Introduction of Saugeye *Sander vitreum x Sander canadense* to Improve Crappie *Pomoxis* Fisheries in Southern Reservoirs: Overall Potential and Fish Community Response

Proposal for Master's Thesis

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Chapter I

Seasonal and Ontogenetic Variation of Saugeye Food Habits in Southern Reservoirs

Introduction

Predator-prey interactions are crucial in shaping fish communities in nearly all aquatic ecosystems (Northcote 1988; Tonn et al. 1992). Predation can directly control dynamic rates in prey populations (Santucci and Wahl 2003) and indirectly alter prey species by affecting growth (Fraser and Gilliam 1992) and competition (Persson 1991), especially in supplementary stocked fisheries (Fayram et al. 2005). Thus, it is important to understand predator-prey interactions in order to successfully manage for predator-prey balance after introducing new top predators into reservoir ecosystems.

Saugeye *Sander vitreum x Sander canadense* are a hybrid predator species created in fish hatcheries with a female Walleye and male Sauger. Saugeye have been introduced in several states throughout the U.S. to supplement declining Walleye fisheries (Denlinger et al. 2006), introduce additional recreational fishing opportunities, and as a biomanipulation tool for improving over-abundant crappie *Pomoxis* spp. fisheries (Boxrucker 2002; Galinat et al. 2002). Saugeye display faster growth (Siegwarth and Summerfelt 1990) and different habitat preferences (Johnson et al. 1988) than its parent species. Consequently, Walleye and saugeye food habits also differ (Johnson et al. 1988; Walter 2000), emphasizing the importance of recognizing predator-prey interactions when stocking saugeye. However, few studies have addressed saugeye food habits (Johnson et al. 1988; Walter 2000; Galinat et al. 2002), and little is known about their food habits at southern latitudes (Leeds 1988).

The purpose of this study will be to determine food habits of Oklahoma saugeye populations. Specifically I will test for lake-, seasonal-, and size-related variation in food habits and saugeye relative weight. Understanding this predator-prey interaction will also be the first step in evaluating the viability of different saugeye management strategies among lakes (Chapter 2; i.e. Stunted crappie management vs. sport fishery management) and will identify potential community-level effects of stocking saugeye into Oklahoma reservoirs (Chapter 3).

Methods

Study Sites and Diet Collection

This study will be conducted in Lake Carl Blackwell (North Central OK; 1356 ha), Lake McMurtry (North Central OK; 467 ha), Lake Lawtonka (Southwest OK; 970 ha), Lake Jean Neustadt (South Central OK, 187 ha) and Thunderbird Reservoir (Central OK; 2165 ha). Lake Carl Blackwell and Lake McMurtry data will be collected by Dray Carl, whereas the remaining lakes will be sampled by Oklahoma Department of Wildlife Conservation personnel.

Saugeye for diet analysis will be sampled seasonally with boat electrofishing, and will be supplemented with 24.4 m, experimental-mesh, monofilament gill nets will be deployed for 2-hr sets if electrofishing catch rates are low. Diet samples for lakes Carl Blackwell and McMurtry will begin in summer 2016 and sampling for lakes Lawtonka, Jean Neustadt, and Thunderbird will begin in fall 2016. Spring, summer, and fall sampling sessions will be approximately two months in duration with samples distributed throughout each two-month interval (minimum of five sampling events per season). Saugeye thermal tolerance is slightly higher than that of Walleye (Zweifel et al. 2010), and Walleye begin to seek thermal refuge at temperatures above 23°C (Ager 1976). Thus, the transition between spring and summer as well as summer and fall seasons will be defined by this temperature threshold, and the summer sampling session will be conducted during peak reservoir water temperatures (July-August; approximately 26 - 29°C). Sampling will initially be conducted during daytime and nighttime. Assuming no difference in diets is seen from the preliminary data, sampling will occur at the time of day that minimizes the percentage of empty saugeye stomachs. At least 40 diets will be collected from each lake during each season.

All collected saugeye will be measured (TL; mm) and weighed (g), and diet contents will be collected via gastric lavage, as recommended for Walleye diet collection (Kamler and Pope 2001; Quist et al. 2002a). Small saugeye stomachs will be flushed with a large syringe (150 mL) and vinyl tubing. Larger saugeye will be flushed using a bilge pump and vinyl tubing (12.7 mm inside diameter) with a control valve. Diet contents will be collected in a 500 micron wire-mesh sieve, rinsed into Whirl-Paks®, and preserved in 95% ethyl alcohol for later identification. Forty saugeye stomachs of varying fish lengths will be dissected post-gastric-lavage in spring 2017 to evaluate the efficiency of our gastric lavage techniques.

