Understanding drivers and correlates of fish productivity: Finding optimal indicators in freshwater fishes

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Abstract

Canadian freshwater commercial and recreational fisheries contribute $8.8 billion in revenue to the economy annually and are a significant subsistence food source for Indigenous communities. Fish production is recognized as the best indicator of fish population fitness and for assessing productive capacity at both the population and community levels and is legislatively required by the Canadian federal government to prevent, mitigate and/or monitor impacts of development in the *Fisheries Act.* However, empirical tests of correlates and drivers of fish productivity are lacking due to the extensive effort and monetary expense required to calculate estimates of production. Using approximately 20-years of data from disturbed and undisturbed freshwater fish populations and the environments that support them at the IISD-Experimental Lakes Area (ELA) this dissertation explored spatiotemporal correlates and drivers of freshwater fish production. Here, I (i) proposed modifications to current estimation methodologies through the use of von Bertalanffy growth models to allow for estimates of negative production, (ii) identified key fine-scale mechanisms of both population- and community-level fish production temporally, as well as population-level production over regional scales, and (iii) based on these analyses, provide recommendations for variables that can be used as surrogates of fish production. I show that physiochemical and limnological factors that influence habitat availability (i.e., total phosphorus, dissolved organic carbon) dictate lower food web dynamics (i.e., prey quantity and access to prey) and resulting life history strategies (i.e., mean weight, mean length, abundance, and body condition), to ultimately shape fish productivity, demonstrating that fish production is primarily driven by factors that shape individual- and population-level bioenergetics.

Lay Summary

Freshwater fish productivity, defined as the rate of weight gained over time by a fish population or community, is considered the best metric for monitoring fish health. Estimates of fish production incorporate other important metrics such as mortality, the size of the fish, how many fish are in the population, and how fast they grow, all of which are sensitive to changes in the environment. Because of this, the Canadian federal government requires fish productivity to be estimated when looking to assess the impacts of development. Yet, the environmental processes that dictate how productive a wild fish population or community is over time are not well understood, as well as across different lakes at local scales. Using approximately 20 years of environmental and fisheries data across time and multiple lakes, I found that freshwater fish productivity is driven by environmental variables like total phosphorus, an important nutrient in freshwater ecosystems, and dissolved organic carbon (the 'tea colour' of a lake or river). Total phosphorus was found to increase with the fish production of Lake Trout, White Sucker, and multiple minnow species by increasing prey availability. While at high concentrations, dissolved organic carbon reduced fish production by shrinking the preferred habitat available to fish by making the lakes darker and colder, which decreased prey for fish. My thesis shows that factors that alter the amount of preferred habitat for fish also changes the amount of prey available and ultimately the amount of energy that fish have to grow and reproduce. Overall, this thesis provides important insights into mechanisms of fish production that may help to protect fish populations in the future.

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CHAPTER 1

General Introduction

Fishes are dynamic in time and space as they occupy a wide array of habitats, are influenced by heterogeneous abiotic and biotic factors, and maintain various ecological roles within freshwater systems. Fish are important ecologically, economically, and culturally, and as a result, have been a main focus of studies seeking to understand the transfer of energy in aquatic ecosystems. Fish production is a foundational concept in fisheries science and estimates of production are good indicators of fish population performance or fitness (Benke, 2010; Randall & Minns, 2000). Production estimates mobilize comprehensive demographic information for a given population such as abundance, biomass, growth and mortality (Dolbeth et al., 2012; Rypel et al., 2015). As production is driven by energy flow (Waters, 1977), it is a useful metric for expressing the bioenergetic state of a population and/or community and for assessing energy flow within entire aquatic ecosystems. Thus, consideration of the effects of various abiotic and biotic drivers on the net production of populations and communities within this framework are critical, particularly in the face of mounting anthropogenic pressures such as climate change.

Fish production is defined as the amount of tissue elaborated per unit time per unit area, while the basis for calculations of fish production is to quantify the rate of biomass change between two sampling periods for a population or community. Assumptions of this rate of change in populations over time are: (i) that mortality causes a decrease in the number of individuals from time t (N_t) to N_{t+t} and; (ii) that growth is the rate at which the weight (W) of surviving individuals increases from W_t to $W_{t+\Delta t}$. Based on these assumptions, production over Δt can be expressed as:

$$[B_{t+\Delta t} - B_t][g/(g-z)] \quad (1)$$

where B_t is biomass at time t and g and z are rates of population growth and mortality, respectively.

Several methodological approaches have been described in the literature for estimating freshwater fish production, which include (i) removal summation, (ii) increment summation, (iii) the Allen curve method, (iv) size-frequency method, and (v) instantaneous growth rate (IGR) method; with the IGR method being the most widely applied (Chapman, 1978; Hayes et al., 2007; Ryder, 1965; Waters, 1977). Although it is recognized that most estimation methods introduce error into estimates due to size exclusion and sampling error (common occurrences with fisheries data), methodologies for estimating production have not been revised since those initially proposed (Garman & Waters, 1983; Newman & Martin, 1983; Ricker, 1946; Waters, 1977). Further, some methods introduce additional error, such as the IGR method that recommends replacement of negative estimates of cohort production with a value of zero, under the argument that new production will simply cancel out negative production (Chapman, 1978). However, it is conceivable for a population to experience a significant decline in production due to excessive mortality or a legitimate loss of biomass associated with ecosystem changes which would result in truly negative production values. Such changes in population abundance or cohort biomass have been previously observed in ecosystems experiencing disturbance and shifts in resource availability (Evans et al., 2005; Guzzo & Blanchfield, 2017; Hanson & Leggett, 1985; Mills et al., 2002; Rennie et al., 2019). Overall, this highlights the need for methodological improvements for estimating fish production and an assessment of the validity of interpreting negative production.

Foundational work has identified several correlates or predictors of fish production, including total phosphorus, primary production, pH (Downing et al., 1990), standing biomass, mean weight, mean air temperature, species richness (Downing & Plante, 1993), latitude (Downing & Plante, 1993; Rypel & David, 2017), mean depth (Prepas, 1983), population production per unit biomass (P/B) ratios (Downing & Plante, 1993), and habitat size (Kelso, 1988; Minns, 1995) to be correlated with freshwater fish production. However, all assessments of these drivers and correlates of fish production to date have been evaluated across (i) very large spatial scales and/or short time-periods, (ii) often combining estimates from multiple estimation methods (Downing et al., 1990; Downing & Plante, 1993; Rypel & David, 2017), (iii) often employ variable sources of fisheries data, some of which are well known to be prone to bias (i.e., commercial fishing yields, sport fishing yields, average commercial catch; Hanson & Leggett, 1982; Oglesby, 1977; Prepas, 1983; Ryder, 1965), or (iv) are based on the application of models of production that rely on significant assumptions (Embke et al., 2019; Jarvis et al., 2020; Rypel & David, 2017). Few other assessments of production have been published or have attempted to estimate or apply robust estimates of production outside of these initial investigations (Downing et al., 1990; Downing & Plante, 1993; Waters, 1977, 1999), with recent analyses applying assessments of what can be best described as components of production (i.e., biomass, growth, abundance; Campana et al., 2020; Craig et al., 2017; Jarvis et al., 2020) or relative estimates of production components (i.e., bCPUE, CPUE; Finstad et al., 2014; Karlsson et al., 2009; Koizumi et al., 2018).

A large component of this recent body of work has looked to understand both temporal and regional mechanisms of fish production associated with dissolved organic carbon (DOC), as the literature agrees that higher concentrations of DOC modifies light attenuation and thermocline depth to alter ecosystem nutrient and thermal dynamics (Craig et al., 2015; Karlsson, Byström, et al., 2009; Sherbo et al., 2023; Tonin et al., 2022). As such, DOC is likely to impact fish productivity, although DOC has yet to be evaluated against direct estimates of fish production. To date, DOC has only been assessed against some components of production (i.e., growth), but mostly against relative estimates of components of production (i.e., relative biomass (bCPUE), relative abundance (CPUE), or yield; Craig et al., 2015, 2017; Finstad et al., 2014; Karlsson et al., 2009; Koizumi et al., 2018; Tonin, 2019). Further, while other work across large geographic scales has shown that production increases with biomass and decreases with body size (Downing et al., 1990; Downing & Plante, 1993), we have a poor understanding generally of the relationships between estimates of production and component estimates (i.e., growth, biomass, abundance), including relative estimates (i.e., bCPUE, CPUE). Overall, this points to the need to establish relationships between fish production and its component parts, as well as investigate regional dynamics of fish production where the impact of climate/latitude is negligible.

While the literature strongly supports the advantage of applying estimates of fish production for resource management purposes, our fundamental understanding of the forces that shape the productivity of freshwater fish populations in their natural environments remains rudimentary due to the intense time and monetary constraints associated with collecting the data required to calculate these estimates. This has further inhibited the development of novel time- and cost-effective tools and predictive models for estimating production, and highlights the need to understand the fundamental mechanisms that drive fish production variation within and among lakes. Recent theoretical work has established clear links between individual bioenergetics and fish productivity, demonstrating that physiochemical and limnological processes constrain available habitat within ecosystems to dictate lower food web dynamics (i.e., access to prey, prey quantity and size) that then shapes life history strategies and ultimately fish productivity (MacLeod et al., 2022). Following this theoretical framework in this dissertation, I will use extensive long-term data sets of disturbed and undisturbed freshwater fish populations and the environments that support them from the IISD-Experimental Lakes Area (ELA) to explore methodological improvements, and spatiotemporal correlates and drivers of fish production.

CHAPTER 2

Using von Bertalanffy growth models to inform estimates of fish production

Abstract

Fish production is a key metric in understanding the state of fish populations, however, estimates are prone to uncertainty when based on sparse size-at-age data. The standard instantaneous growth rate (IGR) method can introduce error into estimates through small sample sizes, as well as the assumption that negative production should be interpreted as no production (and equated to zero), despite empirical evidence of weight loss in individual fish, and fish cohorts over time. Here, we modified the IGR method by taking advantage of long-term data which permitted fitting von Bertalanffy growth models to individual cohorts through time to provide more representative estimates of size-at-age in under-sampled age classes. We used long-term Lake Trout *(Salvelinus namaycush*) data from an experimental IISD-ELA lake to compare standard IGR estimates against those calculated using the proposed von Bertalanffy-modified IGR estimates. My results indicate that the proposed von Bertalanffy-modified IGR method addresses uncertainty in production estimates by using predicted mean weights in instances of low sample sizes, thus avoiding false incidences of negative production, but unlike other production estimation methods identifies and allows legitimate occurrences of negative production. Using this revised method, we estimated that Lake Trout production increased four times background levels during a whole-lake aquaculture experiment (2003-2007) before experiencing a negative rate of production and subsequently returning to pre-manipulation levels upon cessation of nutrient inputs. By comparison, the standard IGR method estimated higher rates of production over all time periods, suggesting standard methods may actually overestimate production when applied to dynamic populations. In conclusion, the proposed von Bertalanffy-modified method

provides a conceptually sound framework for dealing with small sample sizes where long-term data are available.

Introduction

Fish productivity, a form of secondary production, can be defined as the amount of biomass elaborated per unit time per unit area occupied by the assemblage of fish present (often expressed kg ha^{-1} yr^{-1}). Fish production has been defined as one of the best metrics of fish population fitness (Randall et al. 1995), as it explicitly integrates important demographic information of fish populations (i.e., abundance, mortality, biomass, growth). Fish production is firmly founded in bioenergetic principles and has been shown to conceptually relate to habitat availability, primary production, and community composition based on first principles (MacLeod et al., 2022). However, fish production is rarely directly measured and remains understudied due to extensive time and monetary constraints associated with the data required for calculation of these estimates. These constraints have largely inhibited the application and further development of estimation methods of fish production beyond those proposed initially (Garman & Waters, 1983; Newman & Martin, 1983; Ricker, 1946; Waters, 1977).

