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Predicting the impact of a northern pike (*Esox lucius*) invasion on endangered June sucker (*Chasmistes liorus*) and sport fishes in Utah Lake, UT

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PREDICTING THE IMPACT OF A NORTHERN PIKE (*ESOX LUCIUS*) INVASION
ON ENDANGERED JUNE SUCKER (*CHASMISTES LIORUS*)

AND SPORT FISHES IN UTAH LAKE, UT

by

Jamie Reynolds

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2017

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ABSTRACT

Predicting the Impact of a Northern Pike (*Esox lucius*) Invasion on Endangered June Sucker (*Chasmistes liorus*) and Sport Fishes in Utah Lake, UT

by

Jamie Reynolds, Master of Science

Utah State University, 2017

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Invasive species introductions are associated with negative economic and environmental impacts, including reductions in native species populations. Successful invasive species populations often grow rapidly and a new food web equilibrium is established. Invasive, predatory northern pike (*Esox lucius*; hereafter pike) were detected in 2010 in Utah Lake, UT, a highly-degraded ecosystem home to the endemic, endangered June sucker (*Chasmistes liorus*). Here we test whether pike predation could hinder the restoration efforts of June sucker using the number of June sucker consumed by pike at various population densities as our metric. More specifically, we considered pike density at which the population could consume all June sucker stocked a critical threshold. Currently the number of naturally recruited June sucker is drastically lower than the number stocked. Thus, the metric we used to determine whether the pike population could hinder the June sucker restoration efforts is the number of pike that could consume the number of June sucker stocked. We combined pike growth and foraging observations with an energy-budget, bioenergetics consumption model to

quantify lake-wide pike predation on June sucker. We also used an age-structured density dependent population model to estimate the pike population growth trajectory under various mitigation scenarios. Of 125 pike, we found an average pike consumes 0.8-1.0% June sucker and 40% sport fish. According to our bioenergetics model simulations, a population of adult pike at a very high density (60 pike per hectare) has the potential to consume nearly 6 million age-0 June sucker per year, which is likely more June sucker consumed than exist in the environment. In addition, our model suggests that an adult pike density greater than 1.5 pike per hectare has the potential to consume all June sucker stocked annually. Our age-structured population model suggests the pike population will reach equilibrium around 2026 at between 8 and 12 adult pike per hectare with the potential to consume between 0.8 and 1.2 million age-0 June sucker per year, respectively. The growing pike population could hamper restoration efforts and threaten endangered June sucker, a population with a mere 2,000 adults, in jeopardy of extinction. Our findings not only inform pike management efforts, but also highlight the importance of allocating resources toward habitat restoration to provide refuge for juvenile June sucker from predation, preventing the spread of aquatic invasive species, and the need for aquatic invasive species education.

PUBLIC ABSTRACT

Predicting the Impact of a Northern Pike (*Esox lucius*) Invasion on Endangered June
Sucker (*Chasmistes liorus*) and Sport Fishes in Utah Lake, UT

Jamie Reynolds

Invasive species introductions are associated with negative economic and environmental impacts, including reductions in native species populations. Successful invasive species populations often grow rapidly and a new food web structure is established. The ability of invasive species to outcompete and prey upon native species are two characteristics that make them a leading cause of fish extinctions in North America.

Northern pike (*Esox lucius*; hereafter pike) are voracious ambush top predators native to the upper Midwest and Mid-Atlantic regions of the lower 48 United States, Alaska, and southern Canada. Pike have been spreading across the Intermountain West and Pacific Northwest and were detected in 2010 in Utah Lake, UT, a highly degraded ecosystem home to the endemic, endangered June sucker (*Chasmistes liorus*). June suckers are an important indicator species for the lake, meaning they can signal a change in the biological or physical condition of the ecosystem and serve as a measurement of ecosystem health. Captive breeding programs, stocking programs, and habitat restoration projects are major components of the estimated \$50 million-dollar plan to restore the June sucker population. The recent introduction of invasive pike may not only threaten the success of June sucker restoration, but also their downlisting from endangered to threatened.

We tested whether pike predation could hinder the restoration efforts of June sucker., The metric we used to determine whether the pike population could hinder the June sucker restoration efforts is the number of pike that could consume the number of June sucker stocked each year. We combined pike growth and foraging observations with an energy-budget, bioenergetics consumption model to quantify lake-wide pike predation on June sucker. We also used an age-structured density dependent population model to estimate the pike population growth trajectory under various removal scenarios. Of 125 pike we found an average pike consumes 0.8-1.0% June sucker and 40% sport fish. According to our bioenergetics model simulations, a population of adult pike at a very high density (60 pike per hectare) has the potential to consume nearly 6 million age-0 June sucker per year. Our age-structured population model suggests the pike population will stabilize around 2026 at between 8 and 12 adult pike per hectare with the potential to consume between 0.8 and 1.2 million age-0 June sucker per year, respectively. The growing pike population could hamper restoration efforts and threaten endangered June sucker, a population with a mere 2,000 adults, in jeopardy of extinction. Our findings not only inform pike management efforts, but also highlight the importance of preventing the spread of aquatic invasive species and the need for aquatic invasive species education.

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CHAPTER I

INTRODUCTION

Invasive species introductions are associated with negative economic and environmental effects and are a major cause of declines in native species worldwide (Elton 1958; Vitousek 1996; Sala et al. 2000), particularly in aquatic ecosystems (Ricciardi 1999; Pimentel et al. 2005). The ability of invasive species to outcompete and prey upon native species (Cucherousset & Olden 2011) are two characteristics that make them a leading cause of fish extinctions in North America (Miller et al. 1989; Ricciardi 1998; Clavero & García-Berthou 2005). Indeed, the native species abundance is negatively related to invasive species abundance (e.g., McHugh & Budy 2005; Pine et al. 2007). Furthermore, invasive species impacts on native species are often exacerbated in anthropogenically disturbed ecosystems (Byers 2002).

An aquatic invasive apex predator has the ability to change the abundance of prey species multiple trophic levels lower in a cascading effect (Charlebois & Lamberti 1996; Townsend 1996; Carpenter et al. 1985). As such, the removal of the invasive apex predator can result in the recovery of the native fish community (Lepak et al. 2006). However, once an invasive species population establishes, mitigation or eradication can be difficult, if not impossible (Knapp & Matthews 1998; Vander Zanden et al. 2010; Gaeta et al. 2012), which is problematic in the face of endangered species conservation. Utah Lake, UT (Figure 1) is an example of a degraded, turbid, anthropogenically-disturbed ecosystem with a newly introduced apex predator population and a fragile native fish population.

Northern pike (*Esox lucius*) are voracious ambush apex predators that will strike any species of fish (i.e., they cannot be conditioned to consume certain species; Beyerle & Williams 1968; Mauck & Coble 1971). Though native to the upper Midwest and Mid-Atlantic regions of the lower 48 United States (Page & Burr 1991), Alaska, and southern Canada, invasive northern pike have been spreading across the Intermountain West and Pacific Northwest (McMahon & Bennett 1996; Vineyard 2001). Anglers reported a northern pike invasion in Utah Lake, UT in 2010, which was confirmed by the Utah Division of Wildlife Resources (UDWR) in 2011. Observed natural reproduction in 2014 suggests the population is established and growing. The presence of northern pike in Utah Lake is particularly alarming due to their potential to prey upon the lake's endemic and endangered June sucker (*Chasmistes liorus*).

June sucker is one of four lake sucker species (*Chasmistes* spp.) that historically occurred in Utah, Nevada, Oregon, and California. Two of these species are endangered and one is presumed extinct (Miller & Smith 1981; Nature Serve 2014). Distinguishing characteristics of these fishes include a terminal mouth and branched gill rakers that allow them to filter feed zooplankton from the water column (Crowl et al. 1995; Scoppettone & Vineyard 1991). According to early accounts of settlers in Utah Valley, the June sucker population in Utah Lake was abundant during the mid-1800s and they were used for food and fertilizer (Heckmann et al. 1981). However, the population decreased drastically over the next century due to dewatering of spawning tributaries and commercial fishing (USFWS 1999). The June sucker gill net catch rate dropped from 0.68 suckers per hour in the mid-1950s (UDWR, unpublished data) to 0.01 suckers per hour in 1970 (White & Dabb 1970). In 1986 the U.S. Fish and Wildlife Service (USFWS)

listed the June sucker as an endangered species due to decreased population sizes as a result of the synergistic effects of habitat degradation (e.g., loss of submerged vegetation and thus fewer refuge areas for juveniles); increased eutrophic conditions (e.g., low concentration of dissolved oxygen, increased phosphorus concentrations); alteration of hydrologic flows in the Provo River, a main tributary June sucker use for spawning; and introductions of non-native species such as walleye (*Sander vitreus*), white bass (*Morone chrysops*), and common carp (*Cyprinus carpio*; USFWS 1999). June suckers are an important indicator species for the lake, meaning they can signal a change in the biological or physical condition of the ecosystem and serve as a measurement of ecosystem health. Thus, restoring the water quality and degraded habitat are inherent objectives in the June sucker restoration process (JSRIP 2015). Captive breeding programs, stocking programs, and habitat restoration projects are major components of the estimated \$50 million-dollar plan to restore the June sucker population (USFWS 1999). The USFWS is currently considering downlisting the June sucker from endangered to threatened due to protected Provo River flows and spawning and rearing habitat restorations.. However, the recent introduction of invasive northern pike may threaten downlisting.

Andersen et al. (2008) found that northern pike in turbid systems have a higher degree of behavioral variation than northern pike in clear water. For instance, northern pike in turbid water often increase their activity level and increase their residence time in the pelagic zones of lakes. Utah Lake is not only turbid, but also void of submerged vegetation for most of the year. Thus, northern pike in Utah Lake may behave differently and feed in the water column, increasing the probability of encounters with June sucker,

because the lack of littoral vegetation in the lake does not facilitate ambush predatory behavior. The overarching objectives of our research are to test whether northern pike predation could potentially hinder the June sucker restoration efforts and to investigate potential northern pike mitigation strategies. Successful restoration of the June sucker population would mean the number of naturally recruited June sucker in the system is greater than or equal to the number stocked. The number of naturally recruited June sucker in the lake is currently much lower than the number stocked each year. Thus, the metric we used to determine whether the northern pike population could hinder the June sucker restoration efforts is the number of northern pike necessary to consume the number of June sucker stocked.

In chapter 1, we quantified the current (2015-2016) predatory impact of invasive northern pike on endangered June sucker to test whether the presence of northern pike could hinder June sucker restoration efforts. We will use northern pike growth and foraging observations specific to Utah Lake to build an empirically-based, energy-budget consumption model to quantify the number of June sucker consumed by the northern pike population. We will then investigate management strategies of invasive northern pike to prevent the endangered June sucker population from declining.

In chapter 2, we used a density-dependent, age-structured model to predict the growth trajectory of, and identify potential mitigation options for, the Utah Lake northern pike population. This approach will allow us to understand how the northern pike population is growing and predict the effectiveness of management strategies to ensure the persistence of the June sucker population.

CHAPTER II

ESTIMATING INVASIVE NORTHERN PIKE (*ESOX LUCIUS*) CONSUMPTION OF ENDANGERED JUNE SUCKER (*CHASMISTES LIORUS*) AND SPORT FISHES IN UTAH LAKE, UT USING BIOENERGETICS MODELS

Introduction

Invasive species are a leading cause of the loss of biodiversity (Elton 1958; Sala et al. 2000) and are economically costly (Leung et al. 2002; Pimentel et al. 2005), particularly in aquatic systems (Ricciardi 1999; Pimentel et al. 2005). The ability of aquatic invasive species to outcompete and prey upon native species (Cucherousset and Olden 2011) contribute to the classification as the second leading cause of fish extinctions in North America (Miller et al. 1989; Ricciardi 1998; Clavero & García-Berthou 2005), behind only habitat loss. The addition of an apex invasive predator, in particular, can alter the food web structure of ecosystems (Carpenter et al. 1985; Carey & Wahl 2010) and can have detrimental effects on the native community (Mooney & Cleland 2001).

Preventing the initial spread of aquatic invasive species, particularly apex predators, is key, but applying mitigation strategies if they invade and establish is the best option (Vander Zanden & Olden 2008). However, once an invasive is established, quantifying the impacts of an apex predator is critical for both conservation and management. Combinations of empirical and theoretical approaches are commonly used to predict the predatory impact of apex invasives on native species (Paukert et al. 2003; Muhlfeld et al. 2008, Walrath et al. 2015; Scheibel et al. 2016).

Northern pike are voracious apex predators native to the upper Midwest of the lower 48 United States, Alaska, and southern Canada (Page & Burr 1991). As ambush predators, northern pike will consume any species of fish (Beyerle & Williams 1968; Mauck and Coble 1971). This species is invasive across the Intermountain West and Pacific Northwest (McMahon & Bennett 1996; Vineyard 2001) and were first reported by anglers in Utah Lake, UT in 2010 with natural reproduction detected by resource managers in 2014. The invasion of an apex predator with an affinity for sucker species (Diana 1979) is of particular concern in Utah Lake because only a small population of endangered June sucker, an important indicator species (i.e., they can signal a change in the biological or physical condition of the ecosystem and serve as a measurement of ecosystem health; JSRIP 2015), still exist.

June sucker were abundant in Utah Lake during the mid-1800s and were harvested for food and fertilizer (Heckmann et al. 1981). However, the population decreased remarkably over the next century due to the dewatering of spawning tributaries and commercial fishery harvest (USFWS 1999). By 1970, the June sucker gill net catch rate dropped from 0.68 suckers per hour in 1955 (UDWR, unpublished data) to 0.01 suckers per hour (White & Dabb 1970). In 1986 the U.S. Fish and Wildlife Service (USFWS) listed the June sucker as an endangered species due to decreased population sizes as a result of the synergistic effects of habitat degradation (e.g., loss of submerged vegetation and thus fewer refuge areas for juveniles); increased eutrophic conditions (e.g., low concentration of dissolved oxygen, increased phosphorus concentrations); alteration of hydrologic flows in the Provo River, a main tributary June sucker use for spawning; and non-native species introductions (USFWS 1999). Captive breeding

programs, stocking programs, and habitat restoration projects are major components of the estimated \$50 million-dollar plan to restore the June sucker population (USFWS 1999). The USFWS is currently considering downlisting the June sucker from endangered to threatened due to protected Provo River flows and spawning and rearing habitat restorations. Thus, the addition of northern pike to the Utah Lake ecosystem is particularly concerning for the June sucker population (Figure 2).

We are interested in quantifying the potential predatory effects of invasive northern pike on endangered June sucker and the sport fish community in Utah Lake. We used energy-based consumption models, known as bioenergetic models (Hanson et al. 1997; Kitchell et al. 1997) to quantify the potential predatory impact of northern pike on endangered June sucker in Utah Lake. Empirical diet analysis allowed us to understand the proportion and biomass of different prey items consumed by northern pike in Utah Lake, UT. We created a logistic mixed-effects model to estimate the probability of fish consumption as northern pike size varies. We used these findings, in conjunction with northern pike demographic information, lake temperature data, and physiological parameters from literature, to simulate consumption of June sucker by northern pike using a Monte Carlo bioenergetics framework in which we modeled individual. Finally, management of this invasive apex predator is critical to prevent the endangered June sucker population from declining.