Diet Processing and Statistical Comparisons

Saugeye prey items will be identified to the nearest species (fish) or family (invertebrates) in the lab. Total length, standard length, or backbone length of prey (Miller 1960) will be recorded for later conversions to pre-digested weight using regression equations for White Crappie *Pomoxis annularis* and Gizzard Shad *Dorosoma cepedianum* (Carl and Shoup, unpublished data) and regression equations from FishBase (Froese and Pauly 2016) for other prey species. Wet weight (g) for each prey item will also be recorded. Several diet indices will be used to analyze diets to gain a universal view of saugeye food habits (Chipps and Garvey 2007). Frequency of Occurrence (O_i) and Mean Proportion by Number (MN_i) diet indices are used to assess prey preference, though Mean Proportion by Weight (MW_i) is better for evaluating energy flow (Chipps and Garvey 2007).

Fish diets can vary among systems (Vander Zanden et al. 2000), seasons (Quist et al. 2002b), and individual fish size (Liao et al. 2002), thus these comparisons will be analyzed for additional insight into saugeye food habits. Saugeye will be split into three size categories for analyses according to length frequency histograms (200-324mm, 325-449mm, >450mm). When comparing a single prey species or family, analysis of variance (ANOVA) with repeated measures (sample date, lake) to account for autocorrelation will be used. If data not normally distributed, an arcsine transformation will be used (Weinman and Lauer 2007). If data are not normally distributed, a rank transformation will be used (Soupir et al. 2000). Simultaneously comparing all prey categories is also possible through multivariate statistics, assuming prey proportions have a multivariate-normal distribution and similar variance-covariance structure (Chipps and Garvey 2007). These multivariate methods will also be examined using an approach similar to Liao et al. (2002) with Bray-Curtis similarity coefficients for pairwise comparisons. Seasonal variation in saugeye condition will be assessed with repeated measures ANOVA. Saugeye total length versus prey item length will also be plotted to examine potential size ranges of prey vulnerable to saugeye predation (Kaufman et al. 2009).

Prey Availability

Prey availability in the form of presence/absence, abundance, or size structure may also relate to variation in saugeye food habits among lakes and seasons. Therefore, we will seine the nearshore prey assemblage to provide an index of prey availability among lakes and seasons with the goal of identifying large-magnitude differences that might explain variation in saugeye diets among lakes or seasons. Five seine hauls per season at each lake will be taken with a 12.2 m x 1.8 m x 4.8 mm Delta mesh seine with a 1.8 m x 1.8 m x 1.8m x 3.2 mm mesh bag using a pivot technique (one stationary pole on shore while the other pole completes 180° arc). Sites where saugeye are routinely captured will be chosen as seining sites to characterize prey assemblage corresponding with the collected diet data. All fish captured in seine hauls will be identified to species, enumerated, and measured (random first 30 of each species).

Chapter II

Annual Saugeye Consumption of Crappie and Influence on Crappie Growth in Oklahoma Reservoirs

Introduction

High densities of fish can often result in increased intraspecific competition and slow growth rates within a population (Isermann and Paukert 2010), which can be undesirable to fishermen. Components of intraspecific competition that contribute to slowing growth rates include individual variation in foraging ability (Metcalfe 1986), limited prey availability (Mittelbach 1988), or habitat displacement (Abrams 1986). Several fishery management strategies have been developed to combat the associated effects of high-density sportfish populations, including mechanical habitat alterations (Olson et al. 1998; Unmuth et al. 1999) and prey stockings (Noble 1981; Devries and Stein 1990). However, removal of individuals from the population (i.e. thinning) is generally most common (Boxrucker and Irwin 2002).

A convenient strategy for removing individuals from a high-density population is angler harvest (Isermann and Paukert 2010). A protected slot limit would be ideal for high-density, slow-growing crappie populations, where the harvest of smaller fish is promoted, reducing intraspecific competition (Isermann and Paukert 2010). Protected slot length limits can improve growth in recreationally important fisheries such as Largemouth Bass *Micropterus salmoides* (Wilde 1997), Northern Pike *Esox lucius* (Pierce 2010), and Salmonids (Power and Power 1996). However, implementation of a protected slot limit on crappie populations is unrealistic and, due to angler behavior, likely would not remove enough small fish to influence crappie population dynamics.

A high biomass of predators could reduce biomass and maintain desirable growth rates in crappie populations in small impoundments (Willis et al. 1984). Similar to Largemouth Bass and Bluegill *Lepomis macrochirus* dynamics in ponds (Guy and Willis 1990) this management strategy would only be effective if the predators consume enough to influence the prey population size. This predatory-control approach has been the basis of several Oklahoma Department of Wildlife Conservation (ODWC) saugeye introductions. Lakes containing abundant, slow-growing crappie are stocked with saugeye to reduce small crappie abundance and improve growth through density-dependent relief in competition, much as harvest of small fish with a slot limit functions. However, the effectiveness of this strategy has not been fully established.