The most widely applied method for estimating fish production is the instantaneous growth rate (IGR) method, originally described by Ricker (1946). The IGR method calculates the change in production in an age class or cohort of fish across two subsequent sampling periods and requires age- and size-structure data of a population or community (Rypel et al., 2015). Total annual production is then summed across all age classes for the time interval of interest (Rypel et al., 2015; Waters, 1977). Mathematically, this can be expressed as:

$$\hat{P} = \sum \hat{G}\bar{B} \tag{2.1}$$

where $\hat{P}$ is the sum of estimated production for all cohorts of a population within a specified interval, $\hat{G}$ is the instantaneous growth rate for the cohort from time t to t_{+1}, with $\overline{w}_t$ representing the mean cohort weight at time t, which follows:

$$\hat{G} = \log_e \overline{w}_{t+1} - \log_e \overline{w}_t \tag{2.2}$$

where $\overline{B}$ is the mean cohort biomass over the specified interval, following:

$$\overline{B} = (\hat{B}_t + \hat{B}_{t+1})/2 \tag{2.3}$$

and $\hat{B}_t$ is the outcome of the density (N_t) and mean weight of each age class at time t, so that:

$$\hat{B}_t = N_t * \overline{w}_t \tag{2.4}.$$

The, N_t for each cohort is calculated by apportioning population abundance estimates in time t (N_p) across age-classes based on the proportion of caught individuals such that:

$$N_t = (n_{age\text{-}class} / n_{total}) * N_p \tag{2.5}$$

where $n_{age\text{-}class}$ is the number of individuals per age-class, and n_{total} is the total number of individuals across all age classes caught in that sampling period.

Although widely accepted and applied, the IGR method can introduce error into estimates through two main mechanisms: 1) sampling biases (a frequent outcome for most fisheries data) and 2) the assumption that negative production (i.e., negative growth in a cohort between consecutive time periods) should be interpreted as no production (and equated to zero; Chapman, 1978; Hayes et al., 2007; Ricker, 1975). Most fisheries sampling methods are challenged generally with adequately capturing individuals from all available age-classes such that numerical abundance and mean mass for each age class can be accurately characterized. These challenges can occur for several reasons, including (i) gear selectivity, (ii) limited time and resources for sampling to adequately characterize all age classes, as well as (iii) ontogenetic differences and associated behavioural and habitat disparities among age classes leading to differential vulnerability to sampling gear. Even if these issues can be accounted for, calculating means based on a small number of observed individuals from a given age-class (commonly encountered in fisheries science) is inherently problematic, and is more likely to be unrepresentative of the true mean due to a high potential for bias resulting from few observations. For example, overestimation of mean mass at time *t* (represented by $\overline{w}_t$ in equations 2.1 and 2.3) due to a small sample size would result in lower biomass and growth rate than the true mean. This would lead to a lower production estimate over the period of estimation (and vice versa if $\overline{w}_t$ was represented by an underestimated mean weight), due to inaccurate estimates of cohort growth, and consequently, inaccurate estimates of production when using the IGR method.

The IGR method further introduces error into its estimates of production through the general advice to “zero” incidences of negative cohort production, as this method fails to account for legitimate instances of fish weight loss within a cohort over time. While such advice is widely advocated when using the IGR method (Hayes et al., 2007; Mills et al., 2002; Waters, 1977), justifications for this procedure are not clearly founded or described. Vague rationales in the literature have been provided for zeroing negative production based on the premise of negative production being the opposite of tissue elaboration (i.e., production), such that within the context of population dynamics new production will cancel out any negative production (Chapman, 1978). Here, we argue that negative production can and should be considered when there is high certainty that negative production is capturing legitimate loss of cohort mass across time periods. Loss of fish mass over relatively short time periods (up to one year) has been widely observed, often in situations where populations undergo habitat and resource changes resulting in reduced size-at-age and abundance, and increased mortality (Evans et al., 2005a; Guzzo et al., 2017; Hanson & Leggett, 1985; Mills et al., 2002; Rennie et al., 2019). In this instance, if $\overline{w}_{t+1}$ in equation 2.1 is lower than $\overline{w}_t$ due a legitimate loss of mass associated with ecological disturbance (and not because of bias associated with small sample sizes), this then results in negative growth ($\hat{G}$) and therefore a negative production estimate for a given cohort; should the impact be of sufficient magnitude, it is conceivable that the sum of these estimates might be negative for the entire population. The challenge then lies in being able to distinguish false incidences of negative production due to poor sample sizes leading to inaccurate mean weights from true instances of mass loss.

The von Bertalanffy growth model is widely accepted as a descriptor of lifetime somatic growth in fishes (Ricker, 1975; von Bertalanffy, 1957). When applied to a year-class or cohort of fish measured repeatedly over time, the model represents a lifetime growth trajectory of the cohort that is less subject to uncertainties in size-at-age in any single age class. Here, we propose a method for improving fish production estimates by incorporating von Bertalanffy growth models fit to individual cohorts to provide more accurate estimates of size-at-age for age classes represented by low sample sizes, and providing a means for better identifying legitimate instances of negative production. Thus, the application of cohort-specific von Bertalanffy growth models may reduce statistical artefacts from small sample sizes resulting in under- and overestimates of age class mean weights leading to false negative growth estimates. Further, we use data from Lake 375 at the IISD – Experimental Lakes Area (IISD-ELA) to demonstrate observed instances of negative growth that are not a consequence of poor sample sizes (i.e., legitimate loss of weight over time within a cohort) and the effect of this mass loss across several cohorts on population production estimates. Lake 375 underwent experimental aquaculture between 2003-2007 where total phosphorus levels increased three times over background concentrations (Bristow et al., 2008). Increases in Lake Trout *(Salvelinus namaycush)* abundance, size-at-age, and increases in juvenile growth rates in Lake 375 were also observed, with the population returning to pre-manipulation levels upon cessation of aquaculture and nutrient inputs (Rennie et al., 2019). Given observed reductions in Lake Trout size-at-age across several cohorts following the cessation of aquaculture (i.e., nutrient inputs; Rennie et al., 2019), I present these data as an example of true negative production. Finally, we assessed the results of the proposed von Bertalanffy-modified IGR method against the existing IGR production estimation method.

Methods

Data Selection

Long-term data from Lake 375 at IISD-ELA (1989-2013) describing size-at-age and mark-recapture of the Lake Trout population (Rennie et al., 2019) was selected to develop the application of the proposed von Bertalanffy-modified IGR method. Lake Trout were sampled during spawning in autumn (mid-September to late October) each year using a combination of Beamish-style trap nets (Beamish, 1973) and short-set gillnets on spawning shoals (Rennie et al., 2019). Lake Trout abundance was estimated using mark-recapture data and the POPAN Jolly-Seber model (Schwarz & Arnason,

1996) in Program MARK (White & Burnham, 1999), as described and reported in Rennie et al. (2019). Captured fish were measured and weighed, fin rays were taken for ageing on first capture and individuals were tagged using PIT tags near their dorsal fin. Individual ages were determined from (a) fin rays collected at initial sighting, and (b) age assignment in subsequent recaptures of individuals identified by tags based on age at first capture. Further details of sampling methodologies and abundance calculations can be found in Rennie et al. (2019). As production estimates correspond to an interval between sampling periods, we assigned production estimates over any year *t* to *t+1*, given that (i) individuals were sampled in the fall, and (ii) most somatic growth of fish is accumulated over the open water season (Bloomfield et al., 2022; Guzzo et al., 2017; Morbey et al., 2010; von Biela et al., 2021; with growth from resource acquisition in spring and winter of *t+1* primarily occurring in year *t+1* based on fall sampling in each year).

Unmodified Instantaneous Growth Rate Production Calculations

Annual production was calculated using the standard application of the Instantaneous Growth Rate method (Hayes et al., 2007; Ricker, 1946) following equations 2.1- 2.5 (Method A). For a description of the complete method, associated variance calculations and a worked example, see Hayes et al. (2007).

von Bertalanffy-Modified Instantaneous Growth Rate Production Calculations

The proposed modified method follows equations 2.1- 2.5 and the variance estimators described in Hayes et al. (2007), with the key difference being that we used predicted mean weights from a von Bertalanffy growth function fit to a cohort of fish over time in place of observed mean weights in instances where age-classes were determined to have too few individuals to calculate a representative mean weight (Method B). To determine when to use predicted weights in place of observed weights, we conducted a simulation study to identify the minimum number of observations required to accurately describe a mean weight estimate for each age-class from Lake 375 prior to experimental aquaculture (1989-2002). Lake Trout were categorized into age classes from 1 to 20+ and 21+. More specifically, fish are categorized into age classes from 1 to 20+ in the first sampling period and 2 to 21+ in the second sampling period to follow and quantify the rate of production of age cohorts across the two sampling periods. Based on these age-class categories, mean weights of each age-class were calculated using age-specific means based on fish sampled in all years before aquaculture (e.g., representing natural variation in the population). Using these known age-class specific means, normal random distributions around these means were created and a range of n observations (n ranging between 3 and 30) were sampled (with replacement) from the distribution to calculate sample means. For each sample size (n), 100 sample means were calculated. Stability in mean estimates across sample sizes was evaluated by determining the sample size at which the coefficient of variation across the 100 calculated means fell below 10% for each age class (Table S2.1). For age classes with sample sizes below those derived from the simulation study were assigned cohort-based von Bertalanffy predicted mean weights, and sample sizes above values derived from the simulation study were assigned observed mean weights.

To determine cohort-specific von Bertalanffy growth curves, the age of each fish at capture was subtracted from the year of capture to identify the cohort (i.e., year of birth) the fish belonged to. Monophasic von Bertalanffy models for each cohort through time (i.e., cohorts born between 1979-2008) were fit to the long-term Lake 375 Lake Trout data. These growth models have been shown to represent Lake Trout growth accurately (Lester et al., 2021; Shuter et al., 1998). The von Bertalanffy equation used for the monophasic models was as follows:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \tag{2.6}$$

where L_t is the expected or average length at time (or age) t, L_∞ represents the asymptotic average length, K is the Brody growth rate coefficient (yr^{-1}), t_0 is the time or age when the average length is zero (set to zero in this case; Beauchamp et al., 2004). From the growth curve predicted lengths, predicted weights were determined using cohort-specific weight-length regressions.

Cohorts born between 1982-1995 had observable ‘jumps’ of secondary somatic growth during the aquaculture experiment; these fish appeared to have already achieved asymptotic size, but because of a change in ecosystem productivity (due to experimental aquaculture), somatic growth for these individuals was re-initiated (see example in Figure S2.1). These jumps in growth were typically observed to occur following the initiation of aquaculture (e.g., Figure S2.1), and though variable among cohorts, occurred approximately three years following the initiation of aquaculture in 2003 on average across all cohorts where this phenomenon was observed. To ensure that these secondary increases in somatic growth were captured in the calculated production estimates, von Bertalanffy models were fit to all observations in the age class up to this transition in maximum size (Figure S2.1). For each cohort that had an observable jump in somatic growth, we assigned a secondary asymptotic mean weight to describe sizes post-2006, corresponding to the new asymptotic mean size following aquaculture based on observed patterns.

von Bertalanffy-Modified IGR Method Variations

Additional variations of the IGR method were also implemented for comparisons in this study (Table 2.1). Specifically, we assessed variations where 1) we implemented von Bertalanffy predicted weights based on insufficient sample sizes, but set all negative age-class specific production estimates to zero (consistent with existing advice for the standard application of the IGR method (Method C); Hayes et al., 2007; Newman & Martin, 1983; Waters, 1977), and 2) only von Bertalanffy predicted weights were used to calculate production estimates, which prevented any negative production estimates from occurring (Method D).

