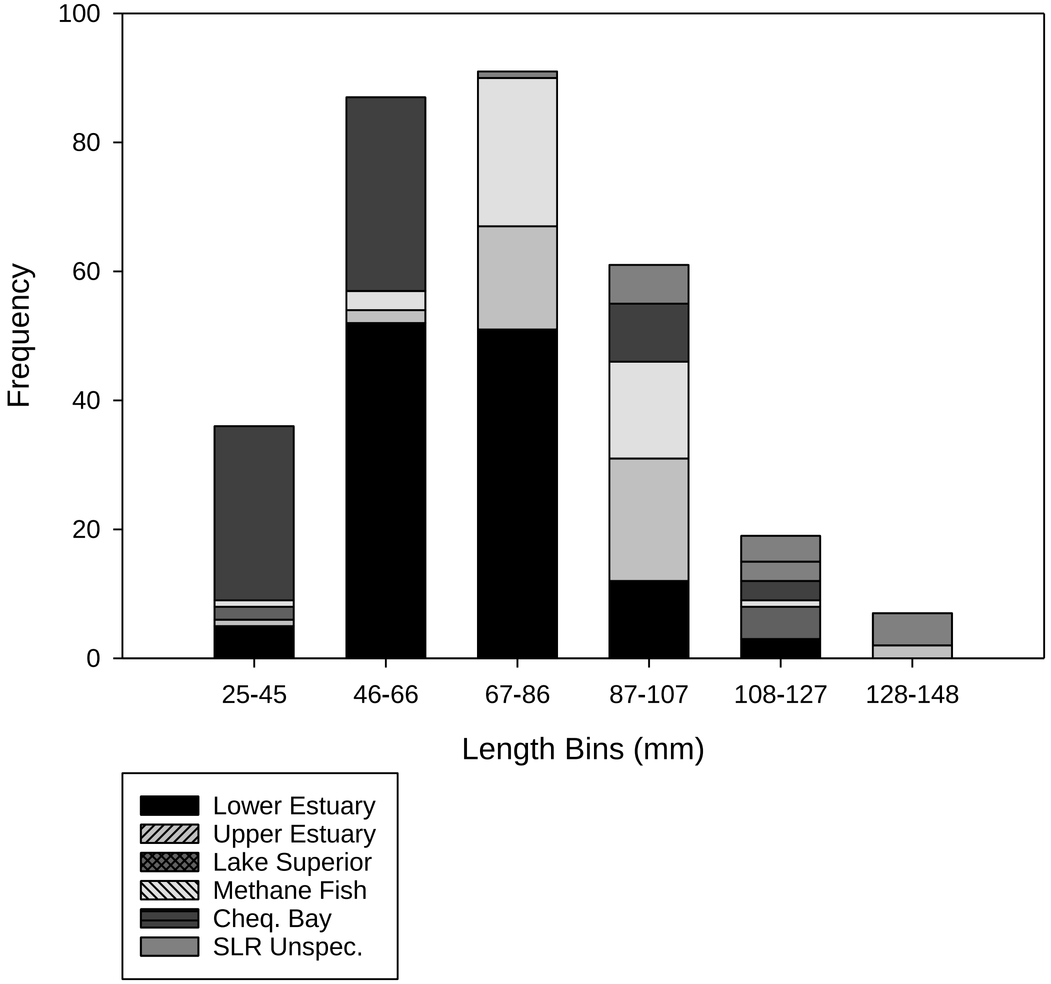

Figure 19. Length frequency of Ruffe (*Gymnocephalus cernua*) by capture location. Ruffe were binned into six different length classes, each encompassing approximately 20 mm. Ruffe locations are identified based on their length.

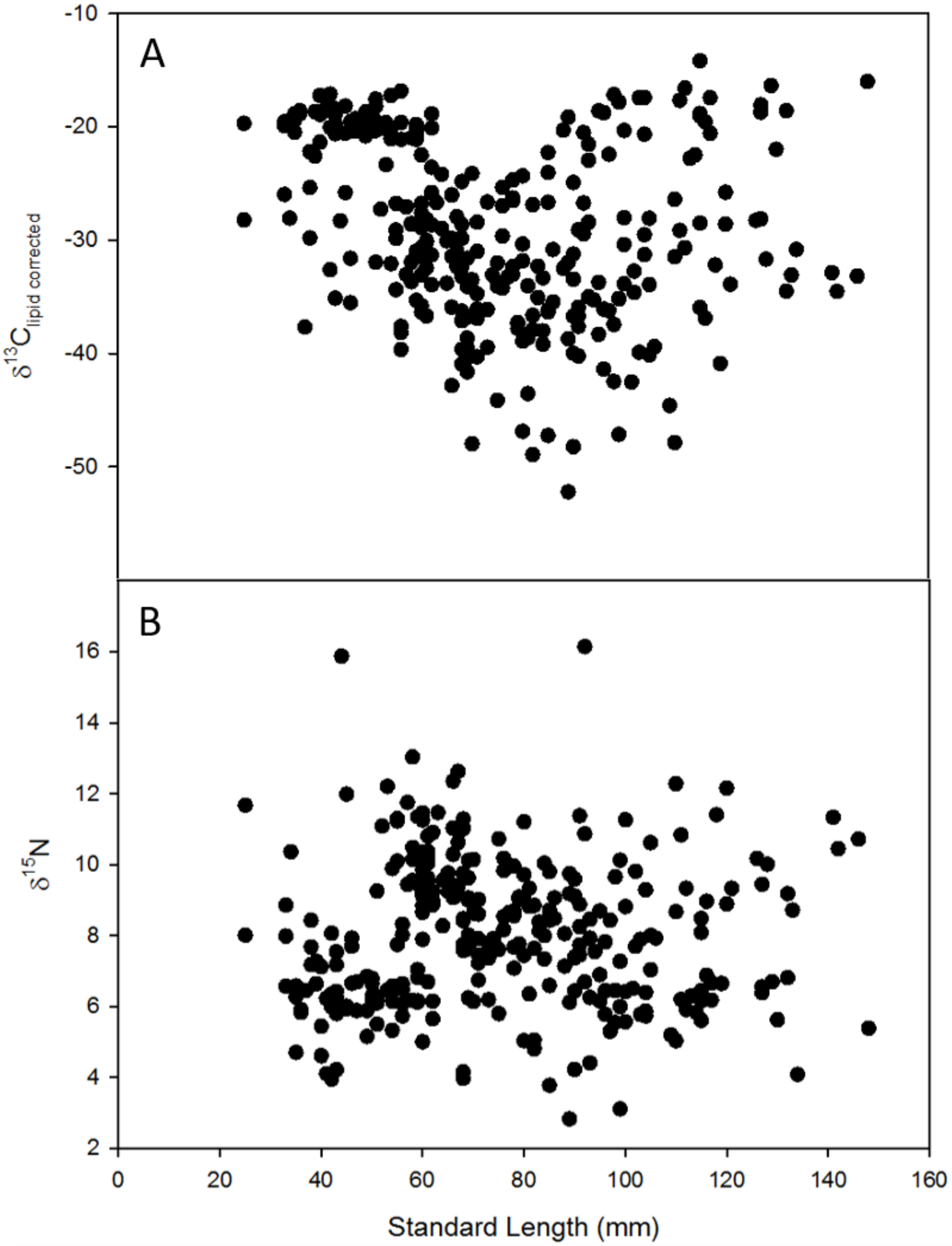

Figure 20. A) δ^{13}Clipid corrected and B) δ^{15}N values by standard length (mm). Points represent individual fish raw isotope values.

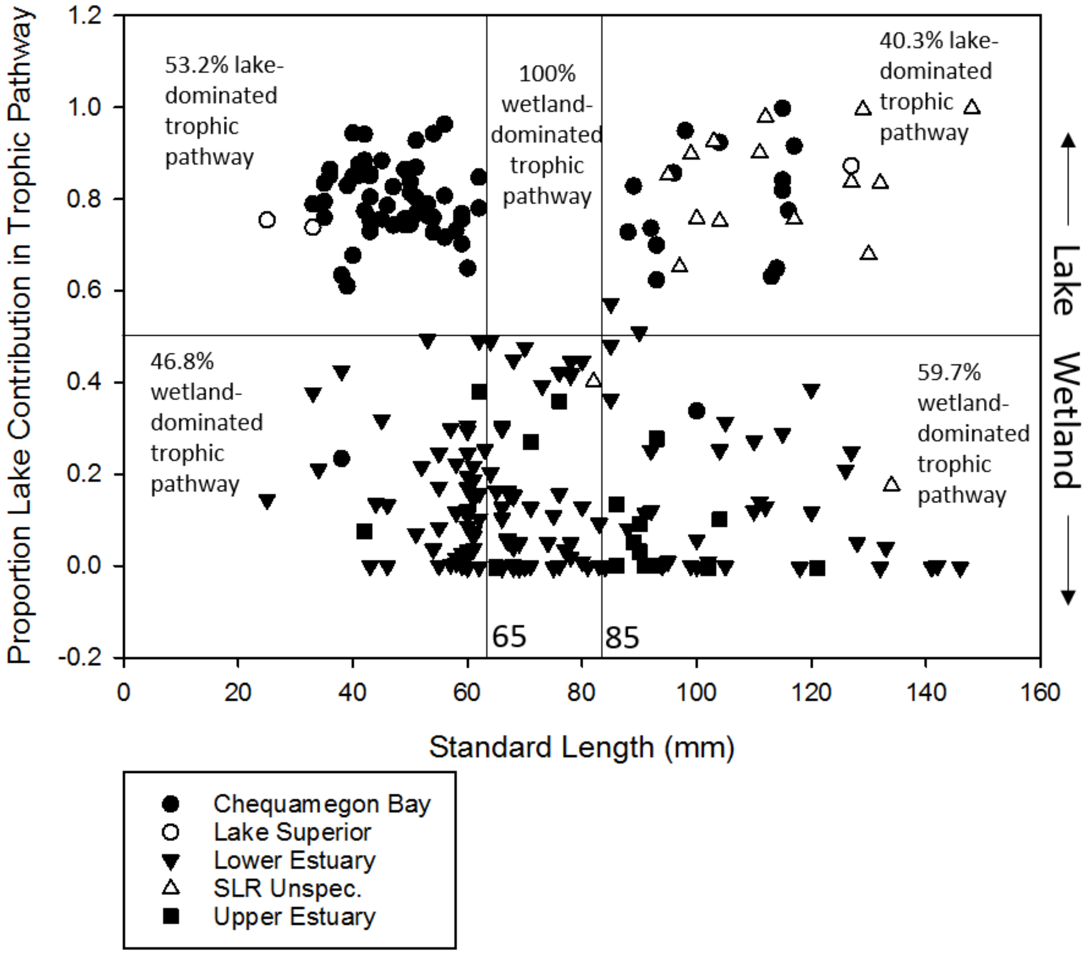

Figure 21. Proportion Lake Superior contribution in trophic pathway. Vertical lines delineate size groupings of Ruffe (*Gymnocephalus cernua*), the horizontal line delineate “lake” vs “wetland” dominated trophic pathway, and shapes indicate capture location. “SLR Unspec.” is in the St. Louis River but in an unspecified location.