Methods

Study site

Utah Lake is located in north-central Utah (PSOMAS and SWCA 2007) and is 38.6 miles long and 20.9 miles wide, spanning >38,445 hectares. A remnant of ancient Lake Bonneville, the lake was once abundant in submerged vegetation and supported a number of cool-water fish species, including Bonneville cutthroat trout (*Oncorhynchus clarki utah*) and mountain whitefish (*Prosopium williamsoni*; Janetski 1990). Sediment build up, pollutants and nutrients, and the increasing need of water demand associated with human development in the region have degraded this system. The ecosystem is now shallow (mean depth of 3 m), eutrophic, generally void of submerged vegetation, and highly turbid (Gaeta et al., unpublished data). Utah Lake was historically home to 13 native fishes (JSRIP 2015). The Utah chub (*Gila atraria*), the Utah sucker (*Catostomus ardens*), and the endemic June sucker (*Chasmistes liorus*) are the only three remaining native species among a number of non-native species, including common carp, channel catfish (*Ictalurus punctatus*), black bullhead (*Ameiurus melas*), white bass, black crappie (*Pomoxis nigromaculatus*), bluegill sunfish (*Lepomis macrochirus*), walleye, largemouth bass (*Micropterus salmoides*), and yellow perch (*Perca flavescens*).

Fish collection and laboratory analyses

The Utah Division of Wildlife Resources (UDWR), anglers, and Loy Fisheries (commercial common carp fishermen) donated northern pike to the Gaeta Lake Ecology Laboratory in 2015 and 2016. Northern pike were collected at ten locations on or near (e.g., Hobble Creek) Utah Lake between 2012 and 2016 by the UDWR using fyke nets, trammel nets, and seines; by anglers donating northern pike in conjunction with a

mandatory harvest regulation; and by Loy Fisheries using commercial seines during common carp removal efforts. Specimens were frozen within 3-5 hours of collection. Once obtained, we weighed and lengthed each individual, extracted calcified hard structures (e.g., cleithra, scales, spines, and otoliths) for age and growth information, and extracted stomachs for diet analysis, which were stored in 95% ethanol.

Diet items were identified to the lowest possible taxonomic unit using differentiating physical characteristics. We confirmed or refuted the identity of a subset of highly digested prey taxa, including all suspected June sucker, via Sanger genetic sequencing. In Sanger sequencing, a polymerase chain reaction (PCR) is used to amplify the sample, dideoxynucleotides are used to terminate the chain after the DNA is primed, and gel electrophoresis is used to analyze the resulting fragments. We categorized the diet items a general macroinvertebrate category or one often fish taxa after genetic analysis: black crappie, bluegill sunfish, common carp, fathead minnow (*Pimephales promelas*), green sunfish (*Lepomis cyanellus*), June sucker, mottled sculpin (*Cottus bairdii*), northern pike, white bass, and unidentifiable fish. Genetic analysis allowed us to confidently identify highly degraded diet items. Utah sucker and June sucker are genetically indistinguishable, thus we conservatively considered any sucker detected by genetic analysis as June sucker. We weighed diet items using a wet weight to the nearest 0.001 g. We calculated the percentage of diet of different taxa by wet weight with the following equation:

$$(1) \quad \frac{1}{P} \sum_{j=1}^P \left(\frac{W_{ij}}{\sum_{i=1}^Q N_{ij}} \right)$$

where, P is the number of fish with food in their stomachs, w is wet weight, i is the prey taxa, j is the fish (northern pike), N is the number in food category i , and Q is the number of food types (Chipps & Garvey 2007).

We used the growth information (i.e., how much weight a northern pike gained during each year of its life as an estimate of annual growth) as inputs for bioenergetics modeling. We used otoliths and cleithra to obtain growth information for each northern pike. Otoliths, the inner ear stones of fishes, and cleithra, the shoulder bone, are calcified structures that accrete layers on a regular interval. The layers stack very close to one another and create rings, known as annuli, during periods of slow growth, such as winter, in temperate regions (e.g., Quist et al. 2012). We used cleithra to confirm the age estimates derived from otoliths. We used the annuli to extract growth information for each individual fish by calculating the length between the origin, or center, of the otolith, and each annulus, and back-calculating the length at each age using the total radius of the otolith and the fish's length at capture (Devries & Frie 1996). We then created a length-at-age model that describes the relationship between the radii length (i.e., distance between the origin of the otolith and annuli) to northern pike length, which was used to back-calculate length-at-age for an individual (Devries & Frie 1996). We built the following length-weight model for Utah Lake northern pike (Figure 3; Anderson & Neumann 1996) to convert the back-calculated length-at-age into a weight-at-age:

$$(2) \quad W = e^{-12.597 + 3.103 \cdot \ln(L)}$$

where W is weight and L is length.

Bioenergetics model

Bioenergetics is a simple energy budget equation (Hanson et al. 1997; Kitchell et al. 1997). The energy consumed by a fish is allocated toward different physiological processes necessary for life (e.g., respiration, metabolism, excretion of wastes), and any energy left over is allocated toward growth, represented in the following equation:

$$(3) \quad C = (R + A + S) + (F + U) + (\Delta B + G)$$

where, C is the amount consumed; R is respiration; A is active metabolism; S is specific dynamic action, such as the energetic costs of digestion; F and U represent egestion and excretion, respectively; ΔB is the change in biomass (growth); and G is gonadal growth (Hanson et al. 1997; Kitchell et al. 1997).

We used the Wisconsin Fish Bioenergetics 3.0 (Hanson et al. 1997) modified to run in R (version 3.3.1; R Core Team 2016) to estimate northern pike consumption in Utah Lake. Bioenergetics model inputs include physiological parameters, growth observations, diet proportions, and temperature across the year (Figure 4). Fixed parameters for the model include respiration, egestion rates, excretion rates, and prey energy densities (Diana 1983; Bevelheimer et al. 1985; Hanson 1997). We used average daily Utah Lake temperature data gathered by the Lake Ecology Laboratory (Gaeta, unpublished data) from April to October 2014 for initial calibration. We averaged temperatures between 2014 and 2015 for the final model run. We assumed the temperature was low and constant. We interpolated between observations.

We used a Monte Carlo modeling approach in which we ran bioenergetics models for individuals in a population of 10,000 northern pike. Each individual in this simulated population was randomly selected from a kernel density distribution fit to a weight-frequency histogram of the 125 northern pike captured in Utah Lake between 2012 and 2016. We chose to select individuals from a kernel density distribution because our observed values may not capture reality due to gear type bias during capture and low sample size. The weight at which an individual was selected, or the draw weight, served as a start weight, or weight at the beginning of a one-year period. We derived end weights, or the weight gained in the one-year period, by applying the start weights to a power function in a weight-at-age model to simulate growth over the course of one year. The start and end weights then served as the growth information for each individual in the bioenergetics model (Figure 5).

We converted the model output, total grams of food consumed per northern pike per year, into number of June sucker of different ages consumed per year. We multiplied the total grams of food consumed by northern pike by the estimated proportion of June sucker in the northern pike diet to obtain the number of June sucker consumed per northern pike per year. We then used June sucker length-at-age information (Belk 1998) and 2015 UDWR sampling data to determine the average weight of an age-0, yearling, age-2, and adult June sucker which we used to calculate the number of age-0, yearling, age-2, and adult June sucker consumed per northern pike year. We calculated northern pike density by dividing the number of northern pike by the average size of Utah Lake, 38,445 hectares.

Mixed effects logistic model

We created a logistic mixed-effects model to estimate the proportion of fish in the diet across northern pike sizes and better inform the estimated proportion of fish and proportion of macroinvertebrates consumed by northern pike for the bioenergetics model. The fish categories were combined to create a total fish consumed category for the purposes of running the logistic mixed effects model. The proportion of fish and the proportion of macroinvertebrates were calculated by dividing the total wet weight of fish and the total wet weight of macroinvertebrates, respectively, by the total wet weight of the diet.

Of the 125 northern pike diets, 53 were empty and excluded from the analysis. Twelve of the remaining 72 diets did not have a capture date (i.e., day of year) associated with them and were also excluded for the model run with potential to add them back into the model if day of year is not a significant variable, according to the model output. Each northern pike observation is nested within a year, capture location, and a gear type (Figure 6). We also discarded eight of the remaining 60 observations where the proportion of fish in a northern pike diet was between 0 and 1, because the model required a binary data structure, leaving the total sample size for the model as 52. The northern pike length and day of year were z-scored to allow for model convergence (Zurr et al. 2009).

We used a hypothesis-driven approach for selecting the logistic mixed effects model, because the data structure provides a very narrow window from which we can select potential covariates and random effects. *A priori* we decided length is the main predictor of the proportion of fish in a northern pike diet. We were also interested in

testing whether day of year influences the relationship between proportion of fish in a northern pike diet and northern pike length based on previous research (Gaeta, unpublished data). We chose to exclude capture location from the analysis because gear type and capture location are related, thus the random effect structure was intercept-only for both year and gear type.

We used R Cran (version 3.3.1; R Core Team 2016) and the ‘arm’ (version 1.9-1; Gelman & Su 2016), ‘Matrix’ (version 1.2-6; Bates & Maechler 2016), and ‘lme4’ (version 1.1-12; Bates et al. 2015) packages to test whether seasonality influenced the relationship between the proportion of fish in northern pike diets and northern pike length. The null model (Equation 4) predicts the proportion of fish in a northern pike diet as a function of 1 with the random effects of year and gear type:

$$(4) \quad \Pr(y_i = 1) = \text{logit}^{-1}(1)$$

where y_i is the proportion of fish in a northern pike diet. Thus, the null model predicts that the proportion of fish in northern pike diets is constant as northern pike length changes and does not take into account changes in season. Our hypothesis (Equation 5) predicts the proportion of fish in a northern pike diet as a function of length plus day of year with the random effects of year and gear type (Zurr et al. 2009):

$$(5) \quad \begin{aligned} \Pr(y_i = 1) &= \text{logit}^{-1}(\beta_{0j[i], k[i]} + \beta_1 x_1 + \beta_2 x_2) \\ \beta_{0j[i]} &\sim N(\mu_{\beta_{0j[i]}}, \sigma^2_{\beta_{0j[i]}}), \text{ for } j = 1, \dots, J \\ \beta_{0k[i]} &\sim N(\mu_{\beta_{0k[i]}}, \sigma^2_{\beta_{0k[i]}}), \text{ for } k = 1, \dots, K \end{aligned}$$

where y_i is the proportion of fish in a northern pike diet, x_1 is northern pike length, x_2 is day of year, $\beta_{0j[i]}$ is the intercept of the i^{th} observation within the j^{th} year and $\beta_{0k[i]}$ is the intercept of the i^{th} observation within the k^{th} year.

Results

Demographic information

All results are based on analyses from 125 northern pike captured between 2012 and 2016. Northern pike length ranged from 82-892 mm with a median length of 422 mm. The heaviest northern pike was 5300 g and the lightest was 3 g. Over 49% of northern pike came from Hobbie Creek, 61% came from Hobbie Creek, Provo Bay, and the mouth of the Provo River combined, and all northern pike came from the east shore of the lake (Table 1).

Diet analysis

Fifty-three (42%) of the 125 northern pike diets were empty. Our pre-genetics estimate of June sucker consumed was 5.6-12.2%. After genetic analysis, however, the average estimate of June sucker consumed dropped to 0.8-1.0% after one diet item was genetically confirmed as a sucker (Figures 7 & 8). The official identity was desert sucker (*Catostomus clarki*), but it is likely the June sucker genetic sequence was not available in GenBank, the National Institute of Health's genetic sequence database. Therefore, we are treating any sucker as a June sucker to be conservative. Macroinvertebrates comprised less than 40% of northern pike diets, sport fishes (e.g., white bass, bluegill sunfish, black crappie, northern pike, and yellow perch) roughly 40%, common carp 5.5%, unknown

fish between 10.9 and 14.1%, and non-sport fishes (e.g., fathead minnow and mottled sculpin) roughly 3%.

Bioenergetics modeling

We found at very high densities (i.e., 60 northern pike per hectare), a population of adult northern pike has the potential to consume nearly six million age-0 June sucker per year. At very low densities (e.g., 1.5 adult northern pike per hectare), northern pike not only have the potential to consume more than the number of June sucker stocked into Utah Lake in 2015, but also more than the number estimated to compose the June sucker population (Figure 9).

Discussion

Our model indicates that while June sucker comprised only 0.8-1.0% of an average northern pike diet, the predatory impact of northern pike has the potential to decimate the June sucker population. The majority of northern pike were captured in Hobble Creek, which provides spawning and rearing habitat for June sucker. Even at low densities, northern pike still have the ability to consume more age-0 June sucker than those naturally recruited (USFWS 1999). Thus, the June sucker population will likely persist only with stocking, and the size at which June sucker are stocked may need to increase (i.e., hatchery managers will be forced to keep them in the facility longer), resulting in greater costs to the UDWR. Similarly, the management and stocking protocols for sport fishes also may need to change to ensure those economically-valuable populations persist. Utah Lake is the state's largest freshwater fishery. White bass, catfish, walleye, and other sport fishes drive license and gear sales, which in turn provide

funding for conservation projects (UDWR 2017). However, 40% of an average northern pike's diet consists of these popular fish species. The illegal addition of northern pike to Utah Lake, despite its already-thriving sport fish community, now jeopardizes the lake both economically and environmentally. In addition, northern pike have the potential to consume sport fishes and drive down license and gear sales. Therefore, our research highlights the need for aquatic invasive species education (Leung et al. 2002; Lodge et al. 2006; Krasny and Lee 2010; Simpson 2010; Vander Zanden et al. 2010).

Our findings are likely gross underestimates based on the density of northern pike alone if we expect the growth rate of the Utah Lake invasive northern pike population to be similar to, or higher than, that of a population in their native range. Northern pike can occur between 3 and 59 northern pike per hectare in their native range (Pierce & Tomcko 2005). However, mitigation efforts may prevent the population from ever reaching the high densities observed in their native range because the northern pike invasion in Utah Lake was detected early.

Our bioenergetics model is calibrated to the invasive northern pike population in Utah Lake. Catch-and-release mark-recapture approaches were not an option to estimate current northern pike abundance given: 1) our concern with predation on endangered June sucker by any northern pike released for such a study; 2) June sucker conservation, and 3) the desire to minimize northern pike natural reproduction. Therefore, our model is the best tool managers have to estimate the predatory effect of northern pike on June sucker and other sport fishes in Utah Lake. Nevertheless, uncertainty and assumptions are commonplace in any modeling effort (Chatfield 2006). We assume our bioenergetics model parameters are accurate and do not differ between native and non-native ranges.

We assume the growth data we calculated from northern pike otoliths is reasonably accurate. We also assume the genetics results for the northern pike diet items are accurate. Future improvements for this model could include: successfully including the logistic mixed-effects model into the bioenergetics model to better inform the proportion of different species of fish and macroinvertebrates consumed; including different prey energy densities accordingly; and increasing our sample size, particularly for the identification of diet items. Our research will help inform management decisions regarding the growing northern pike population in Utah Lake and their influence on June sucker and the sport fish community.

Millions of dollars and countless hours have been devoted to habitat restoration to recover the June sucker population in Utah Lake (JSRIP 2015). A tributary restoration project, for example, was designed to provide optimal June sucker spawning habitat and potentially rearing habitat for juveniles. Although little is known about juvenile June sucker behavior, researchers suspect juveniles rear in the tributaries and in the main lake near tributary mouths. Submerged and emergent vegetation near tributary mouths and throughout the main lake, however, is inundated in the spring but often dries out in the summer months as the lake level drops and thus may or may not be available for these juvenile fish (Gaeta, unpublished data). While the tributary restoration provides valuable spawning habitat, our estimates of June sucker consumption by northern pike highlight the critical need to include restoration of rearing habitat in recovery efforts as refuge habitat from northern pike predation, particularly near the mouths of tributaries.