Method Comparison

Mean percent average differences were calculated among all modified methods described here relative to the standard application of the IGR method. Specifically, production estimates produced with variations of the standard method (Methods B-D) were compared to the standard estimates (Method A) across all years, as well as among time periods (before, during, and after aquaculture). To quantify the average percent difference between the method variations in comparison to the standard method estimates for the time periods assessed, annual standard estimates were subtracted from annual estimates produced by the method variations for each year, divided by the standard estimate and multiplied by 100, and then averaged. To identify any significant differences from standard estimates, confidence intervals (95%) of difference estimates corresponding to each time period (before, after, during experimentation, or across all years) were estimated; confidence intervals for difference estimates that did not include zero were deemed significantly different.

Results

The proposed von Bertalanffy-modified IGR method produced estimates that followed similar temporal patterns to standard estimates over time but produced lower estimates of production and captured instances of negative population production on average (Figure 2.1). This was supported through the assessment of the average percent difference between standard estimates with the proposed method and other method variations (Figure 2.2). Across all years, the von Bertalanffy-modified IGR method (Method B) generated production estimates that were on average 50% lower relative to the standard method (Method A; Figure 2.2i) and produced significantly different estimates both during and after aquaculture that were approximately 30% (Figure 2.2iii) and 60% lower (Figure 2.2iv) on average, respectively. While there were no significant differences between the von Bertalanffy-modified IGR method (Method B) compared to standard IGR estimates (Method A) before aquaculture, estimates were on average 47% lower than standard estimates (1989-2002; Figure 2.2ii).

The most notable difference between estimates calculated by the proposed method (Method B) and the standard IGR (Method A) were observed immediately after the cessation of nutrient inputs in 2008 when production rapidly declined (Figure 2.1). Specifically, after the cessation of nutrient inputs the proposed method (Method B) estimated production to be around negative one kg/ha/yr in 2009 (i.e., a loss of Lake Trout tissues through both reductions in population biomass and individual mass loss) whereas the standard IGR method (Method A) estimated production to be zero kg/ha/yr. Notably, the proposed method (Method B) identified an additional negative annual production estimate in 1994 prior to aquaculture not identified by other methods. Across all years, as well as before and during aquaculture, the other method variations (Method C & D) evaluated produced estimates that were not significantly different from standard estimates (Figure 2.2i, 2.2ii; 2.2iii), although these method variations produced significantly different estimates after aquaculture (Figure 2.2iv). While not significantly different, the von Bertalanffy-modified method with zeroed negative estimates of production (Method C) produced estimates that were 5% higher than the standard estimates over all time periods on average (Figure 2.2i), 30% higher before aquaculture (Figure 2.2ii), 15% lower during aquaculture (Figure 2.2iii), and 30% lower after aquaculture (Figure 2.2iv). Estimates produced using only von Bertalanffy predicted weights (Method D) were less variable across all years compared to other methods, producing estimates approximately 20% and 50% higher though not significantly different relative to standard IGR estimates (Figure 2.2i, 2.2ii). While estimates during and after aquaculture were 35% (Figure 2.2iii) and 70% lower (Figure 2.2iv) respectively, with estimates being significantly different compared to standard estimation methods after aquaculture.

We assessed the frequency that predicted and observed mean weights were used for each annual von Bertalanffy-modified IGR production estimate (Figure 2.3). Predicted mean weights were used at an almost equal frequency (all years=168;

before=87; during=51; after=30) to observed values (all years=171; before=88; during=50; after=33). Similarly, we quantified the frequency of negative production estimates for individual cohorts between the proposed method (where negative production estimates are permitted) and the standard IGR method (where negative production would be set to zero) and found the von Bertalanffy-modified IGR method produced negative production estimates approximately 50% less across time periods (all years=73; before=41; during=25; after=7) in comparison to the standard IGR method (all years=135; before=82; during=45; after=8; Figure 2.4).

Discussion

Here, we demonstrated that the proposed method for using cohort-specific von Bertalanffy predicted weights in place of age-class means that are uncertain due to small sample sizes successfully addressed 1) small sample biases that can introduce questionable production estimates through under- and overestimated age-class mean weights and associated growth estimates, and 2) provided a method to capture legitimate incidences of negative production, while removing expected occurrences of false negative production (that are otherwise likely driven by small sample bias). Further, we argue that negative production can and should be interpreted when legitimate incidences of negative production (i.e., cohort weight loss) are observed, and would be expected, based on knowledge of the system under study. Several examples in the literature show that weight loss in fish can occur under circumstances of resource limitation due to disturbance (Guzzo et al., 2017; Mills et al., 2002; Rennie et al., 2019), competition (Hanson & Leggett, 1985), and under experimental conditions (McKenzie et al., 2014;

Nicieza & Metcalfe, 1997; Queiros et al., 2021). For example, work by Guzzo et al. (2017) found that Lake Trout experienced mass and body condition losses associated with reduced access to littoral prey due to decreased critical spring feeding periods that were driven by increased water temperatures and reduced oxythermal habitat. In Lake 375 specifically, Lake Trout abundance and size-at-age declined dramatically after the cessation of aquaculture, in association with a reduction in nutrient inputs (Rennie et al., 2019). The broader body of literature supports that weight loss of fish can (and does) happen and should therefore be accounted for as a description of a loss of biomass from the system rather than be simply ignored or assumed to be negligible relative to new production (and therefore assumed to be zero, Chapman, 1978) as it is in standard IGR estimates.

The von Bertalanffy-modified IGR method proposed here closely followed the standard IGR estimates over time but produced lower estimates of fish production overall. Specifically, the von Bertalanffy-modified method closely followed the standard IGR estimates prior to aquaculture but produced significantly lower estimates of production during (2003-2007) and after (2008-2010) aquaculture. The lower estimates of production calculated by the proposed method during aquaculture demonstrates that there were likely frequent incidences of overestimated mean weights using the standard IGR method due to small sample size bias. Small sample sizes can also introduce underestimates of production, which would be zeroed using the standard method. I demonstrated that there was a higher frequency of encountering negative estimates of production (that are then zeroed) in the standard method compared to the proposed method. However, despite a high frequency of zeroed negative production estimates, the standard method still produced higher estimates of production than the proposed method. Using cutoff values and predicted von Bertalanffy mean weights in the method proposed here, we provide greater confidence in detecting instances of sample size bias that are potentially introducing inflated biomass and growth estimates, and false incidences of negative production. While the development of this application of this method was only possible with the availability of extensive and temporally-detailed size-at-age data, it provides some guidelines for practitioners concerned about sample size bias in production estimates based on more limited data (i.e., Table S2.1).

An additional outcome of interest from the comparison of the method variations against the proposed method and the standard method is that estimates calculated using all von Bertalanffy predicted weights provided similar estimates to both the proposed and standard estimation methods. While the estimates produced seemed to have more muted responses to population changes than those using all (i.e., standard IGR method) or most (i.e., von Bertalanffy-modified method) of the observed weights, these estimates still followed similar temporal changes in population production and were not significantly different from the standard IGR estimates, except for the last two years of the dataset after aquaculture where estimates seem to be declining when standard estimates are increasing. This highlights the potential for the use of von Bertalanffy predicted weights for estimating population production in systems under equilibrium with sparse data generally, or where years of data are missing among datasets with mostly consistent consecutive sampling periods.

Empirical evidence supports total phosphorus as a driver of fish population production (Downing et al., 1990; Hecky & DePinto, 2020; Mills, 1985). As such, we anticipated Lake Trout production in Lake 375 would track changes in total phosphorus experienced by the ecosystem due to experimental aquaculture (Bristow et al., 2008) and experience a loss in mass after the cessation of nutrients due to the end of the manipulation. We demonstrated that the proposed method captures major population changes during times of disturbance (i.e., during and after aquaculture) after addressing two mechanisms of introduced error. However, we also note that the proposed method may also have the capability to capture population changes associated with natural disturbance. Specifically, the proposed method identified the population likely experienced legitimate negative production between fall of 1993 to fall of 1994 (assigned to the 1994 production year) at a time when the system was not experiencing any experimental alteration or disturbance. Previous work identified that the mount Pinatubo explosion in 1991 led to large declines in fish size-at-age in 1992 and 1993 in other cool water predatory species such as Walleye (*Sander vitreus*) in Minnesota (Schupp, 2002). Additionally, the literature also reports cooler epilimnia and deeper thermoclines in 1992 in Lake Opeongo (King et al., 1999) and in the South Bay of Lake Huron (King et al., 1997), likely due to this volcanic eruption. This cooling effect on aquatic systems is a likely cause for declines in lower food web productivity, leading to declines in secondary production observed here by the proposed method in 1994; notably 1994 production estimates are based on production between 1993 and 1994. This demonstrates the utility of the proposed method in capturing negative production associated with both major global change events and more direct instances of ecosystem disturbance like nutrient manipulations.

We argue that these methodological improvements for calculating freshwater fish production represent valuable modifications to one of the most widely employed and accepted methods of estimating freshwater fish population production. Though the use of growth models to improve under-sampled age-classes relies on the availability of long-term data, we demonstrate that employing growth models to improve certainty around age-class mean weights provides the unique capability of detecting legitimate instances of negative rates of production in freshwater fish populations. Additionally, we show that calculating production using only growth model predicted weights offers an opportunity to calculate production using the IGR method with sparse data to provide estimates that are not significantly different from standard IGR estimates (which are less biased from small sample sizes in individual cohort estimates). Improvements of fish production estimation methods have not been proposed since the initial establishment of methods, even though fish production is understood to be the most sensitive metric for monitoring fish populations. It will be important that further method modifications be investigated in the future to improve current production estimation methods and to provide new approaches to estimating production that are time- and cost-effective.

Table 2.1. Comparison of method variations

Method Variation	Mean Weight Type Used	Negative Production
Standard IGR (Method A)	Observed mean weights only	Zeroed
Von Bertalanffy-modified IGR (Method B)	Observed + von Bertalanffy predicted mean weights	Included
Von Bertalanffy-modified IGR without negative production (Method C)	Observed + von Bertalanffy predicted mean weights	Zeroed
Standard IGR with only von Bertalanffy predicted weights (Method D)	von Bertalanffy predicted mean weights only	NA (see Methods section)