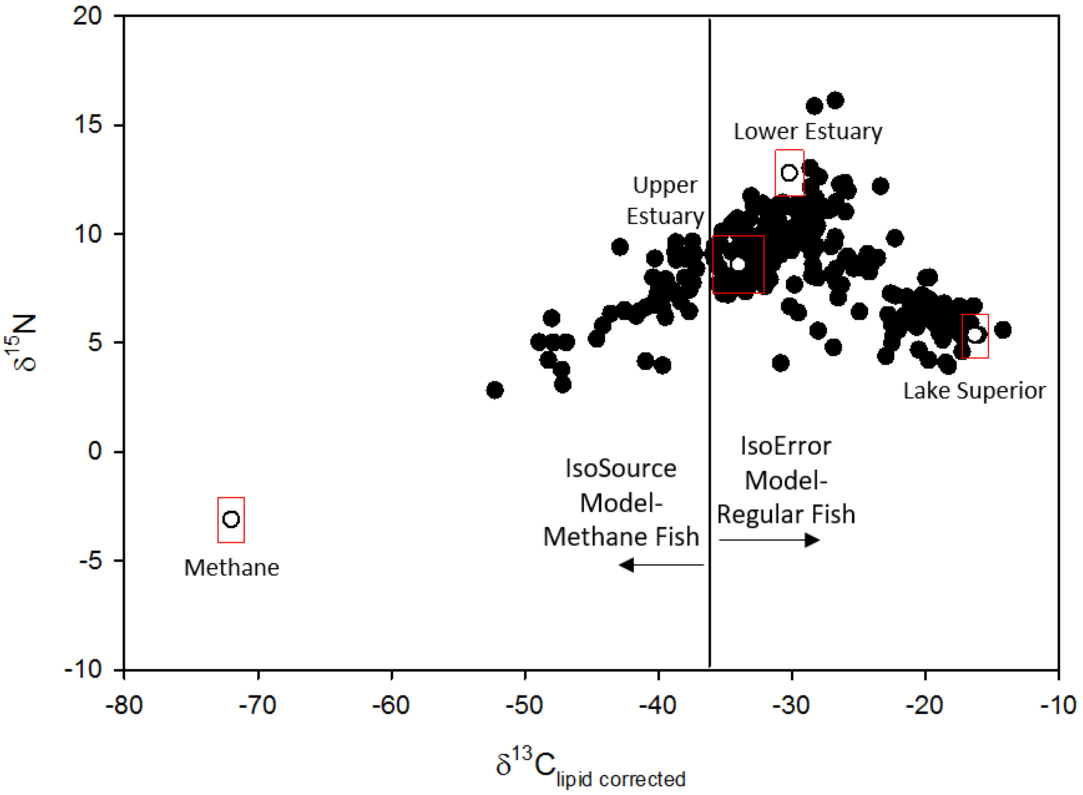

Figure 22. Unfitted stable isotopes model. Open circles are the sources for the IsoError and IsoSource models. The rectangles represent the standard deviation around the sources. Solid points represent fish stable isotopes in the models. The line is drawn at -36‰ $\delta^{13}C$ to differentiate the two models.

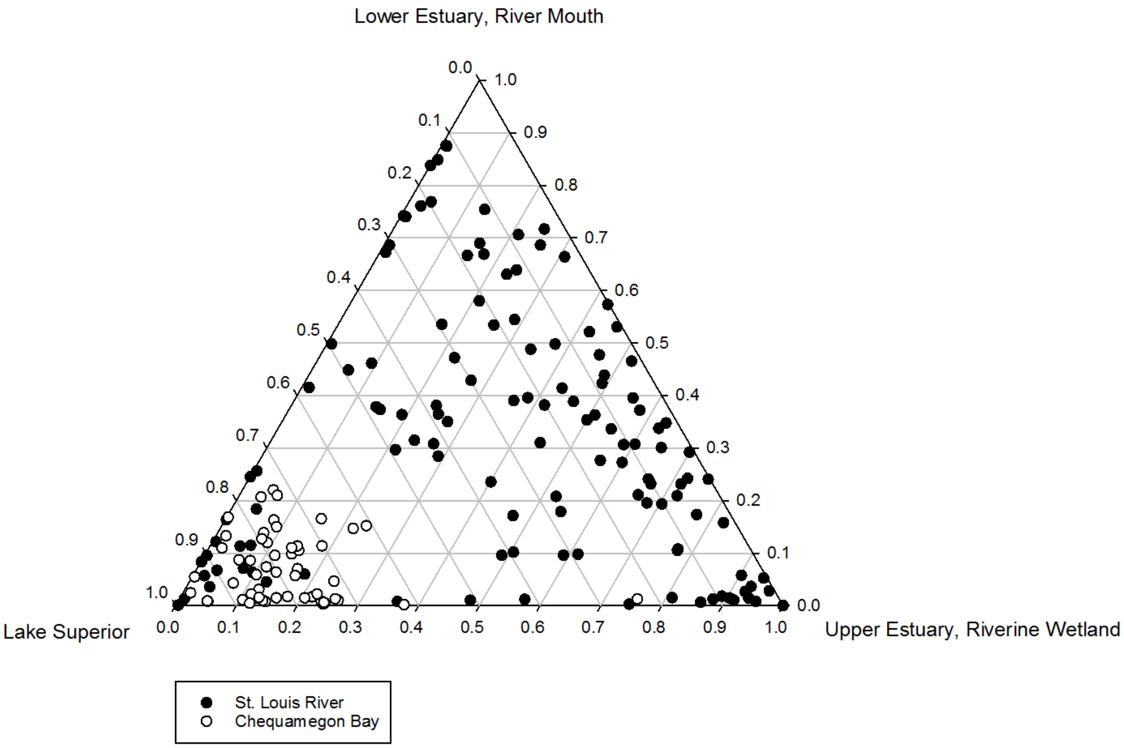

Figure 23. Triangle plot with points from St. Louis River and Chequamegon Bay. The three points of the triangle represent the sources in the IsoError model, and the points show where the individual fish fall along the axes by proportion contribution. At the points of each triangle, St. Louis River sources are listed first, and then a description of the equivalent habitats are listed second.

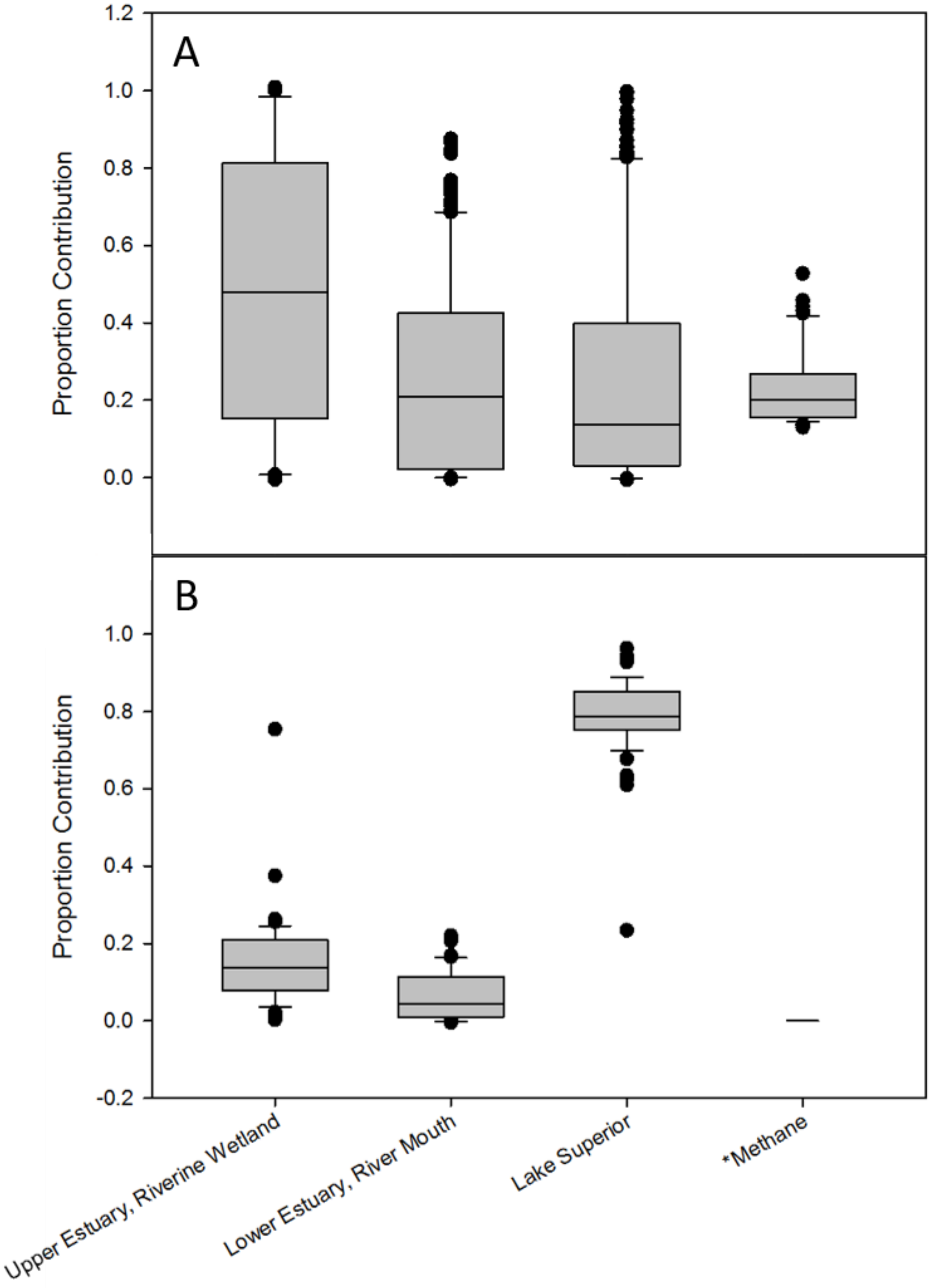

Figure 24. Boxplots of proportion contribution for A) St. Louis River and B) Chequamegon Bay Ruffe (*Gymnocephalus cernua*). At the x-axis major ticks, St. Louis River sources are listed first, and then a description of the equivalent habitats are listed second. Methane-influenced fish were not measured for Chequamegon Bay Ruffe.