Combinations of empirical and theoretical approaches are commonly used to predict the predatory impact of apex invasives on native species (Paukert et al. 2003;

Muhlfeld et al. 2008; Walrath et al. 2015; Scheibel et al. 2016). A Monte Carlo bioenergetics modeling method (Madenjian et al. 1993) in which we modeled individuals, in conjunction with confirmation of the identity of northern pike diet items using genetic analysis, is a novel approach to evaluating the consumption of an endangered species by an invasive apex predator early in the invasion. Our research also highlights the importance of preventing the spread of aquatic invasive species (Leung et al. 2002; Pimentel et al. 2005), mitigating the growth of invasive species populations (Vander Zanden et al. 2010; Lodge et al. 2006), and educating the public (Krasny & Lee 2010) about the consequences of illegal stocking

Tables and Figures

Table 1. Capture location information for northern pike donated to our laboratory in 2015 and 2016.

Location of capture	Number of northern pike	Percentage (%) of total	Location on lake
Hobble Creek	62	49	East
No location	31	24.8	N/A
Mouth of Provo River/Provo Jetty	14	11.2	East
Lincoln Beach area	6	4.8	Southeast
Provo Bay	4	3.2	East
Lindon Boat Harbor	3	2.4	East
Skipper Bay	2	1.6	East
Lindon Boat Harbor	1	0.8	East
American Fork	1	0.8	NE
Rock Island Waterfowl Management Are	1	0.8	Southeast

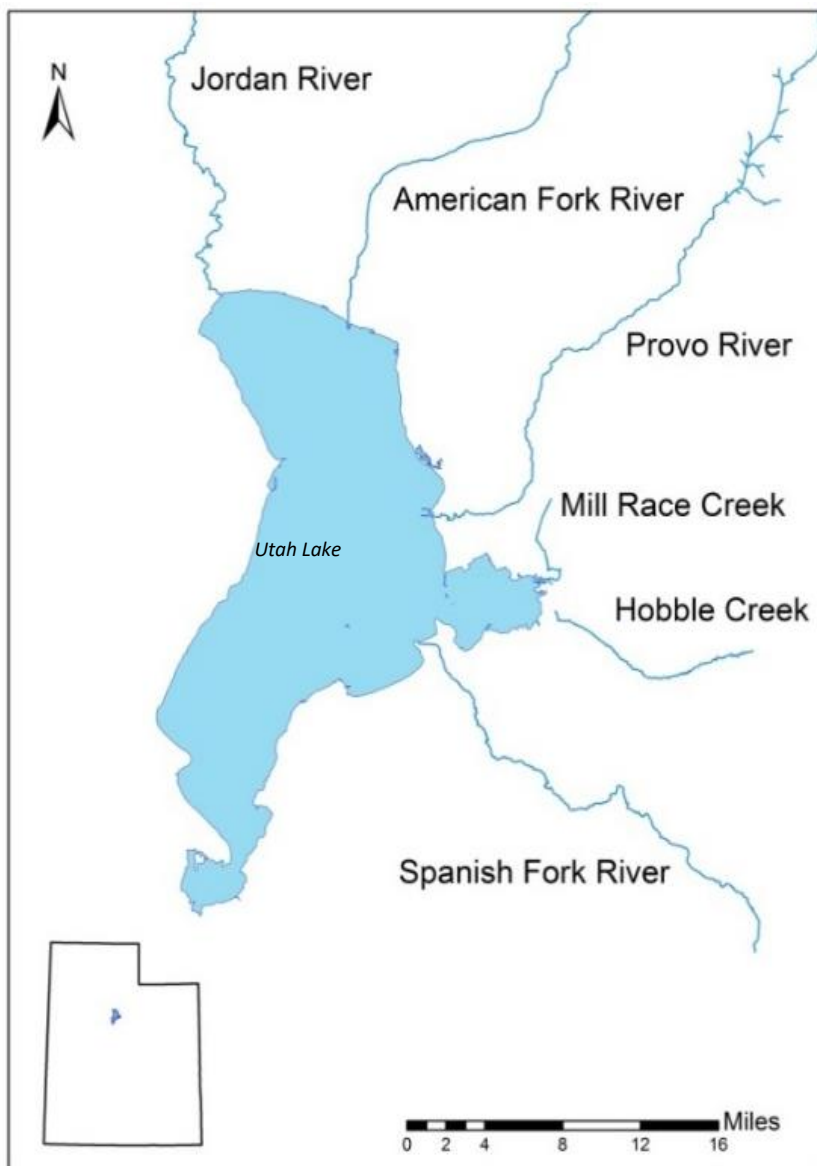


Figure 1. Map of Utah Lake, UT and major tributaries.

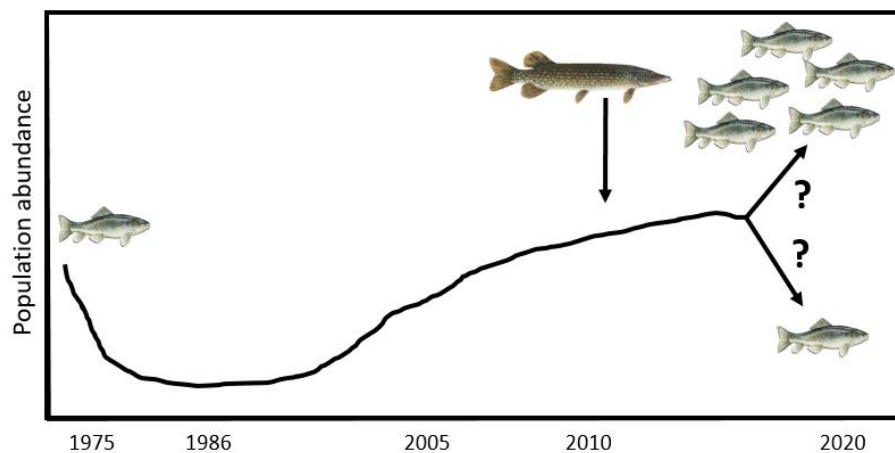


Figure 2. Conceptual model of the June sucker population in Utah Lake, UT showing the population decline prior to 1986, steady increase to present day, and the uncertain future of the population after the addition of northern pike in 2010.

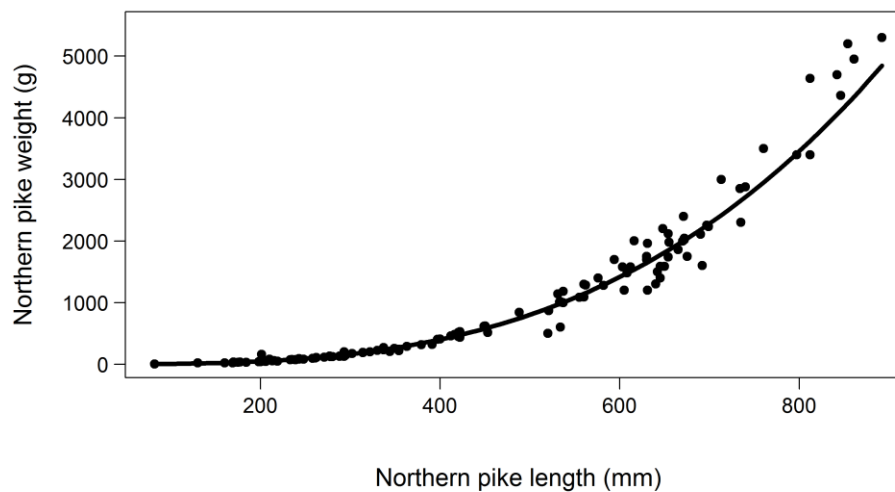


Figure 3. Length-at-weight model for northern pike in Utah Lake, UT. Data used were from northern pike caught between 2012 and 2016.

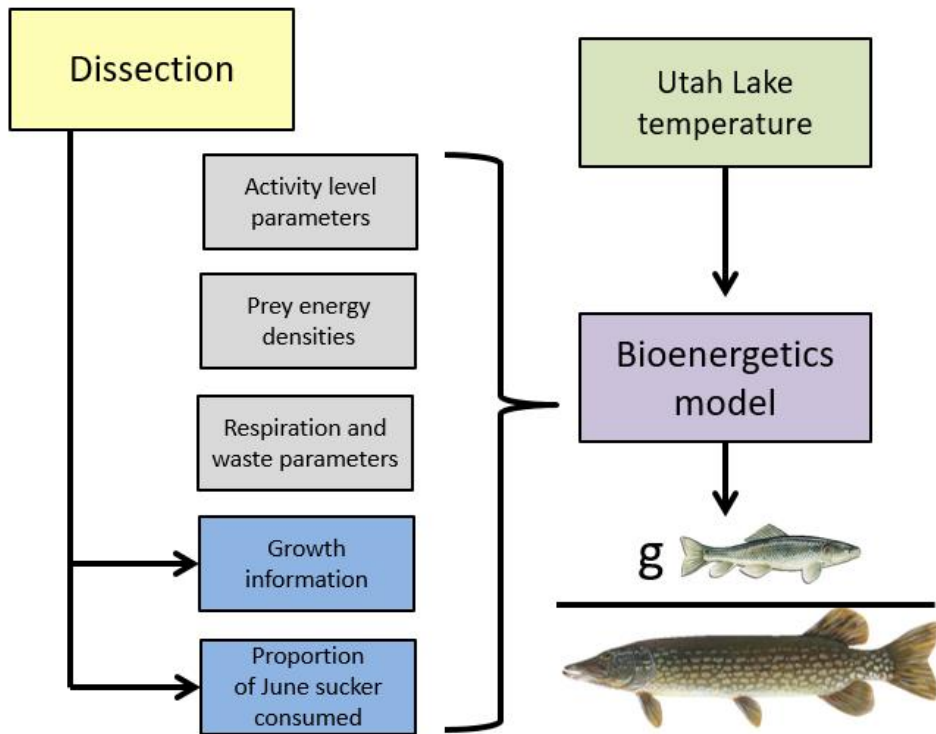


Figure 4. Conceptual model describing the inputs and output of the northern pike bioenergetics model. Parameters (grey) are fixed (e.g., activity level, prey energy density, respiration, and waste) and were estimated from the literature. Growth and diet proportions of June sucker (blue) came from dissection of northern pike. Temperature data (green) came from Utah Lake monitoring efforts in 2014. The bioenergetics model output is grams of June sucker consumed per pike.

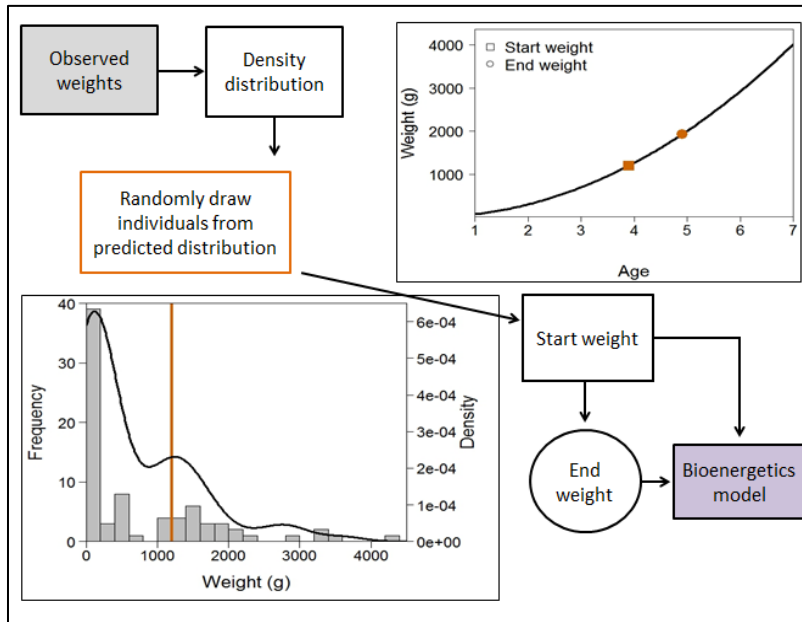


Figure 5. Conceptual model of population-level bioenergetics modeling. The solid black line in the lower left Figure represents a density distribution. The orange represents one northern pike drawn from the density distribution at 1200 g. The orange square in the age-at-weight Figure in the top right represents the draw, or start, weight while the orange circle represents the weight after one year, or end weight. Together, the start and end weight represent the growth over a one year period for that individual. The growth information is included in the bioenergetics model. The process is then repeated for simulated population of northern pike.

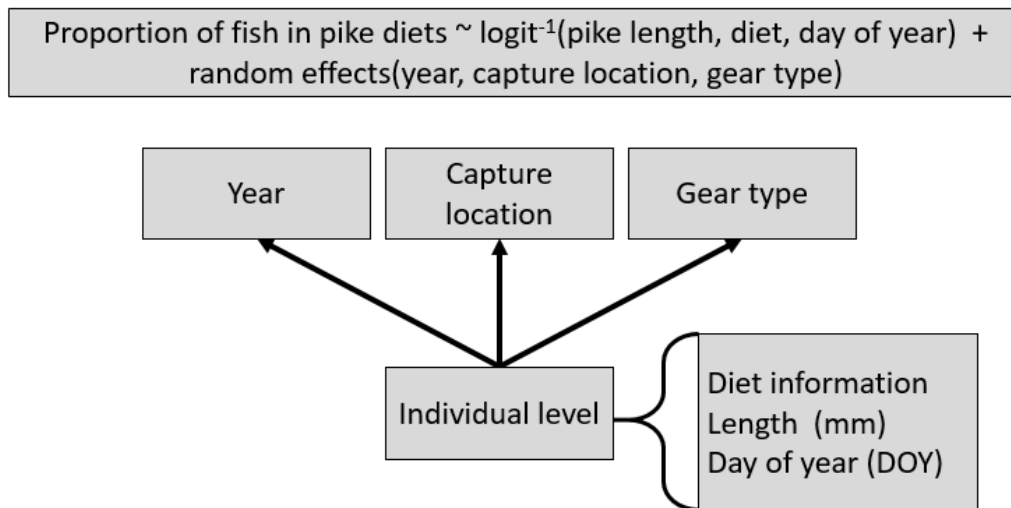


Figure 6. Conceptual model of the data structure for the logistic mixed effects model predicting the proportion of fish in a northern pike diet given northern pike length.



Figure 7. Diet items of northern pike. Clockwise from top right: suspected white bass; smallest northern pike (82 mm) consumed a total of 17% of its body length; 5-6 different fish(es) in one diet; mass of tissue and bones of an unknown fish.

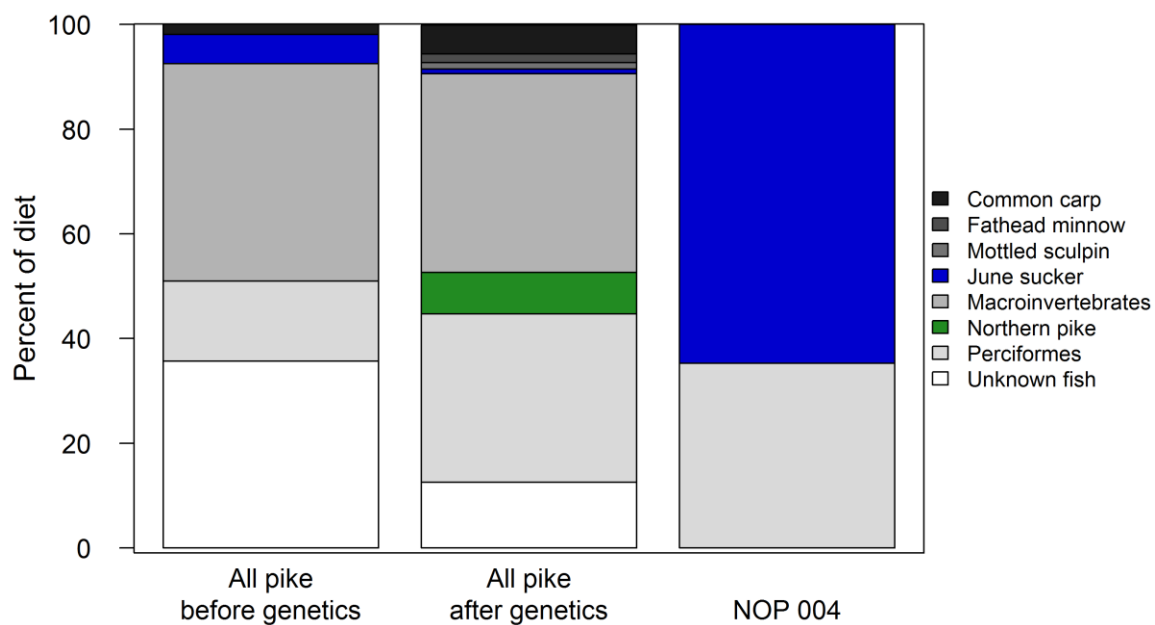


Figure 8. Species composition of northern pike diet items before and after genetic analyses (left and middle panels, respectively). The right panel shows the diet composition of the northern pike that consumed the genetically confirmed sucker.