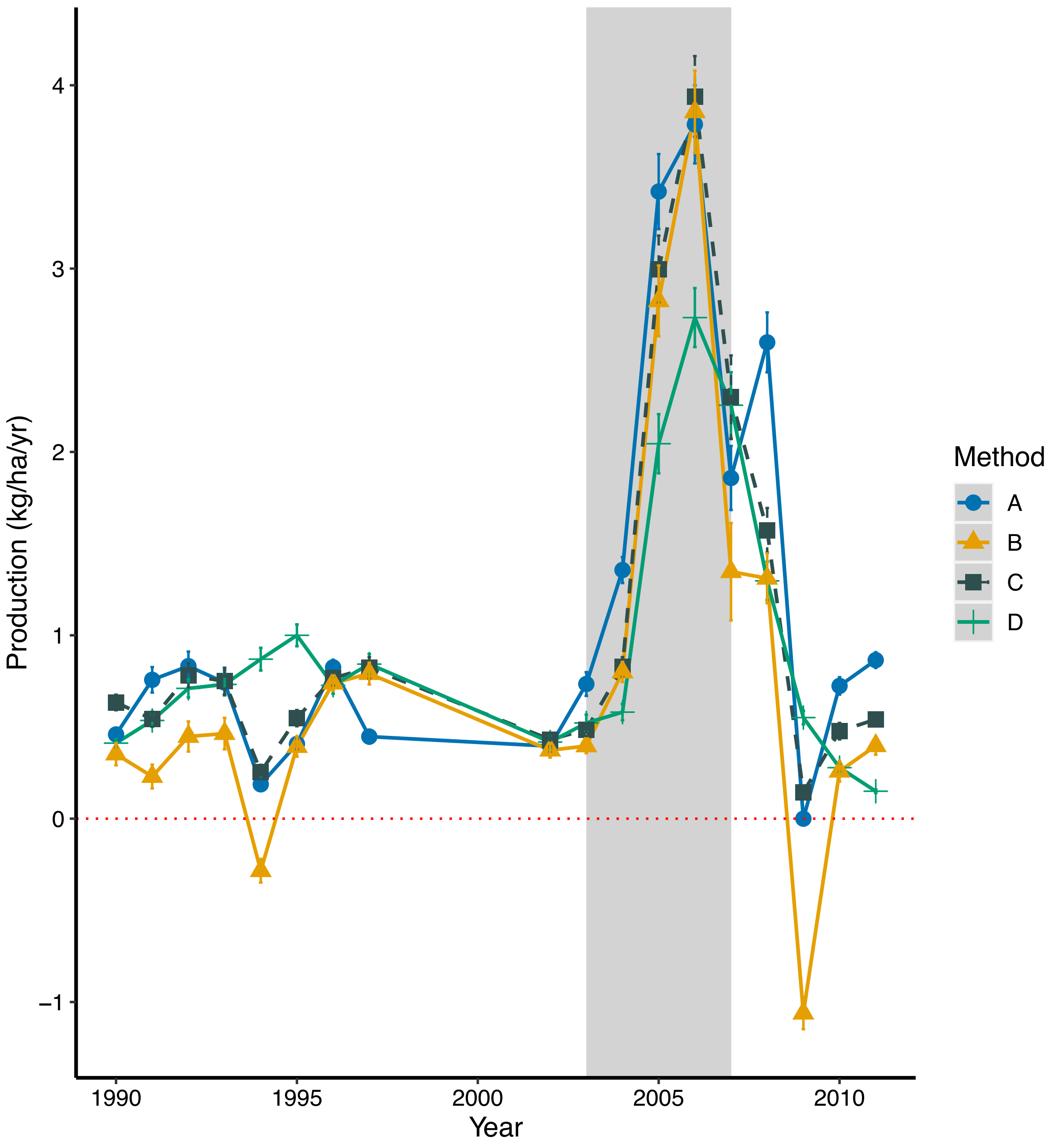


Figure 2.1. Comparison of annual IISD-ELA lake 375 Lake Trout production estimates calculated using different estimation methods (A) standard IGR method, (B) von Bertalanffy-modified IGR method, (C) von Bertalanffy-modified IGR method with zeroed negative production estimates, (D) all von Bertalanffy based predicted weights. Shaded region denotes time period during aquaculture (2003-2007).

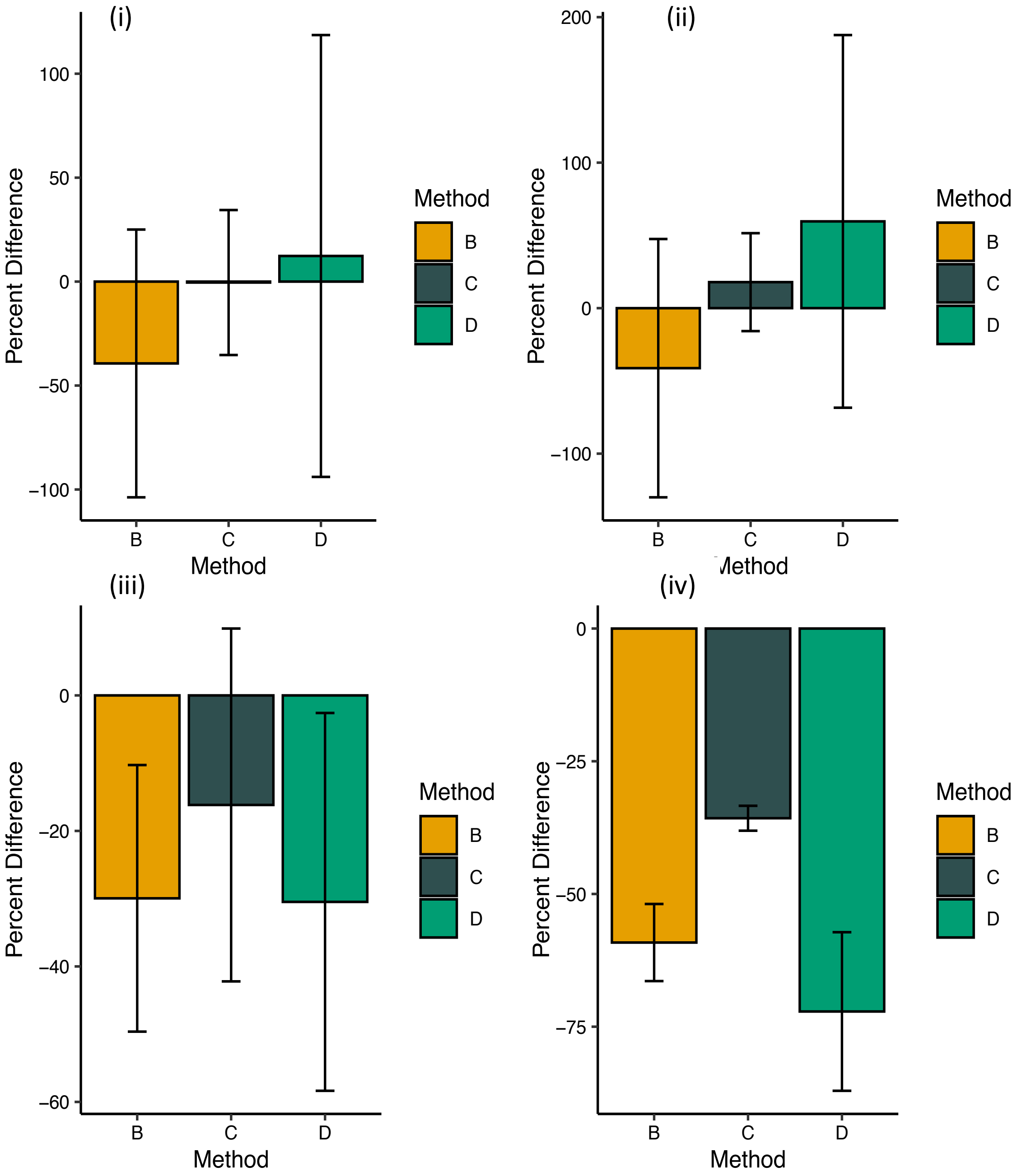


Figure 2.2. Average differences of modified production estimates compared against standard IGR estimates; panel (i) average difference across all time-periods, (ii) time-period before aquaculture (1989-2002); (iii) time-period during aquaculture (2003-2007); (iv) time-period after aquaculture (2008-2010). Method variations include (B) VB-modified IGR method, (C) VB-modified IGR method with no negative production estimates, (D) all VB-based predicted weights. Error bars denote confidence intervals.

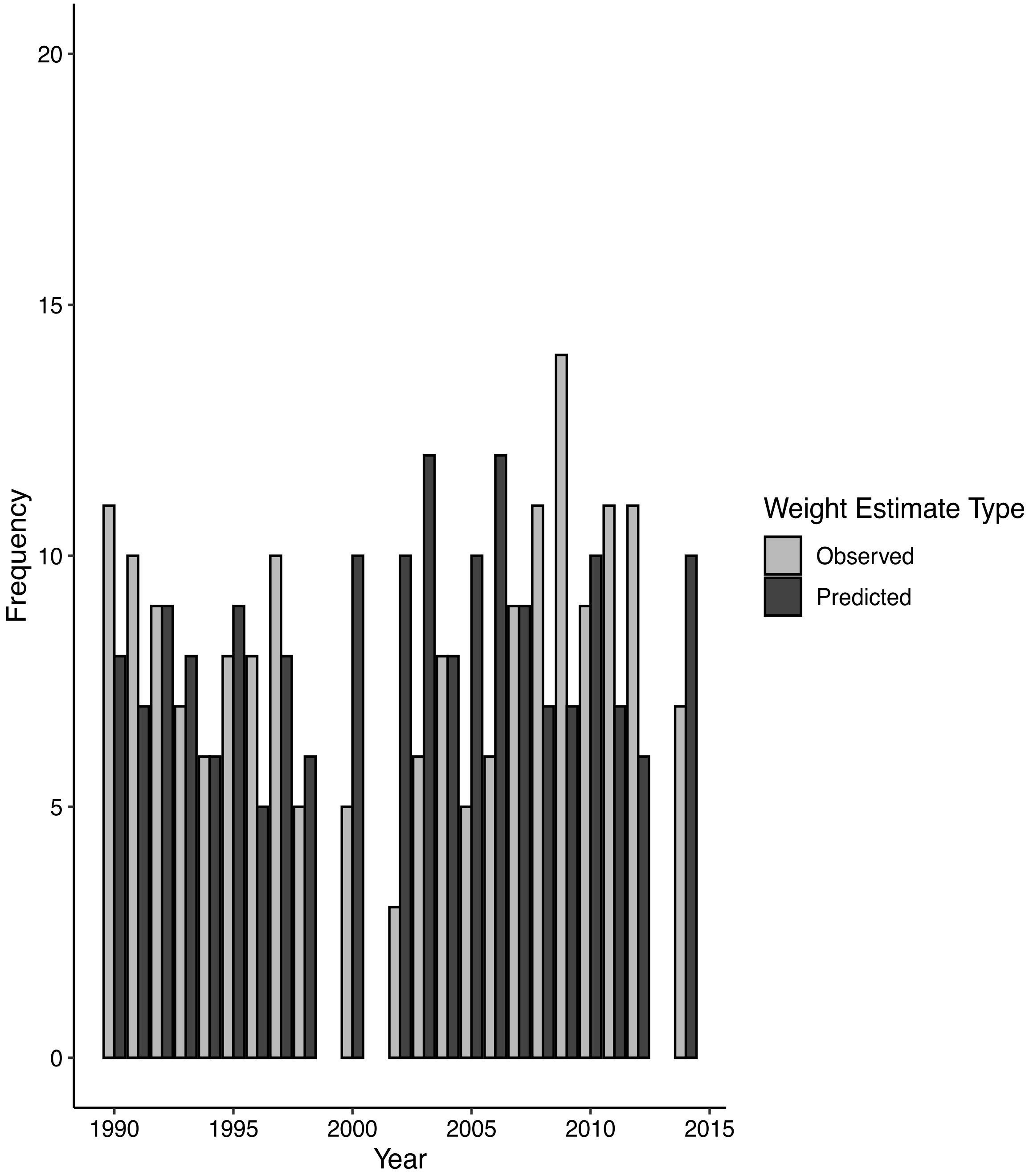


Figure 2.3. A comparison of the frequency of observed and predicted mean (based on 20 possible age classes in each year) used to calculate each annual production estimate in the proposed von Bertalanffy-modified method.