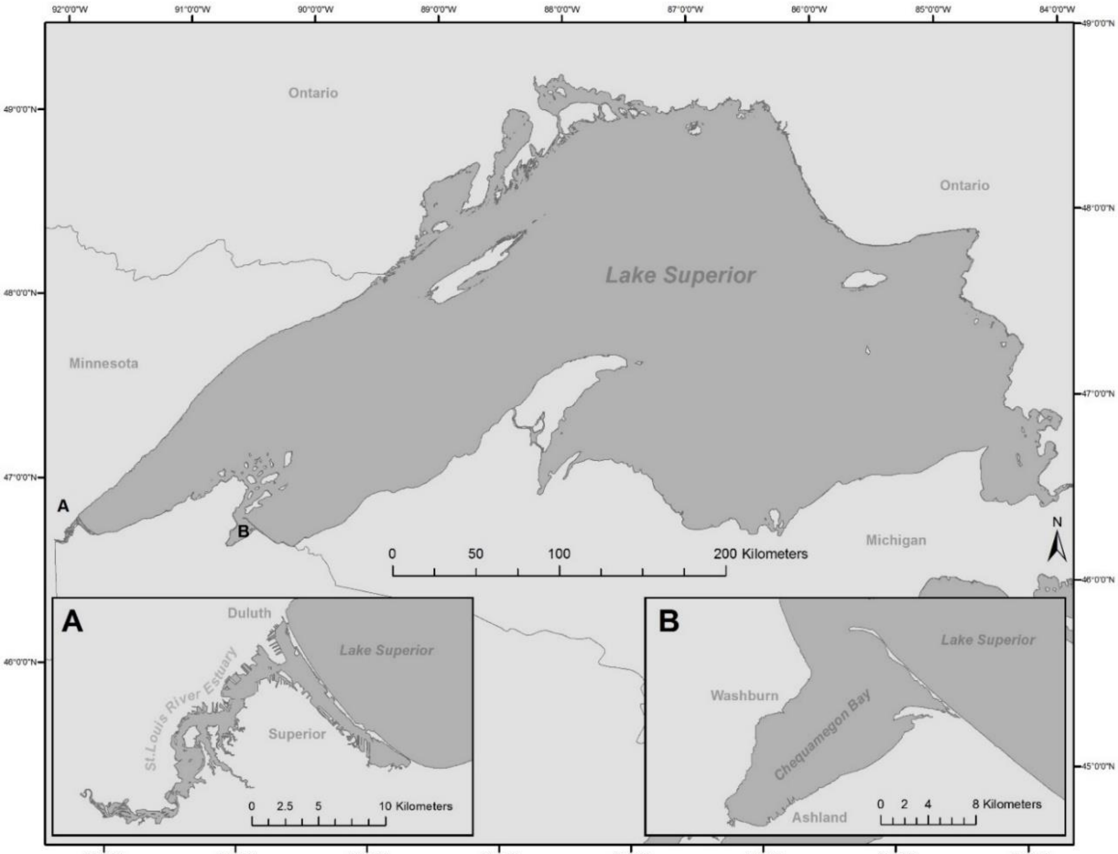

Figure 25. Site map of Lake Superior for Maxent model. Panel A is St. Louis River, WI/MN, and panel B is Chequamegon Bay, WI.

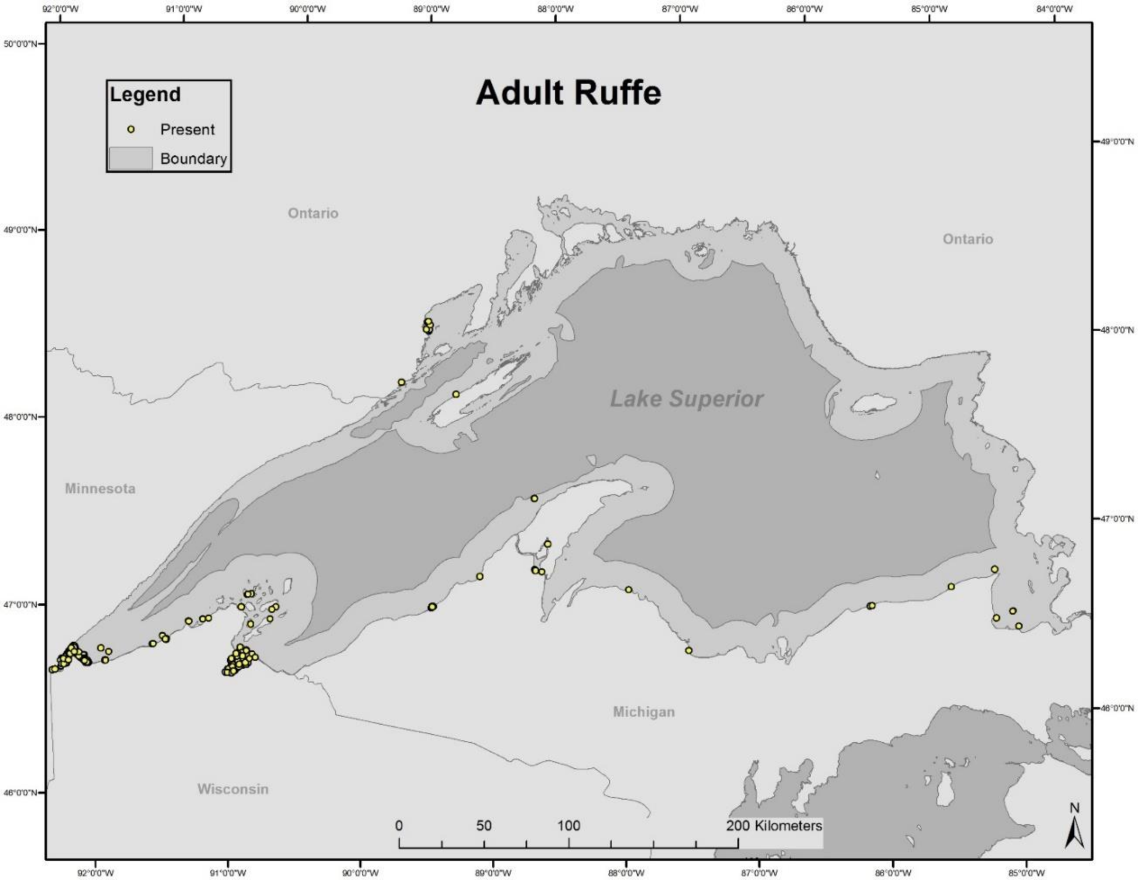

Figure 26. Occurrence points of Ruffe (*Gymnocephalus cernua*) with model buffer at 15 km distance/ 250 m depth. Buffer was created to represent the area where Ruffe can exist. Points represent Ruffe presences from 2005-2015. All overlapping points were removed. Data was gathered from US Geological Survey, US Fish and Wildlife Service, US Environmental Protection Agency, and 1854 Treaty Authority.

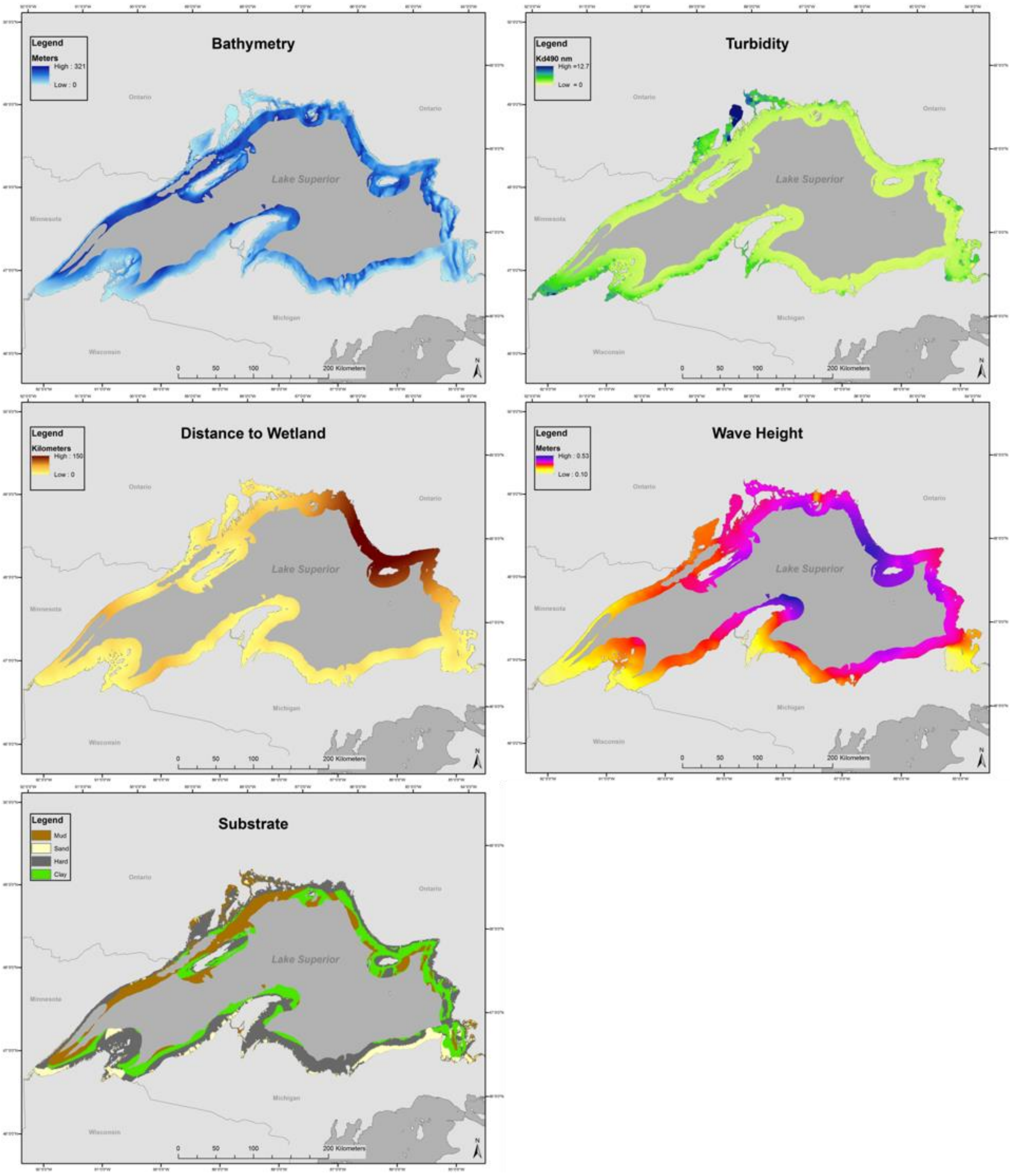

Figure 27. Environmental layers for the Maxent model. Environmental data was created in ArcGIS. It was collected from Michigan Tech Research Institute and Great Lakes Aquatic Habitat Framework. All data was resampled to 30-m resolution.