Crappie grew faster after saugeye introduction in Lake Thunderbird, Oklahoma (Boxrucker 2002) and Richmond Lake, South Dakota (Galinat et al. 2002), suggesting saugeye can effectively reduce competition of small crappie. However, these studies lacked control lakes and the erratic nature of crappie recruitment (Hooe 1991; Allen and Miranda 1998; Dubuc and DeVries 2002) may have accounted for changes in crappie growth independent of saugeye introduction. Further, even without changes in crappie recruitment, inter-annual changes in environmental conditions (temperature, flood versus drought, etc.) could alter crappie growth rates independent of saugeye introductions. Additionally, some Oklahoma reservoirs with established saugeye populations have poor crappie size structure (Ryan Ryswyk ODWC, personal communication), calling into question the effectiveness of this biomanipulation in all systems.

In order for saugeye to effectively control over-abundant crappie populations, they must consume sufficient crappie to alter crappie growth rates. Therefore, investigating annual consumption of crappie by saugeye is the first step in evaluating the effectiveness of this management strategy. The first objective of this study will be to estimate annual saugeye consumption of crappie using a bioenergetics modeling approach with data from three Oklahoma reservoirs. The second objective will be to determine the population-level effect saugeye would have on crappie growth and size structure, given the amount of crappie they consume. By directly estimating crappie consumption by saugeye in multiple lakes, this study will determine whether saugeye introductions can be used to improve crappie growth, and if so, begin to identify conditions this strategy is likely to be effective.

Methods

Study Sites and Model Approach

This study will be conducted in Lake Carl Blackwell (North Central OK), Lake Thunderbird (Central Oklahoma), and Lake Lawtonka (Southwest OK). Reservoirs were chosen using several criteria including: 1) available ODWC interest and help, 2) presence of an established saugeye population, and 3) an attempt to provide a range of saugeye consumption rates seen statewide (i.e., included reservoirs where crappie control appears to have occurred and places where it has not). Anecdotal evidence suggests saugeye predation on crappie is minimal at Lake Lawtonka (Ryan Ryswyk, personal communication) and high at Thunderbird Reservoir (Leeds 1988). Lake Carl Blackwell was chosen to with the assumption that predatory control would be between these other two lakes due to some evidence of moderate crappie predation (Carl and Shoup, unpublished data, spring 2016).

A series of models will be used to estimate saugeye consumption of crappie and potential influences on crappie growth and size structure. First, a saugeye bioenergetics model (Zweifel et al. 2010) using lake-specific saugeye population parameters and diet data will be used to estimate crappie consumption. Next, an age-structured yield-per-recruit model with density-dependent growth (Allen and Miranda 1998) will be used to estimate the change in crappie growth and size structure both with and without consumption by saugeye. A simplified schematic of the overall modeling approach is provided in Figure 1.

Saugeye Bioenergetics

Annual consumption estimates of saugeye will be calculated using the saugeye bioenergetics model of Zweifel et al 2010 modelled within Fish Bioenergetics 3.0 (Hanson 1997). This bioenergetics approach is an established tool for estimating prey biomass consumed by stocked piscivores (Kitchell and Crowder 1986; Lathrop et al. 2002; Evans et al. 2014). Bioenergetics models are based on a balanced energy equation (Hartman and Hayward 2007):

$$C = G + (M + SDA) + F + U$$

where C is consumption, G is growth, M is metabolism, SDA is specific dynamic action, F is egestion, and U is excretion.

One of the most critical inputs when evaluating population-level consumption is population biomass; two options are available for obtaining this estimate. First, a Schnabel mark-recapture (Seber 1982) of age-1 saugeye in the spring can be conducted (to estimate age-0 mortality from the known number of saugeye that were stocked the previous year), and the total mortality rate of age-1+ saugeye can be estimated from a catch curve and used to estimate population size for each age class starting with the known age-1 abundance. Alternatively, I will use the known number of stocked age-0 saugeye, an estimate of first-year mortality from the literature (Stahl et al. 1996), and the mortality rate of age-2+ saugeye from catch-curve analysis to estimate population size, similar to Denlinger et al. (2006).