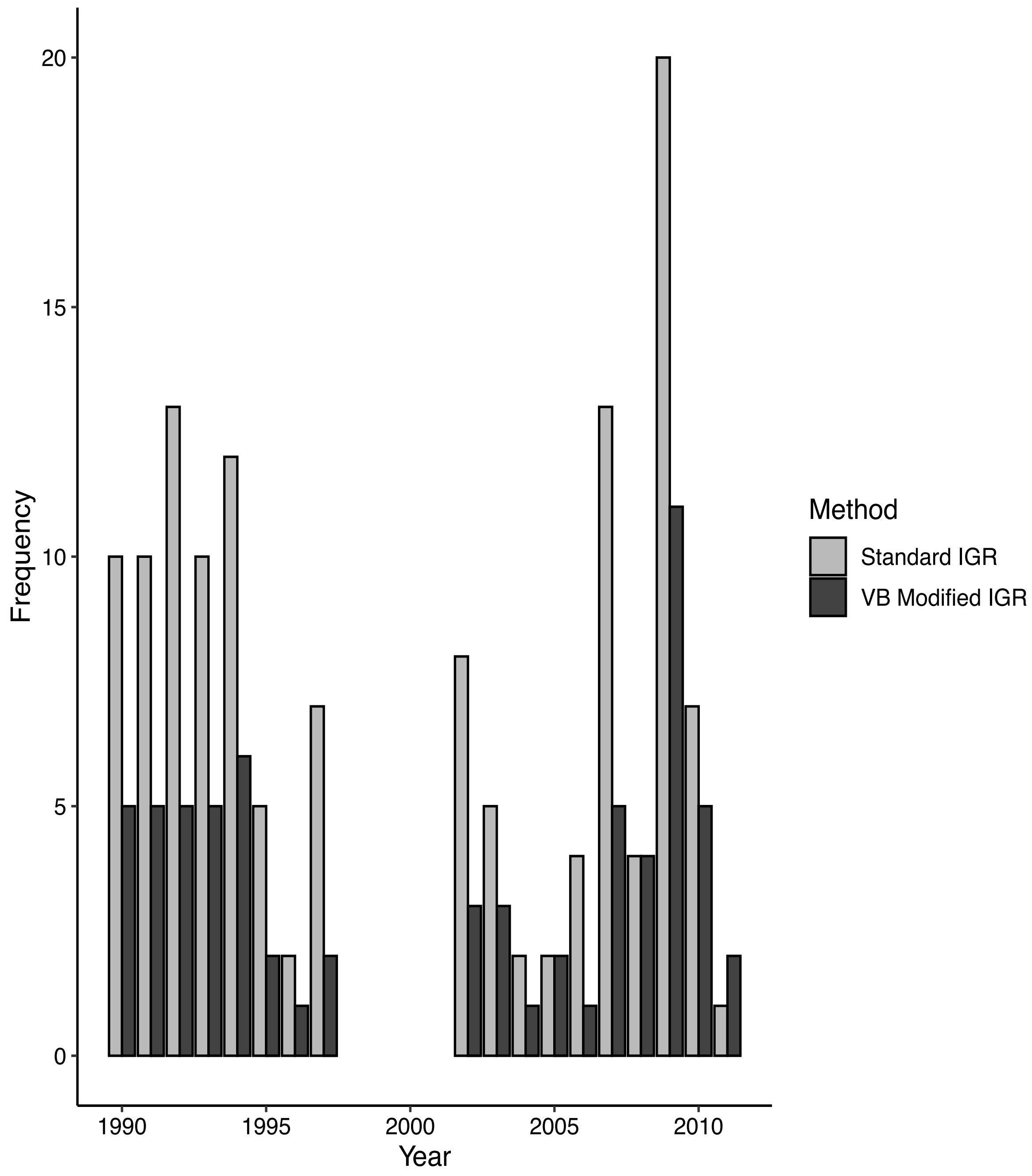


Figure 2.4. A comparison of the frequency of age-class negative production estimates (based on 20 possible age classes in each year) between the standard IGR method and the proposed von Bertalanffy-modified IGR method.

Chapter 2 Supplemental Information

Table S2.1. Minimum number of individuals required to use observed weights over predicted weights (i.e., cut-off value)

Age	Cutoff Value
1	10
2	14
3	11
4	20
5	6
6	3
7	4
8	4
9	5
10	6
11	3
12	4
13	5
14	6
15	9
16	8
17	8
18	6
19	3
20	4
20+	5
21+	7

Table S2.2. von Bertalanffy model parameters for all cohort-specific growth curves and cohort-specific length-weight regression equations. All t_0 values were set to zero in models.

Year	L_∞	*k*	Coefficient Estimate	Intercept Estimate	R^2	df	*F*-value	*p*-value
1979	461.67	0.46	2.85	-10.8	0.59	70	102.7	2.28E-15
1980	455.29	0.40	2.69	-9.89	0.54	41	50.3	1.23E-08
1981	441.34	0.40	3.35	-13.91	0.72	47	123.1	1.00E-14
1982	470.49	0.19	2.76	-10.32	0.57	72	96.5	6.24E-15
1983	437.99	0.72	2.61	-9.44	0.82	63	291.4	2.20E-16
1984	464.37	0.27	2.78	-10.44	0.89	99	865.2	2.20E-16
1985	437.38	0.42	2.89	-11.12	0.94	89	1345	2.20E-16
1986	451.98	0.29	3.09	-12.33	0.98	135	6306	2.20E-16
1987	462.02	0.26	3.01	-11.82	0.98	127	7230	2.20E-16
1988	456.55	0.53	2.99	-11.77	0.96	87	1939	2.20E-16
1989	473.01	0.22	2.97	-11.61	0.94	62	1039	2.20E-16
1990	640.00	0.24	3.28	-13.47	0.98	76	3054	2.20E-16
1991	464.61	0.31	3.27	-13.36	0.91	59	641.8	2.20E-16
1992	461.87	0.33	3.15	-12.69	0.97	58	1929	2.20E-16
1993	467.51	0.48	3.21	-12.99	0.92	56	670.3	2.20E-16
1994	467.26	0.40	3.23	-13.12	0.98	53	2348	2.20E-16
1995	458.88	0.79	3.23	-13.16	0.95	49	866.3	2.20E-16
1996	465.87	0.46	1.78	-4.32	0.49	58	58.8	2.19E-10
1997	473.67	0.63	3.05	-12.05	0.87	100	702.2	2.20E-16
1998	468.54	0.52	3.14	-12.61	0.97	96	2874	2.20E-16
1999	484.39	0.28	3.03	-11.87	0.88	67	505.7	2.20E-16
2000	484.09	0.34	2.98	-11.68	0.87	67	472	2.20E-16
2001	487.17	0.31	3.12	-12.48	0.96	98	2122	2.20E-16
2002	480.46	0.48	3.00	-11.76	0.76	72	230	2.20E-16
2003	461.67	0.66	3.04	-11.97	0.96	128	3027	2.20E-16
2004	469.23	0.79	2.91	-11.16	0.98	74	3475	2.20E-16
2005	454.63	0.74	2.93	-11.28	0.97	61	2037	2.20E-16
2006	616.76	0.74	2.68	-9.83	0.99	9	1123	9.26E-11
2007	594.09	0.19	3.16	-12.69	0.99	15	2125	2.20E-16
2008	459.61	0.91	2.7746	-10.35	0.94	5	89.2	0.000225

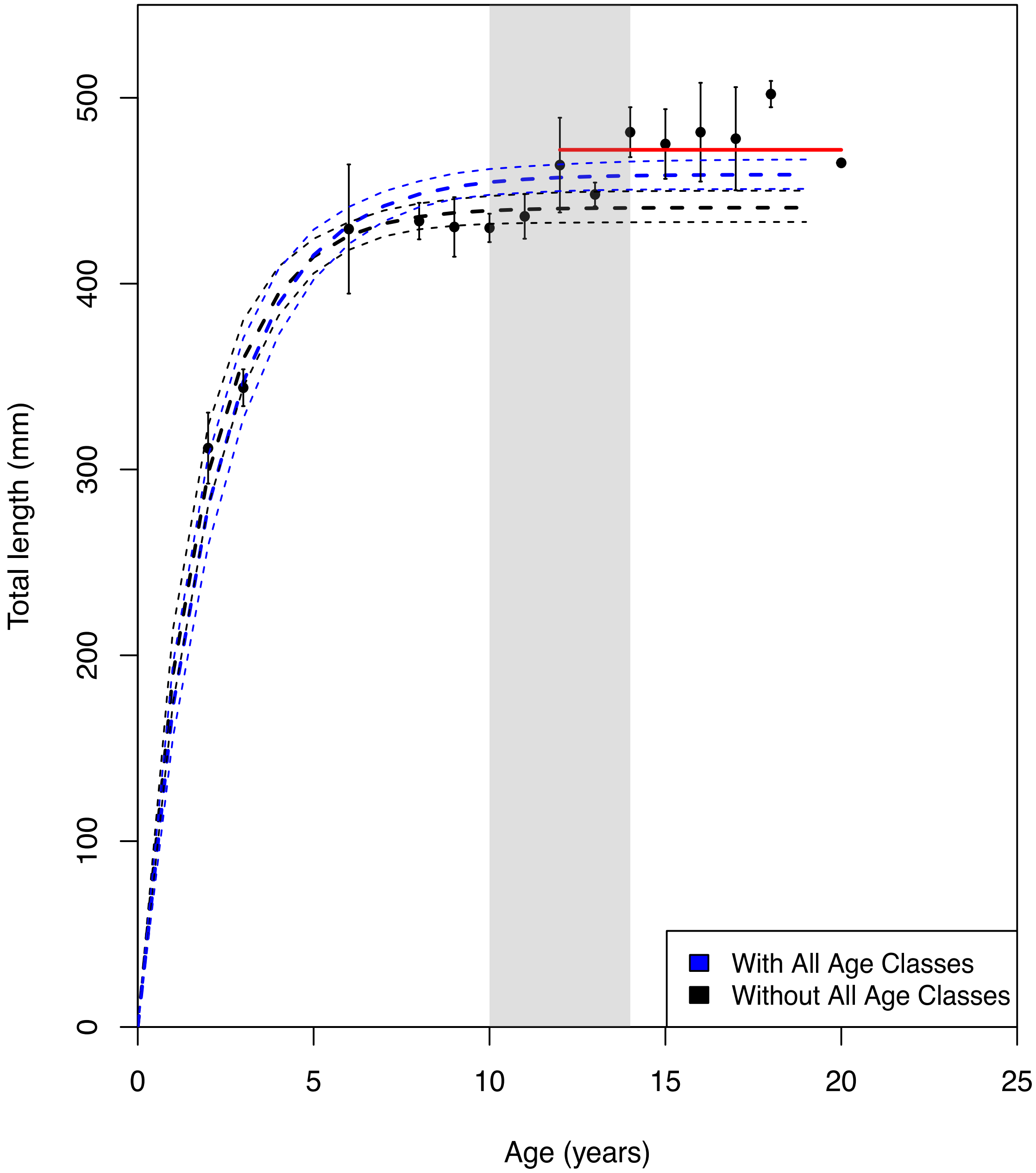


Figure S2.1. Von Bertalanffy models of the 1993 Lake Trout cohort with (blue) and without (black) age-classes that experienced secondary somatic growth due to aquaculture. The red line denotes the mean weight taken for the age-classes that experienced secondary somatic growth that was used in place of model predicted weight in cohorts that experienced these growth changes. Aquaculture is denoted as the shaded region and dashed lines are the growth model 95% confidence intervals.