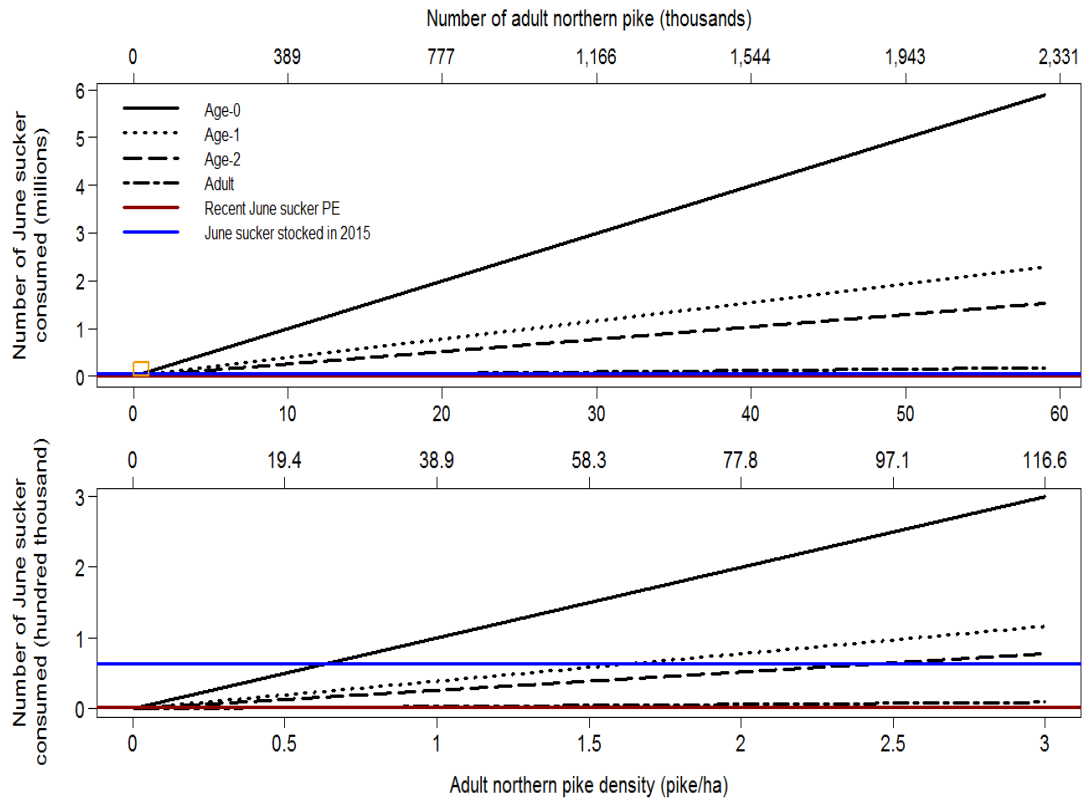


Figure 9. Consumption of age-0, age-1, age-2, and adult June sucker by adult northern pike at high (top panel) and low (bottom panel) densities. The red line represents the most recent June sucker population estimate of 2000 spawning adults in 2013. The blue line represents the number of June sucker stocked in Utah Lake in 2015. The orange square in the top panel highlights the bottom panel.

Literature Cited

- Andersen M, Jacobsen L, Grønkjær P, and Stov C. 2008. Turbidity increases behavioral diversity in northern pike, *Esox lucius* L., during early summer. *Fisheries Management and Ecology* **15**:377-383.
- Anderson, RO, Neumann RM. 1996. Length, Weight, and Associated Structural Indices. Pages 447-482 in Murphy BR, Willis DW, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**:1-48.
- Bates D, Maechler M. 2016. Matrix: Sparse and Dense Matrix Classes and Methods. R package version 1.2-6. <https://CRAN.R-project.org/package=Matrix>
- Belk M, 1998. Age and growth of June sucker (*Chasmistes liorus*). *Great Basin Naturalist* **58**:390-392.
- Bevelhimer MS, Stein RA, Carline RF. 1985. Assessing significance of physiological differences among three Esocids with a bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:57-69.
- Beyerle GB, Williams JE. 1968. Some observations of food selectivity by northern pike in aquaria. *Transactions of the American Fisheries Society* **97**:28-31.
- Byers JE. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* **97**:449-458.
- Carey MP, Wahl DH. 2010. Native fish diversity alters the effects of an invasive species on food webs. *Ecology* **91**:2965-2974. DOI: 10.1890/09-1213.1.
- Carpenter SR, Kitchell JF, Hodgson JR. 1985. Cascading trophic interactions and lake productivity. *Bioscience* **35**:634-639.
- Charlebois PM, Lamberti GA. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. *Journal of the North American Benthological Society* **15**:551-553.
- Chatfield C. 2006. Model Uncertainty. *Encyclopedia of Environmentics* 4. DOI: 10.1002/9780470057339.vam030.
- Chipps SR, Garvey JE. 2007. Assessment of Diets and Feeding Patterns. Page 480 in Guy CS, Brown ML, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.

- Clavero M Garcia-Berthou E. 2005. Invasive species are a leading cause of animal extinctions. *TRENDS in Ecology and Evolution* **20**:110.
- Crowl TA, Petersen ME, Mellenthin R, and Thiede GP. 1995. Trophic interactions of gizzard shad, June sucker and white bass: implications for fishery enhancement and the management of the endangered June sucker. Final report submitted to UDWR, Salt Lake City, UT.
- Cucherousset J, Olden JD. 2011. Ecological impacts of non-native freshwater fishes. *Fisheries* **36**:215-230.
- Devries DR, Frie RV. 1996. Determination of Age and Growth. Pages 483-512 in Murphy BR, Willis DW, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Diana JS. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). *Canadian Journal of Zoology* **57**:2121-2127.
- Diana JS. 1983. An energy budget for northern pike (*Esox lucius*). *Canadian Journal of Zoology* **61**:1968-1975.
- Elton C. 1958. *The Ecology of Invasions by Plants and Animals*. Springer-Science + Business Media, B.V., Netherlands.
- Gaeta JW, Read JS, Kitchell JF, Carpenter SR. 2012. Eradication via destratification: whole-lake mixing to selectively remove rainbow smelt, a cold-water invasive species. *Ecological Applications* **22**:817-827.
- Gelman A, Su Y. 2016. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package version 1.9-3. <https://CRAN.R-project.org/package=arm>.
- Hanson PC, Johnson TB, Schindler DE, Kitchell JF. 1997. *Fish Bioenergetics 3.0 for Windows*. Center for Limnology, University of Wisconsin–Madison, Madison, Wisconsin.
- Heckmann RA, Thompson CW, White DA. 1981. *Fishes of Utah Lake*. Great Basin Naturalist Memoirs, No. 5: Utah Lake Monograph. Brigham Young University, Provo, Utah.
- Janetski JC. 1990. Utah Lake: its role in prehistory of Utah Valley. *Utah Historical Quarterly*.
- June Sucker Recovery Implementation Program (JSRIP). 2015. <http://www.junesuckerrecovery.org/index.html>. Salt Lake City, Utah. Accessed August 11 2015.

- Kitchell JF, Steward DJ, Weininger D. 1997. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* **34**:1922-1935. DOI: 10.1139/f77-258.
- Knapp RA, Matthews KR. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. *Restoration Ecology* **6**:207-213.
- Krasny ME and Lee S. 2010. Social learning as an approach to environmental education: lessons from a program focusing on non-indigenous, invasive species. *Environmental Education Research* **8**:101-119.
- Lepak JM, Kraft CE, Weidel BC. 2006. Rapid food web recovery in response to removal of an introduced apex predator. *Canadian Journal of Fisheries and Aquatic Sciences* **63**:569-575.
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**:2407-2413. DOI: 10.1098/rspb.2002.2179.
- Lodge DM, Williams SL, MacIsaac H, Hayes K, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT, McMichael A. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* **16**:2035-2054.
- Madenjian CP, Carpenter SR, Eck GW, Miller MA. 1993. Accumulation of PCBs by lake trout (*Salvelinus namaycush*): an individual-based model approach. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:97-109.
- Mauck WL, Coble DW. 1971. Vulnerability of some fishes to northern pike (*Esox lucius*) predation. *Journal of the Fisheries Research Board of Canada* **28**:957-969. DOI: 10.1139/f71-141.
- McHugh P, Budy P. 2005. An experimental evaluation of competitive and thermal effects of brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarki utah*) performance along an altitudinal gradient. *Canadian Journal of Fisheries and Aquatic Sciences* **62**:2784-2795.
- McMahon TE, Bennett DH. 1996. Walleye and northern pike: boost or bane to northwest fisheries? *Fisheries* **8**:6-13.
- Miller RR, Smith GR. 1981. Distribution and evolution of *Chasmistes* (Pisces: Catostomidae) in western North America. *Occasional papers of the Museum of Zoology*, No 696. University of Michigan, Ann Arbor, Michigan.

- Miller RR, Williams JD, Williams JW. 1989. Extinctions of North American fishes during the past century. *Fisheries* **14**:22-38.
- Mooney HA, Cleland EE. 2001. The evolutionary impact of invasive species. *PNAS* **98**:5446-5451. DOI: 10.1073/pnas.091093398.
- Muhlfeld CC, Bennett DH, Steinhorst RK, Marotz B, Boyer M. 2008. Using bioenergetics modeling to estimate consumption of native juvenile salmonids by nonnative northern pike in the Upper Flathead River System, Montana. *North American Journal of Fisheries Management* **28**:636-648. DOI: 10.1577/M07-004.1.
- Nature Serve. 2014. *Chasmistes liorus*. The IUCN Red List of Threatened Species 2013: e.T62197A3109722. <http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T62197A3109722.en>. Accessed on 29 March 2017.
- Page LM, Burr BM. 1991. A field guide to freshwater fishes of North America north of Mexico. Houghton Mifflin Company, Boston, Massachusetts.
- Paukert CP, Stancill W, DeBates TJ, Willis DW. 2003. Predatory effects of northern pike and largemouth bass: bioenergetics modeling and ten years of fish community sampling. *Journal of Freshwater Ecology* **18**:13-24.
- Pierce RB, Tomcko CM. 2005. Density and biomass of native northern pike populations in relation to basin-scale characteristics of north-central Minnesota Lakes. *Transactions of the American Fisheries Society* **134**:231-241.
- Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**:273-288.
- Pine WE, Kwak TJ, Rice JA. 2007. Modeling management scenario and the effects of an introduced apex predator on a coastal riverine fish community. *Transactions of the American Fisheries Society* **136**:105-120. DOI: 10.1577/T05-249.1
- PSOMAS and SWCA. 2007. Utah Lake TMDL: Pollutant loading assessment and designated beneficial use impairment assessment, final draft. Prepared for the Utah Division of Water Quality.
- Quist MC, Peg MA, DeVries DR. 2012. Age and growth. Pages 677-731 in Zale AV, Parrish DL, Sutton TM, editors. *Fisheries techniques*, 3rd edition. American Fisheries Society, Bethesda, Maryland.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

- Ricciardi A, Neves RJ, Rasmussen JB. 1998. Impending extinctions of North American freshwater mussels (Unionodia) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* **67**:613-619.
- Ricciardi A, Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* **12**:1220-1222
- Sala OE, et al. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**:1770-1774.
- Scheibel NC, Dembkowski JD, Davis JL, Chipps SR. 2016. Impacts of northern pike on stocked rainbow trout in Pactola Reservoir, South Dakota. *North American Journal of Fisheries Management* **36**:230-240.
- Scoppettone GG, Vineyard G. 1991 Life history and management of four endangered lacustrine suckers *in* Battle against extinction: Native fish management in the American West. Arizona State University Press, Phoenix, Arizona.
- Simpson A, Jarnevich C, Madsen J, Westbrook R, Fournier C, Mehrhoff L, Browne M, Graham J, Sellers E. 2009. Invasive species information networks: collaboration at multiple scales for prevention, early detection, and rapid response to invasive alien species. *Biodiversity* **10**:2-3, 5-13.
- Townsend CR. 1996. Invasion biology and ecological impacts of brown trout (*Salmo trutta*) in New Zealand. *Biological Conservation* **78**:13-22.
- U.S. Fish and Wildlife Service (USFWS). 1999. June sucker (*Chasmistes liorus*) Recovery Plan. U.S. Fish and Wildlife Service, Denver, Colorado.
- Utah Division of Wildlife Resources (UDWR). 2017 <https://wildlife.utah.gov/about-us/64-what-we-do/about-us/191-financial-overview.html>.
- Vander Zanden JM, Olden JD. 2008. A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* **65**:1512-1522.
- Vander Zanden JM, Hansen GJA, Higgin SN, Kornis MS. 2010. A pound of prevention plus a pound of cure: early detection and eradication of invasive species in the Laurentian Great Lakes. *Journal of Great Lakes Research* **36**:199-205.
- Vineyard GL. 2001. Fish species recorded from Nevada. Biological Resources Research Center. University of Nevada, Reno, Nevada.
- Vitousek PM, D'Antonio CM, Loope LL, Westbrook R. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468-478.

Walrath JD, Quist MC, Firehammer JA. 2015. Trophic ecology of nonnative northern pike and their effect on conservation of native Westslope cutthroat trout. *North American Journal of Fisheries Management* **35**:158-177.

White J, Dabb B. 1970. Fish population studies, Utah Lake. Utah Division of Wildlife Resources, Springville, Utah.

Zurr A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer-Verlag, New York, New York.

CHAPTER III

PREDICTING THE POPULATION GROWTH TRAJECTORY OF INVASIVE
NORTHERN PIKE (*ESOX LUCIUS*) IN UTAH LAKE, UT UNDER
DIFFERENT MANAGEMENT SCENARIOS

Introduction

Pollution, habitat degradation, overexploitation, and invasive species are leading causes of species declines and the loss of biodiversity (Wilson 1989; Sala et al. 2000), particularly in aquatic systems (Ricciardi 1999; Pimentel et al. 2005). Invasive species, for instance, are economically costly (Leung et al. 2002, Pimentel et al. 2005), can alter food webs (Carey & Wahl 2010), are a major threat to native species (Elton 1958; Vitousek 1996; Mooney & Cleland 2001; Strayer et al. 2006), and hamper conservation of threatened or endangered species (Mooney & Cleland 2001). Once an invasive species population establishes, mitigation or eradication can be difficult, if not impossible (Knapp and Matthews 1998; Vander Zanden et al. 2010; Gaeta et al. 2012), which is problematic in the face of endangered species conservation.

While preventing the spread of invasive species is optimal, early detection, and the subsequent application of mitigation strategies is the best-case scenario to minimize impacts once an invasive population establishes (Leung et al. 2005; Vander Zanden and Olden 2008; Vander Zanden et al. 2010). In aquatic systems, managers, researchers, and conservationists may slow the growth trajectory of an invasive population and, thereby, minimize predatory effects on the prey base, given early detection and action (e.g., increased harvest, application of chemical treatment, thermal destratification, mechanical

removal; Simberloff 2002; Vander Zanden et al. 2010; Gaeta et al. 2012). The addition of apex predators to a system can have impacts multiple trophic levels below (Carpenter et al. 1985).

Northern pike are an apex predator native to the upper Midwest of the lower 48 United States, Alaska, and Canada (Page & Burr 1991), but are spreading across the Great Plains, the Intermountain West, and Pacific Northwest (McMahon & Bennett 1996; Vineyard 2001; Muhlfeld et al. 2008; Scheibel et al. 2016). As ambush predators, northern pike will consume any unsuspecting fish of suitable size and cannot be conditioned to consume one specific type of fish (Beyerle & Williams 1968; Mauck & Coble 1971). Northern pike are a threat to native species (Muhlfeld et al. 2008), and researchers are using modeling approaches to guide management decisions for this invasive species (Vineyard 2001; Muhlfeld et al. 2008; Scheibel et al. 2016).

Northern pike were first reported by anglers in Utah Lake, UT in 2010 with natural reproduction detected by managers in 2014. The invasion of an apex predator that has an affinity for sucker species (Diana 1979) is of particular concern in Utah Lake as only a small population of June sucker, an important indicator species for the lake (JSRIP 2015), still exist. According to early accounts of settlers in Utah Valley, during the mid-1800s the June sucker population in Utah Lake was abundant and the fish were used for food and fertilizer (Heckmann et al. 1981). However, over the next century the population decreased remarkably due to dewatering of spawning tributaries and commercial fishing (USFWS 1999). The June sucker gill net catch rate dropped from 0.68 suckers per hour in the mid-1950s (UDWR, unpublished data) to 0.01 suckers per hour in 1970 (White & Dabb 1970).

In 1986 the U.S. Fish and Wildlife Service (USFWS) listed the June sucker as an endangered species due to decreased population sizes as a result of the synergistic effects of habitat degradation (e.g., loss of submerged vegetation and thus fewer refuge areas for juveniles); increased eutrophic conditions (e.g., low concentration of dissolved oxygen, increased phosphorus concentrations); alteration of hydrologic flows in the Provo River, a main tributary June sucker use for spawning; and the introduction of non-native species, such as walleye, white bass, and common carp (USFWS 1999). Captive breeding programs, stocking programs, and habitat restoration projects are major components of the estimated \$50 million-dollar plan to restore the June sucker population (USFWS 1999). The USFWS is currently considering downlisting the June sucker from endangered to threatened due to protected Provo River flows and spawning and rearing habitat restorations. Thus, the addition of northern pike to the Utah Lake ecosystem is particularly concerning for the persistence and future of the June sucker population.

The June sucker is an important indicator species for the Utah Lake ecosystem (JSRIP 2015), meaning they can signal a change in the biological or physical condition of the ecosystem and serve as a measurement of ecosystem health. Countless hours and millions of dollars have been devoted to the restoration of the June sucker population over many years and by multiple agencies. The invasion of predatory northern pike is of particular concern because the most recent population estimate of adult June sucker is roughly 2000 spawning adults (Conner 2013), and there is no accurate estimate of juvenile abundance. We had a unique opportunity in Utah Lake to study northern pike early in the invasion, use models to understand how the population is growing, and inform management decisions regarding the conservation of endangered June sucker.

Fortunately, because of this endangered species and the cultural importance of the lake for agriculture, irrigation, and recreation, the fish community is heavily monitored and the invasion was detected while northern pike are still at very low densities. Removal efforts and a mandatory harvest regulation were initiated within two years of detection. However, researchers and managers are uncertain as to the benefits of costly removal efforts when low densities preclude high catch rates. Understanding the growth trajectory of and assessing mitigation options for northern pike, a new, predatory, invasive species, is a necessary step in preventing the decline of the endangered June sucker population. Our goal was to quantify the invasive northern pike population growth trajectory in Utah Lake, UT and assess the effectiveness of mitigation efforts to date. While early detection and early mitigation efforts are the best option once a species invades (Vander Zanden & Olden 2008; Vander Zanden et al. 2010), these efforts are often applied without an *a priori* evaluation of their efficacy.

Understanding an invasive species population's growth trajectory, survival, and reproductive rates can be vital to inform any management efforts. We developed a density-dependent, age-structured population model to estimate the growth trajectory of an invasive northern pike population in Utah Lake. Here we report our evaluation of when the population will reach equilibrium if left unchecked and assess potential mitigation options. Management of this invasive apex predator is critical to prevent the imperiled endangered June sucker population from declining further.

Methods

We used Leslie matrix models developed in R Cran version 3.3.1 (R Core Team 2016) to model the northern pike population under three different mitigation scenarios. Matrix models mathematically express changes in the age structure of a population over time (Lewis 1942; Leslie 1945, 1948; Jensen 1995):

$$(5) \quad N_{t+1} = M * N_t$$

$$M = \begin{bmatrix} F_1 & F_2 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & 0 \end{bmatrix} \text{ and } N_t = \begin{bmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{bmatrix}$$

where F, across the top row of matrix M, represents fertility of each age class and is the product of m_x , fecundity, and S_i , survival probability (Figure 10). Survival probability is on the sub-diagonal and represents survival from age i to age $i+1$. The vector N_t represents the abundance of each age class of the population.

This age-structured model yields an exponentially growing population (Leslie 1945, 1948), and thus a density-dependent population growth term is necessary to mimic the pressures to which organisms are exposed in their environment (Leslie 1959; Jensen 1995). We created a simple density-dependent age structured model specific to northern pike in Utah Lake, UT based on a model created by Jensen (1995) to estimate the abundance of the northern pike population at time $t+1$:

$$(6) \quad N_{t+1} = N_t + D_t * (M - I) * N_t$$

where M is the matrix and N_t is the vector defined in Equation 4, above. D_t is a density-dependent term equal to the abundance of organisms each year relative to the system's carrying capacity, K . I , the identity matrix, is a matrix of zeros with ones along the diagonal.

Model parameterization

The size structure we used for the initial invading population in 2010 was one age-2, three age-3, and one age-4, for a total of five individuals. We chose this size structure because logistically it would be easier for an angler to illegally transport and stock a greater number of smaller northern pike into Utah Lake rather than one large individual. Model parameters including survival and fecundity values and carrying capacity were estimated from Matsumura et al. (2011) to create the following matrix, M , for northern pike in Utah Lake:

(7)

$$M = \begin{bmatrix} 0 & 3.9 & 8.25 & 13.95 & 20.65 & 27.94 & 35.49 \\ 0.73 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.61 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.60 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.60 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.60 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.60 & 0 \end{bmatrix}$$

The model assumed northern pike live to be seven years old, because we did not age any individuals older than age-7 in Utah Lake. We did not include age-0 northern pike in our model because their survival probability is difficult to include without further complicating the model. We assume angler harvest is constant for individuals age-3 and

older. We also assume the estimate of carrying capacity in the model is accurate for Utah Lake and that northern pike were illegally stocked in Utah Lake in 2010, based on initial reports by anglers in 2010, and confirmation by the UDWR in 2011.

Model scenarios

We tested three mitigation scenarios with our model: unmitigated, early mitigation, and late mitigation. In the unmitigated scenario, we allowed the northern pike population to grow without removing individuals. In the early mitigation scenario, we accounted for all individuals removed between 2012 and 2016 by anglers, the UDWR, Loy Fisheries, and USU, and we continued future removal at the same effort as the removal effort in 2015 (i.e., we removed the same proportion of individuals in each age class from 2017 on as were removed in 2015). We also allowed angler harvest to increase as the population became more abundant. We included a 10% harvest increase for age-1 individuals, a 20% increase for age-2 individuals, and a 50% increase for individuals age-3 and older. In the late mitigation scenario, we allowed the northern pike population to grow unmitigated until it reached half of carrying capacity ($1/2 K$), and then removed individuals from the population as well as increased angler harvest at the same rate as in the early mitigation scenario.

Bioenergetics modeling

In chapter 1 we used growth and foraging observations with genetic analysis and bioenergetic models to estimate the predatory impact of northern pike on endangered June sucker in Utah Lake. Bioenergetics is based on a simple energy budget equation (Hanson et al. 1997, Kitchell et al. 1997). The energy consumed by a fish is allocated

toward different physiological processes necessary for life (e.g., respiration, metabolism, excretion of wastes), and any energy left over is allocated toward growth. We used the Wisconsin Fish Bioenergetics 3.0 model (Hanson et al. 1997) modified to run in R (version 3.3.1; R Core Team 2016) to create a population-level bioenergetics model specific to Utah Lake. The population-level model is based on a Monte Carlo bioenergetics modeling approach in which we modeled individuals.

We found at very high densities (i.e., 60 northern pike per hectare), a population of adult northern pike has the potential to consume nearly six million age-0 June sucker per year. At very low densities, northern pike also have the potential to consume more than the number of June sucker stocked into Utah Lake in 2015 and more than the estimated June sucker population, which could threaten the persistence of the June sucker population.

Sensitivity analysis

We conducted a sensitivity analysis on our age-structured density-dependent model. We projected the population growth trajectory to 2050 after altering carrying capacity and age-specific survival, fecundity, and harvest by $\pm 10\%$. We then evaluated the resulting equilibrium (percent change in density in pike per hectare) indicated by consecutive years at the same population size, and identified the first year the population reached or surpassed the final equilibrium. We used the early mitigation scenario as the baseline for the sensitivity analysis.

Results

Our models suggest the northern pike population will reach an abundance equilibrium around 2026 in all scenarios assuming constant environmental conditions. The equilibrium abundance, however, varies across management scenario. The population under the late mitigation scenario reaches equilibrium just before the early mitigation scenario, though both follow a similar growth trajectory. Both the early and late mitigation scenarios stabilize slightly earlier than the unmitigated scenario. Both mitigation scenarios stabilize around 8 adult northern pike per hectare, while the population under the unmitigated scenario stabilizes around 12.3 adult northern pike per hectare (Figure 11).

We applied our bioenergetics modeling results from Chapter 1 to this density-dependent age-structured model by calculating the number of age-0 June sucker adult northern pike could potentially consume as the density of the northern pike population in the age-structured model changes. An unmitigated population of adult northern pike in Utah Lake would have the potential to consume more than 10,000 age-0 June sucker per year in 2018. A population of adult northern pike under the early mitigation scenario would have the potential to consume around 9,000 age-0 June sucker per year in 2018 (Figure 12).

The population in the baseline scenario surpassed equilibrium (330,469 individuals) in 2036. All populations in the sensitivity analysis reached equilibrium between 2035 and 2045. The sensitivity analysis suggests the most sensitive ages and parameters in the model are: survival at age-1, fertility at age-2, harvest at age-2, and carrying capacity (Figure 13). A positive or negative 10% change in each parameter

resulted in a less than or equal to positive or negative 5% change in equilibrium. Thus, from the sensitivity analysis we conclude that our model is fairly robust and that targeting young northern pike is important for removal efforts.

Discussion

Our initial model findings suggest early mitigation efforts have negligible effects on the initial (i.e., through 2020) growth trajectory of the northern pike population when compared to the unmitigated scenario. We attribute the similarity in the growth trajectory between the scenarios to the fecundity of northern pike (Wright and Shoesmith 1988) and the large size of Utah Lake (38,445 ha). While the population is growing quickly, the population density relative to the size of the lake is low, making encounter rates of northern pike during angling or sampling extremely low. Over a longer period of time (i.e., 20 years after invasion), however, both the early and late mitigation scenarios result in the northern pike population reaching a lower equilibrium than in the unmitigated scenario. Our research will help inform management decisions regarding the management of the northern pike population in Utah Lake.

Eradication of northern pike from the lake is highly unlikely due to its large size (Knapp & Matthews 1998; Vander Zanden et al. 2010; Gaeta et al. 2012) and due to restraints imposed by the imperiled status of endangered June sucker. For example, it is not feasible to chemically treat Utah Lake to remove invasive fish species due to cost and the presence of endangered June sucker. Given our bioenergetics modeling results, adult northern pike have the potential to decimate any June sucker natural recruitment via consumption, indicating the June sucker population will likely persist through stocking

efforts only. Our research highlights a need to attempt targeted removal of the invasive northern pike during spawning (Vredenberg 2004). We suggest investing in the stocking of triploid males (Thresher et al. 2014), detection methods (e.g., telemetry, mark-recapture) using Judas techniques to increase capture efficiency (Campbell & Donlan 2005; McCann & Garcelon 2008; Cruz et al. 2009; Bajer et al. 2011), and increased outreach to the public.

Our age-structured and bioenergetics models are calibrated to the invasive northern pike population in Utah Lake. Given our concern with predation on endangered June sucker conservation and the desire to minimize natural reproduction, catch-and-release mark-recapture approaches were not an option to estimate current northern pike abundance. Therefore, our model currently provides the best estimate of northern pike abundance and the only prediction of the population growth trajectory. Nevertheless, uncertainty and assumptions are commonplace in any modeling effort. We assume the survival and fecundity probabilities for the Leslie matrix model are accurate and do not differ among populations or between native and non-native ranges. We also assume the estimate of carrying capacity in the model is accurate for Utah Lake and that northern pike were planted in Utah Lake in 2010, based on initial reports by anglers in 2010 and confirmation by the UDWR in 2011. Future improvements for this model could include: quantifying the variance around our estimates; modeling more than three mitigation scenarios, adding the time of year each individual was removed; estimating angler harvest for different ages of northern pike and including those estimates in the model; and considering environmental influences (e.g., species interactions, the effect of drought, etc.) on northern pike population growth. While we acknowledge model uncertainty, we

hope our model will serve as a useful tool to guide invasive northern pike management decisions in the face of June sucker conservation.

Our findings are consistent with previous studies that suggest eradication of invasive species in large systems is impractical (Knapp & Matthews 1998; Lodge et al. 2006; Vander Zanden et al. 2010; Gaeta et al. 2012). Thus, our work highlights the need for aquatic invasive species education, particularly regarding the spread of invasive species (Vander Zanden & Olden 2008). The cost of preventing the spread of invasive species from entering a system is almost always less than the cost of managing them after invasion (Leung et al. 2002, Pimentel et al. 2005). Our research is unique in that we are studying northern pike near the beginning of the invasion process in Utah Lake. Millions of dollars and countless hours have been spent on habitat restoration projects aimed at restoring the June sucker population. Continuing to pursue those habitat restoration efforts would benefit June sucker, particularly juveniles, as refuge habitat from predators such as northern pike is critical for their survival. We used theoretical modeling approaches to guide management actions aimed at slowing their growth trajectory, thus possibly allowing the endangered June sucker population to persist. Early detection, prevention of spread, and mitigation of an invasive species (Leung et al. 2002; Lodge et al. 2006; Simpson 2010; Vander Zanden et al. 2010) are critical components to controlling the growth of an invasive species population, particularly in the face of endangered species conservation.

Tables and Figures

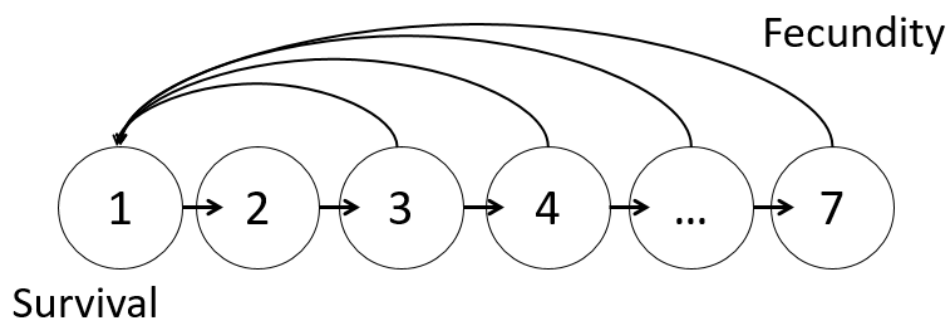


Figure 10. Conceptual model of a Leslie matrix model. The circles represent the abundance of individuals in the first age class to adult (age-3 and older). The arrows to the right represent survival (S_i) of individuals from one age class to the next. The arrows to the left represent fecundity (F_i) from ages i at which the species is capable of reproducing and contributing individuals back to the first age class.

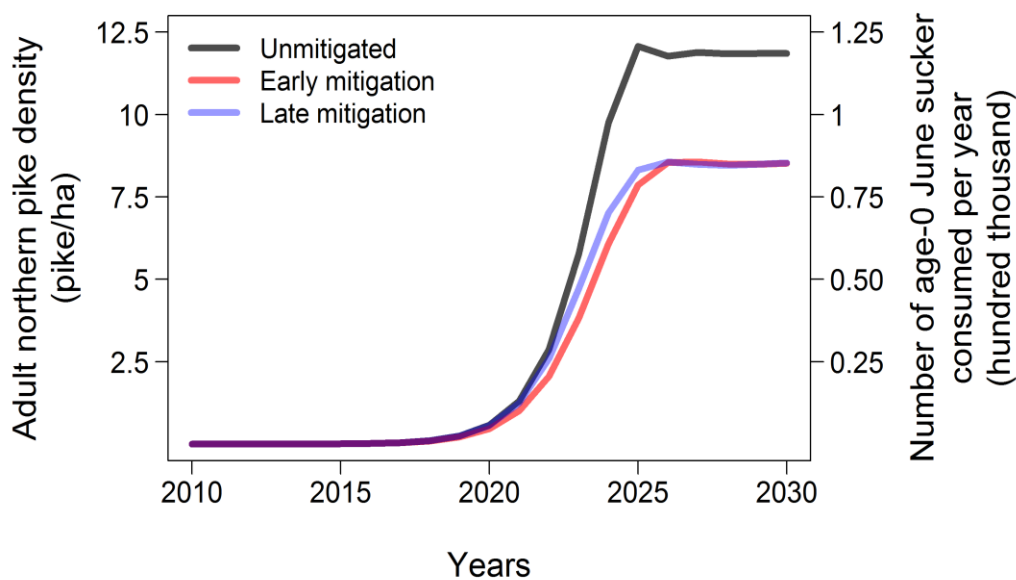


Figure 11. Northern pike population growth trajectory under the unmitigated (black), early mitigation (red), and late mitigation (blue) scenarios between 2010-2030.

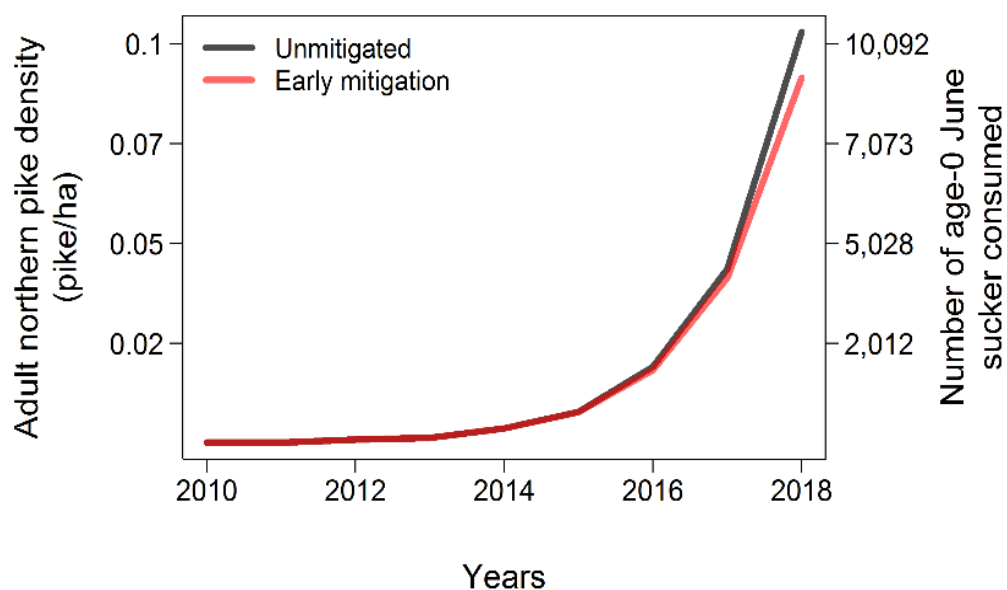


Figure 12. Northern pike growth trajectory under the unmitigated and early mitigation scenarios between 2010-2018.

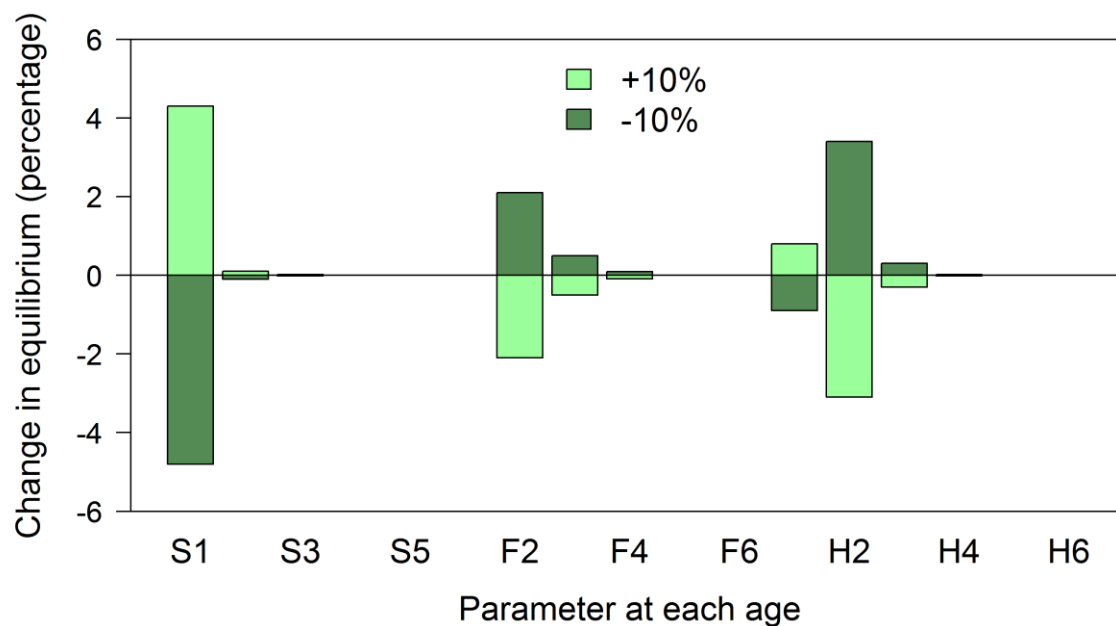


Figure 13. Results of the age-structured density-dependent model sensitivity analysis showing the percent change in equilibrium. Light green indicates a positive 10% change in the age-specific parameters survival (S), fertility (F), and harvest (H). Dark green indicates a negative 10% change in the age-specific parameters.

Literature Cited

- Andersen M, Jacobsen L, Grønkjær P, and Stov C. 2008. Turbidity increases behavioral diversity in northern pike, *Esox lucius* L., during early summer. Fisheries Management and Ecology **15**:377-383.
- Bajer PG, Chizinski CJ, Sorensen PW. 2011. Using the Judas technique to locate and remove wintertime aggregations of invasive common carp. Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications. Lincoln, Nebraska.
- Beyerle GB, Williams JE. 1968. Some observations of food selectivity by northern pike in aquaria. Transactions of the American Fisheries Society **97**:28-31.
- Byers JE. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos **97**:449-458.
- Carey MP, Wahl DH. 2010. Native fish diversity alters the effects of an invasive species on food webs. Ecology **91**:2965-2974. DOI: 10.1890/09-1213.1.
- Campbell KJ, Donlan CJ. 2005. Feral goat eradications on islands. Journal of Conservation Biology **19**:1362-1374. DOI: 10.1111/j.1523-1739.2005.00228.x
- Carpenter SR, Kitchell JF, Hodgson JR. 1985. Cascading trophic interactions and lake productivity. Bioscience **35**:634-639.
- Conner M. 2013. Estimation of population size, survival, and rate of population change for the spawning population of June suckers in Utah Lake using mark-reencounter data. Report for the June Sucker Recovery Implementation Program. Utah State University Department of Wildland Resources, Logan, Utah.
- Cruz F, Carrion V, KJ Campbell, Lavoie C, CJ Donlan. 2009. Bio-economics of large-scale eradication of feral goats from Santiago Island, Galápagos. Journal of Wildlife Management **72**:191-200.
- Diana JS. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). Canadian Journal of Zoology **57**:2121-2127.
- Elton C. 1958. The Ecology of Invasions by Plants and Animals. Springer-Science + Business Media, B.V., Netherlands.
- Gaeta JW, Read JS, Kitchell JF, Carpenter SR. 2012. Eradication via destratification: whole-lake mixing to selectively remove rainbow smelt, a cold-water invasive species. Ecological Applications **22**:817-827.

- Hanson PC, Johnson TB, Schindler DE, Kitchell JF. 1997. Fish Bioenergetics 3.0 for Windows. Center for Limnology, University of Wisconsin–Madison, Madison, Wisconsin.
- Heckmann RA, Thompson CW, White DA. 1981. Fishes of Utah Lake. Great Basin Naturalist Memoirs, No. 5: Utah Lake Monograph. Brigham Young University, Provo, Utah.
- Jensen AL. 1995. Simple density dependent matrix model for population projection. *Ecological Modeling* **77**:43-48.
- June Sucker Recovery Implementation Program (JSRIP). 2015. <http://www.junesuckerrecovery.org/index.html>. Salt Lake City, Utah. Accessed August 11 2015.
- Kitchell JF, Steward DJ, Weininger D. 1997. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* **34**:1922-1935. DOI: 10.1139/f77-258.
- Knapp RA, Matthews KR. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. *Restoration Ecology* **6**:207-213.
- Krasny ME and Lee S. 2010. Social learning as an approach to environmental education: lessons from a program focusing on non-indigenous, invasive species. *Environmental Education Research* **8**:101-119.
- Leslie PH. 1945. On the use of matrices in certain population mathematics. *Biometrika* **33**:183-212.
- Leslie PH. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* **35**:213-245.
- Leslie PH. 1959. The properties of a certain lag type of population growth and the influence of an external random factor on a number of such populations. *Physiological Zoology* **32**:151-159.
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**:2407-2413. DOI: 10.1098/rspb.2002.2179.
- Lewis EG. 1942. On the generation and growth of a population. *Sankhya. Indian Journal of Statistics* **6**:93-96.

- Lodge DM, Williams SL, MacIsaac H, Hayes K, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT, McMichael A. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* **16**:2035-2054.
- Matsumura S, Arlinghaus R, Dieckmann U. 2011. Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits, with an application for northern pike (*Esox lucius*). *Evolutionary Ecology* **25**:711-735.
- Mauck WL, Coble DW. 1971. Vulnerability of some fishes to northern pike (*Esox lucius*) predation. *Journal of the Fisheries Research Board of Canada* **28**:957-969. DOI: 10.1139/f71-141.
- McCann BE, Garcelon DK. 2008. Eradication of feral pigs from Pinnacles National Monument. *Journal of Wildlife Management* **72**:1287-1295. <https://doi.org/10.2193/2007-164>.
- McCauley E, Wilson WG, de Roos AM. 1992. Dynamics of age-structured and spatially structured predator-prey interactions: individual-based models and population-level formulations. *American Society of Naturalists* **142**:412-442.
- McMahon TE, Bennett DH. 1996. Walleye and northern pike: boost or bane to northwest fisheries? *Fisheries* **8**:6-13.
- Mooney HA, Cleland EE. 2001. The evolutionary impact of invasive species. *PNAS* **98**:5446-5451. DOI: 10.1073/pnas.091093398.
- Muhlfeld CC, Bennett DH, Steinhorst RK, Marotz B, Boyer M. 2008. Using bioenergetics modeling to estimate consumption of native juvenile salmonids by nonnative northern pike in the Upper Flathead River System, Montana. *North American Journal of Fisheries Management* **28**:636-648. DOI: 10.1577/M07-004.1.
- Page LM, Burr BM. 1991. A field guide to freshwater fishes of North America north of Mexico. Houghton Mifflin Company, Boston, Massachusetts.
- Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**:273-288.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

- Ricciardi A, Neves RJ, Rasmussen JB. 1998. Impending extinctions of North American freshwater mussels (Unionodia) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* **67**:613-619.
- Ricciardi A, Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* **12**:1220-1222
- Sala OE, et al. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**:1770-1774.
- Scheibel NC, Dembkowski JD, Davis JL, Chipps SR. 2016. Impacts of northern pike on stocked rainbow trout in Pactola Reservoir, South Dakota. *North American Journal of Fisheries Management* **36**:230-240.
- Simberloff D. 2002. Today Tiritiri Matangi, tomorrow the world! Are we aiming too low in invasives control? Pages 4-12 in C. R. Veitch and M. N. Clout, editors. *Proceedings of the international conference on eradication of island invasives. Occasional Paper of the IUCN Species Survival Commission, Gland, Switzerland and Cambridge, United Kingdom.*
- Simpson A, Jarnevich C, Madsen J, Westbrooks R, Fournier C, Mehrhoff L, Browne M, Graham J, Sellers E. 2009. Invasive species information networks: collaboration at multiple scales for prevention, early detection, and rapid response to invasive alien species. *Biodiversity* **10**:2-3, 5-13.
- Thresher RE, Hayes K, Bax NJ, Teem J, Benfey TJ, Gould F. Genetic control of invasive fish: technological options and its role in integrated pest management. *Biological Invasions* **16**:1201-1216.
- U.S. Fish and Wildlife Service (USFWS). 1999. June sucker (*Chasmistes liorus*) Recovery Plan. U.S. Fish and Wildlife Service, Denver, Colorado.
- Utah Division of Wildlife Resources (UDWR). 2017. <https://wildlife.utah.gov/about-us/64-what-we-do/about-us/191-financial-overview.html>.
- Vander Zanden JM, Olden JD. 2008. A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* **65**:1512-1522.
- Vander Zanden JM, Hansen GJA, Higgin SN, Kornis MS. 2010. A pound of prevention plus a pound of cure: early detection and eradication of invasive species in the Laurentian Great Lakes. *Journal of Great Lakes Research* **36**:199-205.
- Vineyard GL. 2001. Fish species recorded from Nevada. Biological Resources Research Center. University of Nevada, Reno, Nevada.

- Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468-478.
- Vredenburg VT. 2004. Reversing introduced species effects: Experimental removal of introduced fish leads to rapid recovery of a declining frog. *Proceedings of the National Academy of Sciences* **101**:7646-7650. DOI: 10.1073/pnas.0402321101.
- White J, Dabb B. 1970. Fish population studies, Utah Lake. Utah Division of Wildlife Resources, Springville, Utah.
- Wright RM, Shoesmith EA. 1988. The reproductive success of pike, *Esox lucius*: aspects of fecundity, egg density and survival. *Journal of Fish Biology* **33**:623-636.

CHAPTER IV

CONCLUSION

Millions of dollars and countless hours have been devoted to habitat restoration to recover the June sucker population in Utah Lake (JSRIP 2015). A tributary restoration project, for example, was designed to provide optimal June sucker spawning habitat and potentially rearing habitat for juveniles. However, the recent introduction of invasive northern pike may not only threaten the success of June sucker restoration, but also their downlisting from endangered to threatened. Our estimates of June sucker consumption by northern pike highlight the critical need to include restoration of rearing habitat in recovery efforts as refuge habitat from northern pike predation, particularly near the mouths of tributaries.

Our bioenergetics model indicates that while June sucker comprise only 0.8-1.0% of an average northern pike diet, the predatory impact of northern pike has the potential to decimate the June sucker population. Even at low densities, northern pike still have the ability to consume more age-0 June sucker than those naturally recruited (USFWS 1999). Thus, the June sucker population will like persist only with stocking, and the size at which June sucker are stocked may need to increase (i.e., hatchery managers will be forced to keep them in the facility longer) in order to escape the gape size of northern pike, resulting in greater costs to the UDWR. Northern pike consumption of sport fishes may have negative consequences for the various fisheries supported by this ecosystem. Similarly, the management and stocking protocols for sport fishes may also need to change to ensure those economically-valuable populations persist.

Our initial age-structured density-dependent model findings from suggest early mitigation efforts have minimal effects on the initial (i.e., through 2020) growth trajectory of the northern pike population when compared to the unmitigated scenario. We attribute the similarity in the growth trajectory between the scenarios to the fecundity of northern pike (Wright and Shoesmith 1988) and the large size of Utah Lake (38,445 ha). While the population is growing quickly, the population density relative to the size of the lake is low, making encounter rates of northern pike during angling or sampling extremely low. Over a longer period of time (i.e., 20 years after invasion), however, both the early and late mitigation scenarios result in the northern pike population reaching a lower equilibrium than in the unmitigated scenario.

Our bioenergetics and age-structured density-dependent models are calibrated to the invasive northern pike population in Utah Lake. Catch-and-release mark-recapture approaches were not an option to estimate current northern pike abundance given: 1) our concern with predation on endangered June sucker by any northern pike released for such a study; 2) June sucker conservation, and 3) the desire to minimize northern pike natural reproduction. Our models are the best tools managers have to predict not only the predatory effect of northern pike on June sucker and other sport fishes in Utah Lake, but also northern pike abundance and the population growth trajectory. Nevertheless, uncertainty and assumptions are commonplace in any modeling effort (Chatfield 2006). Therefore, future improvements for these models could include: successfully incorporating the logistic mixed-effects model into the bioenergetics model to better inform the proportion of different species of fish and macroinvertebrates consumed; including different prey energy densities accordingly; increasing our sample size,

particularly for the identification of diet items; quantifying the variance around our estimates; modeling more than three mitigation scenarios, adding the time of year each individual was removed; estimating angler harvest for different ages of northern pike and including those estimates in the model; and considering environmental influences (e.g., species interactions, the effect of drought, etc.) on northern pike population growth. While we acknowledge model uncertainty, we hope our model will serve as a useful tool to guide invasive northern pike management decisions in the face of June sucker conservation.

Combinations of empirical and theoretical approaches are commonly used to predict the predatory impact of apex invasives on native species (Paukert et al. 2003; Muhlfeld et al. 2008; Walrath et al. 2015; Scheibel et al. 2016). We used theoretical modeling approaches to guide management actions aimed at slowing the northern pike population growth trajectory, thus possibly allowing the endangered June sucker population to persist. Our findings not only highlight a need to attempt targeted removal of the invasive northern pike during spawning (Vredenberg 2004), but they also highlight the importance of preventing the spread of aquatic invasive species (Leung et al. 2002; Pimentel et al. 2005), mitigating the growth of invasive species populations (Lodge et al. 2006; Vander Zanden et al. 2010), and educating the public (Krasny & Lee 2010) about the consequences of illegal stocking, particularly in the face of endangered species conservation.

Literature Cited

- Chatfield C. 2006. Model Uncertainty. Encyclopedia of Environmentics 4.
DOI: 10.1002/9780470057339.vam030.
- June Sucker Recovery Implementation Program (JSRIP). 2015.
<http://www.junesuckerrecovery.org/index.html>. Salt Lake City, Utah. Accessed August 11 2015.
- Krasny ME and Lee S. 2010. Social learning as an approach to environmental education: lessons from a program focusing on non-indigenous, invasive species. Environmental Education Research **8**:101-119.
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London Series B, Biological Sciences **269**:2407-2413. DOI: 10.1098/rspb.2002.2179.
- Lodge DM, Williams SL, MacIsaac H, Hayes K, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT, McMichael A. 2006. Biological invasions: recommendations for U.S. policy and management. Ecological Applications **16**:2035-2054.
- Muhlfeld CC, Bennett DH, Steinhorst RK, Marotz B, Boyer M. 2008. Using bioenergetics modeling to estimate consumption of native juvenile salmonids by nonnative northern pike in the Upper Flathead River System, Montana. North American Journal of Fisheries Management **28**:636-648. DOI: 10.1577/M07-004.1.
- Paukert CP, Stancill W, DeBates TJ, Willis DW. 2003. Predatory effects of northern pike and largemouth bass: bioenergetics modeling and ten years of fish community sampling. Journal of Freshwater Ecology **18**:13-24.
- Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52**:273-288.
- Scheibel NC, Dembkowski JD, Davis JL, Chipps SR. 2016. Impacts of northern pike on stocked rainbow trout in Pactola Reservoir, South Dakota. North American Journal of Fisheries Management **36**:230-240.
- U.S. Fish and Wildlife Service (USFWS). 1999. June sucker (*Chasmistes liorus*) Recovery Plan. U.S. Fish and Wildlife Service, Denver, Colorado.

- Vander Zanden JM, Hansen GJA, Higgin SN, Kornis MS. 2010. A pound of prevention plus a pound of cure: early detection and eradication of invasive species in the Laurentian Great Lakes. *Journal of Great Lakes Research* **36**:199-205.
- Vredenburg VT. 2004. Reversing introduced species effects: Experimental removal of introduced fish leads to rapid recovery of a declining frog. *Proceedings of the National Academy of Sciences* **101**:7646-7650. DOI: 10.1073/pnas.0402321101.
- Walrath JD, Quist MC, Firehammer JA. 2015. Trophic ecology of nonnative northern pike and their effect on conservation of native Westslope cutthroat trout. *North American Journal of Fisheries Management* **35**:158-177.
- Wright RM, Shoesmith EA. 1988. The reproductive success of pike, *Esox lucius*: aspects of fecundity, egg density and survival. *Journal of Fish Biology* **33**:623-636.

APPENDICES

APPENDIX A

GENETICS RESULTS OF NORTHERN PIKE DIETS

Pre- and post-genetics identity of 42% of all northern pike (i.e., only northern pike with diet items in their stomachs) dissected between 2012 and 2016. The “Pike ID” column indicates the northern pike ID number. The “Diet item” column indicates the northern pike ID number followed by the diet item number (e.g., 1,1 is the first diet item of NOP 001). “Visual species/taxa ID” includes the identity of diet items after visual observation. “Post-genetics ID” includes the identity of diet items after genetic analysis.

Pike ID	Diet item	Capture date	Visual species/taxa ID	Post-genetics ID
1	1,1	1/26/2015	macroinvertebrates	
1	1,2	1/26/2015	unknown fish	
2	2,1	2/19/2015	macroinvertebrates	
2	2,2	2/19/2015	unknown fish	
4	4,1	4/27/2015	bluegill	
4	4,2	4/27/2015	unknown, minnow	green sunfish
4	4,3	4/27/2015	possible June sucker	desert sucker
5	5,1	4/27/2015	black crappie	green sunfish
8	8,1	4/27/2015	macroinvertebrates	
8	8,2	4/27/2015	macroinvertebrates	
8	8,3	4/27/2015	white bass, centrarchid, or minnow	green sunfish
9	9,1	4/27/2015	June sucker or fathead minnow	green sunfish
10	10,1	4/27/2015	minnow	green sunfish
10	10,2	4/27/2015	minnow or June sucker	green sunfish
10	10,3	4/27/2015	macroinvertebrate tissue	
10	10,4	4/27/2015	macroinvertebrate	
11	11,1	4/27/2015	beetle	
11	11,2	4/27/2015	grasshopper	
11	11,3	4/27/2015	fish tissue	unknown fish
12	12,1	4/27/2015	grasshopper	
12	12,2	4/27/2015	unknown, fathead minnow	fathead minnow
12	12,3	4/27/2015	unknown	unknown fish
13	13,1	4/27/2015	centrarchid, black crappie	green sunfish
14	14,1	4/27/2015	macroinvertebrates	

15	15,1	no date	white bass	
16	16,1	4/27/2015	macroinvertebrates	
16	16,2	4/27/2015	worm	
17	17,1	6/25/2015	centrarchid	common carp
17	17,2	6/25/2015	unknown fish	common carp
18	18,1	6/25/2015	June sucker or minnow	green sunfish
19	19,1	2/26/2015	macroinvertebrates	
20	20,1	6/12/2015	unknown, minnow	green sunfish
22	22,1	2/14/2015	macroinvertebrates	
24	24,1	6/9/2015	large chunk	white bass
24	24,2	6/9/2015	caudal fin	white bass
25	25,1	2/11/2015	white bass	white bass
27	27,1	no date	fish body	white bass
27	27,2	no date	caudal fin	white bass
30	30,1	no date	white bass	
33	33,1	5/20/2015	unknown fish	northern pike
34	34,1	5/20/2015	tissue	northern pike
42	42,1	2/18/2015	macroinvertebrates	
43	43,1	no date	white bass	
44	44,1	2/18/2015	macroinvertebrates	
45	45,1	2/18/2015	macroinvertebrates	
46	46,1	2/18/2015	macroinvertebrates	
47	47,1	2/17/2015	macroinvertebrates	
51	51,1	2/17/2015	macroinvertebrates	
52	52,1	4/6/2015	possible June sucker	northern pike
53	53,1	4/6/2015	unknown	unknown fish
54	54,1	4/6/2015	macroinvertebrates	
56	56,1	8/4/2015	possible minnow	northern pike
56	56,2	8/4/2015	possible minnow	mottled sculpin
56	56,3	8/4/2015	possible chironomid	
57	57,1	8/4/2015	minnow	northern pike
57	57,2	8/4/2015	minnow	northern pike
57	57,3	8/4/2015	tissue	northern pike
57	57,3	8/4/2015	chironomid	
58	58,1	8/4/2015	possible fathead minnow or June sucker	unknown fish
58	58,2	8/4/2015	possible fathead minnow	unknown fish
58	58,3	8/4/2015	unknown fish	unknown fish
58	58,4	8/4/2015	unknown fish	northern pike
58	58,5	8/4/2015	possible minnow	unknown fish
58	58,6	8/4/2015	tissue	mottled sculpin

58	58,7	8/4/2015	unknown fish	unknown fish
58	58,8	8/4/2015	unknown fish	fathead minnow
59	59,1	8/4/2015	possible minnow	northern pike
59	59,2	8/4/2015	possible minnow	northern pike
59	59,3	8/4/2015	minnow or June sucker	fathead minnow
59	59,4	8/4/2015	possible minnow	unknown fish
60	60,1	2/3/2014	unknown fish	unknown fish
60	60,2	2/3/2014	unknown fish	yellow perch
63	63,1	2/3/2014	possible June sucker	white bass
65	65,1	10/17/2013	possible white bass	green sunfish
68	68,1	4/6/2015	macroinvertebrate	
71	71,1	4/6/2015	macroinvertebrates	
72	72,1	4/6/2015	macroinvertebrates	
73	73,1	4/6/2015	macroinvertebrate	
74	74,1	4/6/2015	macroinvertebrate	
75	75,1	4/6/2015	macroinvertebrate	
76	76,1	4/6/2015	macroinvertebrate	
80	80,1	5/9/2012	carp	
80	80,1	2/3/2016	macroinvertebrate	
81	81,1	3/23/2016	unknown centrarchid	green sunfish
81	81,2	3/23/2016	western mosquitofish	unknown fish
82	82,1	2/19/2016	macroinvertebrate	green sunfish
83	83,1	2/14/16	macroinvertebrate	
84	84,1	2/14/2016	macroinvertebrates	
85	85,1	1/20/2016	macroinvertebrates	
86	86,1	1/22/2016	macroinvertebrates	
87	87,1	1/20/2016	macroinvertebrates	
80	90,1	1/13/2016	macroinvertebrates	
91	91,1	4/25/2016	western mosquitofish	green sunfish
91	91,2	4/25/2016	unknown	green sunfish
94	94,1	2/10/2016	unknown fish	northern pike
97	97,1	3/23/2016	common carp	common carp
99	99,1	no date	common carp	common carp
99	99,2	no date	bluegill sunfish	green sunfish
101	101,1	10/2/2015	unknown fish	green sunfish
102	102,1	no date	white bass	white bass
104	104,1	no date	bones and tissue (connected)	
108	108,1	no date	tissue and bone (disconnected)	
109	109,1	no date	white bass	white bass
109	109,2	no date	white bass	white bass

109	109,3	no date	white bass	white bass
109	109,4	no date	unknown fish	white bass
109	109,5	no date	bones connected	white bass
109	109,6	no date	unknown (bone length)	white bass
109	109,7	no date	bones disconnected	northern pike
111	111,1	5/2/2016	unknown large chunk of tissue	northern pike
111	111,2	5/2/2016	unknown middle chunk of tissue	white bass
111	111,3	5/2/2016	unknown small chunk of tissue	
111	111,4	5/2/2016	unknown (tissue and bone)	white bass
115	115,1	no date	white bass	white bass
115	115,2	no date	white bass	white bass
115	115,3	no date	white bass	white bass
116	116	4/29/2015	bones, no tissue	
122	122	no date	bones	
123	123	no date	bones, some tissue	white bass

APPENDIX B

NORTHERN PIKE GROWTH DATA

Back-calculated growth information for 79 of 125 northern pike. The “Fish ID” column indicates the identity of the northern pike. “Age i” indicates the age at each annulus or the edge of the otolith. “Length at i (um)” indicates the length from the origin of the otolith. “Total Radius (um)” indicates the total length from the origin of the otolith to the edge. “Length at capture (mm)” indicates total length of the pike at capture. “Length at age (Li)” indicates the back-calculated length-at-age in mm.