A subsample of saugeye will be sacrificed for otolith collection during spring 2017 while electrofishing for the mark-recapture estimate in Lake Carl Blackwell and Lake Lawtonka. Saugeye otoliths were recently collected (2014) at Lake Thunderbird so data from this collection event will be used. The results from otolith analysis paired with the size-based population size estimate will provide estimates of abundance-at-age and mean weight-at-age for size-specific inputs into the bioenergetics model. Otolith sample size will be based on recommendations of Coggins et al. (2013) with 10 fish collected per length bin where length bins are calculated using Von Bertalanffy length infinity divided by 30. The best method of fixing saugeye otoliths for aging (i.e. whole mount, cracked, etc.) will be determined and used throughout the study. Two independent readers will age each fish; if a discrepancy in age of an individual fish appears, the otolith will be reexamined together, and a consensus age will be agreed upon.

Another important input for bioenergetics modeling, and specifically for the saugeye – crappie question, is a seasonally-stratified diet composition estimate. A detailed, seasonally-stratified diet study will be conducted (see details in Chapter 1) at each of the study lakes, and these lake- and size-specific diet compositions will be used as bioenergetic inputs. Thermal history data will be collected with HOBO® temperature loggers deployed at two depths above the anticipated thermocline depth in Lake Carl Blackwell and Lake Lawtonka. Bioenergetics outputs are relatively insensitive to small temperature variation typical across distances as small as those between lakes in this study (Evans et al. 2014); therefore, mean thermal history values from Carl Blackwell and Lawtonka will be used for modeling of Thunderbird Reservoir (located between the two reservoirs, latitudinal). Both saugeye and crappie (1223.9 Cal/g wet weight) energy density values will be obtained from the literature. Mortality rates will be estimated from catch curves constructed from spring 2017 saugeye sampling data. These data will be used within Fish Bioenergetics 3.0 to estimate annual saugeye consumption of crappie in each study lake.

Density-Dependent Crappie Growth and Population Modeling

Predation will only improve growth rates of small crappie if intraspecific competition is currently in effect (McInerny and Cross 1999; Boxrucker 2002). Pope et al. (2004) found significant crappie density-dependent growth typically only occurs through age-2, and crappie growth is not controlled by a density-dependent mechanism after age-2 in Texas reservoirs. Therefore, we will model expected changes in growth of age-0 through age-2 crappie using a density-dependent growth model. Allen and Miranda (1998) built a relationship based on paired age-0 crappie density and incremental growth measurements. This relationship will be used to estimate the relative change in crappie growth that occurs with and without consumption by saugeye. The estimate of consumed crappie will be added to high, medium, and low crappie densities (cove rotenone sampling; Arkansas Game and Fish Commission, unpublished data) and modeled with lake-specific population dynamics (age-structure, growth, etc.) to evaluate relative influences on crappie population size structure (PSD and mean length-at-age).

Black Crappie *Pomoxis nigromaculatus* and White Crappie *Pomoxis annularis* will be collected for otolith analysis to provide model parameters for each study lake, and separate models will be constructed for each species. Crappie will be sampled with 12.7-mm mesh modified fyke nets (two 0.91 X 1.83 m rectangular frames and four 76.2 cm hoops with 20.1 m lead) for a minimum of 20 net nights. Upon collection, each crappie will be measured for total length and weight, placed in a Whirl-pak® with a unique identifier, and frozen for later otolith dissection. Otolith sample size (Coggins et al. 2013), fixing, and aging processes will be similar to saugeye (detailed above).

Chapter III

Modeling Fish Community Response after Saugeye Introductions in Arkansas Reservoirs using Ecopath with Ecosim

Introduction

Introducing new fish species by stocking is commonplace within the history of inland fisheries management (Trushenski et al. 2010). Introductions are made for a variety of purposes including the creation of trophy fisheries (Simonson and Hewett 1999), filling voids in a reservoir ecosystem such as creating a pelagic fishery (Axon and Whitehurst 1985), or to produce “put-and-take” fisheries where most stocked fish end up in the creel (Miko et al. 1995). Producing fish for stocking is oftentimes expensive (Trushenski et al. 2010); therefore, it can be important for the stocking to provide an economic return by creating or improving a recreationally important fishery.

However, in some cases, stocking fish to create a recreational fishery can cause intentional or unintentional fish community responses that causes a decline in fishery quality.

Several fish species introductions have generated profound community or even ecosystem-level effects in lakes and reservoirs. Bluegill and Largemouth Bass condition have been improved following Grass Carp *Ctenopharyngodon idella* introductions through bottom-up pathways (Bain 1993), and the transition of alternative stable states (clear to turbid state) in lakes has been well-documented after introductions of Common Carp *Cyprinus carpio* (Weber and Brown 2009) with negative effects on native fishes (Weber and Brown 2011). However, new fishery introductions are typically predators (Cucherousset and Olden 2011), and top-down effects from increased stocking of top predators have also caused a reverse in alternative stable states (turbid to clear state) in lakes, demonstrating a clear, ecosystem-level response (Lathrop et al. 2002). Many repercussions of stocking predatory sportfish have been documented across the United States involving numerous ecosystem pathways (Parker et al. 2001; Knapp et al. 2012).

In Southern reservoirs, species richness is frequently increased by stocking additional sportfish for recreational benefits (Axon and Whitehurst 1985). However, in many cases predator-prey relationships are unbalanced due to a lack of available prey biomass (Ney 1990) or high predator demand (Cyterski et al. 2003; Vatland et al. 2008). Predator-prey balance has been frequently assessed with single-species bioenergetics approaches (Irwin et al. 2003; Denlinger et al. 2006), overlooking potential prey limitation caused by interactions among other piscivore species and the prey base (Ney 1990). Thus, to accurately estimate predator demand and effects of introducing a new predatory species into reservoir food webs, all piscivores must be considered simultaneously (Evans et al. 2014). For example, Kinter and Ludsin (2012) used an ecosystem modeling approach to determine the community-level influence of introducing Hybrid Striped Bass

Morone chrysops x Morone saxatilis into Southern reservoirs. Similar studies with other stocked piscivores, such as saugeye, are needed to better illuminate the effects of such predator introductions.

Saugeye are frequently stocked to create new fisheries, supplement declining Walleye fisheries, or help manage overcrowded crappie populations (Boxrucker 2002). Saugeye diets can contain relatively high proportions of *Lepomis* spp. and *Pomoxis* spp. (Leeds 1988; Galinat et al. 2002), and saugeye routinely switch to alternative prey sources when Gizzard Shad biomass is low (Denlinger et al. 2006). Consuming large amounts of a mesopredators, (e.g., White Crappie; trophic level 3.8 – 4.4), may influence community dynamics through middle-out pathways (Boxrucker 2002; Froese and Pauly 2016). Inverse relationships between the abundance of Largemouth Bass and Walleye populations are common in temperate lakes (Fayram et al. 2005), and Hybrid Striped Bass introductions may reduce Largemouth Bass biomass by up to 20% (Kinter and Ludsin 2012). Saugeye are often stocked with little thought to reservoir fish community dynamics, though these introductions could negatively affect prey availability for native piscivore populations.

As fisheries management progresses toward more holistic, ecosystem-based management strategies (Eby et al. 2006), it is increasingly important to identify possible influences of new predator introductions on existing fish communities. The purpose of this study is to compare fish community dynamics before and after saugeye introductions in four Arkansas reservoirs using the mass-balance ecosystem modeling approach of Ecopath with Ecosim. We will also simulate saugeye introductions with the Ecosim function in each reservoir, which will be compared to real-world, post-saugeye introduction Ecopath models to evaluate model performance and help identify the presence of confounding variables.

Methods

Study Sites and Ecopath with Ecosim

Study lakes will be selected from Arkansas Game and Fish's historic (1975 – 2008) annual cove rotenone data. Lakes will be selected based on 1) at least four years of available data before and after saugeye introduction and 2) having an "established" saugeye population. Saugeye populations will be considered "established" after consecutive observations (years) of saugeye biomass greater than 0.05 kg/ha. Four Arkansas reservoirs (Frierson, Gillham, Hinkle, and Hogue) fit these criteria, and more details about available data for each lake are given in Table 2.

Ecopath with Ecosim (EwE) is the most commonly used software for modeling marine and freshwater ecosystems (Colléter et al. 2013). Ecopath is a static, mass-balanced model that can be used to initiate temporal, dynamic simulations (Ecosim) to observe temporal changes in ecosystem dynamics. Details of EwE can be found in Christensen and Walters (2004), but a condensed description is provided below. Ecopath equations partition annual production and consumption of each food web group as:

Production = predation + net migration + biomass accumulation + yield + other mortality

Consumption = production + respiration + unassimilated food

Next, these production and consumption equations are expressed in terms of rates within the Ecopath master equation:

$$B_i \cdot P/B_i = \sum B_j \cdot \frac{Q}{B_j} \cdot DC_{ij} + NM_i \cdot B_i + BA_i \cdot B_i + F_i \cdot B_i + B_i \cdot P/B_i \cdot (1 - EE_i)$$

where B_i is the biomass of group i, P/B_i is production to biomass ratio of group i, B_j is the biomass of predator j, Q/B_i is the consumption to biomass ratio of consumer i, DC_{ij} is the diet fraction of prey i for predator j, NM_i is the annual net migration rate of group i, BA_i is the biomass accumulation rate for group i, F_i is the annual fishing mortality rate of group i, and EE_i is the ecotrophic efficiency for group i (Christensen and Walters 2004). Ecopath uses B, P/B, Q/B, and DC inputs and solves this equation for EE to balance the model. Ecosim then uses a differential equation with values derived from the Ecopath master equation:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i) \times B_i$$

where dB_i/dt represents the growth rate during the time interval dt of group i in terms of its biomass (B_i), g_i is the net growth efficiency, Q_{ji} is the total consumption by group i, Q_{ij} is the predation by all predators on group i, $M0_i$ is the non-predation natural mortality rate, F_i is fishing mortality rate, e_i is emigration rate, and I_i is immigration rate (Christensen and Walters 2004). Ecosim predicts consumption rates based on the Lotka-Volterra model, which can be modified with “foraging arena” properties by adjusting prey vulnerabilities with detailed search rate, hiding, seasonal, or mediation factors (Christensen and Walters 2004).

EwE Input Values, Modeling, and Evaluation

To evaluate the effect of saugeye introductions on reservoir fish communities, we will first compare Ecopath models constructed from before and after saugeye introductions (“Pre-saugeye” and “Post-saugeye” models; Table 2). Food web groups will constitute everything from predatory fish to phytoplankton, and closely related species will be grouped together into functional groups for Ecopath modeling. For example, Bluegill, Redear Sunfish *Lepomis microlophus,* and Longear Sunfish *Lepomis megalotis* would be grouped into an omnivorous Sunfish spp. functional group. A species must be present in at least 50% of annual samples to be included in the model. Food web groups will also be split into one, two, or three “life stages” according to life history and ontogenetic diet shifts. Mean fish biomasses for each model will also be adjusted using the relationship developed by Bayley and Austen (1990) to account for rotenone sampling bias related to mean species length.

The production/biomass (P/B) ratio is associated with the turnover rate of a food web group and is equivalent to instantaneous total annual mortality *Z* (Heymans et al. 2016). Production of fish groups will be estimated with an empirical formula (Downing and Plante 1993) that incorporates fish species biomass and maximum observed individual mass. This value of production will be divided by observed biomass (cove rotenone sampling) for each food web group to provide P/B estimates. Similarly, consumption/biomass (Q/B) ratios will be calculated using the empirical ratio of Palomares and Pauly (1998) as suggested by Heymans et al. (2016), where weight infinity and aspect ratio of the tail will be taken from median values in FishBase (Froese and Pauly 2016) and mean annual temperature data from nearby Kentucky Lake, KY (E. Ganus, Tennessee Wildlife Resource Agency, unpublished data).

Diet compositions of all food web groups will be estimated from published literature values from Southern reservoirs except for saugeye, where diet data from Chapter 1 will be used. Creel data for fishing mortality *F*, an important parameter for EwE modeling, are not available for any of the study lakes. However, instantaneous total annual mortality *Z* is known, and *Z* is equal to *F* plus natural mortality *M*, and *M* can be estimated from another Pauly empirical equation (Pauly 1980), so *F* will be derived from *Z* and *M*. Median FishBase (Froese and Pauly 2016) values will be used for Von Bertalanffy length infinity and Broady growth coefficient (*K*).

Benthic invertebrate biomass (Hanson and Peters 1984) and production (Plante and Downing 1989) will be estimated from empirical relationships. Lake-specific data from the Arkansas Department of Environmental Quality will be used to estimate zooplankton biomass (sampled with a Wisconsin Net) for both the Pre (1989) and Post (1999) models (ADEQ 1999); while literature values will be used for zooplankton P/B and Q/B ratios. Chlorophyll-*a* (ADEQ 1999) will be converted to phytoplankton biomass (Kasprzak et al. 2008) for Pre (1989) and Post (1999) models, and P/B and Q/B ratios will be estimated from the literature for model inputs.

After all input parameters are collected, but prior to balancing the model, parameters will be evaluated with a set of pre-balance (PREBAL) diagnostics based on general ecological and fisheries principles as recommended by Link (2010). For example, trophic levels should span 5-7 orders of magnitude and the slope of the biomass should decline by 5-10% across trophic levels (Welch 1968; Link 2010; Heymans et al. 2016). Once PREBAL criteria are met, standards for balancing the model (Figure 2) will be followed to maintain laws of thermodynamics (Darwall et al. 2010).

Several Ecopath tools will be used to help identify changes in ecosystem dynamics between Pre- and Post-saugeye models. Simple trophic level (calculated by EwE) or biomass changes within a food web group can be evaluated to provide coarse effects of introducing saugeye. Mixed Trophic Impacts (MTI) will provide values in a matrix of both direct (predation) and indirect (competition) impacts of any group on all other groups in the ecosystem (Christensen and Walters 2004) and can be used to evaluate the impact of an introduced species (Colvin et al. 2015). Similarly, niche overlaps will be assessed using both Prey Overlap Index and Predator Overlap Index (values between 0 and 1) to compare the Pre- and Post-saugeye models (Pianka 1973; Christensen et al. 2005). A keystone species is defined as one that has relatively low biomass but a strong structuring role in the ecosystem (Power et al. 1996). An index of keystoneness for each food web group within EwE will be used to identify changes in ecosystem dynamics (Libralato et al. 2006).

Finally, simulations of saugeye introductions will be applied to models of the four lakes using Ecosim. I will use Langseth et al. (2012)'s Method 1 to simulate a saugeye invasion in EwE. In this method, the original Pre-saugeye models will be adjusted and balanced to include saugeye, and saugeye biomass will be forced to zero for the first several years of the simulation using a time series forcing function and the pre-introduction ecosystem will be allowed to stabilize again. Next, beginning at the year of introduction, saugeye biomass will be forced to observed levels in each available year of data after the introduction. Ecosim will then simulate the influence of the increasing saugeye population on each of the other food web groups through time. I will then compare these simulated values to my original Post-saugeye Ecopath models that were fit with real data. This will validate EwE's ability to accurately simulate the ecosystem's behavior after saugeye were introduced (Pine III et al. 2007) and to help identify the presence of potential confounding variables (i.e., factors other than saugeye introduction that drove community changes) within the time period of the study.

Tables and Figures

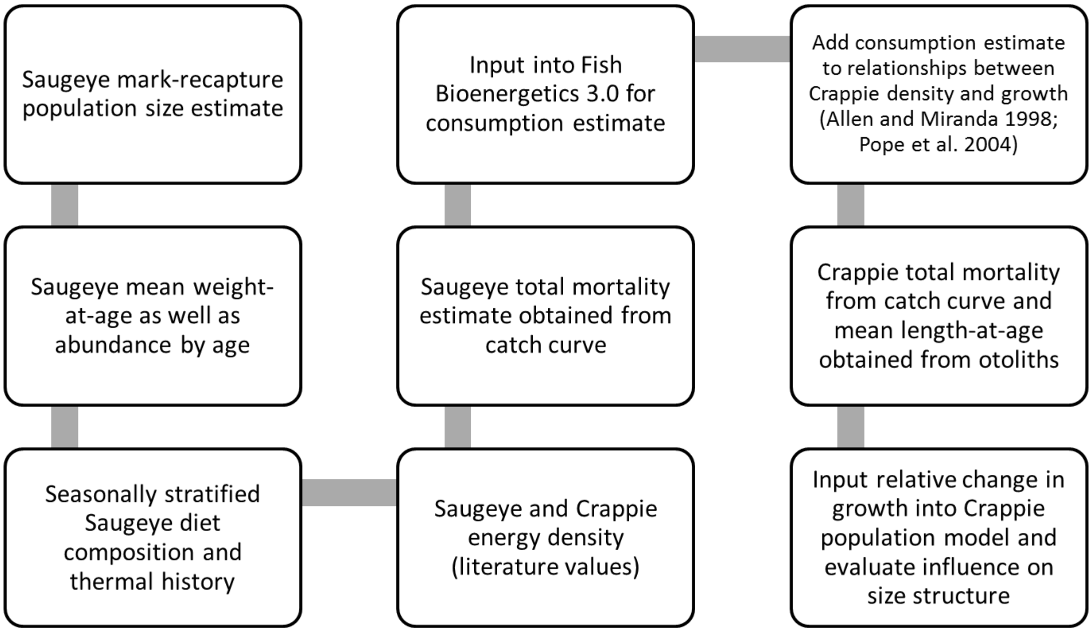
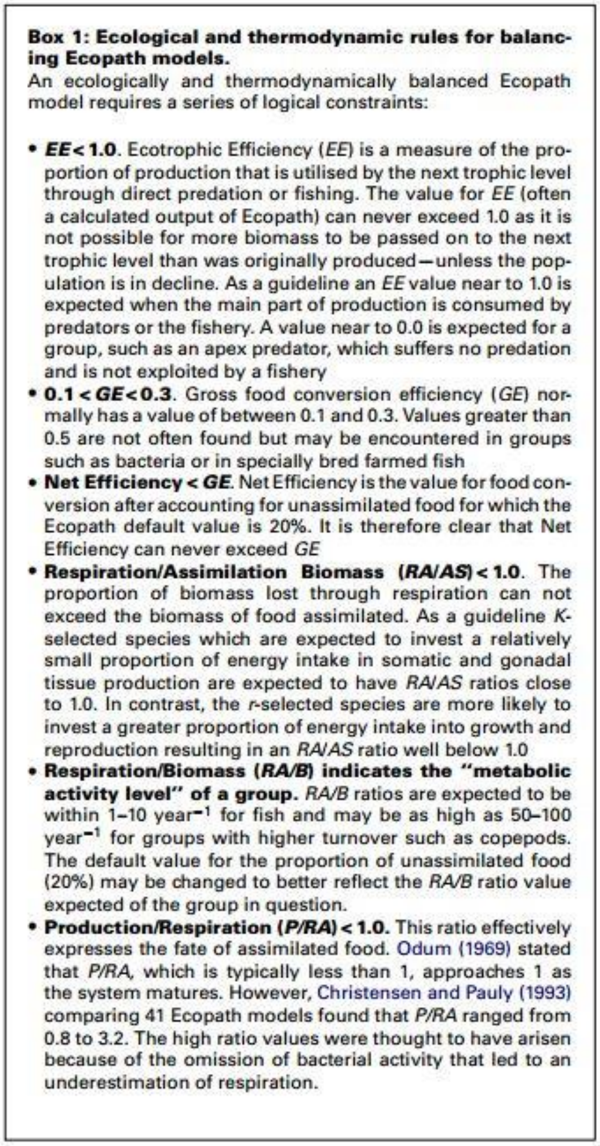


Figure 1. Flowchart of bioenergetics and population modeling approach for estimating saugeye consumption and influence on crappie growth. Modified from Beauchamp et al. (2007).

Table 2. Lake characteristics and data availability for the 4 Arkansas study lakes. Saugeye were considered established after consecutive years with saugeye biomass greater than 0.05 kg/ha. Pre saugeye introduction models will use available data up to the year saugeye were first sampled. Post saugeye introduction models will use available data from the year of saugeye establishment to the last available sample year.

	Lake Frierson	Gillham Lake	Lake Hinkle	Lake Hogue
Water Body Type	Impoundment	Impoundment	Impoundment	Impoundment
Surface Area (ha)	136	554	388	113
Location	Northeast AR	Western AR	Western AR	Northeast AR
Year saugeye First Sampled	1997	1990	1993	1995
Year saugeye Established	2002	1992	1995	1995
First Year in Pre Model	1985	1979	1975	1985
Last Year in Post Model	2008	2008	2006	2005
Total Years in Pre Model	9	6	16	4
Total Years in Post Model	6	7	10	12



Box 1: Ecological and thermodynamic rules for balancing Ecopath models.

An ecologically and thermodynamically balanced Ecopath model requires a series of logical constraints:

- ***EE*****< 1.0**. Ecotrophic Efficiency (*EE*) is a measure of the proportion of production that is utilised by the next trophic level through direct predation or fishing. The value for *EE* (often a calculated output of Ecopath) can never exceed 1.0 as it is not possible for more biomass to be passed on to the next trophic level than was originally produced—unless the population is in decline. As a guideline an *EE* value near to 1.0 is expected when the main part of production is consumed by predators or the fishery. A value near to 0.0 is expected for a group, such as an apex predator, which suffers no predation and is not exploited by a fishery
- **0.1 < *GE* < 0.3**. Gross food conversion efficiency (*GE*) normally has a value of between 0.1 and 0.3. Values greater than 0.5 are not often found but may be encountered in groups such as bacteria or in specially bred farmed fish
- **Net Efficiency < *GE***. Net Efficiency is the value for food conversion after accounting for unassimilated food for which the Ecopath default value is 20%. It is therefore clear that Net Efficiency can never exceed *GE*
- **Respiration/Assimilation Biomass (*RA*/*AS*) < 1.0**. The proportion of biomass lost through respiration can not exceed the biomass of food assimilated. As a guideline *K*-selected species which are expected to invest a relatively small proportion of energy intake in somatic and gonadal tissue production are expected to have *RA*/*AS* ratios close to 1.0. In contrast, the *r*-selected species are more likely to invest a greater proportion of energy intake into growth and reproduction resulting in an *RA*/*AS* ratio well below 1.0
- **Respiration/Biomass (*RA*/*B*) indicates the "metabolic activity level" of a group.** *RA*/*B* ratios are expected to be within 1–10 year^{-1} for fish and may be as high as 50–100 year^{-1} for groups with higher turnover such as copepods. The default value for the proportion of unassimilated food (20%) may be changed to better reflect the *RA*/*B* ratio value expected of the group in question.
- **Production/Respiration (*P*/*RA*) < 1.0.** This ratio effectively expresses the fate of assimilated food. Odum (1969) stated that *P*/*RA*, which is typically less than 1, approaches 1 as the system matures. However, Christensen and Pauly (1993) comparing 41 Ecopath models found that *P*/*RA* ranged from 0.8 to 3.2. The high ratio values were thought to have arisen because of the omission of bacterial activity that led to an underestimation of respiration.

Figure 2. General rules to follow when balancing Ecopath models to create ecologically and thermodynamically sound models. Figure borrowed from Darwall et al. (2010).

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