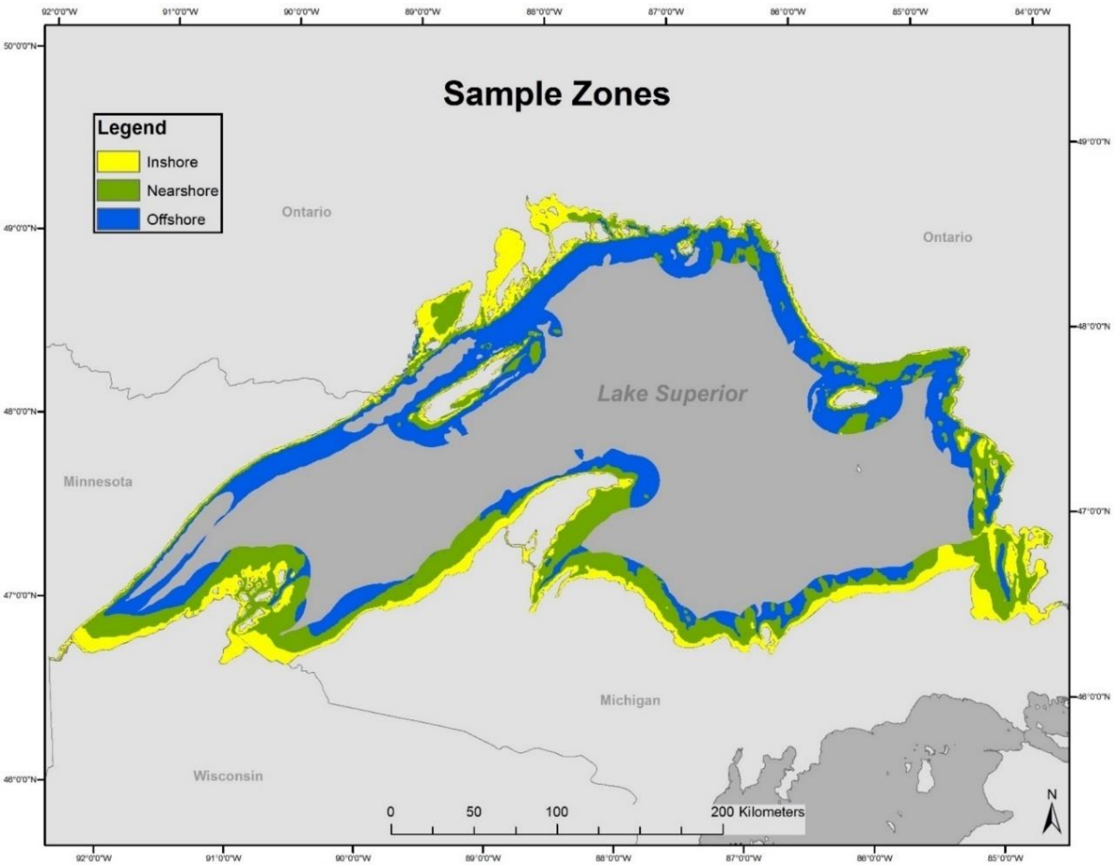

Figure 28. Proportion of suitable area within the buffer of three zones: in-shore (<30 m), nearshore (<100 m), and offshore (>100 m). Area was predicted using Maxent and ArcGIS. Area (km^2) and percent of buffer can be found in Table 14.

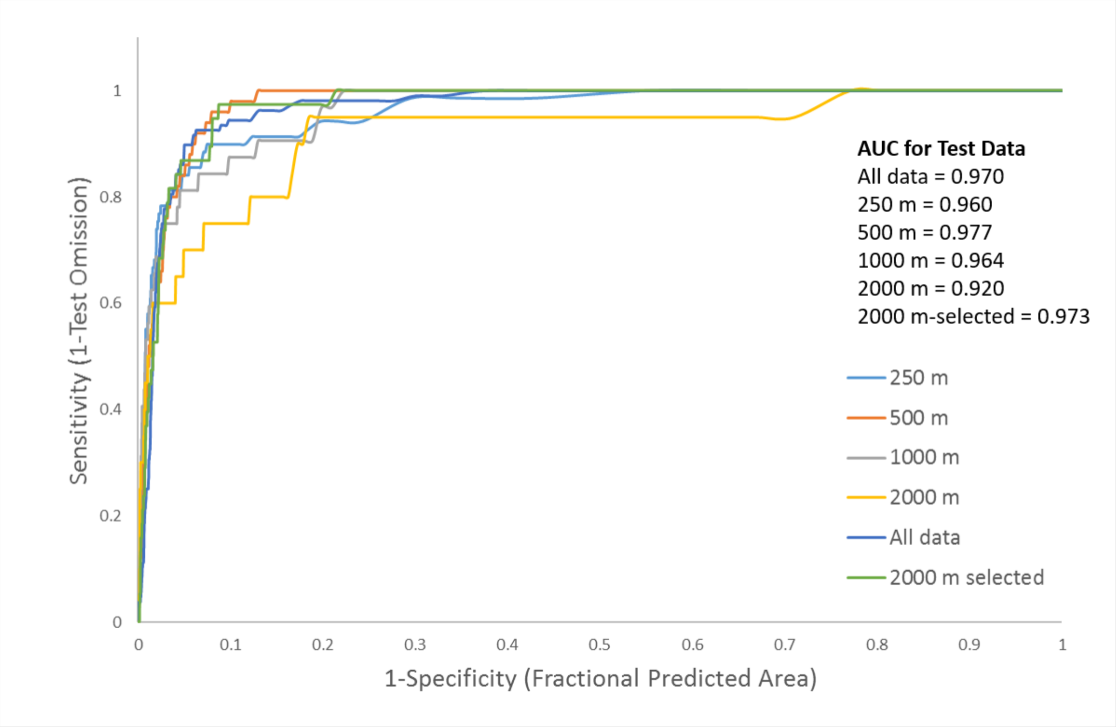

Figure 29. Receiver operator characteristic (ROC) plot for the six distance-buffered Maxent models. Area under the curve (AUC) scores are displayed to compare the six models. An AUC score above 0.75 is “potentially useful” (Elith 2002).

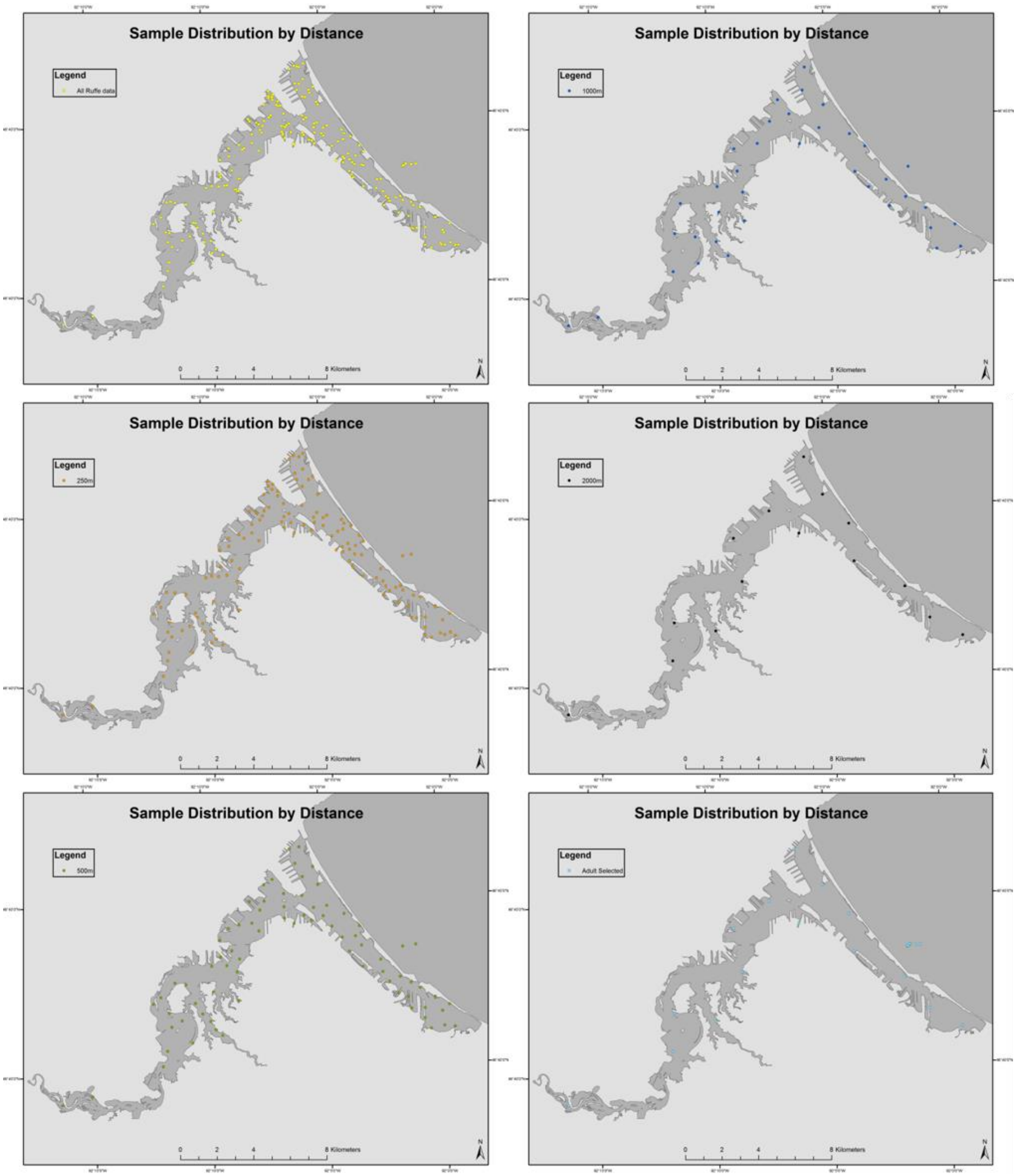

Figure 30. Example of cluster removal for each model distance buffer in the St. Louis River, WI/MN. Occurrence points for Ruffe (*Gymnocephalus cernua*) were very clustered in the St. Louis River and Chequamegon Bay, WI. We applied these distance buffers to the data to remove the clustering. There was a 250, 500, 1000, 2000, and 2000-m selected buffer. The 2000-m selected buffer removed clustering only in St. Louis River and Chequamegon Bay, while the other buffers removed clustering in all of Lake Superior. Points were removed using a computer algorithm that chose a point and removed that points within the chosen distance surrounding that point.

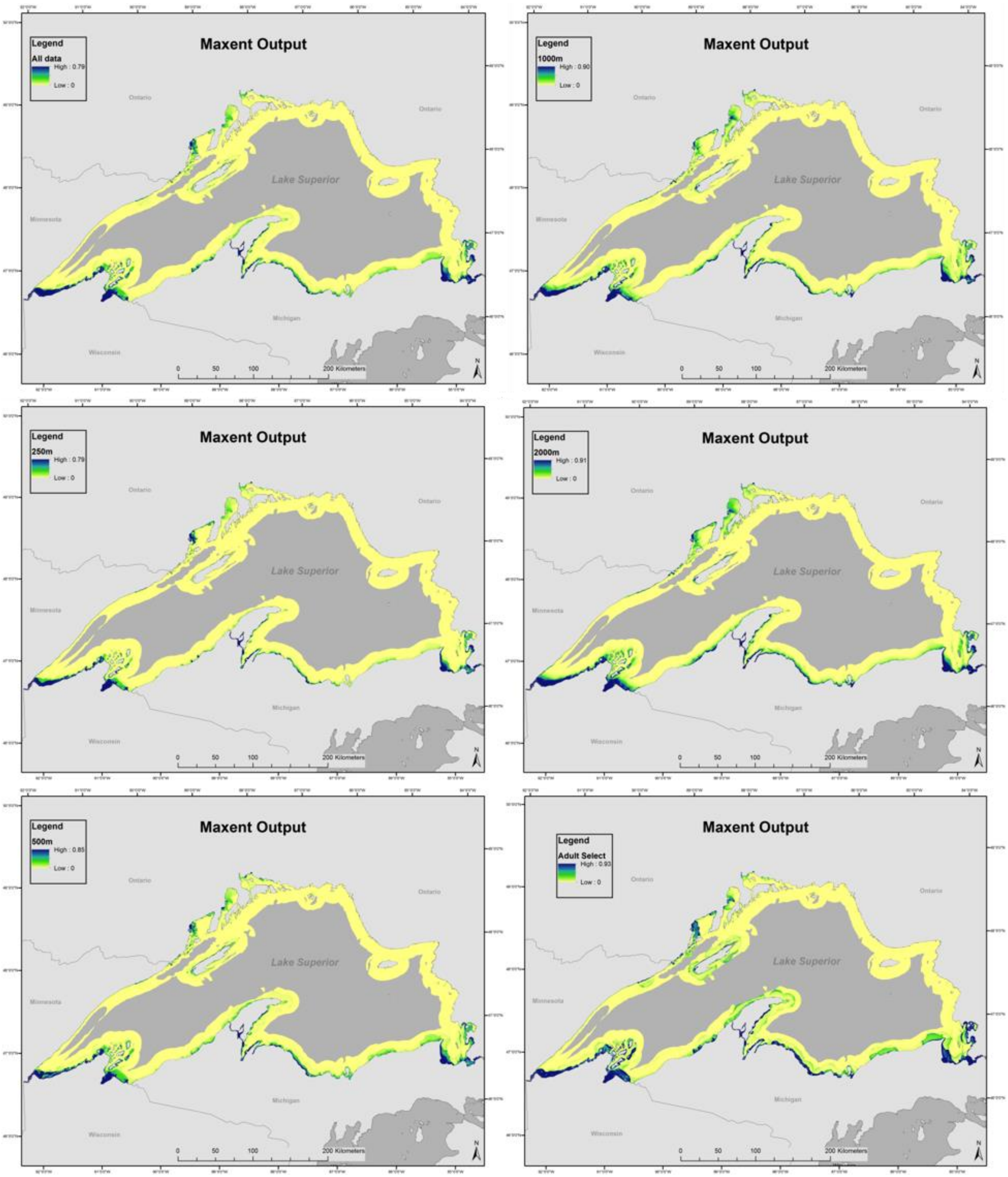

Figure 31. Maxent prediction maps of suitable habitat for Ruffe (*Gymnocephalus cernua*). These maps are an output of the Maxent model. The dark regions represent high suitability and the light regions represent no suitability.

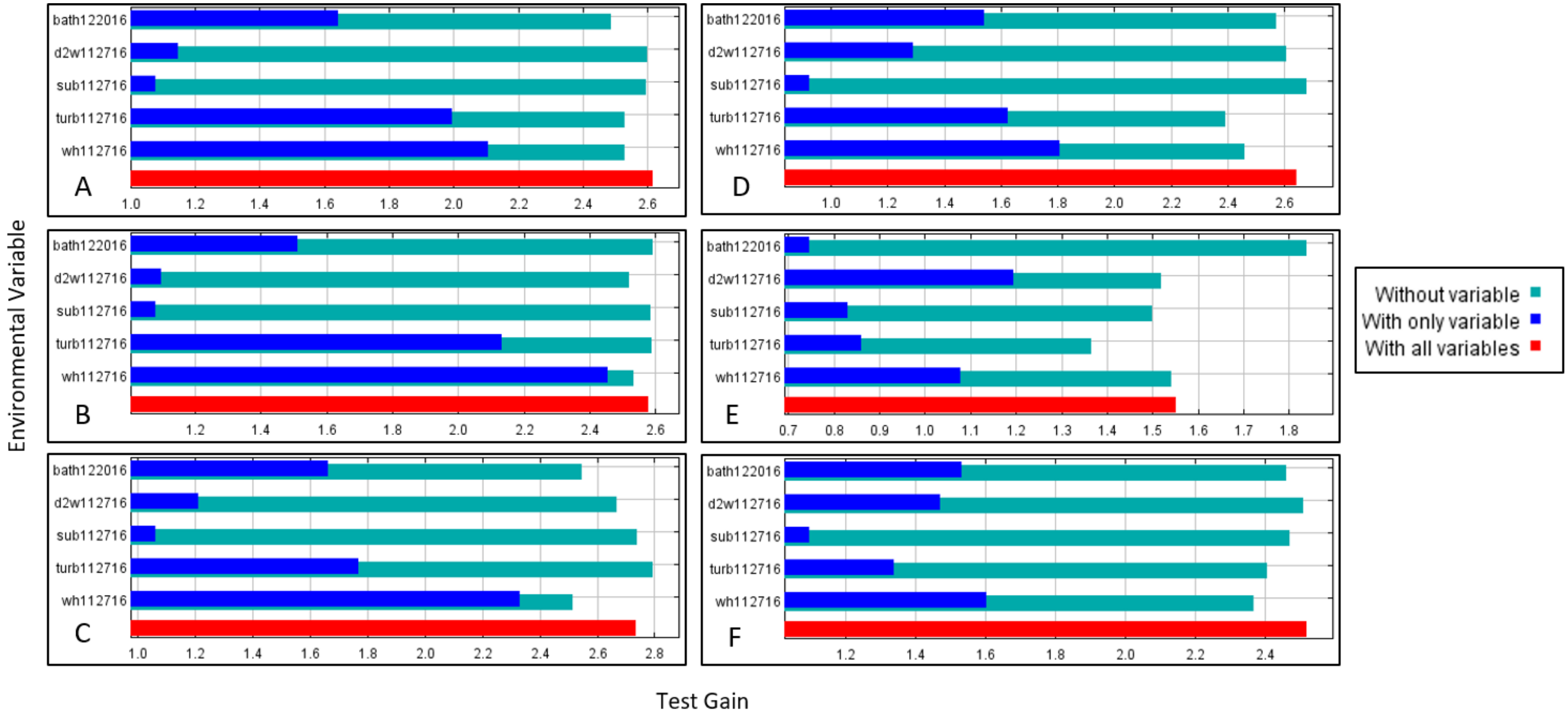

Figure 32. Jackknife test gain outputs from each model. A) model with all data, B) 250-m model, C) 500-m model, D) 1000-m model, E) 2000-m model, and F) 2000-m selected model. These are an output from Maxent that determine which environmental variables are most important to the model.

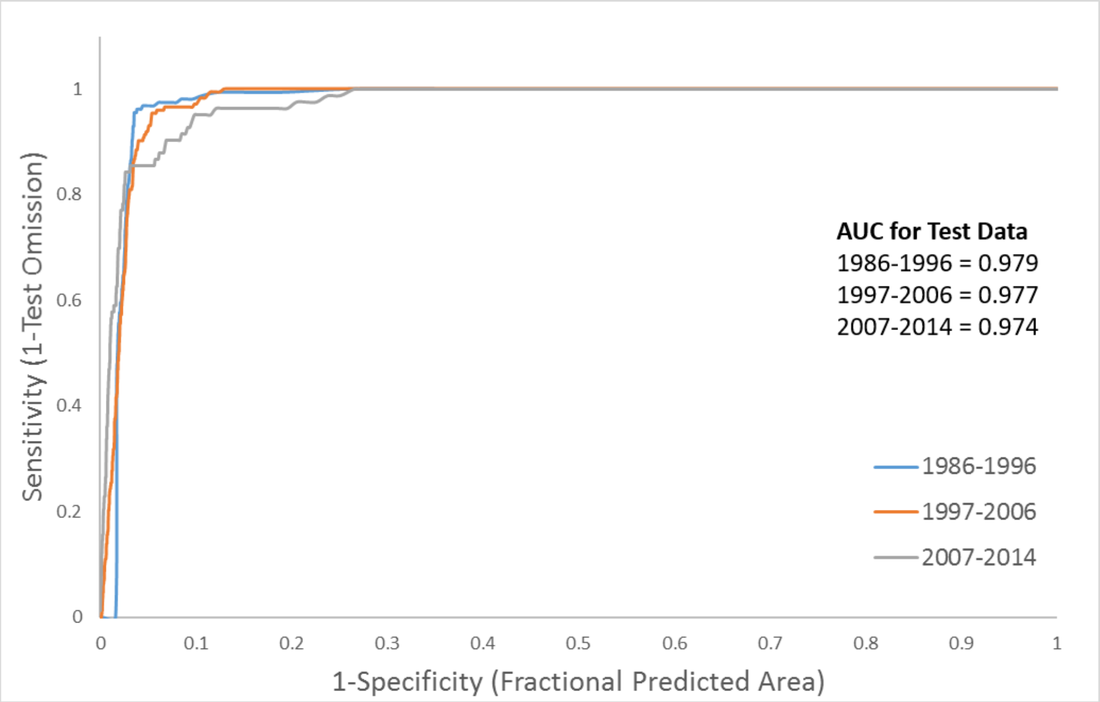

Figure 33. Receiver operator characteristic (ROC) plot for separate time series. Area under the curve (AUC) scores are displayed to compare the three time frames. An AUC score above 0.75 is “potentially useful” (Elith 2002).

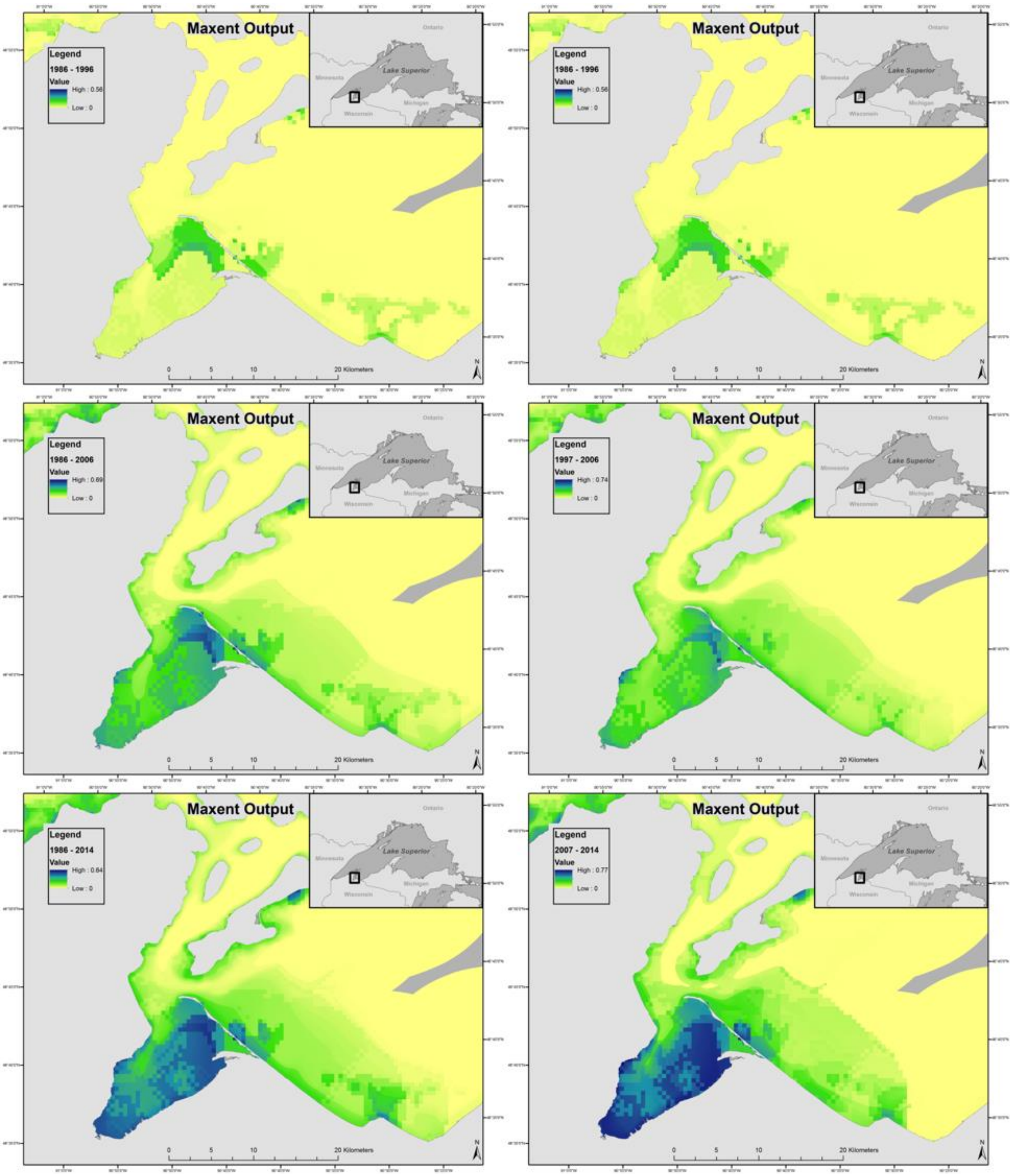

Figure 34. Chequamegon Bay for the cumulative (column 1) and separate (column 2) time series analyses. These are Maxent output predictive maps of suitable habitat. The dark regions represent high suitability and the light regions represent no suitability.

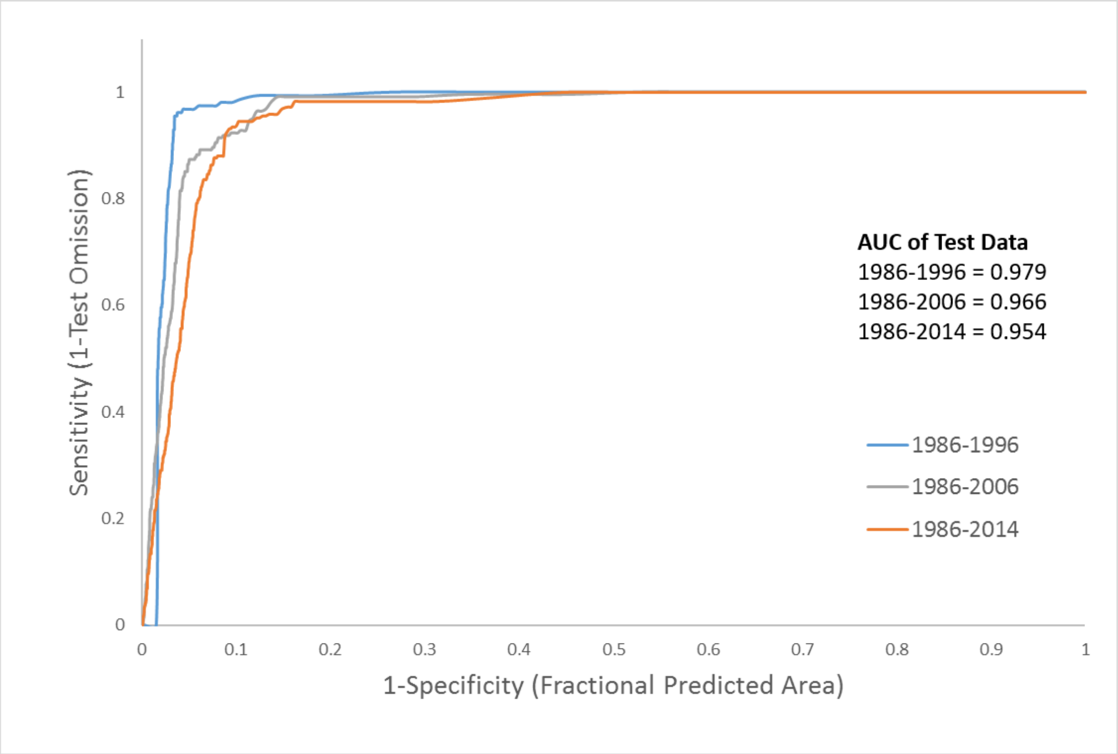

Figure 35. Receiver operator characteristic (ROC) plot for cumulative time series. Area under the curve (AUC) scores are displayed to compare the three time frames. An AUC score above 0.75 is “potentially useful” (Elith 2002).

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Appendices

Tables

Table A-1. Time-series catch per unit effort (CPUE) data, natural logarithm-transformed (ln(CPUE+1)), for St. Louis River, MN/WI from 1993-2015 (Chapter 2). Competitor and Ruffe (*Gymnocephalus cernua*) data was collected via a bottom trawl (USFWS) and predator data was collected via gill nets (MNDNR) (see methods of Chapter 2 for details). Gaps in the data were imputed using a cubic spline method.

Year	Ruffe	Emerald Shiner	Johnny Darter	Round Goby	Spottail Shiner	Trout Perch	Yellow Perch	Muskellunge	Smallmouth Bass	Northern Pike	Walleye
1993	6.381	3.990	2.263	0.000	4.110	4.397	3.377	0.047	0.047	1.204	1.204
1994	6.746	5.050	1.992	0.000	4.734	5.183	4.672	0.074	0.143	1.019	1.669
1995	7.576	5.060	1.986	0.000	5.461	5.989	5.570	0.091	0.047	1.362	1.580
1996	7.271	4.069	1.945	0.000	5.370	5.667	5.021	0.134	0.091	1.551	1.700
1997	7.304	4.358	1.794	0.000	5.172	5.347	5.814	0.179	0.140	1.598	1.708
1998	7.332	4.089	1.907	2.154	5.726	4.959	5.661	0.174	0.214	1.540	1.743
1999	6.992	5.170	1.823	3.206	5.668	4.617	3.785	0.091	0.341	1.386	1.977
2000	6.990	5.120	1.821	3.260	5.905	5.303	3.238	0.047	0.389	1.232	2.192
2001	6.927	5.293	3.194	2.887	5.782	5.168	3.734	0.145	0.283	1.196	2.244
2002	7.043	4.583	2.624	3.647	5.029	5.293	3.408	0.214	0.251	1.130	2.067
2003	7.020	4.426	2.125	3.327	4.369	4.889	4.918	0.140	0.470	0.956	1.629
2004	6.348	4.132	2.670	4.434	4.894	5.132	4.128	0.095	0.531	1.224	1.649
2005	6.503	4.432	3.190	5.961	5.080	5.751	4.137	0.047	0.251	1.530	1.897
2006	6.874	5.190	3.402	6.460	6.101	6.237	4.474	0.049	0.588	1.224	1.946
2007	6.701	5.676	3.470	6.402	6.978	6.538	3.406	0.070	0.479	0.970	2.001
2008	6.486	5.340	3.970	6.506	7.034	6.652	3.268	0.147	0.100	0.927	2.046
2009	6.380	3.813	4.313	6.622	6.585	6.775	4.137	0.223	0.095	0.811	1.981
2010	6.291	2.650	4.205	6.387	5.584	7.058	4.240	0.047	0.174	0.566	1.743
2011	5.931	4.557	3.122	5.064	4.408	7.073	3.025	0.001	0.163	0.439	1.615

2012	3.902	5.829	1.709	3.223	4.454	6.161	2.365	0.104	0.100	0.574	1.648
2013	5.041	7.611	2.569	3.693	4.937	8.112	2.739	0.174	0.047	0.907	1.718
2014	4.613	6.036	1.312	3.187	5.264	7.738	4.489	0.134	0.047	1.204	1.838
2015	4.532	6.099	0.000	4.564	5.283	6.781	2.678	0.134	0.047	1.016	2.326

Table A-2. Time-series catch per unit effort (CPUE) data, natural logarithm-transformed (ln(CPUE+1)), for Chequamegon Bay, WI, USA from 1993-2015 (Chapter 2). Competitor and Ruffe (*Gymnocephalus cernua*) data was collected via a bottom trawl (USFWS) and predator data was collected via creel surveys (see methods of Chapter 2 for details). Gaps in the data were imputed using a cubic spline method.

Year	Ruffe	Emerald Shiner	Johnny Darter	Spottail Shiner	Trout Perch	Yellow Perch	Northern Pike	Walleye
1993	0.000	3.291	2.634	3.865	4.065	2.468	0.045	6.772
1994	0.061	2.703	2.721	4.328	5.077	4.430	0.051	7.321
1995	0.000	0.000	3.449	2.785	3.857	3.837	0.030	4.554
1996	0.000	2.288	2.657	3.999	3.507	4.691	0.038	6.928
1997	0.061	1.201	1.895	2.525	4.142	2.479	0.049	4.522
1998	1.895	4.457	2.379	4.794	4.314	5.594	0.024	4.644
1999	0.531	0.531	2.122	3.300	2.715	4.862	0.000	0.000
2000	0.000	0.000	0.000	0.000	2.323	0.000	0.033	6.279
2001	0.000	0.963	0.462	0.000	3.057	0.375	0.124	5.991
2002	1.112	0.000	0.732	0.000	1.702	0.000	0.048	4.727
2003	1.926	0.331	0.536	3.615	5.097	1.455	0.009	3.892
2004	0.919	0.000	0.000	0.000	3.279	3.352	0.017	3.807
2005	3.937	0.000	0.000	0.000	4.274	0.000	0.059	7.771
2006	3.622	0.000	0.000	0.000	4.044	2.418	0.015	4.248
2007	0.000	0.000	0.681	0.000	2.362	3.234	0.015	6.297
2008	1.007	0.000	0.000	1.677	3.383	1.754	0.089	7.265
2009	1.686	0.000	3.610	0.307	2.157	3.510	0.013	4.043
2010	4.472	1.821	4.194	3.166	4.187	4.404	0.009	3.466
2011	5.433	3.020	3.312	5.513	3.258	5.168	0.028	7.011
2012	5.312	4.042	3.200	4.844	3.708	5.053	0.015	4.369
2013	1.897	0.107	2.902	1.504	1.736	5.697	0.010	3.664

2014	3.182	3.029	3.951	4.217	3.261	4.573	0.032	7.375
2015	3.396	0.000	2.336	0.646	2.798	4.062	0.023	4.804

Table A-3. Raw time-series catch per unit effort (CPUE) data for St. Louis River, MN/WI, USA from 1993-2015. Competitor and Ruffe (*Gymnocephalus cernua*) data was collected via a bottom trawl (USFWS) and predator data was collected via gill nets (MNDNR) (see methods of Chapter 2 for details). Data has not been imputed or log-transformed (Chapter 2).

Year	Emerald Shiner	Johnny Darter	Round Goby	Ruffe	Spottail Shiner	Trout Perch	Yellow Perch	Muskellunge	Northern Pike	Smallmouth Bass	Walleye
1993	53.067	8.616	0.000	589.258	59.917	80.214	28.269	0.048	2.333	0.048	2.333
1994	155.065	6.329	0.000	849.555	112.756	177.298	105.886	0.077	1.769	0.154	4.308
1995	156.537	6.285	0.000	1950.291	234.370	398.129	261.475	0.095	2.905	0.048	3.857
1996	57.514	5.995	0.000	1436.605	213.848	288.040	150.575	0.143	3.714	0.095	4.476
1997	77.138	5.016	0.000	1485.162	175.334	208.966	333.943				
1998	58.653	5.733	7.622	1527.257	305.746	141.441	286.525	0.190	3.667	0.238	4.714
1999	174.965	5.191	23.684	1086.615	288.419	100.182	43.044				
2000	166.263	5.177	25.048	1084.519	366.047	199.866	24.475	0.048	2.429	0.476	7.952
2001	197.962	23.397	16.935	1018.504	323.384	174.533	40.829				
2002	96.809	12.790	37.370	1144.294	151.798	197.850	29.204	0.238	2.095	0.286	6.905
2003	82.630	7.373	26.867	1117.847	77.971	131.831	135.726	0.150	1.600	0.600	4.100
2004	61.319	13.434	83.260	570.108	132.511	168.299	61.061	0.100	2.400	0.700	4.200
2005								0.048	3.619	0.286	5.667
2006	178.514	29.034	637.747	966.136	445.420	510.100	86.732	0.050	2.400	0.800	6.000
2007	290.642	31.140	601.875	811.931	1071.823	690.106	29.132				
2008								0.158	1.526	0.105	6.737
2009								0.250	1.250	0.100	6.250
2010	13.159	65.997	593.018	538.523	265.244	1161.175	68.408	0.048	0.762	0.190	4.714
2011	94.325	21.698	157.208	375.490	81.065	1179.106	19.588				
2012	339.026	4.521	24.109	48.518	84.983	472.828	9.643				
2013	2018.484	12.055	39.177	153.692	138.322	3333.300	14.465	0.190	1.476	0.048	4.571
2014	417.077	2.712	23.205	99.749	192.265	2293.922	87.997	0.143	2.333	0.048	5.286
2015	444.500	0.000	94.927	91.914	195.881	879.960	13.561	0.143	1.762	0.048	9.238

Table A-4. Raw time-series catch per unit effort (CPUE) data for Chequamegon Bay, WI, from 1993-2015. Competitor and Ruffe (*Gymnocephalus cernua*) data was collected via a bottom trawl (USFWS) and predator data was collected via creel surveys (see methods of Chapter 2 for details). Data has not been imputed or log-transformed (Chapter 2).

Year	Walleye	Northern Pike	Smallmouth Bass	Muskellunge	Emerald Shiner	Johnny Darter	Ruffe	Spottail Shiner	Trout Perch	Yellow Perch
1993	872.000	149.000	421.000	0.000	25.871	12.936	0.000	46.719	57.269	10.801
1994	1511.000	470.000	0.000	0.000	13.919	14.192	0.063	74.809	159.372	82.909
1995	94.000	0.000	5.000	0.000	0.000	30.456	0.000	15.196	46.342	45.401
1996	1019.000	137.000	0.000	0.000	8.854	13.251	0.000	53.564	32.339	108.006
1997	91.000	66.000	0.000	0.000	2.323	5.652	0.063	11.492	61.915	10.926
1998	103.000	43.000	0.000	0.000	85.212	9.796	5.652	119.749	73.721	267.755
1999	0.000	0.000	0.000	0.000	0.700	7.348	0.700	26.123	14.110	128.280
2000	532.000	275.000	0.000	0.000	0.000	0.000	0.000	0.000	9.209	0.000
2001	399.000	97.000	0.000	0.000	1.620	0.588	0.000	0.000	20.261	0.455
2002	112.000	72.000	0.000	0.000	0.000	1.079	2.041	0.000	4.486	0.000
2003	48.000	5.000	0.000	0.000	0.392	0.709	5.863	36.135	162.533	3.284
2004	44.000	9.000	0.000	0.000	0.000	0.000	1.507	0.000	25.553	27.556
2005	2370.000	312.000	0.000	0.000	0.000	0.000	50.270	0.000	70.840	0.000
2006	69.000	101.000	0.000	0.000						
2007	542.000	88.000	0.000	0.000	0.000	0.975	0.000	0.000	9.615	24.385
2008	1428.000	57.000	0.000	0.000	0.000	0.000	1.738	4.348	28.470	4.780
2009	56.000	10.000	0.000	0.000	0.000	35.966	4.398	0.360	7.644	32.434
2010	31.000	0.000	0.000	0.000	5.180	65.269	86.554	22.707	64.850	80.791
2011	1108.000	329.000	0.000	0.000	19.493	26.448	227.729	246.788	25.006	174.574
2012	78.000	272.000	0.000	0.000	55.966	23.525	201.809	125.999	39.756	155.445
2013	38.000	57.000	0.000	0.000	0.112	17.204	5.667	3.501	4.675	297.057
2014	1595.000	394.000	0.000	0.000	19.675	50.967	23.086	66.829	25.064	95.819
2015	121.000	37.000	0.000	0.000	0.000	9.338	28.853	0.908	15.412	57.065

Table A-5. Calculations of predicted percent area from the Maxent model (Chapter 4). Area is in meters divided by meters of the buffer and multiplied by 100 to get the percentage.

	Percent area predicted from buffer	**Percent area predicted from Lake Superior**	**Depth (m)**					
			<30		<100		>100	
			Count	Area (m^2)	Count	Area (m^2)	Count	Area (m^2)
Full adult model	(5254259/ 36413732)*100 = **14%**	(4728833100/82097000000)*100 = **5.76%**	(4812688/36413732)*100 = **13.22%**	4331419200	(365269/36413732)*100 = **1.00%**	328742100	(76302/36413732)*100 = **0.21%**	68671800
250 m	(2168114/ 36413732)*100 = **6%**	(1951302600/82097000000)*100 = **2.38%**	(2160894/36413732)*100 = **5.93%**	1944804600	(7220/36413732)*100 = **0.020%**	6498000		
500 m	(3147913/ 36413732)*100 = **8%**	(2833121700/82097000000)*100 = **3.45%**	(3090323/36413732)*100 = **8.49%**	2781290700	(57589/36413732)*100 = **0.16%**	51830100	(1/36413732)*100 = **2.75e-6%**	900
1000 m	(7452951/ 36413732)*100 = **20%**	(6707655900/82097000000)*100 = **8.17%**	(5964854/36413732)*100 = **16.38%**	5368368600	(1275697/36413732)*100 = **3.50%**	1148127300	(212400/36413732)*100 = **0.58%**	191160000
2000 m	(6415621/ 36413732)*100 =**17%**	(5774058900/82097000000)*100 = **7.03%**	(5646215/36413732)*100 = **15.51%**	5081593500	(769363/36413732)*100 = **2.11%**	692426700	(43/36413732)*100 = **1.18e-4%**	38700
2000 m selected removal	(7935392/ 36413732)*100 = **22%**	(7141852800/82097000000)*100 = **8.70%**	(5628547/36413732)*100 = **15.46%**	5065692300	(1230191/36413732)*100 = **3.38%**	1107171900	(1076654/36413732)*100 = **2.96%**	968988600

Figures

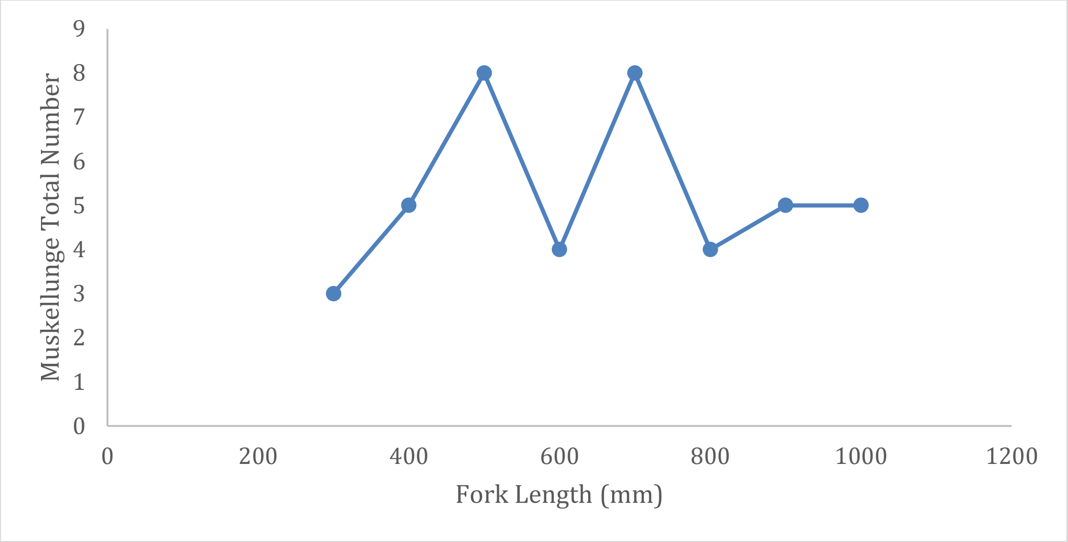

Figure A-1. Catch curve for Muskellunge (*Esox masquinongy*) in Minnesota Department of Natural Resources' gill nets from 1993-2015 (Chapter 2). Data was calculated using Microsoft Excel.

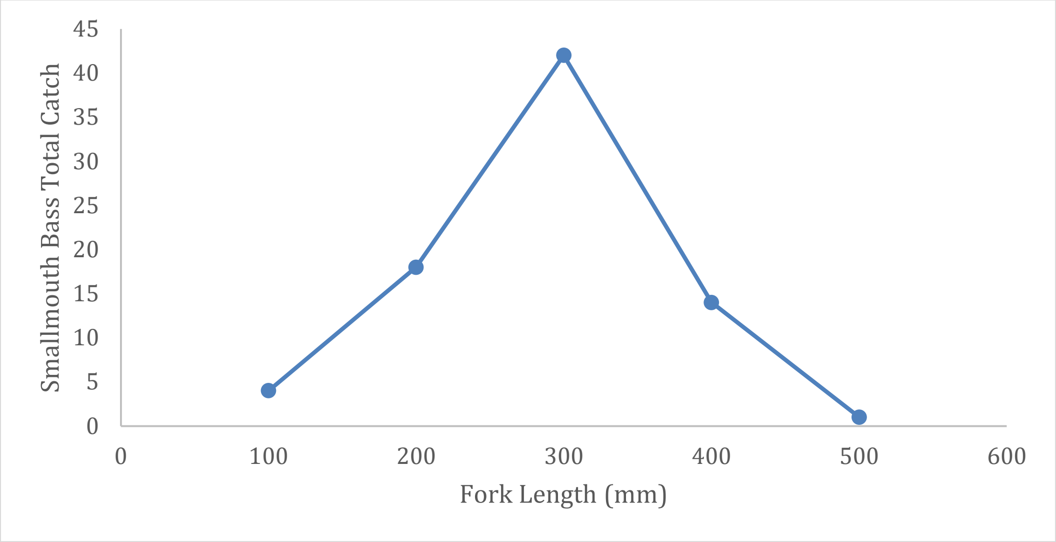

Figure A-2. Catch curve for Smallmouth Bass (*Micropterus dolomieu*) in Minnesota Department of Natural Resources' gill nets from 1993-2015 (Chapter 2). Data was calculated using Microsoft Excel.

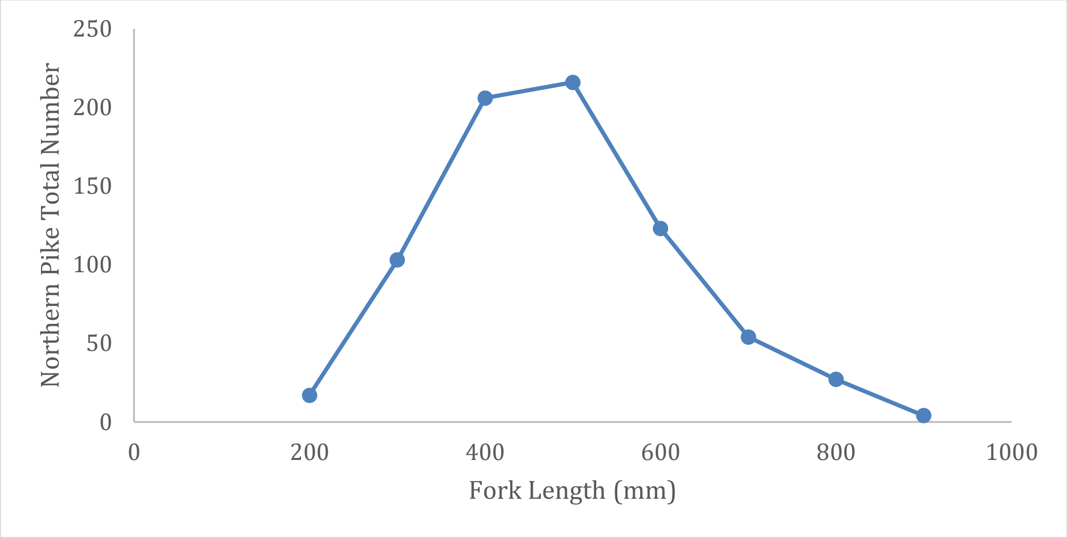

Figure A-3. Catch curve for Northern Pike (*Esox lucius*) in Minnesota Department of Natural Resources' gill nets from 1993-2015 (Chapter 2). Data was calculated using Microsoft Excel.

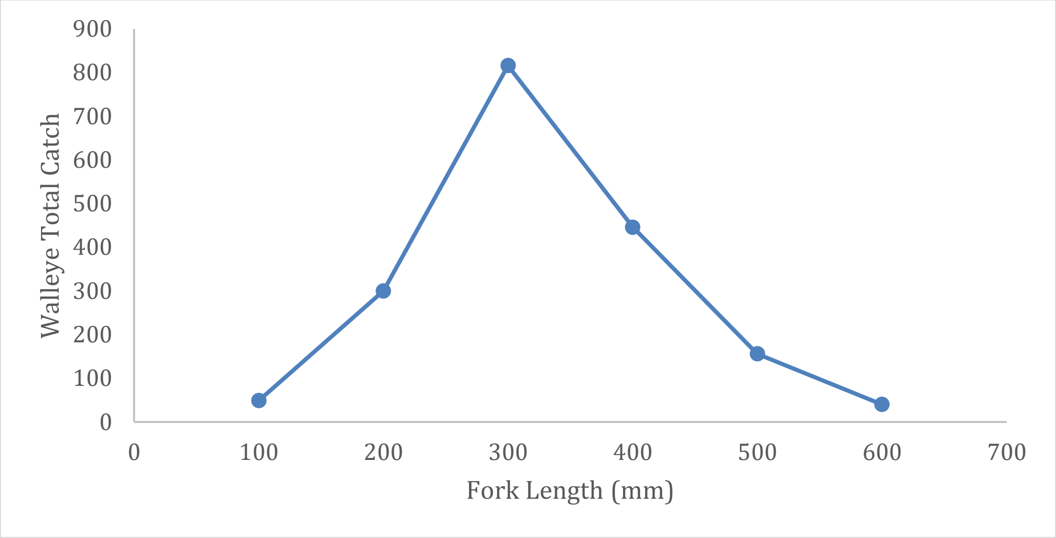

Figure A-4. Catch curve for Walleye (*Sander vitreus*) in Minnesota Department of Natural Resources' gill nets from 1993-2015 (Chapter 2). Data was calculated using Microsoft Excel.