Fish ID	Age i	Length at i (um)	Total Radius (um)	Length at capture (mm)	Length at age (Li)
UTLNOP001	1	930.02	1051.29	293	260.1715423
UTLNOP001	edge	1051.29	1051.29	293	293
UTLNOP002	1	976.02	1114.74	277	243.5762377
UTLNOP002	edge	1114.74	1114.74	277	277
UTLNOP003	1	1023.8	1508.33	450	308.1453643
UTLNOP003	2	1189.09	1508.33	450	356.536904
UTLNOP003	3	1339.92	1508.33	450	400.6950257
UTLNOP003	edge	1508.33	1508.33	450	450
UTLNOP004	1	894.42	1068.61	240	202.2494061
UTLNOP004	edge	1068.61	1068.61	240	240
UTLNOP005	1	692.55	855.35	233	190.2534612
UTLNOP005	edge	855.35	855.35	233	233
UTLNOP006	1	658.71	799.7	280	232.1177015
UTLNOP006	edge	799.7	799.7	280	280
UTLNOP007	1	587.08	869.8	295	201.8467179
UTLNOP007	edge	869.8	869.8	295	295
UTLNOP008	1	891.69	1042.5	271	233.0132394
UTLNOP008	edge	1042.5	1042.5	271	271
UTLNOP009	1	872.15	1102.38	235	187.6771025
UTLNOP009	edge	1102.38	1102.38	235	235
UTLNOP010	1	846.39	1233.77	201	140.530452
UTLNOP010	2	1065.81	1233.77	201	174.7816478
UTLNOP010	edge	1233.77	1233.77	201	201

UTLNOP011	1	865.25	1031.55	288	242.9262595
UTLNOP011	edge	1031.55	1031.55	288	288
UTLNOP012	1	624.41	751.12	215	180.1493518
UTLNOP012	edge	751.12	751.12	215	215
UTLNOP013	1	686.88	813.79	177	150.7085035
UTLNOP013	edge	813.79	813.79	177	177
UTLNOP014	1	586.05	727.19	219	178.1266758
UTLNOP014	edge	727.19	727.19	219	219
UTLNOP015	1	999.47	1860.33	594	323.0206536
UTLNOP015	2	1431.26	1860.33	594	458.9384242
UTLNOP015	3	1772.37	1860.33	594	566.3121724
UTLNOP015	edge	1860.33	1860.33	594	594
UTLNOP016	edge	876.97	876.97	170	170
UTLNOP017	edge	280.2	280.2	82	82
UTLNOP018	1	934.85	1077.74	288	250.9311197
UTLNOP018	edge	1077.74	1077.74	288	288
UTLNOP019	1	988.92	1200.21	314	260.2026553
UTLNOP019	edge	1200.21	1200.21	314	314
UTLNOP020	1	625.5	706.02	210	187.0091119
UTLNOP020	edge	706.02	706.02	210	210
UTLNOP021	1	896.3	1626.9	560	312.2947606
UTLNOP021	2	1259.59	1626.9	560	435.4659027
UTLNOP021	3	1444.26	1626.9	560	498.0770806
UTLNOP021	edge	1626.9	1626.9	560	560
UTLNOP022	1	1090.43	1335.57	449	368.1309833
UTLNOP022	edge	1335.57	1335.57	449	449
UTLNOP023	1	1092.96	1453.16	421	318.7298315
UTLNOP023	edge	1453.16	1453.16	421	421
UTLNOP024	1	944.35	2065.48	812	375.8162283
UTLNOP024	2	1416.07	2065.48	812	559.3423214
UTLNOP024	3	1638.77	2065.48	812	645.9853744
UTLNOP024	4	1817.35	2065.48	812	715.4632208
UTLNOP024	edge	2065.48	2065.48	812	812
UTLNOP025	1	954.46	1890.39	655	334.8740055
UTLNOP025	2	1364.69	1890.39	655	475.1892927
UTLNOP025	3	1699.17	1890.39	655	589.5950096
UTLNOP025	edge	1890.39	1890.39	655	655
UTLNOP026	1	980.29	2125.38	797	372.1317303
UTLNOP026	2	1260.39	2125.38	797	476.0585852
UTLNOP026	3	1482.6	2125.38	797	558.5062341

UTLNOP026	4	1589.84	2125.38	797	598.2960089
UTLNOP026	5	1729.81	2125.38	797	650.2297536
UTLNOP026	6	1857.28	2125.38	797	697.5255563
UTLNOP026	7	1943.96	2125.38	797	729.6868617
UTLNOP026	edge	2125.38	2125.38	797	797
UTLNOP027	1	776.73	1847.51	760	324.3934051
UTLNOP027	2	966.31	1847.51	760	401.5169022
UTLNOP027	3	1289.39	1847.51	760	532.9498564
UTLNOP027	4	1489.71	1847.51	760	614.4425188
UTLNOP027	5	1710.16	1847.51	760	704.1243152
UTLNOP027	6	1822.4	1847.51	760	749.7849403
UTLNOP027	edge	1847.51	1847.51	760	760
UTLNOP028	1	752.03	1598.93	605	289.0061347
UTLNOP028	2	993.17	1598.93	605	378.979875
UTLNOP028	3	1292.59	1598.93	605	490.6989483
UTLNOP028	4	1491.23	1598.93	605	564.815162
UTLNOP028	edge	1598.93	1598.93	605	605
UTLNOP029	1	812.73	1805.74	631	288.6261832
UTLNOP029	2	1056.43	1805.74	631	372.6500089
UTLNOP029	3	1463.37	1805.74	631	512.9563512
UTLNOP029	4	1703.2	1805.74	631	595.6458634
UTLNOP029	edge	1805.74	1805.74	631	631
UTLNOP030	1	970.86	1840.33	642	342.6583073
UTLNOP030	2	1310.74	1840.33	642	459.672413
UTLNOP030	3	1513.67	1840.33	642	529.5372844
UTLNOP030	4	1671.17	1840.33	642	583.761486
UTLNOP030	edge	1840.33	1840.33	642	642
UTLNOP031	1	1089.88	1878.6	648	379.4716146
UTLNOP031	2	1471.04	1878.6	648	509.2417223
UTLNOP031	3	1619.63	1878.6	648	559.8308196
UTLNOP031	4	1731.57	1878.6	648	597.9420219
UTLNOP031	edge	1878.6	1878.6	648	648
UTLNOP032	1	960.18	1922.42	692	349.8387441
UTLNOP032	2	1437.31	1922.42	692	519.5005748
UTLNOP032	3	1626.91	1922.42	692	586.9201106
UTLNOP032	4	1777.68	1922.42	692	640.532154
UTLNOP032	edge	1922.42	1922.42	692	692
UTLNOP033	1	762.29	1498.96	665	342.316169
UTLNOP033	2	1090.07	1498.96	665	485.8937629
UTLNOP033	3	1231.94	1498.96	665	548.0371312

UTLNOP033	4	1414.22	1498.96	665	627.8813066
UTLNOP033	edge	1498.96	1498.96	665	665
UTLNOP034	1	689.75	1655.99	672	284.8073227
UTLNOP034	2	1169.83	1655.99	672	477.1854695
UTLNOP034	3	1431.46	1655.99	672	582.0261096
UTLNOP034	4	1529.27	1655.99	672	621.2206325
UTLNOP034	edge	1655.99	1655.99	672	672
UTLNOP035	1	1023.15	1813.46	645	367.5726275
UTLNOP035	2	1426.56	1813.46	645	509.1841171
UTLNOP035	3	1588.27	1813.46	645	565.9501714
UTLNOP035	4	1732.18	1813.46	645	616.4677825
UTLNOP035	edge	1813.46	1813.46	645	645
UTLNOP036	1	796.54	1527.88	534	282.4193846
UTLNOP036	2	1084.12	1527.88	534	381.3467691
UTLNOP036	3	1381.59	1527.88	534	483.6763089
UTLNOP036	edge	1527.88	1527.88	534	534
UTLNOP037	1	827.78	2064.2	640	261.6885438
UTLNOP037	2	1272.28	2064.2	640	397.6936572
UTLNOP037	3	1660.14	2064.2	640	516.3684452
UTLNOP037	4	1833.87	2064.2	640	569.5251794
UTLNOP037	edge	2064.2	2064.2	640	640
UTLNOP038	1	662.14	1730.1	735	286.4888987
UTLNOP038	2	881.64	1730.1	735	378.6723014
UTLNOP038	3	1159.3	1730.1	735	495.281156
UTLNOP038	4	1307.92	1730.1	735	557.6970891
UTLNOP038	5	1444.26	1730.1	735	614.9557912
UTLNOP038	edge	1730.1	1730.1	735	735
UTLNOP039	1	635.75	1142.75	520	293.0246073
UTLNOP039	2	936.68	1142.75	520	427.7459188
UTLNOP039	3	1055.66	1142.75	520	481.0112683
UTLNOP039	edge	1142.75	1142.75	520	520
UTLNOP040	1	1097.79	2078.83	670	357.7829098
UTLNOP040	2	1543.58	2078.83	670	499.6560818
UTLNOP040	3	1692.67	2078.83	670	547.104143
UTLNOP040	4	1840.39	2078.83	670	594.1162002
UTLNOP040	5	1990.74	2078.83	670	641.9652578
UTLNOP040	edge	2078.83	2078.83	670	670
UTLNOP041	1	711.75	1971.44	846	310.8055497
UTLNOP041	2	1086.05	1971.44	846	469.8314074
UTLNOP041	3	1350.61	1971.44	846	582.232906

UTLNOP041	4	1538.29	1971.44	846	661.9710118
UTLNOP041	5	1705.03	1971.44	846	732.8125066
UTLNOP041	6	1863.84	1971.44	846	800.2848456
UTLNOP041	edge	1971.44	1971.44	846	846
UTLNOP042	1	1127.67	1507.88	582	437.3700202
UTLNOP042	2	1434.6	1507.88	582	554.124655
UTLNOP042	3	1482.44	1507.88	582	572.3227514
UTLNOP042	edge	1507.88	1507.88	582	582
UTLNOP043	1	1026.99	1946.45	650	346.9270511
UTLNOP043	2	1336.88	1946.45	650	449.0731761
UTLNOP043	3	1540.49	1946.45	650	516.1872247
UTLNOP043	4	1678.51	1946.45	650	561.6814588
UTLNOP043	5	1782	1946.45	650	595.7938938
UTLNOP043	edge	1946.45	1946.45	650	650
UTLNOP044	1	756.48	1215.95	422	265.7170959
UTLNOP044	2	1009.61	1215.95	422	351.816061
UTLNOP044	edge	1215.95	1215.95	422	422
UTLNOP045	1	751.47	913.85	322	266.2788814
UTLNOP045	edge	913.85	913.85	322	322
UTLNOP046	1	659.14	1222.42	608	331.7143901
UTLNOP046	2	839.98	1222.42	608	420.4153731
UTLNOP046	3	915.09	1222.42	608	457.2563974
UTLNOP046	4	1005.01	1222.42	608	501.3616417
UTLNOP046	5	1109.76	1222.42	608	552.7409161
UTLNOP046	edge	1222.42	1222.42	608	608
UTLNOP047	1	827.88	1177.78	354	251.3306212
UTLNOP047	2	1044.99	1177.78	354	315.0361051
UTLNOP047	edge	1177.78	1177.78	354	354
UTLNOP048	1	643.4	1288.95	416	211.865065
UTLNOP048	2	1187.67	1288.95	416	383.9733774
UTLNOP048	edge	1288.95	1288.95	416	416
UTLNOP049	1	614.26	1436.76	555	242.0943825
UTLNOP049	2	991.39	1436.76	555	385.5668391
UTLNOP049	3	1208.06	1436.76	555	467.9951189
UTLNOP049	edge	1436.76	1436.76	555	555
UTLNOP050	1	822.47	1773.74	645	303.5920319
UTLNOP050	2	1100.94	1773.74	645	403.534085
UTLNOP050	3	1345.6	1773.74	645	491.3418299
UTLNOP050	4	1522.58	1773.74	645	554.8594245
UTLNOP050	5	1673.53	1773.74	645	609.0349296

UTLNOP050	edge	1773.74	1773.74	645	645
UTLNOP051	1	648.54	910.12	391	281.0387947
UTLNOP051	2	783.12	910.12	391	337.6126115
UTLNOP051	edge	910.12	910.12	391	391
UTLNOP052	1	849.09	1112.57	314	241.6298541
UTLNOP052	edge	1112.57	1112.57	314	314
UTLNOP053	1	980.07	1371.92	344	248.1482437
UTLNOP053	2	1241.44	1371.92	344	312.0828451
UTLNOP053	edge	1371.92	1371.92	344	344
UTLNOP054	1	715.74	926.18	248	193.5620726
UTLNOP054	edge	926.18	926.18	248	248
UTLNOP055	edge	738.17	738.17	200	200
UTLNOP056	edge	608.32	608.32	170	170
UTLNOP057	edge	516.95	516.95	160	160
UTLNOP058	edge	659.7	659.7	175	175
UTLNOP059	edge	498.97	498.97	130	130
UTLNOP060	1	1082.35	2098.68	740	385.7121311
UTLNOP060	2	1359.85	2098.68	740	482.4473289
UTLNOP060	3	1689.19	2098.68	740	597.2537075
UTLNOP060	4	1931.76	2098.68	740	681.8124713
UTLNOP060	5	2035.12	2098.68	740	717.8432823
UTLNOP060	edge	2098.68	2098.68	740	740
UTLNOP061	1	683.36	1699.65	612	251.0889412
UTLNOP061	2	1100.82	1699.65	612	399.3398643
UTLNOP061	3	1336.35	1699.65	612	482.9827041
UTLNOP061	4	1589.88	1699.65	612	573.0178129
UTLNOP061	edge	1699.65	1699.65	612	612
UTLNOP062	1	887.55	1622.84	576	318.8315477
UTLNOP062	2	1281.84	1622.84	576	456.7348907
UTLNOP062	3	1449.78	1622.84	576	515.4720826
UTLNOP062	edge	1622.84	1622.84	576	576
UTLNOP063	1	1041.38	1713.35	630	386.2145316
UTLNOP063	2	1352.19	1713.35	630	498.9739724
UTLNOP063	3	1485.76	1713.35	630	547.4321253
UTLNOP063	4	1603.41	1713.35	630	590.1146266
UTLNOP063	edge	1713.35	1713.35	630	630
UTLNOP064	1	508.9	729.03	261	184.7306603
UTLNOP064	edge	729.03	729.03	261	261
UTLNOP065	1	663.08	1235.66	420	229.2774694
UTLNOP065	2	1046.48	1235.66	420	356.9854198

UTLNOP065	edge	1235.66	1235.66	420	420
UTLNOP066	edge	639.77	639.77	206	206
UTLNOP067	1	1180.32	1571.29	397	300.310635
UTLNOP067	2	1474.5	1571.29	397	373.0632181
UTLNOP067	edge	1571.29	1571.29	397	397
UTLNOP068	1	932.06	1110.23	243	205.3529356
UTLNOP068	edge	1110.23	1110.23	243	243
UTLNOP069	1	690.08	814.12	201	171.6568275
UTLNOP069	edge	814.12	814.12	201	201
UTLNOP070	1	776.55	946	213	176.3533029
UTLNOP070	edge	946	946	213	213
UTLNOP071	1	685.47	867.37	258	205.6573769
UTLNOP071	edge	867.37	867.37	258	258
UTLNOP072	edge	940.99	940.99	239	239
UTLNOP073	1	728.25	892.31	198	163.1420074
UTLNOP073	edge	892.31	892.31	198	198
UTLNOP074	1	627.41	767.53	200	165.0233987
UTLNOP074	edge	767.53	767.53	200	200
UTLNOP075	1	866.43	960.05	198	179.5119881
UTLNOP075	edge	960.05	960.05	198	198
UTLNOP076	1	774.27	853.96	184	167.6142593
UTLNOP076	edge	853.96	853.96	184	184
UTLNOP077	1	553.11	682.47	170	139.3711337
UTLNOP077	edge	682.47	682.47	170	170
UTLNOP078	1	702.88	777.81	169	153.5296297
UTLNOP078	edge	777.81	777.81	169	169
UTLNOP079	1	956.17	1857.34	675	351.5746119
UTLNOP079	2	1264.36	1857.34	675	462.1824554
UTLNOP079	3	1521.06	1857.34	675	554.3107965
UTLNOP079	4	1677.34	1857.34	675	610.3989038
UTLNOP079	5	1784.12	1857.34	675	648.7217096
UTLNOP079	edge	1857.34	1857.34	675	675

APPENDIX C

NORTHERN PIKE LENGTH-FREQUENCY HISTOGRAMS

Length-frequency histograms for northern pike captured between 2012 and 2016.