CHAPTER 3

Identifying drivers of fish population- and community-level production during a whole-lake nutrient manipulation

Abstract

The Canadian federal *Fisheries Act* prohibits development activities that impact the productive capacity of fish habitat, which requires the assessment of fish productivity or components of productivity since fish production is recognized as a sensitive indicator of fish population and community fitness. However, the extensive data requirements to estimate fish production directly have hindered its application broadly, and as a result has limited our understanding of drivers and predictors of freshwater fish productivity. To better understand mechanisms and predictors of population and community production, we used comprehensive long-term data from Lake 375 at the IISD-ELA from species comprising the majority of fish community biomass (99%); Lake Trout (*Salvelinus namaycush)*, White Sucker *(Catostomus commersonii)*, Fathead Minnow (*Pimephales promelas*), and Northern Pearl Dace *(Margariscus margarita).* Lake 375 experienced a whole-lake aquaculture experiment, resulting in dramatic increases in total phosphorus concentrations during aquaculture before rapidly returning to pre-manipulation levels upon aquaculture cessation. Population production estimates for all species increased with these changes in nutrients, with estimates of community production predominantly driven by White Sucker and Lake Trout production. Additionally, minnow catch-per-unit-effort (CPUE) estimates provided strong explanatory power for both White Sucker, Lake Trout and community production estimates. Only White Sucker production was strongly associated with species-specific life-history metrics (i.e., body condition, mean fork length, mean weight). White Sucker production was also strongly related to Lake Trout production, the top predator in the lake. The dominance of White Sucker in the fish community and strong correlations with other species population metrics emphasizes the

potential utility of White Sucker as an indicator species. This study provides insight into complex physiochemical, limnological and inter-species relationships that shape population and community production and offers unique insight into fine-scale long-term temporal population and community production dynamics to identify a broader set of potential predictors of production.

Introduction

Freshwater fish productivity is a sensitive descriptor of population fitness in the wild. Production is defined as the amount of biomass produced over time in the area occupied by a given species or community (Randall & Minns, 2000; Waters, 1977). In Canada, the federal *Fisheries Act* acknowledges the link between productivity of fish populations and communities are linked to their habitat and legislatively requires productivity (or components of productivity) to be assessed to determine anthropogenic impacts associated with development (Government of Canada, 2019). Despite the sensitivity of fish productivity as a monitoring tool, estimating fish productivity directly is time- and cost-prohibitive given that a single estimate of production requires cohort-specific information for both body size and population size data from a population over two consecutive sampling periods (Hayes et al., 2007; Waters, 1977).

To date, seminal work has found fish production to be correlated with total phosphorus, primary production (Downing et al., 1990), standing biomass, mean weight, mean air temperature, latitude, species richness, and production rate per unit biomass (P/B ratios; Downing & Plante, 1993), mean depth (Prepas, 1983). Largely, across studies these correlative relationships have been investigated over (i) large spatial scales and/or short time periods; (ii) using multiple production estimation methods (i.e., Allen curve, cohort, instantaneous growth rate (IGR), size-frequency methods; Downing et al., 1990; Downing & Plante, 1993; Rypel & David, 2017); (iii) often using models of production founded on theoretical assumptions of production (i.e., using one sampling period to calculate population production, Embke et al., 2019; relying on P/B ratios to estimate production, Jarvis et al., 2020; or using a generalized model of production, Rypel &

David, 2017); (iv) or rely on production estimates calculated using data derived from commercial fisheries (i.e., commercial fishing yields, sport fishing yields, average commercial catch; Hanson & Leggett, 1982; Oglesby, 1977; Prepas, 1983; Ryder, 1965) which is known to suffer from biases in size selectivity (Millar, 1992; Quang & Geiger, 2002), and likely resulting in biased production estimates. Since these early investigations, few other assessments of production have been published (see Embke et al., 2019; Rypel & David, 2017 as some recent but rare examples), with most recent analyses only assessing components of production (i.e., biomass, growth, abundance; Campana et al., 2020; Craig et al., 2017; Finstad et al., 2014; Jarvis et al., 2020; Koizumi et al., 2018). Outside of initial investigations that focused on assessing production across large spatial scales (Downing et al., 1990; Downing & Plante, 1993; Waters, 1977, 1999), limited work has been conducted using robust estimates of production, highlighting the need to investigate fine-scale temporal mechanisms of wild fish production using comprehensive long-term data.

Recent syntheses of the literature have led to conceptual models that clearly demonstrate the influence of bottom-up processes (i.e., resource availability) in shaping individual bioenergetics and life history traits, which ultimately dictate the productive capacity of freshwater fishes (de Kerckhove, 2015; MacLeod et al., 2022; Smokorowski & Pratt, 2007). These syntheses demonstrate how usable habitat, shaped through factors such as light attenuation, temperature, dissolved oxygen availability and prey size and quantity (among other factors) likely act together to influence individual bioenergetics, which when scaled to population, shape population and community production. Within an ecosystem (i.e., available space), species are constrained within their usable space, which is dictated by both abiotic (i.e., optimal temperature, available oxygen, factors affecting light availability) and biotic factors (i.e., prey size and quantity; MacLeod et al., 2022). Empirical evidence supports these mechanisms as drivers of production; for example, when fish exist within their species-specific thermal optima or niche, fish are able to maintain peak consumption and basal metabolic needs without consequence (Fry et al., 1947; Hasnain et al., 2010; Magnuson et al., 1979; McMeans et al., 2020; Pörtner, 2002). Outside of these optimal temperature ranges, fish performance decreases and leads to increased energy expenditure to maintain basal metabolic requirements, ultimately decreasing productive capacity. Oxygen availability further dictates the volume of usable habitat since fish metabolism and physiology are aerobic, and a loss of optimal oxythermal habitat can result in declines in growth and body condition by limiting access to prey resources and increasing metabolic costs associated with foraging outside of optimal habitat areas (Guzzo & Blanchfield, 2017). While oxygen and temperature constrain usable space within an ecosystem, nutrient availability is expected to modulate available resources within that space (i.e., prey size and quantity, oxygen availability). Experimental increases in nutrients have been shown to increase abundance, recruitment, growth, condition and size-at-maturation of both apex species (e.g., *Salvelinus namaycush, Coregonus clupeaformis;* Mills, 1985; Rennie et al., 2019), and mid-trophic fishes such as minnows due to increases in productivity through bottom-up controls (Rennie et al., 2019; Schindler, 1990). Size and quantity of available prey can introduce additional constraints such that the benefit of acquiring food increases as prey become bigger, while smaller prey result in increased energy expenditure to acquire an equivalent amount of biomass (Giacomini et al., 2013). Consequently, shifts in life history strategies (e.g., size-at-age, condition, growth) are anticipated in accordance with changes in prey size and quantity/availability.

Given these links between resources and life history traits, life history metrics may provide more direct measures of productivity than environmental drivers, as production estimates are based on changes in the mean weight of age (or length) classes in the population over time (MacLeod et al., 2022). Life history theory dictates that the bioenergetic processes that determine the amount of energy allocated to fitness-enhancing traits (such as somatic growth and reproduction), ultimately shape production (Lester et al., 2004; Shuter et al., 2016). However, life history strategies are constrained by environmental conditions, and reflect the outcome of physiological interactions between an organism and their environment in how energy is utilized optimally. Indeed, these strategies are directly related to production as growth (one component of production) is the rate of individual production and is the consequence of food availability, and the allocation of energy to reproduction (Lester et al., 2004; Shuter et al., 2016). Similarly, adult abundance is the net result of (i) survival rates to maturation (mortality/survival), (ii) how long it takes to reach maturation (growth rate; size- and/or age-at-maturity), and (iii) how much an individual invests in gametes (reproductive investment; Andersen & Beyer, 2006). While physiochemical, limnological, and lower food web processes (i.e., food availability) shape usable habitat thereby setting the constraints for production), life history traits reflect the optimal strategies for success within those constraints (e.g., life history strategies find the optimal production or fitness given a suite of environmental limits/thresholds).

Given this theoretical basis by which abiotic and biotic factors act as drivers and constraints on individual metabolism and bioenergetics, we can hypothesize their influence on life-history strategies and ultimately population and community production. Specifically, I hypothesized that individual species and community estimates of production would follow changes in (i) total phosphorus, (ii) prey availability (i.e., zooplankton biomass, minnow catch-per-unit-effort; CPUE), (iii) available habitat, (iv) temperature (growing degree days; GDD), as well as (v) various life history metrics (i.e., max fork length, max weight, mean fork length, mean weight, body condition). Here I test these hypotheses using approximately 20 years of fisheries and environmental data with the goal of (1) gaining insight into fundamental mechanisms that act as drivers and constraints to shape productive capacity of both populations and communities; and (2) helping to identify possible predictors of production that are more time- and cost-effective than producing traditional estimates of production.

Methods

Site Description

We explored long-term temporal variation in environmental and fish population and community data from Lake 375 at the IISD-Experimental Lakes Area (IISD-ELA). Lake 375 was manipulated from 2003-2007 to evaluate potential impacts of aquaculture on freshwater ecosystems (Bristow et al., 2008; Paterson et al., 2010, 2011; Rennie et al., 2019). Each year, 10,000 penned Rainbow Trout (*Oncorhynchus mykiss*) were maintained annually during the manipulation (Bristow et al., 2008). During this time, total phosphorus in the ecosystem increased five times that of background concentrations due to excess feces and fish food. This increase in available nutrients resulted in (i) a reduction in optimal cold-water oxythermal habitat due primarily to the development of a large hypoxic zone in the hypolimnion (Paterson et al., 2010a; Rennie et al., 2019); (ii) increases in phytoplankton biomass and abundance of some zooplankton species (i.e., *Bosmina* cf. *longirostris, Diacyclops thomasi;* Paterson et al., 2010); (iii) declines in *Mysis diluviana* (Paterson et al., 2011); (iv) increases in Late Trout (*Salvelinus namaycush)* population abundance, size- and age-at maturity, and body condition; (v) declines in White Sucker *(Catostomus commersonii)* abundance and body condition, combined with increases in White Sucker mean size- and age-at maturity (Rennie et al., 2019); and (vi) dramatic increases in fall minnow abundance, but, no observable change in spring minnow abundance, combined with a reduction in young-of-year size of Fathead Minnow, suggesting increased overwinter mortality (Rennie et al., 2019). Changes in isotopic values of carbon and nitrogen of these organisms during aquaculture indicated clear associations with aquaculture feed and waste products, strongly suggesting that these population-level changes were associated with nutrients introduced to the system from aquaculture (Wellman et al., 2017).

Data Selection

Long-term (1989-2013) size, age, and mark-recapture data for Lake Trout and White Sucker from Lake 375 at the IISD-ELA were selected, alongside weight, length, and catch-per-unit-effort (CPUE) data of minnow populations in Lake 375 to calculate population and community production estimates (Rennie et al., 2019). Sampling of fishes occurred in spring and fall, primarily using Beamish-style trap nets for all species

(Beamish, 1973), with the exception of Lake Trout which were sampled primarily during fall spawning (mid-September to October) using a combination of short-set gillnets (10-20 minutes in duration) and trap nets (Rennie et al., 2019). Minnows were captured in the fall using both Beamish-style trap nets (Beamish, 1973) and Gee-style minnow traps. The minnow community was comprised of Fathead Minnow *(Pimephales promelas)*, Northern Pearl Dace *(Margariscus margarita*), Finescale Dace (*Chrosomus neogaeus*), and Northern Redbelly Dace (*Chrosomus eos*). All Lake Trout and the majority of captured White Sucker (those >100mm) also had weights measured and fin-rays were collected on first sighting for aging and were given a unique mark on their dorsal fin to indicate their capture history. A subset of fish (primarily Lake Trout) were given a unique identifying tag, either a sew-on Carlin tag under the dorsal fin, VI tag injected behind the left or right eye, PIT tag injected under the dorsal fin, or some combination of the three. Aged individuals (based on cross-sections of collected fin rays) with unique tag identifiers had ages assigned on subsequent captures based on initial age determination (from fin rays) and time since initial capture. Minnows captured in trap nets were identified to the species level, from which a subset was measured. Additionally, minnow traps were used to supplement trap net sampling, and were measured for length and weight.

Lower food web, physiochemical and limnological variables, and life history variables were selected based on published theoretical and empirical work demonstrating relationships between fish production or related parameters (i.e., growth, biomass, abundance) and data availability. To identify putative predictors of production, we assessed the following physiochemical and limnological variables: (i) mean total epilimnetic phosphorus concentrations (Bristow et al., 2008), (ii) cumulative growing degree days above 0°C (GDD_0), (iii) volume of optimal habitat for cold-water species (i.e., volume of water that contains 4 mg/L O_2 and was 15°C; Rennie et al., 2019). We knew that cold-water habitat was directly impacted in Lake 375 due to the development of a hypoxic zone in the hypolimnion which led to declines in Mysis (Paterson et al., 2011), and other work at IISD-ELA that demonstrated reductions in cold-water habitat led to changes in behaviour and condition of Lake Trout (Guzzo et al., 2017). As there were no reported changes to cool-water habitat or known major climatic variations that would have led to reductions in cool-water habitat, we chose to assess optimal habitat for cold-water species only to assess the degree to which known changes in optimal habitat for cold-water species impacted Lake Trout production and ultimately community production. Lower food web indices selected for analyses were: (iv) zooplankton biomass (Paterson et al., 2010a), and (v) fall minnow CPUE (Rennie et al., 2019). Life history predictors selected were: (vi) mean fork length, (vii) max fork length (i.e., 95% percentile), (viii) mean weight, (ix) max weight (i.e., 95% percentile), and (x) body condition. Body condition was estimated using the relative weight method (Wege & Anderson, 1978), based on species-specific equations for Lake Trout (Piccolo et al., 1993) and for White Sucker (Bister et al., 2000). We did not assess body condition of Fathead Minnows since weight data were not collected for minnows captured with trap nets (see *Production Estimates* for details on how weight was estimated to calculate production). Because total phosphorus/primary productivity is well established as one of the main drivers of fish production (Downing et al., 1990; Downing & Plante, 1993), we chose to assess linear relationships for all species, based on strong ($\rho > 0.6$) but inconsistent significant rank-correlations after correction for multiple comparisons (see results).

Production Estimates

All population and community production estimates were calculated using the standard Instantaneous Growth Rate (IGR) method first described by Ricker (1946; for a full example see Hayes et al., 2007). Standard production estimation followed:

$$\hat{P} = \sum \hat{G}\bar{B} \tag{3.1}$$

where $\hat{P}$ is the sum of estimated production for all cohorts of a population within a specified time interval, $\hat{G}$ is the instantaneous growth rate for a cohort from time t to t_{+1}, with $\bar{w}_t$ representing mean cohort weight at time t, calculated as:

$$\hat{G} = \log_e \bar{w}_{t+1} - \log_e \bar{w}_t \tag{3.2}$$

and $\bar{B}$ is the mean cohort biomass from time t to t_{+1}, calculated as:

$$\bar{B} = (\hat{B}_t + \hat{B}_{t+1})/2 \tag{3.3}$$

where $\hat{B}_t$ is the product of the density (N_t) and mean weight of each age class at time t:

$$\hat{B}_t = N_t * \bar{w}_t \tag{3.4}$$

Lastly, N_t is calculated by apportioning population abundance estimates (N_p) to age-classes based on the proportion of caught individuals in time t, such that:

$$N_t = (n_{age\text{-}class} / n_{total}) * N_p \tag{3.5}$$

where $n_{age\text{-}class}$ is the number of individuals per age-class, n_{total} is the total number of individuals across all age classes caught in that sampling period.

To estimate community production, we chose to focus on the four species in the lake with sufficient data for production estimates: Lake Trout, White Sucker, Fathead

Minnow, and Northern Pearl Dace based primarily on data availability. We also confirmed that these four species comprised the majority of the standing biomass of the fish community in this lake by quantifying percent total captured biomass represented by these species captured in the lake over time. Annual total captured biomass was calculated by quantifying the total annual catch per species, multiplied by the mean weight of individuals caught in the corresponding sampling period. A single mean estimate of captured biomass by species was calculated from annual estimates. The sum of these annual mean estimates over all species captured over all years was used to calculate the proportion of biomass contributed per species. This analysis demonstrated that these four species accounted for 99% of the captured fish community biomass (see Table S3.1).

Lake Trout Production Estimates

Annual Lake Trout abundance estimates were calculated using long-term (1989-2013) fall mark-recapture data and the POPAN formulation of the Jolly-Seber model (Schwarz & Arnason, 1996) using Program MARK (White & Burnham, 1999), as reported in Rennie et al. (2019). Annual population production estimates were calculated using the von Bertalanffy-modified Instantaneous Growth Rate (IGR) method described in Chapter 2 of this thesis. In short, predicted weights (using von Bertalanffy models applied to cohorts) were used in place of observed weights for age-classes when small sample sizes occurred (as identified through a simulation study, details in Chapter 2) and estimates were calculated using a modification of the IGR method that allows for negative estimates of production.

Since Lake Trout production estimates were based on individuals sampled in the fall during spawning, we adjusted the year of the calculated production estimates to be the year of sampling + 1 to better reflect the production of the cohorts being modelled. For instance, Lake Trout production estimates spanning from fall of 2010 to 2011 would be reported as a 2011 production estimate, since this time span best represents the period of tissue elaboration over the 2011 growing season (and only a small portion of 2010 during the coldest part of the year, over which growth is assumed to be negligible).

White Sucker Production Estimates

Annual White Sucker abundance estimates were calculated using the Schnabel method (Schnabel, 1938) from individuals observed over multiple occasions during a 4-6 week period during spring. Collection periods for White Sucker spanned from 1989-2009. Abundance was linearly interpolated in 2004 using abundance estimates from 2003 and 2005 since size-at-age data existed for 2004, but a lack of recaptures prevented the estimation of an accurate Schnabel estimate in this year. As only a subset of captured White Sucker were aged in each year, annual age-length keys were developed to assign ages to unaged individuals captured in each year (Ogle, 2015). Though White Sucker exhibit sexual size dimorphism, the average annual sex ratio in the population is approximately equal (~60:40% male:female; Figure S3.1), indicating that a single growth curve applied to this population is broadly representative of growth for the population as a whole (Figure S3.2). Annual population production estimates were calculated for the White Sucker population using the standard IGR method (equations 3.1-3.5). White

Sucker production was not calculated using the von Bertalanffy-modified method, which has yet to be developed for application to this species.

Fathead Minnow and Northern Pearl Dace Production Estimates

We calculated estimates of production for Fathead Minnow and Northern Pearl Dace between consecutive years during fall sampling periods. Spring estimates of abundance tended to be much lower and showed little change during aquaculture relative to fall estimates, which was speculated to be related to overwinter mortality (Rennie et al., 2019), but could potentially also be due to differential catchability associated with seasonal behavioural differences. To avoid potential biases related to catchability, production was calculated for minnow species between fall to fall in adjacent years with sufficient data.

Only Fathead Minnow and Northern Pearl Dace were assessed from the minnow community, for several reasons. First, previous analyses identified that Fathead Minnow comprised the majority of the minnow community (~80-90%) both before and after aquaculture, while Fathead Minnow and Northern Pearl Dace combined comprised the majority of the minnow community during aquaculture (~80-90%; Rennie et al., 2019, Figure B1). Lastly, while we were able to convert capture data to population estimates for Fathead Minnow and Northern Pearl Dace (see below), no similar equations exist to permit calculations for Northern Redbelly Dace or Finescale Dace.

Fall minnow abundance estimates were calculated using catch-per-unit-effort (CPUE) estimates and converted to abundance estimates using equations published elsewhere (Guzzo et al., 2014). For Fathead Minnow over all time periods (1993-2011)

CPUE estimates from trap nets were used to estimate abundance. For Northern Pearl Dace, abundance estimates were based on CPUE estimates of individuals caught using minnow traps for years during aquaculture (2003-2007). Northern Pearl Dace abundance estimates were limited to minnow trap captures as abundance and trap net CPUE are not significantly related for this species (Guzzo et al., 2014). Estimates of production for Northern Pearl Dace were only calculated during aquaculture for inclusion in community production estimates since this species was only a significant portion of the community during that time period (Rennie et al., 2019 Figure S3.1). Production estimates for this species were only included in community production estimates, and not included in correlative analyses due to too few observations to evaluate population production estimates against predictors (n = 5). Lastly, while we were able to convert relative abundance data to population estimates for Fathead Minnows and Northern Pearl Dace (see below), no similar equations currently exist to permit calculations for Northern Redbelly Dace or Finescale Dace. Further, these species were only minor components of the fish community based on standing biomass estimates (Table S3.1).

To calculate both Fathead Minnow and Northern Pearl Dace production estimates, minnows were binned using species-specific length groups in place of grouping individuals by age-class since minnows were not aged (Figure S3.3 & S3.4). Minnow production estimates were calculated using a length-based application of the standard IGR method where production was evaluated across subsequent length groups between sampling periods (see equations 3.1-3.5; Hayes et al., 2007; Ricker, 1946). We did not apply a length-based von Bertalanffy-modified IGR method (like that presented in Chapter 2) as no such validated method currently exists. To identify the appropriate frequency and width of length groups for binning of both species, population data were assessed using size-frequency plots (Figures S3.5 & S3.6). Based on the species-specific size-frequency plots, both species were binned using incremental 10 mm length groups (e.g., length group 2 = 21-30 mm, length group 3 = 31- 40 mm), though the width of the first and last length groups differed based on species due to differences in species size (e.g., Fathead Minnow length group 1 = 0 - 20 mm and length group 6 = > 60 mm; Pearl Dace length group 1 = 0-50 mm and length group 6 = > 90 mm). Abundance was apportioned to length classes using the same approach described for apportioning abundance to age classes following equation 3.5. Weight data were not collected for Fathead Minnow captured in trap nets. To assign weights to individuals captured in trap nets, length and weight data from individuals captured in minnow traps were used to calculate length-weight regressions (Table S3.2). For all years prior to aquaculture (1989-2002), weights were assigned using a length-weight regression calculated using 2010 data as young-of-year mean weights of the population in 2010 had returned to pre-aquaculture weights (Rennie et al., 2019), suggesting a size-structure for this species comparable to pre-manipulation conditions. For years during aquaculture (2003-2007), and years immediately after manipulation (2008 and 2009), annual length-weight regressions were used to assign weights to captured individuals (Table S3.2). Northern Pearl Dace individual weights were recorded during aquaculture (capture in minnow traps) such that length-weight regressions did not need to be applied.

Lastly, for Fathead Minnow we estimated production for years where we had no existing data (1994-1995) by calculating production that occurred between two years of existing data (1993, 1996) and divided the estimate by three to determine an average amount of production that occurred annually between 1993-1996. These estimates were calculated during years where Lake 375 was under natural conditions (pre-aquaculture) and Fathead Minnow populations were not expected to experience significant changes during this time. As with Lake Trout, we adjusted the year of the calculated production estimates for minnow species to be year of sampling + 1 to ensure we were capturing tissue elaboration that occurred from fall of one year to fall of the next.

Community Production Estimates

Annual community production estimates were calculated by summing individual species production estimates, as well as species variance estimates. In instances where we were missing only one or two species-specific production estimates (occurring during the period prior to aquaculture) we applied a value representing an average of production estimates prior to aquaculture for that species (1990-1997, 2002, 2003), which were then included in the corresponding community production estimates. Since the production of each species should not change significantly prior to aquaculture when the system was under natural conditions, we believed that an average estimate of this time period was sufficient to include in the interpolated community estimates, which all occurred prior to aquaculture. Additionally, we chose an average value of White Sucker production prior to aquaculture for inclusion in the 2010 community production estimate under the assumption that by 2010 much of the fish community had returned to equilibrium following the cessation of nutrient inputs. We followed the same methodology for estimates of variance around community production estimates. Notably, we did not assess body condition as a predictor of community estimates since not all species had sufficient weight data and relative body condition is calculated using weights of individuals within a group divided by a species-specific standard weight (Pope & Kruse, 2007).

Statistical Analyses

One-way analysis of variance was used to assess significant differences in annual production estimates across time periods in Lake 375 associated with experimental aquaculture (i.e., before manipulation, 1989-2002; during experimental aquaculture, 2003-2007; and after experimental aquaculture, 2008-2010) for each species and for community production estimates. Northern Pearl Dace were excluded from this analysis as they were only represented by production estimates during aquaculture, however, the species estimates were included in community estimates. Data were assessed for normality and homogeneity using residual plots and a Shapiro-Wilk's test for normality.

To identify environmental and life history correlates of species and community production estimates, the potential presence of time lags between putative predictors and production estimates were assessed. We assessed multiple time lags (0-3 years of the predictor variables prior to a given production estimate) using Spearman's (rank order) correlation. We chose to apply Spearman's rank correlation analyses as a non-parametric assessment (i.e., ability to deal with any non-linearity associations between variables), thus providing conservative (rank-based) estimates of association. While some ecosystem changes were immediate (i.e., increases in total phosphorus; Bristow et al., 2008), other reported ecosystem changes typically lagged in response by 1-3 years over the course of the five year experiment (i.e., White Sucker and Lake Trout life history traits, fall minnow abundance, changes in optimal cold-water habitat, Rennie et al., 2019;

phytoplankton and zooplankton biomass, Paterson et al., 2010; changes in δ13C and δ15N in the benthic, zooplankton, and fish communities, Wellman et al., 2017). Ecological time lags were identified for each predictor for each population and community estimates based on the strongest significant correlation coefficient across all four-time lags evaluated (0-3 years; Table 3.1, see also Fig S3.8-3.10). To identify significant correlates and account for multiple tests, we applied false discovery rate (FDR) corrected *p*-values to evaluate significance (Table 3.1) following a Benjamini-Hotchberg procedure (Benjamini & Hochberg, 1995) to all correlates using the bruceR package in program R (Bao, 2023).

After significant correlates and their appropriate lags were identified, we explored potential predictive relationships between these variables with both species and community production estimates for Lake 375 using linear regression. Each model included a single predictor and a single species or community production estimate to maintain a reasonable ratio of observations to predictors. Correlations among predictor variables were identified using correlation matrices (see supplemental correlation heat maps, Figures S3.7-3.10). All data were assessed for normality and heterogeneity using residuals plots and the Shapiro-Wilk's test for normality. If models did not meet assumptions of normality and heterogeneity, data were log transformed and re-assessed again for normality and heterogeneity until model assumptions were met. Only log transformations were required to meet model assumptions when untransformed data did not meet assumptions of normality and heterogeneity.

Results

Species-specific and community-level production estimates varied over time before aquaculture, and all four species and corresponding community estimates increased at the beginning of experimental aquaculture, with White Sucker and community estimates declining in 2006 (three years after initiation and two years prior to cessation of aquaculture), Lake Trout and Northern Pearl Dace experienced declines in 2007 (four years after initiation and one year prior to cessation of aquaculture), and Fathead Minnow production declined in 2009, immediately after the cessation of aquaculture (Figure 3.1). After aquaculture, White Sucker, Northern Pearl Dace, and Fathead Minnow production returned to pre-aquaculture levels rapidly, whereas community estimates normalized after two years, and Lake Trout returned to pre-aquaculture levels three years after the cessation of experimental aquaculture (2010) only after experiencing a high rate of negative production in 2009 (Figure 3.1).

During aquaculture, White Sucker production increased 10 times that of pre-aquaculture production, while Lake Trout, the top predator of the system, experienced increases in production four times that of the population's production prior to experimental aquaculture. Fathead Minnows did not contribute significantly to community production but did increase three times that of background levels, and Northern Pearl Dace experienced a 1-fold increase in production during experimental aquaculture. One-way analysis of variance of species-specific and community production estimates between time periods (i.e., before: 1989-2002, during: 2003-2007, after: 2008-2010) indicated that production was significantly different between time periods (Community, $F_{2,18} = 21.61$, $p < 0.0001$; Fathead Minnow, $F_{2,8} = 11.27$, $p < 0.01$; Lake

Trout, $F_{2,14} = 4.74$, $p < 0.05$; White Sucker, $F_{2,93} = 7.90$, $p < 0.05$). Tukey's post-hoc analyses identified that (i) there were no significant differences between before and after time periods for any species and community estimates; (ii) all species and community estimates were found to be significantly greater during aquaculture compared with before aquaculture time periods ($p < 0.05$); and (iii) only community and Fathead Minnow estimates were significantly different between during and after aquaculture time periods, with both being significantly lower after aquaculture ($p < 0.01$). Notably, in 2009, White Sucker production was greater than the community production estimate due to Lake Trout population experiencing substantial negative production associated with a dramatic loss of mean weight among cohorts in the population (as previously reported and discussed in Chapter 2).

Ecological time lags between environmental variables and species/community production estimates were found to vary by species and putative predictors (Table 3.1). Several predictors (total phosphorus, minnow CPUE, and optimal cold-water habitat) were strongly significantly correlated across all species and the community (with the exception of Fathead Minnow production with total phosphorus and minnow CPUE; Table 3.2). Notably, total phosphorus was significant across all time lags for all community and White Sucker population estimates (not including White Sucker production 3 year lag; Figures S3.8-3.11).

Individual regression analyses of total phosphorus (log transformed where appropriate to ensure linearity) indicated similar significant, positive relationships with similar time lags ranging between 0-2 years for community (Figure 3.2a, $p < 0.01$; 2 year lag), Fathead Minnow (Figure 3.2b, $p < 0.05$; 0 year lag), Lake Trout (Figure 3.2c, $p <$

0.01; 0 year lag), and White Sucker estimates (Figure 3.2d, $p < 0.01$; 1 year lag). Fall minnow CPUE was found to be positively related with time lags ranging between 0-1 years for community (Figure 3.3a, $p < 0.01$; 0 year lag), Lake Trout (Figure 3.3b, $p < 0.01$; 0 year lag), and White Sucker estimates (Figure 3.3c, $p < 0.01$, 1 year lag; Table 3.2). We found significant negative relationships between optimal habitat for cold-water species with 2-3 year time lags for community (Figure 3.4a, $p < 0.001$, 2 year lag), Lake Trout (Figure 3.4b, $p < 0.01$, 2 year lag), and White Sucker populations (Figure 3.4c, $p < 0.05$, 3 year lag). Regression analyses also found strong significant relationships between White Sucker production and White Sucker life history traits across similar time lags, specifically, (i) mean weight (Figure 3.5a, $p < 0.001$, 2 year lag), (ii) mean fork length (Figure 3.5b, $p < 0.001$, 2 year lag), and (iii) body condition (Figure 3.5c, $p < 0.05$, 1 year lag). Lastly, we identified a strong positive significant relationship between White Sucker and Lake Trout production (Figure 3.5d, $p < 0.001$, 1 year lag).

While several putative predictor variables were correlated with production, we also identified strong correlations among some predictor variables ($\rho > 0.5$). Specifically, a number of variables were highly correlated ($\rho > 0.6$) with total phosphorus such as (i) minnow CPUE (community, Lake Trout, White Sucker, $p < 0.05$), (ii) body condition (Lake Trout and White Sucker, $p < 0.05$), and (iii) optimal cold-water habitat (community, White Sucker, Lake Trout; Figures S3.8-3.11). Additionally, minnow CPUE and Lake Trout and White Sucker body condition were significantly correlated ($\rho = 0.9$, 0.88, respectively; $p < 0.05$), and optimal cold-water habitat was strongly correlated with Lake Trout mean fork length and mean weight ($\rho > 0.6$; Figure S3.9). Optimal cold-water habitat was strongly negatively correlated with White Sucker mean fork length (ρ

> - 0.6) and was significantly negatively correlated with White Sucker mean weight, max fork length, and max weight (ρ > - 0.7; $p < 0.05$; Figures S3.10). Additionally, most life history variables were significantly correlated with one another within species and community estimates (Figures S3.8-3.11).

Discussion

Total phosphorus is known to be a driver of fish population production based on seminal empirical evidence (Downing et al., 1990; Hecky & DePinto, 2020; Mills, 1985). Here, I confirm this relationship and demonstrate that an entire fish community experienced significant increases in production associated with major nutrient inputs from experimental aquaculture, with production returning to pre-manipulation levels when nutrient inputs ceased. Additionally, I demonstrate that changes in community production were predominantly driven by changes in production of the White Sucker population, which make up ~50% of the total captured biomass in the lake. Contributions to community production by Lake Trout were moderate, while Northern Pearl Dace production had a larger contribution than Fathead Minnow production, which was comparatively negligible.

During aquaculture, Lake Trout production seemed to be driven by a combination of increases in abundance and size-at-age (Figure S3.5), with Lake Trout abundance increasing almost 50% during aquaculture (Rennie et al., 2019). By contrast, White Sucker production appeared to be driven exclusively by increases in size-at-age of individuals (Figure S3.2), as White Sucker abundance actually declined during the experiment (Rennie et al., 2019). Interestingly, while population and community production reached peak rates during aquaculture, there were simultaneous declines in population metrics that were not reflected in the production estimates. Specifically, while White Sucker were experiencing massive increases in production during aquaculture (in comparison to pre-aquaculture rates), the population was undergoing declines in recruitment, body condition, and abundance (Rennie et al., 2019). These large rates of White Sucker production, up to 15 kg/ha/yr in 2005, were driven primarily by large increases in cohort weight from 2003-2005 (Figure S3.2), before cohort weights began to decline in subsequent years (2006, 2007). However, in 2006 and 2007, White Sucker production remained high (2006 = 10 kg/ha/yr; 2007 = 5 kg/ha/yr) even while the population was experiencing declines in abundance, body condition, mean weight, and recruitment (Rennie et al., 2019). Although, in 2006, only individuals up to age six were captured, with older individuals up to age 17 captured in subsequent years, which may have introduced some inflation into both the 2006 and 2007 production estimates. However, given the magnitude of the change in production during these years it is unlikely these differences in production estimates were due alone to the missing age classes in 2006. It is also plausible that Rainbow Trout, which were released into the system as part of the experiment and occupied the nearshore region, could have competed with White Sucker for shared resources or potentially predated on White Sucker to contribute to the observed population declines (Charles et al., 2017). Overall, this highlights the need to understand population changes to fully comprehend changes in population production.

Besides total phosphorus, a number of predictors of population and community production were identified that can be categorized as physiochemical and limnological, lower food web and life history predictors. These included (i) minnow CPUE (lower food web), (ii) optimal habitat for cold-water species (physiochemical and limnological) and (iii) White Sucker body condition, mean weight, mean fork length (life history), in addition to a strong relationship between White Sucker and Lake Trout production. One of the strongest predictors (with the exception on total phosphorus) was minnow CPUE, which was positively related to community, Lake Trout, and (perhaps surprisingly) White Sucker production. Minnows are often a main prey item for Lake Trout (Guy et al., 2011; Kennedy et al., 2019), which is supported by the strong link between Lake Trout production and minnow CPUE reported here. The observed correspondence between minnow abundance and White Sucker production likely reflects a shared response to increases in primary production and/or resource availability. Main prey items for both minnows and White Sucker are lower food web prey items including zooplankton and benthic invertebrates (Chen & Harvey, 1995; Lammens & Hoogenboezem, 1991; Trippel & Harvey, 1987), and consequently minnow CPUE may act as an index of White Sucker production due to similarities in prey reliance. