

THE EFFECTS OF TEMPERATURE, LATITUDINAL ORIGIN, AND DAM ESCAPEMENT
ON MANAGEMENT OF MUSKELLUNGE

BY

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THESIS

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Abstract

Muskellunge *Esox masquinongy* are commonly stocked to either maintain or supplement populations across the Midwestern United States. The objectives of most fish stockings are to maximize survival and growth. Many potential factors influencing stocking success of muskellunge have been identified including temperature, predation, handling stress, competition, prey availability, habitat, dam escapement, and genetic or latitudinal origin. Much work remains to be done exploring the significance and interaction between several of these variables. My thesis focuses on temperature, source latitude of populations, and dam escapement as factors influencing growth and survival of muskellunge. Three different genetic groupings of muskellunge have been identified as the Upper Mississippi, Ohio, and St. Lawrence River drainage stocks. Different populations occurring across a range of latitudes and climates exist within each of these stocks. A recent and increasingly popular strategy in muskellunge management is to identify and utilize populations with perceived growth advantages for stocking. However, there is little understanding of how stocks, and populations within stocks, may vary in their physiological tolerance to thermal stress and the implications when relocating fish. In the first study I examined thermal tolerance among populations representing several stocks of muskellunge from varying latitudes using lethal chronic thermal maxima and sub-lethal physiological stress response experiments. Contrary to expectations, I found few indications that muskellunge populations included in this study differed in their capacity to withstand heat challenges. Other sources of mortality should be examined to explain survival differences among these populations that may be observed in the field. I also expected physiological differences at the population level to influence growth rates of muskellunge. In the second study I attempted to understand thermal adaptation of growth among latitudinally separated muskellunge populations

using bioenergetics modeling to explore whether approaches refined to the population level would improve accuracy and usefulness of future modeling efforts. Bioenergetics modeling simulations indicated that growth rates of muskellunge populations may be adapted to native thermal environments. In addition to many other known factors, survival of muskellunge stocked into reservoirs may also be influenced by dam escapement. Escapement from reservoirs has been identified as one of the unknown factors in muskellunge management, thought to have the potential to greatly reduce abundance and structure populations. Laboratory studies of a simulated spillway and field evaluations utilizing a PIT tag interrogating antennae found dam escapement of muskellunge to be more prevalent during the day. Field evaluations of escapement also found 20% of a reservoir population to escape in one year, with adults escaping more than juveniles. Results of my thesis demonstrate that interactions between latitudinal origin and temperature may have influences on growth more so than survival of stocked muskellunge, and that dam escapement is an important factor influencing management of reservoir populations.

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Chapter 1: Introduction to issues in Muskellunge Management

Introduction and Literature Review

The objectives of most fish stocking programs are to maximize survival and growth rate of hatchery fish. Muskellunge *Esox masquinongy* are commonly stocked to either maintain or supplement populations both within and outside of their native range (Kerr 2011). In North America 46% of muskellunge waters are the result of deliberate or unintentional stocking and over one million fry, fingerlings, and yearlings were stocked in 2010 (Kerr 2011). In Illinois around 25,000 muskellunge fingerlings (>125 mm) are stocked annually while neighboring Wisconsin stocks approximately 50,000 (IDNR, WIDNR). Many factors including temperature, predation, handling stress, competition with existing species, prey availability, habitat, dam escapement, and genetic origin have been cited as factors influencing performance (growth and survival) of stocked muskellunge (Wahl 1999). Although many of these factors have been previously examined, much remains to be done exploring the significance and interaction among several of these variables.

Genetic origin or source stock could interact with several other factors to influence growth and survival of muskellunge. A stock is defined as an intra-specific group of randomly mating individuals that are temporally or spatially separated from other groups (Ihssen et al. 1981). The natural range of muskellunge extends from the Lake of the Woods area of Canada to the St. Lawrence River, down through the Great Lakes and into the Ohio River and its tributaries in Kentucky (Crossman 1986). Initially, the muskellunge was divided into three separate subspecies thought to occur in the Great Lakes (*Lucius masquinongy masquinongy*), Wisconsin and Minnesota (*Lucius masquinongy immaculatus*), and the Ohio river and its tributaries (*Lucius*

masquinongy ohiensis, Crossman 1986). Although the classification of sub-species has been dropped, muskellunge were later shown to be genetically clustered into stocks occurring within the physical boundaries of these major river drainages. We now recognize three stocks of muskellunge to occur in the Upper Mississippi River basin, the Ohio River basin, and the St. Lawrence River basin (Koppelman and Philipp 1986). Because stocks are isolated from one another spatially along a latitudinal gradient they are subject to differing environments and there is potential for adaptive physiological and behavioral differences (Ihssen et al. 1981). These differences may be observed at the stock or population level. I refer to populations as unique groups of fish that are physically and thus presumably genetically, isolated from one another at the sub-stock level.

Management based on the uniqueness of fish stocks and populations, specifically with regard to their thermal adaptations, has been recommended (Ihssen et al. 1981, Philipp et al. 1981, Munch and Conover 2002, Casselman 2007). Several studies have examined intra-stock population differences in muskellunge at a local scale by relocating populations within a major river drainage (Younk 1992, Margenau 1997, Wingate and Younk 2007). Previous studies have explored differences in performance characteristics among muskellunge populations exposed to temperature regimes outside their native regime (Clapp and Wahl 1996, Wagner and Wahl 2007, Wolter 2011). A single stock or population that has superior growth and survival across a range of environments seems unlikely and has yet to be identified. Despite this, the practice of selecting muskellunge from one locale and stocking them in another is commonplace. It is also common for a region without native muskellunge to establish and maintain populations through introductions of fish from other regions (Kerr 2011). In both of these instances the differences

among populations and stocks should be carefully considered to achieve the goals of optimizing hatchery resources and preserving genetic integrity.

The ultimate success of muskellunge stocking can be affected by many factors, and appropriately there has been a great deal of research directed at developing optimal stocking practices. Muskellunge are most often stocked as fingerlings that are >250 mm in length in the fall of their first year (Margenau 1992; Wahl and Stein 1993). Stress associated with handling, transport, or temperature shock contributes significantly to initial mortality following stocking (Mather et al. 1986; Margenau 1999). At small sizes and naïve to threats to predation posed by other fish and birds, muskellunge are extremely vulnerable to predation which can often account for a significant portion of the overall mortality of a stocking year class (Stein et al. 1981; Wahl and Stein 1993; Szendrey and Wahl 1995). Available prey populations and rearing methods have also been shown to influence stocking success as hatchery reared fish attempt to assimilate into their new environment (Szendrey and Wahl 1995; Wahl et al. 2012). Beginning to feed in the wild and achieving fast growth is an important determinant of ultimate stocking success by decreasing the potential for predation and increasing metabolic energy reserves needed to withstand winter (Jonas et al. 1996). There is evidence to suggest that growth, and subsequent survival, may differ between muskellunge stocks from different latitudes (Clapp and Wahl 1996; Wolter et al. 2011) and a number of ideas have been proposed to explain these differences. The theory of thermal adaptation states that all physiological functions of an organism are adapted to the temperature range most often encountered by the ancestors of that organism over generational time (Lonsdale and Levinton 1985). Thermal adaptation has been shown previously for fish (Galarowicz and Wahl 2003; Belk et al., 2005) and predicts that muskellunge stocks and populations originating from low latitudes would show maximum growth at warmer climates and

reduced growth at colder climates, whereas the opposite pattern would occur for high latitude fish. Determining growth differences related to the latitude and thermal environment of populations of muskellunge would have both ecological and management significance.

Individuals from a year class that survive winter and successfully feed and grow are subject to several other sources of mortality, harvest and angling related stress being well studied examples (Beggs et al. 1980; Landsman et al. 2011). In field studies, fish from higher latitudes have showed decreased survival through summer when stocked into lower Midwestern lakes, suggesting that thermal stress may play a role in determining survival (Wolter et al. 2011). In general, little is known about the effects of high summer temperatures on muskellunge survival, and in particular, whether populations of differing latitudinal origin possess the same physiological capacity to withstand heat challenges. Two theories exist related to the speed and magnitude of evolutionary change in thermal physiology (Hertz et al. 1983). The conservative theory suggests that thermal physiology is constrained, does not evolve readily, and provides only minor benefits to the organism, limiting differences within ecologically diverged taxa and stocks within species (Brown 1971). The labile theory of thermal adaptation suggests that thermal physiology evolves rapidly and can vary greatly within a species (Huey 1982). Under the labile theory, latitudinally separated muskellunge stocks and populations have different thermal limits and stress responses. Under the conservative theory, responses to a thermal challenge would be similar among stocks. Exploring intra-specific thermal tolerance differentiation of muskellunge would help to understand the ecology of the species and could lead to more informed management decisions that increase survival of stocked fish.

In the lower Midwest many muskellunge populations are established in reservoirs. Dam or spillway “escapement” has been cited as another source of fish loss in these populations

(Wahl 1999; Kerr 2011). Although the result may not be lethal, when fish pass over a spillway it detracts from the ultimate goal of creating an abundant population of adult fish in the lake (Louder 1958; Lewis et al. 1968). In some instances escaped fish can contribute to very productive tailwater fisheries that are supplemented or sustained by annual influxes of these fish (Trammell et al. 1993, Schultz et al. 2003). In the outflow of smaller impoundments, fish kills are common as oxygen and prey resources can be inadequate to support these large-bodied fishes. There is also potential for escaping predators to have negative effects on downstream ecosystems and native fishes (Martinez et al., 1994; Spoelstra 2008). Understanding the magnitude and factors influencing muskellunge escapement would facilitate development of both short- and long-term solutions to prevent escapement in instances where it is problematic and provide information that would be useful to managing reservoir and tailwater populations. Additionally, because of differences in behavior and thermal preference (Wagner and Wahl, 2007) out-migration may differ between stocks or populations and may explain patterns of survival observed in reservoirs.

In this study I hope to fill gaps in our understanding of muskellunge ecology and management by examining the interaction between temperature and source latitude on growth and survival. Differences in thermal tolerance among muskellunge stocks were explored using lethal and sub-lethal thermal tolerance experiments. Bioenergetics modeling was used to explore differences in muskellunge growth and thermal adaptation at the population level under varying thermal regimes. Lastly, laboratory experiments and remote PIT tag interrogation technology were used to obtain comprehensive data on dam escapement in the field. The results of these three studies have implications for selecting and managing different source populations of

muskellunge as well as adapting management and working toward solutions for losses of fish over spillways.

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Chapter 2: Responses of Muskellunge Stocks to Heat Stress

Abstract

The muskellunge species *Esox masquinongy* has been separated into three stocks that correspond to a gradient of latitudes with potential implications for thermal adaptation. Decisions regarding muskellunge introductions are often made without important information about differing thermal stress response among sources. We tested thermal tolerance of populations representing the Upper Mississippi River drainage stock (Leech Lake, Minnesota), Ohio River drainage stock (Clearfork Lake, Ohio), and fish from the Illinois hatchery system by determining both the lethal chronic thermal maxima and sub-lethal physiological stress response. The Ohio population had a higher chronic thermal maxima than fish from the Illinois hatchery system with the Minnesota population intermediate. All three groups of fish showed similar responses of hematocrit, plasma glucose, and cortisol levels following an abrupt temperature increase. The lack of difference in thermal response among populations suggests that heat related mortality may not contribute to differences in survival of muskellunge stocks in the southern portion of the species range.

Introduction

Temperature affects essentially all physical and biochemical processes in ectotherms (Huey 1982). Both prolonged and acute exposure to adverse temperatures are common lethal agents (Beitinger et al. 2000), making the ability to cope with thermal extremes highly relevant to species survival (Anderson et al. 2003). Accordingly, the thermal regime that a set of organisms are exposed to is a strong selective agent driving the adaptation of genetic stocks (Angilletta et al. 2002; Angilletta et al. 2006). As our understanding of intra-species differences in growth and survival of fish continues to expand, genetics and latitudinal origin have become important considerations when introducing fish into a new system or stocking to maintain existing populations (Philipp 1981; Younk 1992; Wahl 1999; Miller et al. 2009). The focus on genetically different stocks and populations as operational units in fisheries management (Maclean and Evans 1981; Kapuscinski and Philipp 1988) puts an increased emphasis on the need to understand differences among these groups, particularly within species where range expansion through introductions are common.

Muskellunge *Esox masquinongy* in the Midwestern United States are genetically grouped into stocks by major river drainage (Upper Mississippi River, St. Lawrence River, and Ohio River), which correspond to a gradient of latitudes and associated temperature regimes with the potential to drive thermal adaptations (Koppelman and Philipp 1986). As a trophy species, muskellunge stocking source is often selected solely based on perceived growth rate and maximum body size, in part due to a general lack of information on intra-species differences in thermal tolerance of sportfish (Fields et al. 1987). This can result in muskellunge a population representative of a specific stock being introduced outside its native environment (Kerr 2011),

which could affect survival. Upper Mississippi River drainage fish in particular have been introduced in many locations based on observed growth advantages within their native range (Wingate and Younk 2007), but show differences in rates of survival compared to Ohio River drainage and local hatchery fish in Illinois lakes (Wagner and Wahl 2007, Wolter et al. 2011). While Upper Mississippi River drainage fish have shown comparable survival to Ohio River drainage fish and Illinois hatchery system fish overwinter, survival of Upper Mississippi River fish has been shown to be lower through summer (Wolter et al. 2011). Muskellunge stocked in the southern Midwest are often subject to summer temperatures that are warmer than optimum for the species (Wagner and Wahl 2007). Because of these findings, heat related stress has been hypothesized, but not confirmed, as a factor contributing to survival differences among muskellunge populations representative of these stocks (Wagner and Wahl 2007; Wolter et al. 2011).

In an effort to better understand post-stocking survival, we tested the thermal tolerance of muskellunge populations representative of the Upper Mississippi River drainage stock, Ohio River drainage stock, and progeny of the Illinois hatchery system using both prolonged lethal and acute sub-lethal techniques. Chronic thermal maxima studies provide insight into thermal tolerance at the organismal level and have previously been used to identify differences between genetic stocks of largemouth bass (Fields et al. 1987). Chronic lethal maxima trials simulate more natural thermal conditions than other thermal tolerance methods by allowing fish time to attempt to acclimate to increasing temperature (Fields et al. 1987; Beitinger et al. 2000). Organismal death occurs only after lower levels of organization fail to maintain homeostasis. Therefore, we were also interested in examining physiological response to an acute sub-lethal thermal challenge with the goal of linking these two measures. We examined several parameters

that have been previously used as indicators of physiological stress in fish. Plasma glucose is an energy related parameter that has been shown to be sensitive to a variety of stressors in muskellunge (Mather et al. 1974; Miles et al. 1974; Landsman et al. 2011). Increases in percent hematocrit are indicative of stress response as red blood cell count and size increase to facilitate oxygen delivery (Miles et al. 1974). Cortisol is representative of acute stress reaction in fish and may be evolutionarily linked to survival (Lyytikainen et al. 2002). Cumulative effects of sub-lethal physiological stress have been shown to have implications for survival (Barton et al. 1986; Kwak and Henry 1995) as well as growth (Gregory and Wood 1999). Our objective is to increase our understanding of thermal adaptation of groups of fish from differing latitudes and provide insight about survival of stocked fish outside their native environments. We hypothesize that the high latitude muskellunge population representative of the Upper Mississippi River drainage stock will have decreased physiological capacity to cope with heat stress which will be manifested in lower chronic thermal maxima values and higher cortisol, glucose, and hematocrit responses following a heat challenge in comparison to low latitude populations.

Materials and Methods

Chronic Thermal Maxima

Equal sized fingerling muskellunge typical of those available to agencies for fall stocking (average 270mm) from the Leech Lake, Minnesota population, 46°35' North latitude, Upper Mississippi River drainage stock), Clearfork Lake Ohio population (39°30', Ohio River drainage stock), and Jake Wolf Hatchery Illinois population (40°40') were compared in these trials. Fish from the Jake Wolf Hatchery are not a unique genetic stock or population, but rather are the

progeny of broodstock comprised of muskellunge representing several stocks and populations that now inhabit a spring-fed lake in central Illinois. The specific ancestry of these fish is largely unknown due to mixing of broodstock, but field data on their growth and survival is readily available for comparison purposes (Wolter et al. 2011). There was no difference in mean length of trial fish among stocks (ANOVA, $F= 0.33$, $P= 0.72$).

Fish were allowed to acclimate in the laboratory at water temperatures of 20°C for three weeks prior to the experiment and were fed daily rations of fathead minnows. Fish were starved for 24 hours prior to the beginning of trials. During a trial fish of each stock (N=20) were individually placed into aerated 37 liter aquaria inside of a thermally regulated environmental chamber under natural night and day light cycles (14D:10N). After a 24 hour acclimation period at water temperatures of 20°C, fish were subjected to a constant 1°C increase in water temperature every 12 hours until total mortality occurred (Beitinger et al. 2000). Tanks were siphoned and a 10% water change occurred daily to maintain water quality. Water temperature (to the nearest tenth of a degree) and dissolved oxygen levels in each tank were measured with a YSI (Yellow Springs Incorporated) sonde and recorded six times each day. Once water temperature reached 27°C, temperatures were measured every 15-30 minutes. A control group (N=10 from each stock) were held in the chamber under identical conditions for seven days without a temperature increase. Mortality was determined as lack of opercular movement (Fields et al. 1987). Temperature at the time of mortality was recorded for each fish and compared between stocks using one-way ANOVA and Tukey means separation.

Sub-lethal thermal stress response

Fish sources and handling were identical to those used for chronic thermal maxima trials. During each trial three fish of each stock (total nine fish) were held individually in aerated 18L opaque tanks that were part of a re-circulating water system. Trial fish were held at 20°C for 24 hours in the re-circulating system. After 24 hours the water temperature was increased rapidly to 28°C by mechanically switching the water source of the recirculating system between an ambient and heated reserve. Water temperatures were maintained at 28°C for an additional six hours (Vandlandeghem et al. 2010). The magnitude of change and final temperature were selected based on the published thermal maxima and optima values for the species (Scott 1964; Ferguson 1958; Reynolds and Casterlin 1979) and observed summer thermal habitat in the field (Wagner and Wahl 2007). Control fish (N=10 for each stock) were not subjected to an increase in water temperature but were held at a constant 20°C for 30 hours in the re-circulating system. Control and treatment trials were run alternately until N=10 and control and treatment fish from each stock had been sampled. At the conclusion of each trial period fish were anesthetized with buffered tricaine methanesulfonate (MS-222) and blood was immediately taken from the gill arch (Houston 1990) using methods and instruments similar to Vandlandeghem et al. (2010). Whole blood was portioned into aliquots of plasma and packed red blood cells via centrifuge, both of which were immediately frozen in liquid nitrogen (Suski et al. 2003).

Percent hematocrit was examined immediately after blood samples were drawn by determining the percent packed red blood cells after centrifuging a capillary tube of whole blood. Plasma glucose (mmol/l) was determined enzymatically with a spectrophotometer (Lowry and Passonneau 1972). Cortisol (ng/ml) was determined using a commercially available enzyme linking immunoassay kit (Enzo Life Sciences, Farmingdale NY). Data were analyzed using two-way ANOVA with the main effects being treatment and population. The interaction between

treatment and population was also included in the ANOVA as a means to determine how responses to the heat challenge may differ among groups of muskellunge. Tukey adjusted means separation was used to compare differences between stocks and treatments.

Results

Chronic thermal maxima

We observed 100% survival for control fish during the seven day period indicating that mortality during treatment runs was due to increasing temperature and not starvation or handling stress. Throughout treatment and control runs dissolved oxygen levels in all tanks were $>6\text{mg/L}$. All fish included in the treatment trials experienced mortality within six days from the start of a trial. The Ohio River drainage fish showed a significantly higher chronic thermal maxima value (30.4 , confidence interval $\pm 0.2^\circ\text{C}$) than the Illinois hatchery population ($30.1 \pm 0.2^\circ\text{C}$), with fish from the Upper Mississippi River drainage stock being intermediate ($30.2 \pm 0.2^\circ\text{C}$, $P=0.03$, Figure 1).

Sub-lethal stress response

Treatment fish were observed to have changes in coloration and rapid opercular movement during heat challenges indicating physiological disturbance. Three fish (two Illinois, one Minnesota) died, presumably from thermal stress, during one of the six hour heat shock periods. We did not sample tissues from these fish and they were replaced in subsequent trials to preserve sample size.

Percent hematocrit increased significantly between control (mean 28.5%) and heat stressed fish (mean 31.9%, Table 1, Figure 2, $P < 0.01$). There was no difference in percent hematocrit among stocks ($P = 0.50$, Table 1) nor was there an interaction between stock and treatment ($P = 0.69$) that would suggest that these three groups of fish responded differently to the increase in temperature. Plasma glucose values showed no difference between treatment, stock, or the interaction between the two (Table 1, Figure 3, $P > 0.05$). There appeared to be a trend of higher plasma cortisol levels in treatment fish (mean 70.2 ng/ml) in comparison to controls (mean 52.6 ng/ml), but differences were not significant at these sample sizes and level of alpha (Table 1, Figure 4, $P = 0.25$). There was no statistical difference in cortisol levels between stocks or an interaction between stock and treatment.

Discussion

Chronic thermal maxima studies incorporating genetic stocks of largemouth bass (now recognized as separate species) existing across a latitudinal gradient found large differences in thermal tolerance (Fields et al. 1987). In this study, chronic thermal maxima values did not indicate differences in thermal tolerance among separated populations of muskellunge (Ohio and Upper Mississippi River drainages) occurring across a comparable latitudinal gradient. Similarly, examination of physiological stress parameters following a sub-lethal heat challenge did not reveal differences between muskellunge stocks or interactions between stocks and treatments. Hematocrit percentages increased between control and heat shock trials (28.5 to 31.9%) and were largely within ranges previously recorded for muskellunge exposed to stressors (29-33%, Miles et al. 1974). Magnitude of glucose values in our study were consistent with the range

previously reported for muskellunge exposed to thermal stress (Mather et al. 1986) but generally fell in between the guidelines for stressed (>5 mmol/l) and unstressed (<4 mmol/l) fish outlined by Iwama (1998). Plasma cortisol values in this study were highly variable for both control and treatment groups. Levels of physiological stress parameters measured in control fish in this study may be cause for concern. Glucose and cortisol values of fish in the control groups (mean 4.2 mmol/l and 52.6 ng/ml respectively) were higher than controls in other studies of muskellunge stress response. Landsman et al. 2011 found glucose levels of <3 mmol/l and cortisol levels near 10 ng/ml in unstressed control fish. Elevated levels of these parameters in this study may indicate that trial fish were chronically stressed from confinement, handling, noise, or other unknown factors, although efforts were made to limit these sources of stress. Nonetheless, if fish were chronically stressed it could limit their capacity to respond to additional stressors (i.e. temperature shock).

Adaptation through selective processes can lead to different thermal performance functions and limits among conspecific groups of ectotherms (Angilletta et al. 2002). We expected fish from high latitudes (Upper Mississippi River drainage) to be adapted to a cooler thermal regime and thus show lower chronic thermal maxima values and more indication of physiological distress following a temperature increase in comparison to the fish from lower latitudes (Ohio River drainage). The lack of such a pattern indicates that these groups of fish do not differ in their thermal response (at least for warm temperatures) despite geographic isolation along a latitudinal cline. With the exception of the Ohio River stock showing a higher chronic thermal maxima, both the high and low latitude stocks showed a similar response to progeny from the Illinois hatchery system comprised of mixed genetic stocks.

Separating the influence of genetic adaptation and environmental influence on the phenotypic expression of organisms is an important and often difficult component of understanding differences among populations (Whitehead et al. 2011). In our study all populations of fish were brought into a common laboratory environment and held for three weeks prior to trials, allowing fish to acclimate but also creating a scenario where phenotypic flexibility could allow muskellunge stocks to conform physiologically to their new environment, muting important adaptive differences (O'Connor et al. 2011).

Similar responses to a common thermal challenge between the high latitude Upper Mississippi River drainage stock and low latitude Ohio River drainage stock have management implications. Similar thermal performance, particularly in the chronic thermal maxima trials, indicates that these stocks should survive at similar rates following stocking if temperature is the primary factor limiting survival in lakes typical of the southern Midwest. In instances where geographically dispersed source populations are being used to establish and maintain muskellunge fisheries, factors other than heat related mortality, such as immune deficiency (Harper and Wolf 2009), behavioral differences, or emigration, are more likely explanations of observed differences in survival between these two stocks. We emphasize that our results should not serve to encourage stocking decisions that abandon sound conservation genetics principles (Kapusinski and Philipp 1988).

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Tables

Table 1. Results of two-way ANOVA examining the effects of treatment (heat shock), stock, and treatment x stock on length, percent hematocrit, glucose, and cortisol of muskellunge.

Parameter	N	Effect	df	SS	F	P
Length (mm)	60	Whole Model	5	2022.13	1.17	0.34
		Trial	1	135	0.39	0.54
		Population	2	1467.43	2.12	0.13
		Trial x Population	2	419.7	0.6	0.55
		Error	54	18696.2		
Hematocrit (%)	56	Whole Model	5	195.29	3.45	<0.01
		Trial	1	170.62	15.06	<0.001
		Population	2	15.96	0.7	0.5
		Trial x Population	2	8.7	0.38	0.68
		Error	50	566.33		
Glucose (mmol/l)	57	Whole Model	5	4.12	0.21	0.96
		Trial	1	0.64	0.16	0.69
		Population	2	0.99	0.13	0.88
		Trial x Population	2	2.49	0.31	0.73
		Error	51	202.2		
Cortisol (ng/ml)	53	Whole Model	5	16384.92	0.97	0.45
		Trial	1	4727.97	1.4	0.24
		Population	2	9244.61	1.37	0.26
		Trial x Population	2	2376.35	0.35	0.71
		Error	47	158971.7		

Figures

Figure 1. Chronic thermal maxima values for three populations of muskellunge including Leech Lake, Minnesota (MN, Upper Mississippi River drainage stock), Ohio, Clearfork Lake (OH, Ohio River drainage stock) and the Illinois hatchery progeny (IL). Letters denote statistical groupings determined by Tukey means separation.

Figure 2. Percent hematocrit, glucose, and cortisol values for three populations of muskellunge following control (C) and an abrupt 8°C heat shock treatment (T) trials. Trials included populations from Leech Lake, Minnesota (MN, Upper Mississippi River drainage stock), Ohio, Clearfork Lake (OH, Ohio River drainage stock) and the Illinois hatchery system (IL)

Figure 1.

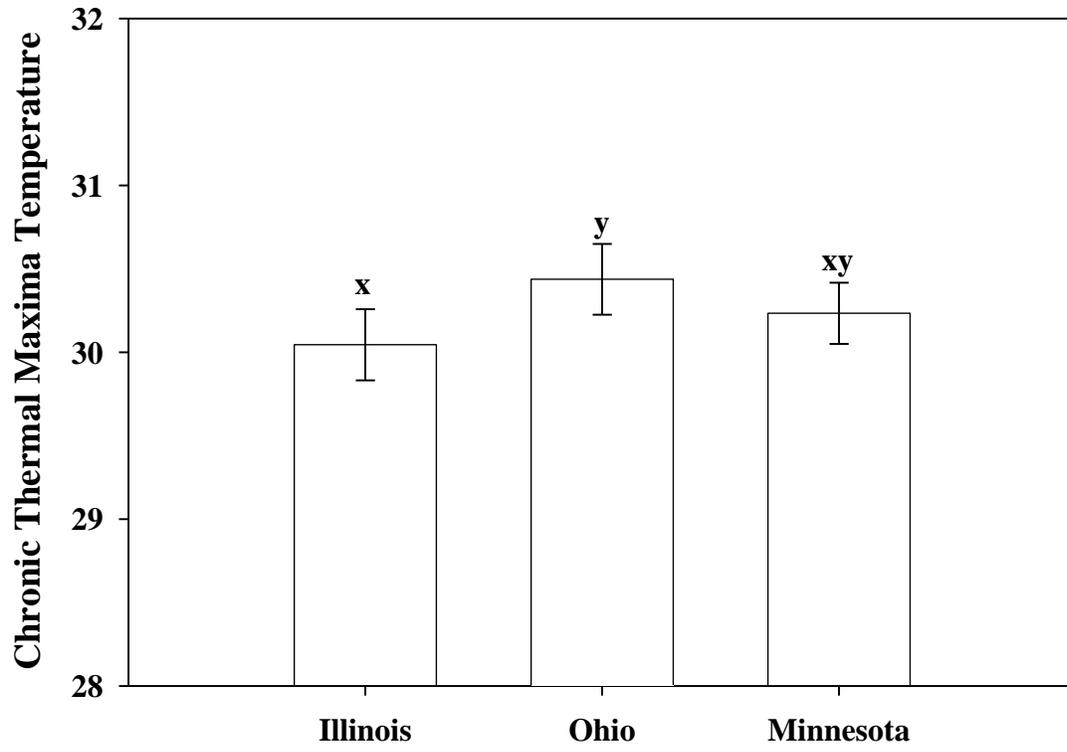
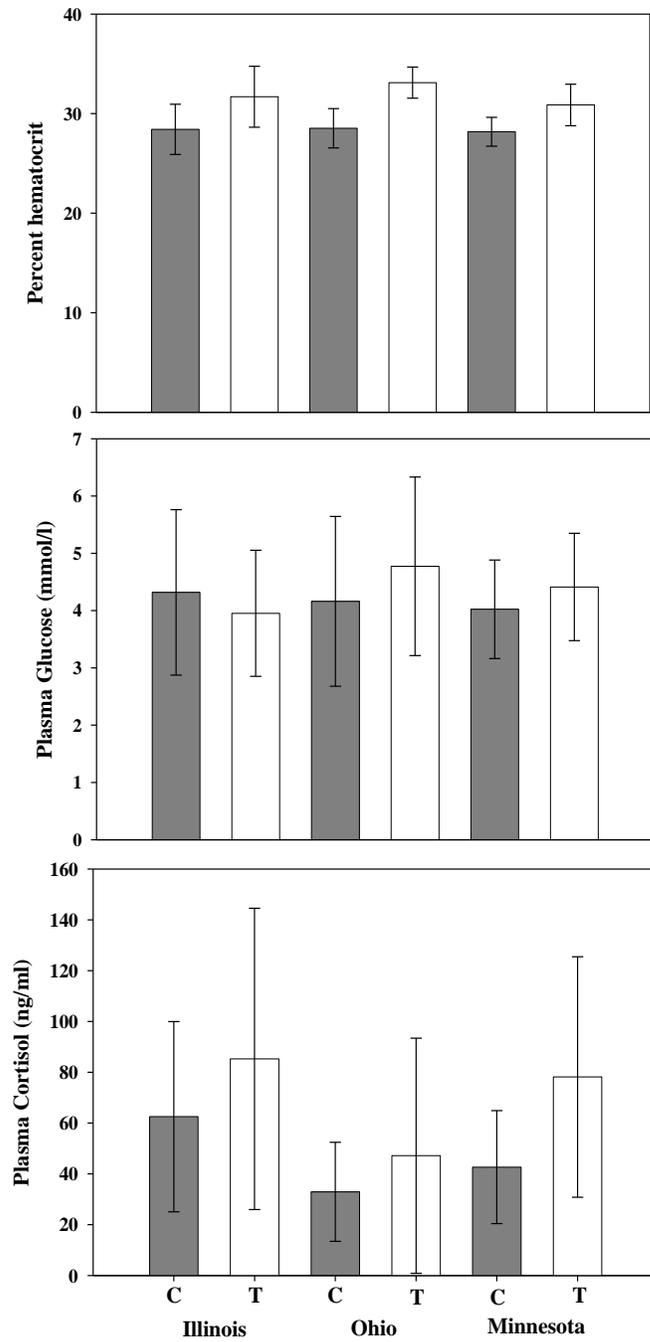


Figure 2.



Chapter 3: Development and Evaluation of a Population-Specific Bioenergetics Model for Muskellunge

Abstract

Muskellunge *Esox masquinongy* are a popular sportfish with populations occurring across a latitudinal gradient that could drive local adaptation of metabolic and food consumption rates in order to optimize growth. Current bioenergetics models for muskellunge, and most other sportfish, do not account for these intra-species differences. We created models for five individual populations of muskellunge from varying latitudes and conducted simulations under differing thermal regimes to explore the influence of temperature on growth patterns. We also created a general range-wide model to compare population-specific model accuracy using growth observed in the laboratory and field. Population specific model predictions provided a better fit to observed laboratory growth rates for individual muskellunge populations than a range-wide model or the current muskellunge bioenergetics model developed with a single population. Simulation exercises provided evidence of thermal adaptation where populations from high latitudes showed increased growth under a cool thermal regime whereas those from low latitudes grew faster in a warm thermal regime. However, when compared to field data the population-specific models accounting for thermal adaptation showed similar predictive power to a generalized range-wide species model. Comparisons of model predictions to field growth may have been limited by mortality, phenotypic plasticity, or low sample sizes. Comparisons to laboratory growth and bioenergetics simulations indicate that muskellunge populations are adapted to specific thermal regimes and population-specific growth differences can result.

Introduction

Temperature is paramount to growth of ectotherms as it dictates essentially all physiological processes (Christie 1988; Beitinger et al. 2000; Angilletta et al. 2002). Thermal adaptation in ectotherms occurs when populations differentiate metabolic efficiency to optimize fitness traits, such as growth, in a given thermal environment (Levinton and Monahan 1983). Growth rates among latitudinally distinct populations or stocks of fish have been shown to be maximized under specific thermal regimes (Galarowicz and Wahl 2003; Angilletta et al. 2006). Appropriately, the thermal history of genetically distinct groups of fish is being increasingly taken into account in an effort to maximize growth rate and survival of sportfish that are stocked to establish or maintain recreational populations (Kapusinski and Philipp 1988).

Muskellunge *Esox masquinongy* are a popular sportfish that are commonly reared in hatcheries and stocked to create trophy fisheries where fast growth and large maximum size are important management goals (Margenau 1999; Kerr 2011). Populations of muskellunge have been shown to be physically and genetically clustered by major river drainages into an Upper Mississippi River stock, an Ohio River stock, and a St. Lawrence River stock (Koppelman and Philipp 1986). The populations within these stocks are found across a gradient of thermal environments that have the potential to affect their evolution on a generational scale (Ihssen et al. 1981; Angilletta et al. 2006). Several studies have found superior growth of one muskellunge population over others within a region, findings which have led to significant management successes (Younk and Strand 1992; Wingate and Younk 2007). As a result, much attention has been directed at selecting muskellunge populations that achieve fast growth and largest maximum body size in stocking scenarios (Wingate and Younk 2007). Currently there are no

tools to make predictions regarding growth of individual muskellunge populations in varying thermal environments which could aid stocking decisions.

Bioenergetics models have been used to predict growth of individuals and fish populations with mixed success (Hansen et al. 1993; Chipps and Wahl 2008). These models are based on a mass-balance equation incorporating consumption, waste, and metabolic cost. Many components of this basic energy budget are heavily influenced by temperature (Angilletta et al. 2002), making thermal environment one of the most important predictors of growth (Lonsdale and Levinton 1985; Wahl 1999). Intra-specific differences in growth rate and metabolism are often attributed to local thermal adaptation to encountered environmental conditions (Angilletta 2001) and have been reported in Atlantic silversides *Medinia medinia* (Munch and Conover 2002), gobiids (Barlow 1961), walleye *Stizostedion vitreum* (Galarowicz and Wahl 2003), and northern pike *Esox lucius* (Armstrong and Hawkins 2008), among others. Rates of consumption and metabolism of muskellunge vary among populations associated with a gradient of latitudes and these local adaptations could influence growth (Clapp and Wahl 1996). Due to the importance of thermal environment in bioenergetics modeling, large errors in growth predictions could occur when local adaptations are not accounted for in models (Galarowicz and Wahl 2003). Errors could also occur if a single population with associated local adaptations is used to describe growth of a different population or a species as a whole. Such failure to appropriately account for thermal adaptation has been cited as a potential limitation to bioenergetics modeling accuracy and calls have been made to refine modeling of sportfish species to the stock or population level (Munch and Conover 2002; Chipps and Wahl 2008). The current bioenergetics model for muskellunge was developed using fish from a single Ohio population (Bevelhimer 1985) but population-specific models may be required if thermal adaptation is present in the

species. Similarly, species-level models may be improved when bioenergetics parameters are developed using multiple populations representative of the heterogeneity of thermal environments within the range of the species. Our objective was to evaluate thermal adaptation of muskellunge populations and explore alternative bioenergetics modeling approaches. We created specific bioenergetics models for five different populations of muskellunge in addition to a range-wide species model incorporating multiple populations from varying latitudes. We then conducted simulations under varying climatic regimes to explore the influence of thermal environment on growth of muskellunge populations. We also compared the usefulness of both the population-specific and range-wide muskellunge models to each other and to the original muskellunge model (Bevelhimer 1985) using laboratory and field growth data. By evaluating a population-level and more inclusive species-level approach, we hope to increase understanding and accuracy of muskellunge growth modeling and contribute to the discussion on the influence of thermal environment on growth of distinct populations. The results and models generated from this study can also be used to make qualitative management recommendations on broodstock selection when muskellunge are being introduced or stocked to supplement populations.

Materials and Methods

Model Building

Our models follow the framework developed for yellow perch by Kitchell et al. (1977) that was also used to generate the Bevelhimer et al. (1985) muskellunge model (hereafter abbreviated BVM):

Equation 1. $G = C - (M + F + U)$ where

G = specific growth ($g \cdot g^{-1} \cdot d^{-1}$), C = specific rate of food consumption, M = specific rate of metabolism (including specific dynamic action), F = specific rate of egestion, and U = specific rate of excretion. C ($g \cdot g^{-1} \cdot d^{-1}$) is equal to $C_{max} \cdot P$, where C_{max} is the ad libitum food consumption at a given temperature and P is the ration level or proportion of C_{max} actually consumed in the field which can vary between 0 and 1.0. The equation for C_{max} for all stocks followed the form:

Equation 2. $C_{max} (g \cdot g^{-1} \cdot d^{-1}) = a^1 \cdot B^{b_1} \cdot e^{(xT+yT^2+zT^3)}$

Where a_1 is an intercept constant, B is biomass (grams), b_1 is the weight dependent constant, and T is temperature (Bevelhimer et al. 1985). The weight dependent parameter b_1 was borrowed from northern pike (Diana 1982; Bevelhimer et al. 1985) and developed using fish $\leq 1200g$. Population specific parameters (a_1 , x , y , and z) describe a third order polynomial equation with T , T^2 , and T^3 as the independent variables and $\ln(C_{max}) - (-0.18 \cdot \ln 9B_0)$ as the dependent variable (Bevelhimer et al. 1985). Excretion and egestion were both modeled as proportionate losses of ingested energy with $U = 0.07 \cdot C$ and $F = 0.13 \cdot C$ (Bevelhimer et al. 1985; Wahl and Stein 1991).

Metabolic rate ($g \cdot g^{-1} \cdot d^{-1}$) for each population was fit to:

Equation 3. $(a_2 \cdot B^{b^2} \cdot e^{mT}) \cdot A + SDA \cdot C$

Where a_2 is the intercept value, B is biomass (grams), b^2 is the weight dependent constant, m is the temperature dependent constant, T is temperature, A is activity, and SDA is specific dynamic action. Weight dependent parameter b_2 is identical to b_1 following the form of the Bevelhimer et al. (1985) model which assumed a similar relationship between biomass and

metabolism as with consumption. The A multiplier was modified from 1.13 (Bevelhimer 1985) to 1.04 as per the recommendation of Wahl and Stein (1991). SDA was set at 14% of the energy consumed (C). Parameters a_2 and m are population-specific and were obtained using linear regression where $\ln(\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}) - (-0.18 \cdot \ln(\text{Biomass}))$ was the dependent variable and T was the independent variable. Parameter a_2 was converted from its original form of $\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ to $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ for use in the model by multiplying $a_2 \cdot (3.24 \text{ cal} \cdot \text{mg O}_2^{-1}) \cdot (1 \text{ g} \cdot 860 \text{ cal}^{-1}) \cdot (24 \text{ h} \cdot \text{d}^{-1})$ (Bevelhimer et al. 1985).

We built population-specific models (PSM's) for Minnesota (Leech Lake, 46°35', hereby abbreviated MNM), Wisconsin (Minoqua Chain, 45°30' North latitude, WIM), New York (Lake Chautauqua, 42°47', NYM), Ohio (Clear Fork Lake, 39°30', OHM), and Kentucky (Cave Run Lake, 37°35', KYM) populations. Maximum food consumption (C_{max}) and metabolic rate data incorporated into these models were those reported by Clapp and Wahl (1996). The C_{max} values were obtained for each population through 10 replicate ad libitum feeding trials with juvenile fish (13-17g) at 5, 10, 15, 25, and 27.5°C. Oxygen consumption trials were conducted in replicate (N=10) for one hour in closed vessel respirometers at the same temperature increments and fish sizes as C_{max} trials. Clapp and Wahl (1996) provide further information on fish sources, handling, and experimental procedure. In addition to the PSM's we built a range-wide model (RWM) where data from all five populations were pooled and parameters were generated using the same methods as above. The RWM essentially represents the mean consumption and metabolism rates for the five populations. We assembled models and conducted simulations in STELLA modeling software (copyright Isee Systems 1985-2005).

Model Fitting and Simulations

Fit of consumption and metabolic rate equations for individual populations and range-wide data was assessed using R^2 values. Growth predictions for the population-specific models were then compared to observed laboratory growth reported by Clapp and Wahl (1996). Growth data came from 10 replicate 14-day ad libitum feeding trails at 5, 10, 15, 25, and 27.5°C for 13-17g fish from each population. Growth was determined as grams of growth per gram of initial fish biomass per trial day. Models were used to predict growth rate ($g \cdot g^{-1} \cdot d^{-1}$) of these fish in each thermal environment at ad libitum ration level ($P = 1.0$). Growth rates predicted by the RWM and BVM were also compared to observed laboratory growth. Accuracy of models was assessed by calculating squared residuals between model predictions and observed growth rate at each temperature increment and population combination (Eq. 4).

Equation 4. Squared residual = $\frac{(\text{Predicted} - \text{Observed})^2}{\text{Observed}}$

Analysis of variance with Tukey adjusted means separation was used to determine differences in mean squared residuals among model types, populations, and temperature increments. Model type, population and temperature were used as class variables in a global analysis. Differences in accuracy among populations and across temperature increments were also assessed within each model type (PSM's, RWM, and BVM).

Growth predictions in a simulated stocking scenario were compared among model types. All populations were assigned the same starting weight of 50 grams. Proportion of maximum consumption (P) was held constant at 0.45 for all models, within the expected range of P values for esocids in the field (Bevelhimer 1985). Simulations were run from October 30, a typical fall

stocking date, through August 24 of the following year (300 days). The simulation used a central Illinois lake (Lake Mingo, North latitude, 40°7') water temperature regime. Temperatures during the simulations ranged between 4 and 28 degrees Celsius. At the conclusion of the 300 day simulation, differences in final biomass predicted by each model were compared.

To simulate growth of the five populations of muskellunge under varying thermal regimes we again used annual temperature data from Lake Mingo. To create differing thermal regimes we examined approximate changes in heating and cooling degree days observed between Lake Mingo and the broodstock locations of the northernmost (Leech Lake, Minnesota) and southernmost (Cave Run, Kentucky) populations for which models were developed. To create a warm thermal regime (Cave Run Kentucky) Lake Mingo daily temperatures were multiplied by 1.1, a cool thermal regime (Leech Lake Minnesota) was created by multiplying temperatures by 0.8. The ration level was again set at P=0.45 for these simulations and the starting weight for all populations was 50g. Simulations were run from October 30 through August 24 of the following year (300 days).

Field Comparisons

Model predictions were compared to field growth using data from four year classes consisting of four populations stocked into Lake Mingo (central Illinois, 40°7' North latitude) and Pierce Lake (northern Illinois, 42°20'). Mean biomass of each stocking class and population combination was used as the starting biomass when running models. Electrofishing sampling dates in the spring following stocking were used as the endpoints for these comparisons. Daily temperatures used in these simulations were derived as averages of 6-20 readings throughout the day from loggers placed at 1m depth into each lake. Daily temperatures ranged from 4-28°C

during the simulation period. Although studies have shown that heterogeneity of thermal environments in reservoirs can impact growth potential of fish (Budy et al. 2011), muskellunge from various populations included in this study have been shown to inhabit similar thermal habitat following stocking (Wagner et al. 2007) so no adjustments for temperature selection were made. Prior to simulations the ration parameter was iteratively tested to determine the level (0.45) at which RWM predictions had minimal mean raw error in comparison to field growth of all population/year class combinations. Additional error between RWM predictions and observed growth could then be assumed to be the result of population-specific growth. For each year class and population the corresponding PSM's were run along with the RWM. We then examined whether the PSM approach successfully reduced absolute error rates further in comparison to the RWM approach.

Error rates between model predictions and observed field data was assessed by grams of error (Eq. 5) and percent error (Eq. 6).

Equation 5.
$$\text{grams error} = \text{biomass(g) predicted} - \text{biomass(g) observed}$$

Equation 6.
$$\text{percent error} = \frac{\text{biomass(g) predicted} - \text{biomass(g) observed}}{\text{biomass(g) observed}} \cdot 100$$

One-tailed paired t-tests were conducted to determine whether mean absolute grams of error and mean absolute percent error were lower for the PSM approach in comparison to the RWM approach. Significance was determined at $P=0.05$. We also compared model success by calculating an index of model reliability for each approach. The statistical variation of the index k method for assessing model reliability (Legget and Williams 1981; Wahl and Stein 1991

Whitledge and Hayward 1997) describes model accuracy by comparing x_i observations to y_i model predictions within a factor of k (Eq. 7):

Equation 7.
$$k = \exp \sqrt{\frac{1}{n} \sum \left(\frac{\log_{y_i}}{\log_{x_i}} \right)^2}$$

Results

Model Fitting and Simulations

Polynomial equations adequately described laboratory derived C_{\max} of individual muskellunge populations ($R^2 > 0.75$, Table 2). Similarly, linear equations describing metabolic rate of populations provided a good fit to laboratory data ($R^2 > 0.55$, Table 3). PSM and RWM parameters were generally similar in magnitude and sign to the parameters developed by Bevelhimer et al. (1985) although specific values varied, particularly for parameters describing C_{\max} (Table 2). The intercept (a_1) describing the C_{\max} equation varied from the Bevelhimer et al. (1985) value by 1 to 564% among the PSM's. In addition, the coefficients describing the temperature and consumption relationship for the PSM's varied from those developed by Bevelhimer et al. (1985) by $x=10-183\%$, $y=2-203\%$, and $z=17-161\%$. Clapp and Wahl (1996) found relatively similar rates of food consumption among these same five muskellunge populations at 5 and 10°C. In that study the Wisconsin population showed the highest rates of food consumption at 15 and 25°C while the Ohio population showed the highest food consumption at 27.5°C. These same patterns are evident in the equations predicting food consumption for the PSM's representing these populations (Figure 3). Equations for PSM's (and

thus also the RWM) typically predicted higher food consumption rates than those predicted by the BVM, except at high temperatures (Figure 3). The temperature at which peak consumption occurred was highest for the OHM (27.1°C), followed by the KYM (24.6), MNM (23.3°C), and NYM and WIM (22.4°C). The relationship between metabolism and temperature was more similar between model types (Figure 3). Clapp and Wahl (1996) similarly found no differences in metabolic oxygen consumption among muskellunge populations at 5, 15, and 25°C and relatively small differences at 10 and 27.5°C. Values of metabolic rate parameters varied between the PSM's and BVM by $a_2=3-39\%$ and $m=4-45\%$ (Table 3).

The BVM typically predicted growth rates that were lower than those observed in the laboratory at 5, 10, and 15°C, but over predicted growth of some populations at 25 and 27.5°C (Figure 4). Comparison of model predicted growth to observed laboratory growth found significant differences in residuals among model types (ANOVA, $F=2.61$, $P=<0.01$). The PSM's had significantly lower mean squared residuals (0.0025) than the RWM (0.0050) and BVM (0.0068) which were not different from one another. The PSM and BVM did not show differences in error rate among populations ($P=0.95$ and 0.26 respectively). The RWM had lower residual error for the Wisconsin and Ohio populations ($P=0.02$) than the Kentucky population, with the Minnesota and New York populations being intermediate. Residual errors were not different among temperature increments for any of the model types ($P=>0.05$). Comparisons among models in a simulated stocking scenario yielded large differences in predicted final biomass (Table 4). The WIM predicted the largest final biomass, 437g higher than lowest predicted final biomass generated by the BVM. Biomass predictions generated by the WIM differed from other model types by the largest average (+318g), while the MNM predictions were most similar to those from other model types, differing on average by only -8g. The BVM

predicted the lowest growth, 192g lower on average than the PSM's. Simulations in warm and cool thermal regimes resulted in different patterns of growth among the five muskellunge populations. In the cool thermal regime the WIM predicted the fastest growth followed by the NYM, OHM, MNM, and KYM (Figure 5). In contrast, in the warm thermal regime the OHM predicted the fastest growth followed by the WIM, MNM, KYM and NYM (Figure 5). Models for the three highest latitude populations predicted higher final biomass (WIM +341g, NYM +169g, MNM +27g) in the cool thermal regime as compared to the warm thermal regime (Figure 5). Models for the two lowest latitude populations predicted faster growth (OHM +116g, KYM +1g) in the warm thermal regime compared to the cool thermal regime.

Field Comparisons

The RWM predictions deviated from observed growth in the field (Table 4) on average by -3.6g and -0.8% (Table 6). When adjusted for sign, the RWM had an absolute mean error of 26.4g and 20.6%. Biomass predictions generated by the PSM's did not have lower mean absolute error (26.3g, $P=0.49$) or absolute percent error (19.2%, $P=0.27$) from observed field growth in comparison to the RWM approach. The RWM approach did have a slightly better reliability Index k value (1.06) than the PSM approach (1.11). When examined individually none of the PSM's had any substantial differences in mean predictability in comparison to one another. There was also no evidence of differences in error rates across study lakes, although these comparisons were limited by sample size. Field data were not available for the Wisconsin population so evaluations of predictive ability of WIM could not be completed.

Discussion

Bioenergetics models have had mixed success in predicting growth and food consumption in fish (Ney 1993; Chipps et al. 2000a; Chipps and Wahl 2008). Among others, studies of seasonal changes in metabolism (Chipps et al. 2000b; Shoenbeck et al. 2008), fluctuation in energy density (Jonas et al. 1996), and the variable nature of activity rates (Madon and Culver 1993) have explained sources of variability and error in bioenergetics model predictions. Failure to recognize and account for intra-species physiological differences caused by local adaptation is another possible source of error (Munch and Conover 2002; Galarowicz and Wahl 2003; Armstrong and Hawkins 2008). By incorporating observed intra-species differences in food consumption and metabolism we expected PSM's accounting for thermal adaptation would explain more observed variability in muskellunge field growth than a general species model. The theory of thermal adaptation in poikilotherms argues that organisms from higher latitudes exhibit increased fitness in temperature regimes common at high latitudes and vice versa for low latitudes (Levinton and Monahan 1983). Predicted food consumption for the high latitude populations in the current study (Wisconsin, New York, Minnesota) peaked at lower temperatures and declined more precipitously at high temperatures in comparison to low latitude populations (Ohio, Kentucky, and the Ohio population in Bevelhimer et al. 1985). Simulations using these population-specific food consumption and metabolic rates showed large potential differences in growth rate among populations as well as interactions between temperature and population. As predicted by thermal adaptation, low latitude fish (Kentucky, Ohio) showed increased growth in a warm thermal regime compared to a cold one and in a cold thermal regime fish from high latitudes (Wisconsin, Minnesota, New York) grew faster in comparison to their growth in a warmer environment. Comparisons of model predictions to

observed field growth, suggested that individual PSM's had similar predictive accuracy as a general species model found that a species model was adequate to describe these populations. Several explanations may exist for why PSM's were no more effective than the RWM despite other evidence to suggest differential growth among populations related to thermal adaptation. Size and survival are strongly linked following stocking (Szendry and Wahl 1995; Wahl 1999). Smaller, slower growing individuals are often subject to higher rates of mortality (Johnson and Margenau 1993; Szendry and Wahl 1996; Lyons 1997; Wahl 1999), which could lead to overestimates of growth. Faster growing individuals that survive long enough to recruit into the population and be sampled may be bioenergetically dissimilar from the mean of the population (Tyler and Bolduc 2008). Low overall survival of stocked muskellunge has been observed in these lakes (Wolter et al. 2011), supporting the idea that observed growth rates may not be representative of actual growth rates. Additionally, low catch rates limited sample size for comparisons between model predictions and field growth. In addition, field comparisons occurred overwinter when the scope for growth is reduced compared to the summer growing season. Growth simulations conducted over 300 days showed growth differentiation to be greatest during the final 100 days of the simulation when temperatures and growth rates were highest. Future field evaluations over a longer time span may find population-specific growth patterns related to temperature which would provide justification for the use of PSM's.

Phenotypic expression of traits (such as growth) consists of both an environmental and genetic component (Lonsdale and Levinton 1985), but the relative importance in determining growth rates and the reversibility of genetic adaptation in response to a new environment are often debated (Barlow 1961; Begg et al. 1999; Conover 2009). The semi-labile nature of most physiological processes, termed phenotypic plasticity (Piersma and Drent 2003) afford

individuals a limited amount of variability in trait expression to suit experienced environments (Angilletta 2004) and is one possible explanation for homogenized growth rates of muskellunge populations in the field. Separating the influence of environment and genetics requires a common environment experiment (Begg et al. 1999; Galarowicz and Wahl 2003) like those performed by Clapp and Wahl (1996). Phenotypic plasticity could only explain the similarities in accuracy between the PSM's and RWM if phenotypic responses to the environment occur over a greater temporal scale than the laboratory trials used to determine physiological rates for these populations. Further understanding of phenotypic plasticity in muskellunge would help not only in the context of this study and bioenergetics modeling, but also for stocking programs across the range of the species.

Rates of metabolism and consumption varied among muskellunge populations but alone did not provide obvious evidence of thermal adaptation (Clapp and Wahl 1996). However, when these rates were synthesized into a bioenergetics model and simulations were conducted, functions describing food consumption and predicted growth provide evidence of some degree of thermal adaptation (Belk et al. 2005). Generally higher growth rates for low latitude fish occurred at high temperatures whereas higher growth rates occurred at low temperatures for high latitude fish. Other factors influenced muskellunge growth rates since not all observed patterns in this study and Clapp and Wahl (1996) can be explained fully by latitudinal effects (i.e. Ohio fish outgrowing Minnesota fish in the cool thermal regime simulation). Muskellunge inhabit both lakes and rivers, though there is evidence to suggest the species is more suited for riverine systems (Crossman 1986). Lotic populations typically have a different thermal history than lentic populations at the same latitude (Germano and Bury 2009). Adaptations in growth rate or other life history characteristics for an individual population could be more dependent on habitat than

on latitude (Rypel et al. 2006; Paukert and Fisher 2001; Blanck and Lamouroux 2007). Biotic interactions may also explain some differences in growth rates between muskellunge populations. Trade-off 's have been shown to occur between metabolic rate and growth when populations evolve in prey limited environments (Munch and Conover 2002). In the absence of sufficient prey, high rates of metabolism, consumption, and thus growth are negatively selected for resulting in populations with lower intrinsic growth rates. Predation risk can have similar effects by reducing foraging, resulting in selection for lower food consumption and growth rates (Lankford et al. 2001). Interactions with competitor species can also influence adaptive growth rates. Populations of pumpkinseed *Lepomis gibbosus* evolving in the presence of bluegill *Lepomis macrochirus* showed growth rates that compensated for the level of competition, equaling growth of allopatric populations under natural environments and exceeding growth when removed from competition (Arendt and Wilson 1999). A similar response could occur for muskellunge populations that have evolved sympatrically with northern pike given that strong competitive interaction between these species exists (Inskip 1986). Without extensive long-term data on the habitat, predation history, prey availability, and competitive interactions of the muskellunge populations, the effects of these factors on adaptive rates of consumption, metabolism, and growth are unknown.

Differences between the PSM's and RWM developed in this study and the model developed by Bevelhimer et al. (1985) could be the result of several factors. The equation for C_{\max} generated by Bevelhimer et al. (1985) predicts lower consumption across a majority of the temperature gradient than those of the PSM's (Clapp and Wahl 1996). We also found differences between the model parameters for the OHM and the BVM which were developed using fish from the same Ohio population. Although fish handling and experimental procedures

were similar between the two studies differences in parameters existed. Size of prey, size of study organisms, differences in condition, changes in broodstock through time or temperature increments at which rates were observed, could lead to differences in parameters. As a result the BVM consistently predicted slower growth than the PSM's and RWM.

Bioenergetics model errors could result from several components highlighted in recent literature reviews (Hansen et al. 1993; Chipps and Wahl 2008). Several of the parameters included in the muskellunge bioenergetics model were borrowed from other species which can affect model accuracy (Ney 1993; Wahl and Stein 1991). The weight dependent exponent b_1 is borrowed from northern pike (Diana 1982), and is used for the biomass-metabolism relationship despite being developed for consumption (Bevelhimer et al. 1985). Allometric growth rate could vary among populations within a species in the same manner as other physiological traits (Galarowicz and Wahl 2003) and should be further examined. Model parameters not related to consumption or metabolic rate were assumed not to vary among populations. However, a study of European salmon showed variation in digestion rates among populations related to latitude (Nicieza et al. 1994) suggesting that other model parameters (i.e. excretion, egestion, specific dynamic action, and activity) should be examined for intra-species differences that might improve bioenergetics modeling efforts.

Including laboratory derived, population-specific rates of metabolism and consumption into bioenergetics models can increase our understanding and accuracy of growth models of fishes (Wahl 1999; Munch and Conover 2002). Modeling additional sources of intra-species variation in activity rate and conversion efficiency as well as responses to resource limitation, competition, and predation risk will only further these efforts. We found that PSM's provided a

better fit to laboratory growth than models derived of a single population (BVM) and a species-level model (RWM). Simulations predicted variable growth that may be representative of thermal adaptation. Disconnects between growth differentiation of populations in simulations and observed growth differentiation in the field may be a result of phenotypic plasticity, differences in survival, or limited sample size. We would encourage further evaluations of the PSM's developed in this study and development of PSM's for other species in light of the indications of intra-species growth differences across temperature gradients derived from our simulations. Identifying physiological differences among populations that have the ability to influence growth, and further understanding factors driving these differences, will have implications for stocking and management programs.

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Tables

Table 2. Bioenergetics model parameters describing maximum consumption rate functions of the Bevelhimer et al. (1985) muskellunge model compared to the population-specific and range-wide and muskellunge models developed in this study. Data used to develop the parameters are from feeding trials at 5, 10, 15, 25, and 27.5°C (Clapp and Wahl 1996). Parameters a_1 , x , y , and z were calculated on a population-specific basis and the associated adjusted R^2 of the polynomial regression fit used to determine these parameters is shown.

Model	Parameters						Adjusted R^2	
	a_1	b_1	x	y	z	F		U
Bevelhimer et al. (1985)	0.0126	-0.18	0.0600	0.0075	-2.16×10^{-4}	0.13	0.07	-
Ohio	0.0128	-0.18	0.2425	-0.006	3.64×10^{-5}	0.13	0.07	0.90
New York	0.0219	-0.18	0.0450	0.0106	-3.45×10^{-4}	0.13	0.07	0.78
Minnesota	0.0243	-0.18	0.0539	0.0077	-2.53×10^{-4}	0.13	0.07	0.86
Kentucky	0.0137	-0.18	0.1766	-0.0014	-6.00×10^{-5}	0.13	0.07	0.88
Wisconsin	0.0837	-0.18	-0.1700	0.0227	-5.63×10^{-4}	0.13	0.07	0.87
Range-wide	0.0224	-0.18	0.0900	0.0051	-2.01×10^{-4}	0.13	0.07	0.84

Table 3. Bioenergetics model parameters describing maximum consumption rate functions of the Bevelhimer et al. (1985) muskellunge model compared to the population-specific and range-wide and muskellunge models developed in this study. Data used to develop the parameters are from feeding trials at 5, 10, 15, 25, and 27.5°C (Clapp and Wahl 1996). Parameters a_2 , and m were calculated on a population-specific basis and the associated adjusted R^2 of the linear regression fit used to determine these parameters is shown.

Model	Parameters			Adjusted R^2
	a_2	b_2	m	
Bevelhimer et al. (1985)	0.103	-0.18	0.055	-
Ohio	0.086	-0.18	0.058	0.63
New York	0.063	-0.18	0.080	0.63
Minnesota	0.086	-0.18	0.057	0.55
Kentucky	0.068	-0.18	0.065	0.68
Wisconsin	0.106	-0.18	0.053	0.59
Range-wide	0.080	-0.18	0.062	0.61

Table 4. Comparison of predicted growth for five populations of muskellunge from bioenergetics models following a simulated 300-day stocking event in Lake Mingo, Illinois. Temperature data was obtained from loggers placed at a depth of 1m in the lake. Ration level was P=0.45 for all model types. Predicted growth for each population is compared to values for each of the other populations and to those from the range-wide (RWM) and Bevelhimer et al. 1985 model (BVM).

Model	Initial	Final	Growth (g)	Growth difference (g)							Mean
	Biomass (g)	Biomass (g)		MN	WI	NY	OH	KY	RW	BV	Difference (g)
MNM	50	305	255	-	-279	20	-95	79	72	158	-8
WIM	50	584	534	279	-	299	184	358	351	437	318
NYM	50	285	235	-20	-299	-	-115	59	52	138	-31
OHM	50	400	350	95	-184	115	-	174	167	253	103
KYM	50	226	176	-79	-358	-59	-174	-	-7	79	-100
RWM	50	233	183	-72	-351	-52	-167	7	-	86	-92
BVM	50	147	97	-158	-437	-138	-253	-79	-86	-	-192

Table 5. Field data used to evaluate accuracy of muskellunge bioenergetics model predictions. The lakes were stocked in fall with four populations over four years and then sampled the following spring. Mean biomass with 95% confidence intervals were calculated at time of stocking and again during sampling and were used as the start and end points in the bioenergetics models.

Simulation	Lake	Stocking			Sampling		
		Population	Date	Biomass (g)	Date	N	Biomass (g)
1	Mingo	KY	October 30, 2002	155±8	March 26, 2003	11	163±21
2	Pierce	KY	September 19, 2004	76±5	April, 15, 2005	7	188±51
3	Mingo	MN	October 31, 2003	60±8	March 17, 2004	6	107±16
4	Mingo	MN	October 11, 2005	48±4	March 29, 2006	5	61±23
5	Pierce	MN	October 29, 2004	96±10	April 19, 2005	6	98±25
6	Pierce	NY	September 19, 2003	44±2	April 8, 2004	11	101±10
7	Mingo	NY	September 28, 2005	45±2	March 29, 2006	3	93±68
8	Mingo	OH	September 4, 2003	56±2	May 5, 2004	4	145±52
9	Mingo	OH	September 14, 2004	74±5	March 17, 2005	4	186±26

Table 6. Predictions of biomass from two types of muskellunge bioenergetics models, range-wide and population specific, and their accuracy relative to observed field data.

Ration levels for the simulations were set to 0.45.

Simulation	Observed Biomass	Range-wide					Population-specific				
		Predicted Biomass (g)	Error				Predicted Biomass (g)	Error			
			g	g (absolute)	%	% (absolute)		g	g (absolute)	%	% (absolute)
1	163±21	184	21	21	12.9	12.9	174	11	11	6.7	6.7
2	188±51	138	-50	50	-26.6	26.6	118	-70	70	-37.2	37.2
3	107±16	74	-33	33	-30.8	30.8	69	-38	38	-35.5	35.5
4	61±23	76	15	15	24.6	24.6	69	8	8	13.1	13.1
5	98±25	114	16	16	16.3	16.3	106	8	8	8.2	8.2
6	101±10	81	-20	20	-19.8	19.8	83	-18	18	-17.8	17.8
7	93±68	89	-4	4	-4.3	4.3	92	-1	1	-1.1	1.1
8	145±52	196	51	51	35.2	35.2	199	54	54	37.2	37.2
9	186±26	158	-28	28	-15.1	15.1	157	-29	29	-15.6	15.6
Mean			-3.6	26.4	-0.8	20.6		-8.3	26.3	-4.7	19.2

Figures

Figure 3. Maximum food consumption and metabolic rate (oxygen consumption) of muskellunge populations resulting from population-specific and range-wide equations across a range of temperatures. The model from Bevelhimer et al. (1985) was developed using an Ohio population but is currently used to model the muskellunge species. All modeled rates are for a 50g juvenile muskellunge at maximum ration ($P=1.0$).

Figure 4. Observed daily growth rates of muskellunge populations in the laboratory (black dots, error bars represent 95% confidence intervals) and predicted growth from bioenergetics models (dotted line) specific to Minnesota (MN), Wisconsin (WI), New York (NY), Ohio (OH), Kentucky (KY) populations. Growth rates predicted by the Bevelhimer et al. (1985) muskellunge bioenergetics model (solid line) and a range-wide bioenergetics model (dashed line) developed in this study with data pooled from multiple populations are also shown.

Figure 5. Simulated growth of five populations of muskellunge under a cool and warm variant of the Lake Mingo Illinois thermal regime during a 300 day simulation using population-specific bioenergetics models. A range-wide model consisting of pooled data from all 5 populations is also shown. Starting biomass was 50g and ration level was held constant at ($P=0.45$) for all simulations and all populations.

Figure 3.

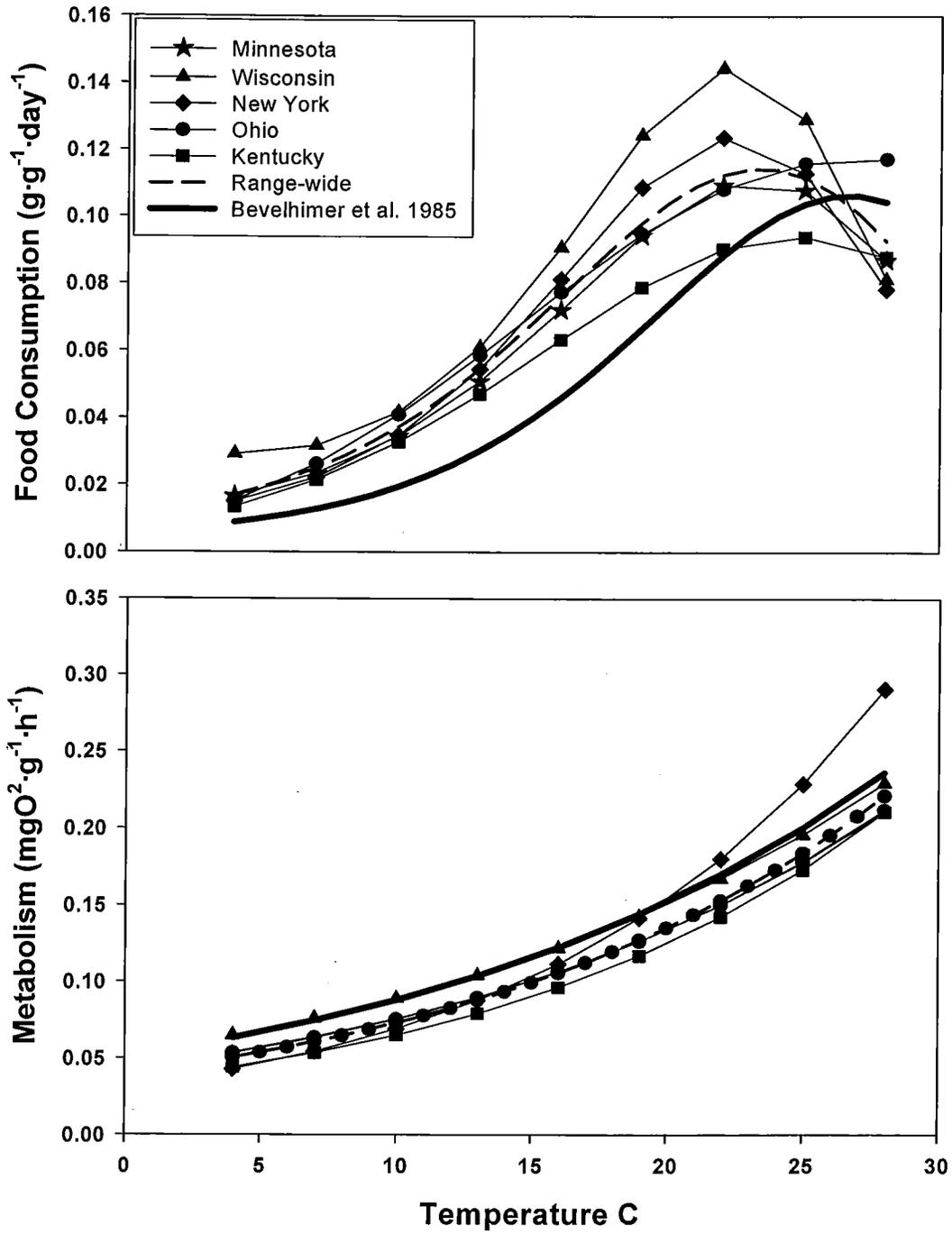


Figure 4.

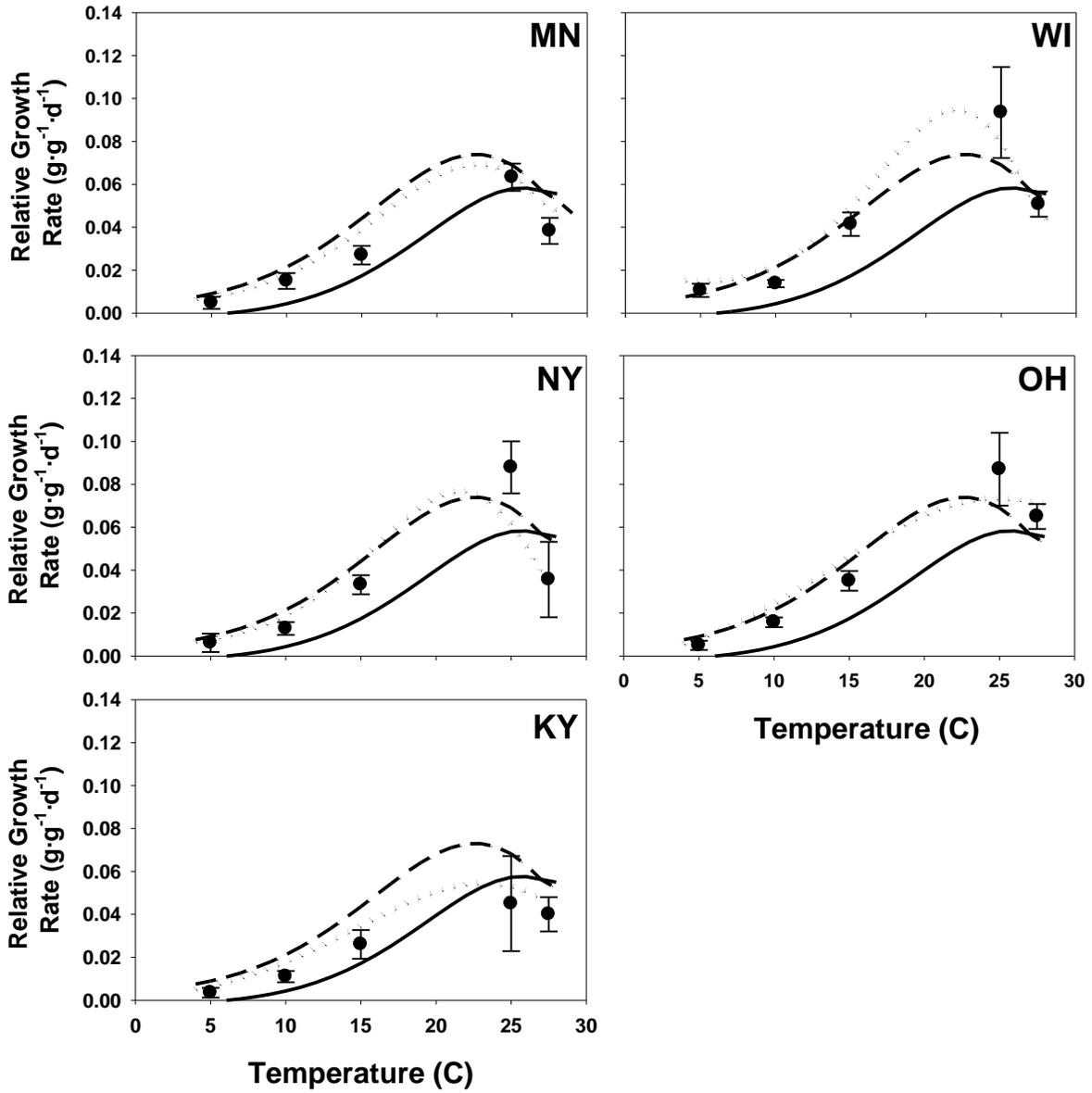
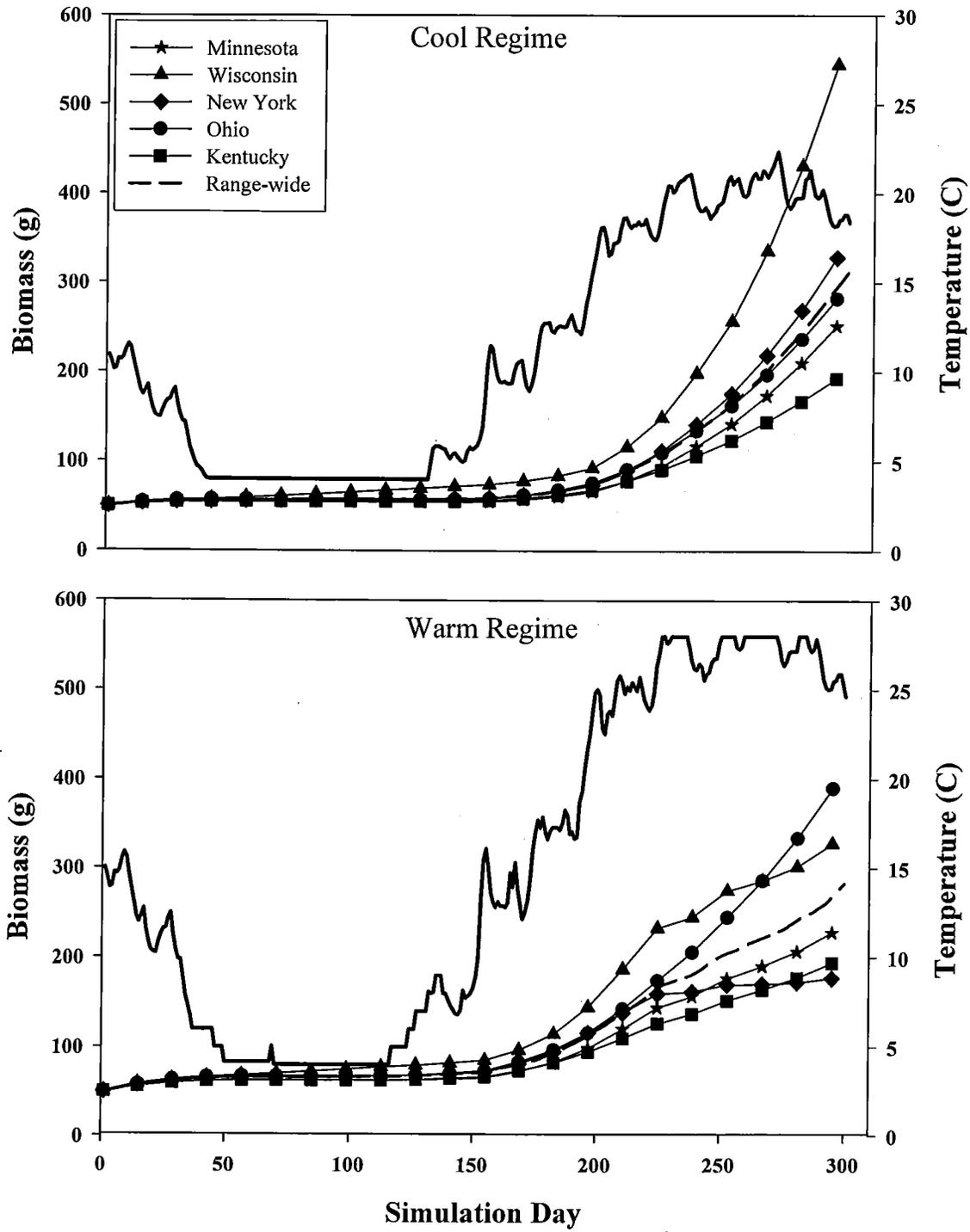


Figure 5.



Chapter 4: Dam Escapement of Muskellunge: Mechanisms and Importance

Abstract

Losses of fish over dams or spillways are highly variable, unpredictable, and a concern to fish managers. Muskellunge *Esox masquinongy* occur in low densities in many Midwestern reservoirs and dam escapement is frequently observed. Little is known regarding the factors influencing rates of muskellunge dam escapement or the proportion of reservoir populations that escape annually. We used a controlled laboratory experiment to examine how muskellunge interact with flow over a barrier at varying levels of turbidity, flow rate, habitat, and ambient light. We also employed an antenna capable of reading passive integrated transponder tags implanted in fish to monitor escapement over a dam. Both laboratory and field studies found muskellunge were more likely to escape during the day than at night. About 20% of a reservoir muskellunge population escaped within one year, with escapement occurring during late-spring but not during fall. Adults were more likely to escape than juveniles, and both sexes escaped at equal rates. Methods developed here can be used to provide useful information to managers and develop mitigation practices to limit escapement in situations where it is not desirable.

Introduction

Losses of fish over spillways are highly variable, unpredictable, and a concern to fish managers (Hergenrader and Bliss 1971; Axon and Whitehurst 1985; Wahl 1999; Paller et al. 2006). In coastal North America, both upstream and downstream dam passage of salmonids is universally considered to be positive (Connor et al. 2000), and is often accommodated (Raymond 1988; Champman et al. 1997). But in the Midwestern United States “dam escapement”, the permanent emigration of fish past the impounding barrier of a reservoir, detractors from the goal of establishing and maintaining sportfish populations in reservoirs (Louder 1958; Wahl 1999). Factors thought to contribute to dam escapement of sportfishes include movement related to spawning or foraging, spillway design, habitat preference, and amount of overflow (Louder 1958; Lewis et al. 1968; Paller et al. 2006). Previous research has highlighted the magnitude of the dam escapement problem with a large proportion largemouth bass stocked into a new impoundment (31%) escaping within a year and 10,000 fish estimated to have escaped from a 65 ha lake in Illinois (Louder 1958, Lewis 1968). Losses of fish over spillways have been shown to be species-specific, but vary between lakes (Lewis et al. 1968, Paller et al. 2006). Size-specific losses have also been identified with adults often more prone to escapement than juveniles (Lewis et al. 1968; Navarro 1993; Paller et al. 2006).

In some tailwaters high density fisheries can be created (Jacobs and Swink 1983). When sufficient outflow creates consistent riverine conditions large bodied fishes often thrive (Harrison and Hadley 1979) and escapement has been described as essentially an annual stocking program for these systems (Jacobs and Swink 1983; Trammell et al. 1993; Schultz et al. 2003). Although the potential exists for productive tailwater fisheries, the influx of unwanted and often nonnative

fish also carries a risk of negative effects on resident fish communities (Martinez et al. 1994; Spoelstra et al. 2008). Negative consequences for escapees can also be high as habitat, prey availability, and thermal conditions in the outflow of smaller impoundments are often not adequate to support large-bodied fish. In these scenarios losses due to escapement are costly when considering the resources invested into rearing and stocking sportfish (Szendrey and Wahl 1995).

Muskellunge are often stocked into reservoirs to create recreational fishing opportunities. Muskellunge escapement over spillways is frequently observed and reported anecdotally across the Midwestern United States (Storck and Newman 1992; Wahl 1999). Because these fish are stocked in low numbers, have limited potential for natural reproduction in many environments (Dombeck et al. 1984), and preventative barriers are often infeasible or ineffective at high flows (Plosila and White 1970), escapement could be one of the primary factors limiting development of abundant reservoir muskellunge populations (Louder 1958). However, at this time we do not have a clear understanding of the mechanisms and magnitude of muskellunge spillway escapement that would be useful in developing and implementing mitigation efforts and making management decisions. Important information on the conditions (season, flow, diel period, temperature, spillway design) associated with escapement and the traits of fish (sex, size, maturity) that are the most susceptible to escapement are needed. Estimates of the proportion of a population escaping annually from reservoirs will aid in making management recommendations and can be used to justify specific remedial actions. To address these issues we conducted laboratory and field evaluations to quantify conditions under which muskellunge escapement occurs and describe the traits and proportion of muskellunge escaping from a reservoir.

Materials and Methods

Laboratory Experiment

In the laboratory we examined a variety of environmental variables for their effect on muskellunge movement with flow over a simulated barrier. In a 4.6 x 1 x 0.5 meter fiberglass tank we created a spillway by blocking off one end with a notched (2cm x 18cm) board, simulating a dam (Figure 6). Pumps (1/4 hsp, 0.2 gallons/s) were used to move water from below the spillway back to the other end of the tank creating a closed loop. The upper meter of the tank was partitioned off with a net so that fish in the trial arena could not encounter the area pumps discharged water. Previous field studies have shown that spillway overflow height is an important determinant of escapement (Lewis et al. 1968; Paller et al. 2006). Resulting overflow heights were greater than the body depth (1.25-1.75cm) of a juvenile muskellunge and water velocity at the face of the simulated dam (6 cm/s) was comparable to velocities observed at the Lake Sam Dale spillway at similar levels of overflow (4 cm/s). Water depth was 0.34m in the trial arena when pumps were running, whereas the water level in the catch basin was 0.24m preventing fish from moving back into the test arena after escaping. The trial arena was 378L in volume and 1.98m long, an approximate distance of 15 body lengths for an average fish used in the trials. Three identical tanks were used in these experiments for replication and were housed indoors. Tanks were surrounded by opaque curtains to prevent fish from being disturbed during trials. A juvenile muskellunge (100-180 mm in length) randomly selected from one of four pools of fish (~200) was placed into the trial arena and allowed to acclimate for 1 hour under trial conditions with no flow over the barrier. After acclimation, the pumps were turned on to begin the 2 hour trial. Two light levels included day (fish acclimated in light, trial run in light) and

night (fish acclimated in dark, trial run in dark). Flow levels included “no flow” (2 cm height/ 0 m/s), “low flow” (1cm height/ 6 cm/s), and “high flow” (2cm height/ 10cm/s). The “no flow” treatment was included to test whether observed escapement was a response to flow or the result of random movements of fish throughout the tank. In these treatments the tank was filled to 2cm above dam height so that fish could cross the dam in the absence of flow. Escapement in “no flow” trials was determined through direct and video recorded observations since fish had the potential to cross back over the dam after escaping. Habitat treatments included either presence or absence of simulated vegetation (20cm strands of yellow nylon rope attached to a 60 x 60cm wire screen) placed in the center of the tank. Turbidity was altered by adding Bentonite clay and included clear (0-1 nephelometric turbidity units) and turbid (15-30 nephelometric turbidity units) levels. Following a trial, fish were temporarily separated from the trial pool of muskellunge to ensure that the same fish did not experience another trial within 48 hours. Water temperature and turbidity measurements were made at the beginning of each trial. All 24 treatment combinations were replicated 20 times and conducted in a full factorial randomized design in the summers of 2010 and 2011. The light level factor could not be randomized as fish were kept on a natural night and day light cycle (14D:10N) throughout trials. Data collected were binomial with fish either “escaping” or “not escaping” during the 2 hour trial. Logistic multiple regression analysis was used to identify the importance of each variable in determining escapement rate using PROC GENMOD (SAS 9.2). Turbidity, light, and habitat were coded with 1’s or 0’s based on presence or absence, flow rate (cm/s) and length of fish were included as continuous variables. Differences among the three levels of flow rate were determined by least squared means. Significance was determined at $P=0.05$.

Reservoir Experiment

Lake Sam Dale located in southern Illinois was selected for the field portion of this study based on a history of muskellunge escapement as determined through personal observations and conversations with local biologists and muskellunge angler groups. Lake Sam Dale is a 194 acre impoundment with a “drop-box” style spillway design (dimensions: 5.5 x 2.4m) receiving overflow from the lake on three sides with the one side abutting the shoreline. Overflowing water is routed under an earthen dam through two large concrete shoots before descending down a spillway outflow structure into a small creek below. The watershed that feeds Lake Sam Dale is 4,342 acres and is primarily cropland (Illinois Environmental Protection Agency Report). The lake has an established population of adult muskellunge and receives an annual fall stocking of approximately 200-300 fingerlings.

Prior to monitoring escapement, the muskellunge population in Lake Sam Dale was surveyed in the early spring using overnight fyke net sets and nighttime shoreline electrofishing. Muskellunge of all sizes were marked with an individually numbered PIT tag (half duplex, 23 mm, Texas Instruments) inserted into the dorsal musculature (Younk et al. 2011) and were given an additional caudal fin clip to estimate tag loss. Fish were tagged between February 21 and March 25, 2011, which was prior to the main spring precipitation and overflow events. Following tagging, all fish were immediately released into the middle portion of the lake. Any fish that was observed to be in poor condition was either not tagged or was removed from the analysis, but these instances were few. A Schnabel multiple mark-recapture population estimate was conducted based on 14 recapture events yielding 28 recaptured individuals (Schnabel 1938, Seber 1982). Length, weight, and sex of each fish were determined and ages were determined by

counting annuli on scales taken at the time of sampling. All PIT tagged fish were also given a caudal clip and late-spring electrofishing samples were used to assess tag retention.

A PIT tag antennae (Zydlewski et al. 2006) was used to collect tag information from fish as they passed over the spillway of the lake. We conducted preliminary trials prior to field experiments to ensure that the system was effective. A known number of tagged fish were placed into an outflow of an experimental pond facility and observations of antennae performance were made as fish passed downstream. Preliminary trials showed that tags could be captured even when passing at considerable velocity and tags were read by the antennae at a variety of orientations relative to the direction of flow.

The PIT antenna at Lake Sam Dale was installed directly on the spillway to receive and record the PIT tag numbers of escaping muskellunge. The antennae consisted of a single rectangular loop (Connolly 2008) of THHN 12 gauge wire spanning the 4.9m width of the spillway outflow structure with an approximate height of 0.61m. The antenna was suspended vertically 15cm above the concrete face of the spillway outflow structure to avoid interference from rebar and other imbedded metals (Connolly 2008). The antenna was positioned on the spillway outflow at a downstream point where tagged fish, once passing, could not physically return to the lake or reencounter the antenna. The antennae was attached to high strength low-stretch tech cord (Endura Braid, New England Ropes) and wrapped in electrical tape to reduce drag during high flow. The antennae wire was connected to a half-duplex interrogator which linked to a data logger (components from OregonRFID) and 12V power source. The PIT tag antenna scanned for tags 10 times per second and was activated whenever there was flow over the spillway. The coverage of the antennae was tested at installation and periodically throughout

the sample period by passing tags through by hand with no gaps in antenna coverage detected at any time. A temperature logger placed at 0.5m depth at mid-lake was used to obtain daily temperature values. Secchi depth (cm) was taken weekly at mid-lake during periods of high flow to characterize turbidity.

Peak periods of escapement and their associated environmental conditions including total daily precipitation (cm), water clarity (secchi depth), and water temperature were determined by examining daily tag detections by the PIT tag antennae. A Chi-square test was used to examine patterns in escapement between day and night using time stamps for tag detections recorded by the data logger. Sunrise and sunset times were used to classify daytime (half hour before sunrise) thru nighttime (half hour after sunset). We compared observed daytime escapement rates to those expected if escapement was random. Demographic characteristics including mean length and age were compared between the escaped and tagged population using a two-tailed t-test. A Chi-square test was used to examine differences in rates of escapement between adult males and females, and between juveniles (ages 1 and 2) and adults (ages 3+). Significance for all analysis was determined at $P=0.05$.

Results

Laboratory Experiment

Trial fish ranged from 100-180mm (mean 133, SD 20). We did not observe any relationships between length of trial fish and rate of escapement (Table 7, $P=0.93$). Of the main effects examined only flow rate and light level had significant effects on rates of escapement

(Table 7). Rate of escapement was nearly 3 times higher during the day (61%) as compared to night (21%, Figure 7). Some escapement was observed during the “no flow” treatment, where fish passed over the dam under their own power (Figure 7). However, trials conducted under “no flow” conditions had significantly lower rates of escapement (30%) than those where flow was present ($P=0.01$). There was no difference between escapement rates in trials with low (43%) and high flow rates (51%, $P=0.15$). Presence or absence of turbid water conditions and habitat did not have significant effects on rates of escapement (Figure 7, $P=0.49$ and 0.99 respectively).

Field Experiment

Fish were tagged ($N=118$) between February 21 and March 25, 2011. One tagged fish was discovered dead shortly after sampling and was removed from analysis. Muskellunge were recaptured ($N=28$) with fyke nets and electrofishing gear after receiving PIT tags and a caudal clip. Mark-recapture estimated 190 ± 6 muskellunge were established in the lake at the time sampling occurred. Fish recaptured by electrofishing in April showed high (100%) tag retention, similar to rates in the literature (Younk et al. 2010).

The PIT tag antenna and data logger were activated on February 22 when flow first passed over the spillway. In the spring, 24 individual tags (20.6% of the tagged population) were detected by the antennae between March 10 and May 3 (Figure 8). Most tagged fish were detected multiple times as they passed through the read range of the antennae. The length and age of escaping fish (811mm confidence interval 32mm, 3.3 ± 0.25 years) were significantly higher than those for the tagged population (744 ± 26 mm, 2.9 ± 0.17 years, Figure 9, t-test, $P=0.03$ and 0.04 respectively). None of the tagged age-1 fish ($N=16$, 400-450mm) from the fall stocking were observed escaping the lake (Figure 9), with disproportionately higher escapement of adults

compared to juvenile fish (Chi square 4.22, $P=0.04$). The sex ratio of escaping adult fish (11F:13M) was similar to the ratio of the tagged population as a whole (53F:49M, Chi-square 0.04, $P=>0.05$).

Precipitation events in the area typically resulted in an increase in overflow at the spillway within 24 hours. Duration of overflow was variable and presumably related to rainfall intensity, duration, ground saturation, and delayed runoff from previous events. From late February to mid-May there was an almost continuous baseline flow of water over the spillway (~5cm overflow height) between pulses from specific precipitation events. Two fish escaped on days in March that were not associated with a specific precipitation event (cumulative precipitation <0.1cm for 3 days prior, Figure 8). The majority of escapement (22 of 24 fish) followed two events in early and late April that had 2 and 8cm respective daily rainfall at their peak (Figure 8). Exact peak overflow heights were difficult to determine, but these precipitation events led to >13cm and >25cm of overflow height respectively. Periods of low water clarity typically followed precipitation events. Secchi depth readings during the two peak escapement events were 37cm (April 12) and 23cm (April 29), both lower than the average secchi depth for Lake Sam Dale in spring of 2011 (43cm). Most escapement occurred at water temperatures over 14°C (Figure 8). A majority of fish escaped during daylight hours (19 of 24), with peak escapement happening in the afternoon/evening (Figure 10). The observed numbers of escaping fish during daylight hours was significantly higher than that expected if escapement occurred randomly throughout the diel cycle (Chi square 5.12, $P=0.03$).

The water level of Lake Sam Dale dropped several inches below normal pool during the summer of 2011 due to evaporative processes which resulted in no summer days with spillway

overflow. Precipitation throughout the fall gradually raised the water level until late November when several days of overflow occurred. A single precipitation event of >1.25cm over 2 days resulted in an overflow height of >15cm. However, during this period no tagged muskellunge escaped (Figure 8).

Discussion

We found that in the field sexually mature muskellunge (>800mm, age 3+) were more likely to escape than juveniles and most escapement occurred in proximity to the spawning season for lower latitude populations (Parsons 1959) and not in the fall. We also showed that muskellunge were more likely to escape during the day than at night in both the laboratory and field. Others have suggested that escapement is an active behavior related to spawning or post-spawning behavior (Louder 1958), a hypothesis that appears to be supported by our observations of escaping muskellunge at Lake Sam Dale. It has also been hypothesized that stocked muskellunge with no homing instinct may move more randomly during the spawning season (Weeks and Hansen 2009), which in reservoirs may increase the chance of encountering spillways. During summer months muskellunge have a defined home range, but spawning activity often forces movement outside of home ranges and congregates the population (Miller and Menzel 1986; Crossman 1990). Muskellunge have also been shown to alter habitat selectivity in response to changes in flow, selecting shallower habitat as flow increases (Harrison and Hadley 1979; Brenden et al. 2006). These movement patterns may explain in part why dam escapement can occur in many impoundments.

We expected that if fish were being passively swept over dams in high flows during periods of low activity that escapement would be higher at night. Studies of radio tagged muskellunge have found activity occurs primarily during the day with peaks in the early morning and late evening hours (Reynolds and Casterlin 1979; Miller and Menzel 1986). In our laboratory experiment, escapement was three times higher during the day and 80% of escapement in the field experiment was shown during daylight hours with concentrations of escapement in the morning and evening. These results suggest that escapement is an active and non-random behavior.

Annual emigration of muskellunge has been suggested to be one of the primary factors structuring reservoir populations (Wahl 1999). We found escapement of adult fish to be over 20% in a single year. By applying this escapement rate to the population estimate we generated we estimate that between 35 and 40 muskellunge escaped lake Sam Dale in 2011. Cumulative over many years these levels would account for a high proportion of population mortality. Reductions in abundance in the lake resulting from dam escapement are obvious, but escapement of primarily large adult fish would also affect size structure. We predict smaller mean lengths and lower PSD values for muskellunge populations in reservoirs that have high annual reductions in adult standing stock from escapement. In contrast, escapement could be expected to annually re-stock downstream systems. In instances where thermal habitat and prey resources are adequate to support tailwater fisheries escapement may be considered beneficial. However, in many instances downstream systems may not have adequate thermal and oxygen levels to sustain large fish through summer months if fish cannot move to other habitats.

Estimates of annual escapement derived from the PIT tag antennae method were high (20%) but are likely conservative. Tag loss for muskellunge was low, but any undetected tag loss would lead to underestimation of escapement rates. Similarly, any rate of tag capture by the array of less than 100% would lead to underestimated escapement rates. Tag orientation is an important factor that determines the effectiveness of antennas in capturing tags (Aymes and Rives 2009). We conducted preliminary trials on a controlled outflow that showed a majority of fish in these environments orient themselves parallel to current. We inserted tags in the dorsal musculature so they would be oriented along the body axis of the study fish resulting in tags passing perpendicular to the axis of the antenna. However, any fish that did not pass by the antennae parallel to the direction of flow would be less likely to have its tag captured. Swimming speed of passing fish has also been shown to decrease tag readability (Aymes and Rives 2009). High flow rates can also compromise read efficiency of PIT tag antennas (Connolly et al. 2008), a finding that has implications for work on spillways where flow is flashy and often intense. Because outflow was typically extremely turbid, observations of fish orientation and passing speed could not be made and thus detection probability is unknown. Studies of tag reading efficiency with a similar PIT tag detection system and offered a modest correction factor to account for detection probabilities of between 70 and 100% for downstream passing fish (Connolly et al. 2008; Aymes and Rives 2009). As a result we believe that raw estimates of escapement from tag detection in this study are conservative in relation to actual numbers of escaping fish.

Possible solutions to dam escapement include barrier nets (Stober et al. 1983) or barrier bars (Powell and Spencer 1979; Schultz et al. 2003). However, physical barriers are costly and infeasible in many scenarios where they can become compromised by debris and extreme flows

(Plosila and White 1970). Sound, light, or bubble barriers have been shown to be effective at limiting movement of other species (Patrick et al. 1985), and should be evaluated as a method to limit dam escapement of muskellunge and other reservoir sportfish. PIT tag detection systems such as the one used in this study can be employed to conduct such evaluations in the field. The data generated by our study can be used to develop strategies to mitigate escapement. Stocking rates can be adjusted to compensate for escapement but effects on population abundance are unknown. On systems where water discharge is regulated by gates or other mechanisms, peak times for escapement (both seasonally and daily) can be identified and avoided for water discharge by resource managers (Jacobs and Swink 1983). We found 80% of muskellunge escapement to happen during daylight hours and similar patterns have been found for largemouth bass (Lewis 1968). In situations with flexibility in the timing of water discharges, preferential releases of water at night may limit escapement rates of muskellunge. Other species that are active at night may then have increased rates of escapement at these times (Lewis et al. 1968). Our laboratory study suggests that habitat manipulations may not be effective in limiting muskellunge interactions with spillways, but field evaluations of this approach may still have merit. Estimating dam escapement from reservoirs using a PIT tag detecting antennae can aid in understanding population dynamics of both reservoir and tailwater fish populations, determining magnitude of effects of escaped fish on downstream populations, coordinating fish rescues from tailwater areas, and evaluating mitigation structures and strategies. Expanding knowledge on fish escapement from reservoirs is necessary in light of the overall magnitude, persistence, and potential cost of outmigration.

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Tables

Table 7. Multiple logistic regression analysis examining the main-effects of flow, light, turbidity, fish length, and habitat on muskellunge escapement from a simulated spillway.

Variable	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	-1.936	0.8447	5.25	0.0219
Flow	17.4247	4.4999	14.99	<0.01
Light	1.8464	0.2193	70.89	<0.01
Turbidity	0.1445	0.2114	0.47	0.4942
Length	-0.0005	0.0057	0.01	0.9312
Habitat	-0.0008	0.2112	0	0.997

Figures

Figure 6. Aerial diagram of the experimental setup used to test the effects of light, flow rate, habitat, and turbidity on muskellunge interaction with flow over a spillway. Approximate tank dimensions are 4.6mL x 1mW x 0.5mD.

Figure 7. Rates of escapement of muskellunge from a simulated dam and spillway under varying levels of light (A), turbidity (B), flow rate (C), and habitat availability (D). Significant differences between levels were assessed using logistic multiple regression. Significance was determined at $P=0.05$ and significantly different statistical groupings are denoted with letters.

Figure 8. Daily precipitation (solid line) and water temperature (dotted line) in the spring and fall 2011 at Lake Sam Dale, Illinois (top panels). Daily number of fish escaping over the dam are shown as vertical bars (lower panel) Escapement was determined by tag detections on a PIT tag antennae covering the lower portion of the spillway.

Figure 9. Length histogram of the tagged and escaped portion of the muskellunge population in Lake Sam Dale, Illinois in 2011.

Figure 10. Ordinal timing of escapement for muskellunge leaving Lake Sam Dale, Illinois in the spring of 2011. Escapement timing was determined by first detection of PIT tags by an antenna covering the spillway below the dam.

Figure 6.

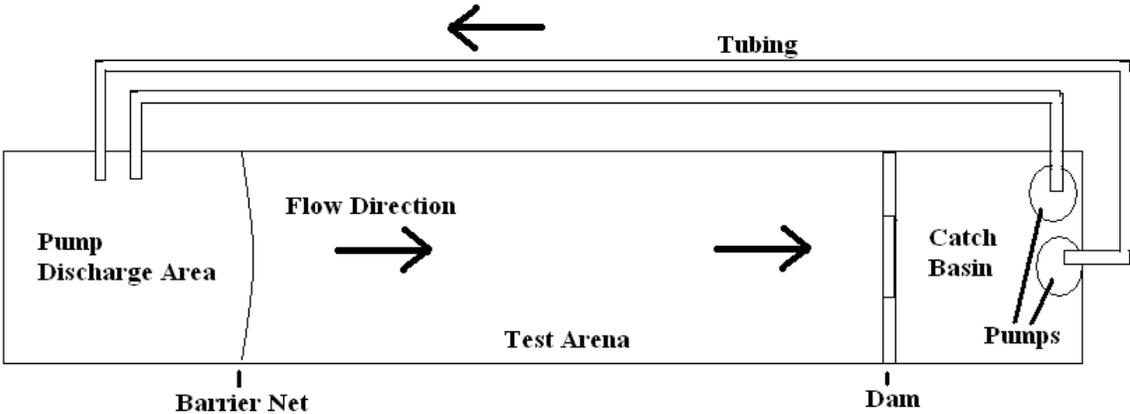


Figure 7.

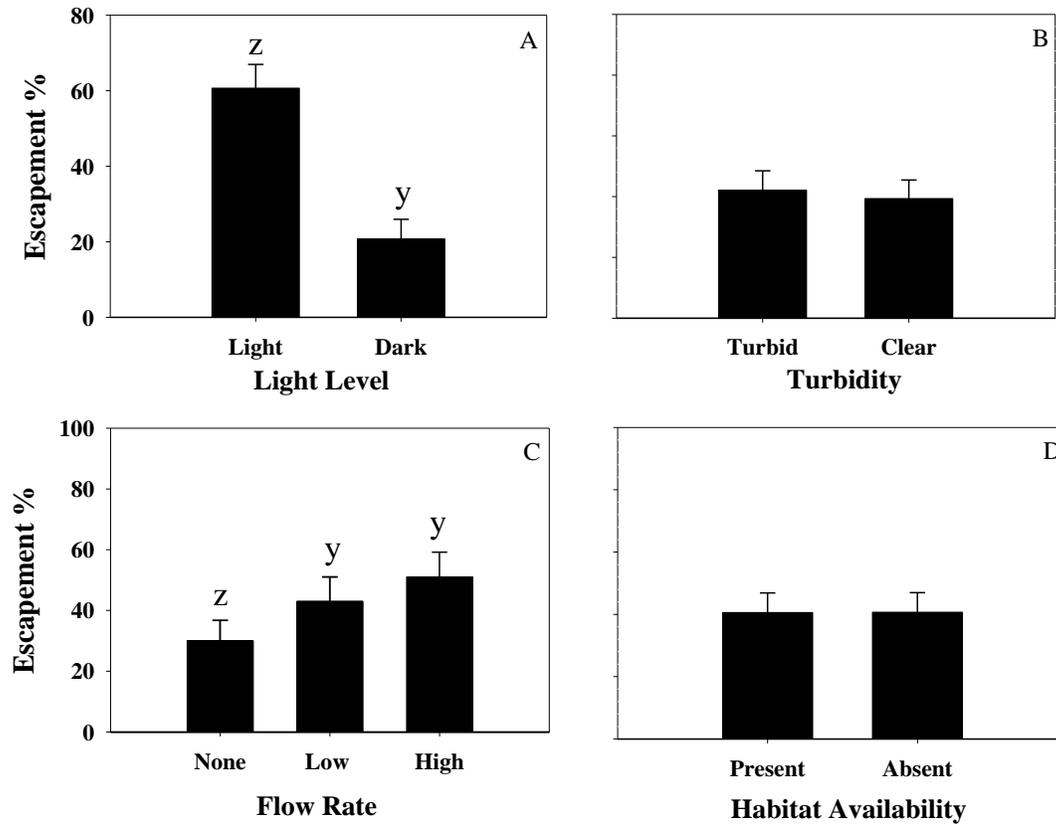


Figure 8.

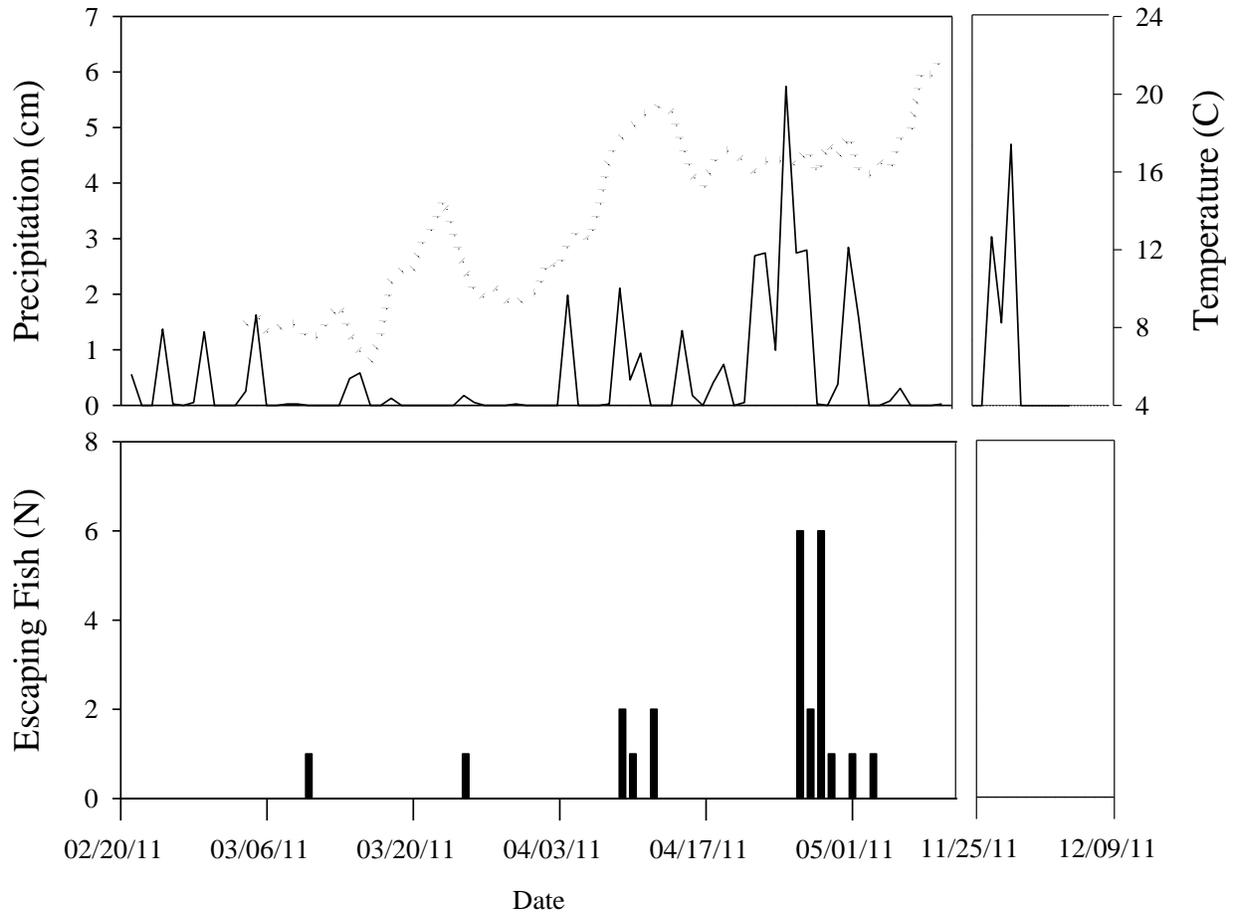


Figure 9.

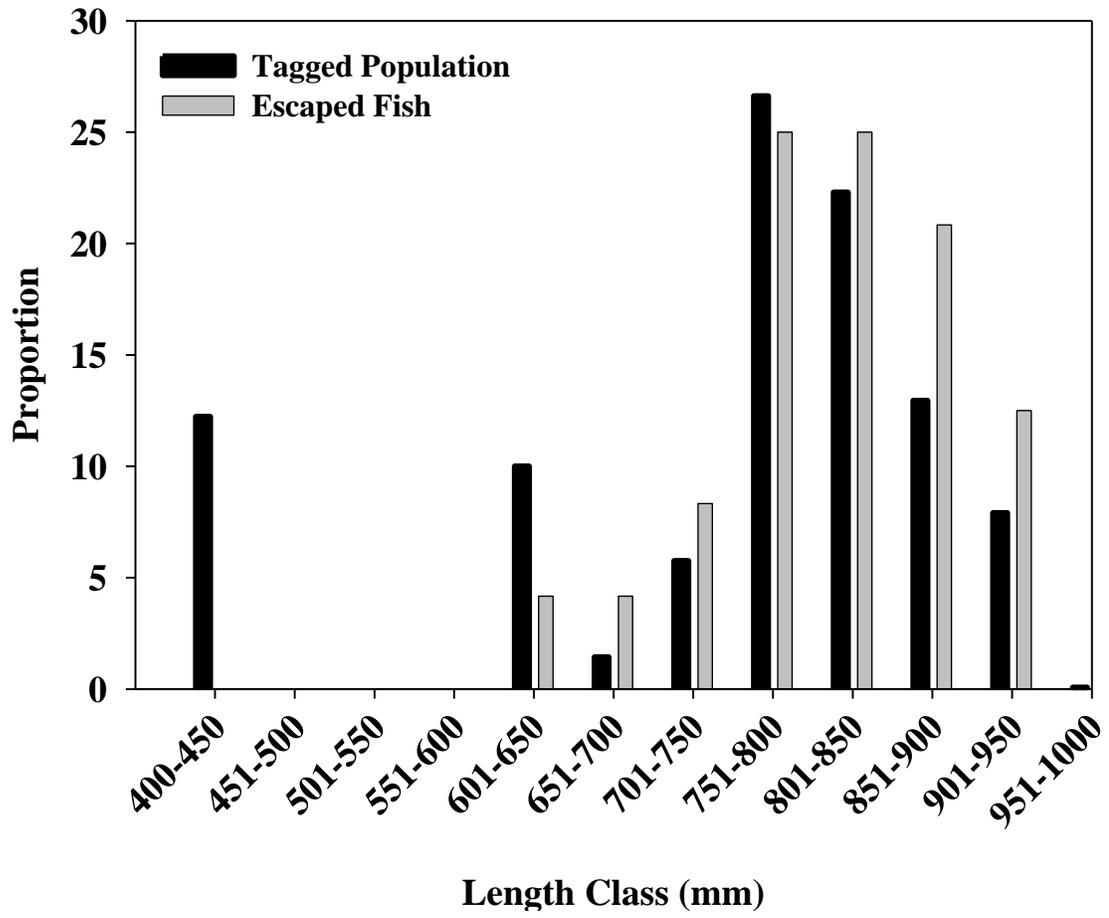
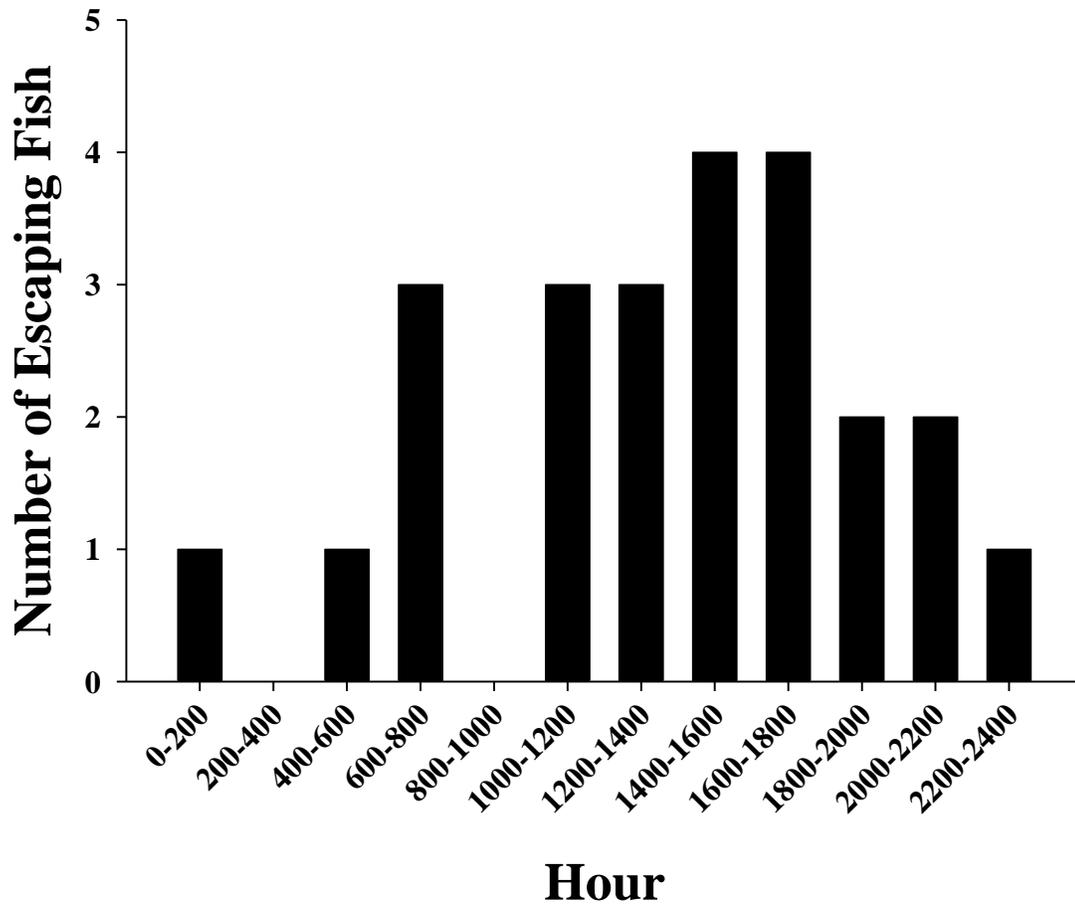


Figure 10.



Summary and Conclusions

I examined several factors thought to influence the short- and long-term growth and survival of muskellunge, with particular emphasis on conditions present in the lower Midwest. Heat related stress had been proposed as an explanation for intra-species survival patterns observed in other studies, wherein fish from high latitudes showed poor survival in lower Midwestern lakes that are warmer than lakes in their native range. Lethal chronic thermal maxima and several sub-lethal physiological stress indicators did not reveal any differences suggesting fish from high latitudes (Leech Lake, Minnesota) would not have decreased capacity to withstand bouts of adversely high water temperature than fish from low latitudes (Clearfork Lake, Ohio). From a management perspective, these results suggest that heat related stress does not explain different patterns of survival among these groups of muskellunge at temperatures commonly encountered in Illinois lakes.

Juvenile growth rate is an important determinant of muskellunge stocking success. Fast growth results reduced threat of predation, higher survival overwinter, and increased reproductive output at earlier ages. Transplanting populations with high growth rates for stocking in new waterbodies or as a supplement to existing populations is common. I developed population-specific bioenergetics models for muskellunge that can be used as a tool to evaluate potential stocking success based on growth rates. I also used these models to examine thermal adaptation of muskellunge across a latitudinal gradient and evaluate potential sources of error in bioenergetics modeling. Consumption equations were different among populations with high latitude populations (Minnesota, Wisconsin, New York) having higher consumption at lower temperatures than low latitude populations (Ohio, Kentucky) suggesting some degree of thermal

adaptation. Simulated growth rates under warm and cool thermal regimes also indicated adaptation was present with high latitude fish showing faster growth in the cool thermal regime and low latitude populations showing faster growth in the warm thermal regime. However, comparisons of model growth predictions to those in the field indicated that population-specific models incorporating thermal adaptation were no more accurate than a general species model. Evidence of thermal adaptation in the field may have been obscured by mortality or low sample size. Comparisons of population-specific models to the current muskellunge bioenergetics model (Bevelhimer et al. 1985) should be made with caution due to differences in parameter development methodology. Evidence of thermal adaptation from these models warrant further field evaluations. Evidence of thermal adaptation in muskellunge growth rates has a variety of management implications for selecting broodstock for both new and supplemental stockings.

Escapement of fish from a reservoir over the impounding barrier is an often cited source of fish loss. Escapement of muskellunge from Midwestern reservoirs is thought to be a major component of muskellunge stocking success, however there was previously little data of use to managers. We used a laboratory study to test in replicate the effect of variables including light, flow, turbidity, and habitat on muskellunge interactions with a simulated spillway. In the field we used a PIT tag antennae to capture information on muskellunge escaping from Lake Sam Dale, Illinois. Laboratory and field experiments both showed that photoperiod had an important effect on escapement as fish were more likely to escape during the day than at night. The PIT tag antennae system I employed identified 20.6% of the tagged population escaping from the reservoir. Examining the demographics of escaping fish in comparison to the population showed that adults were more likely to escape than juveniles. Escapement was focused around several precipitation events occurring in late April. The timing and demographics of muskellunge

suggest that escapement may be related to post-spawning behavior as fish disperse from spawning areas. Results of my study can aid in determining population dynamics of muskellunge populations in both reservoirs and tailwaters, be used to assess potential impacts of escaped fish on downstream systems, help coordinate fish rescues, and evaluate mitigation structures and strategies.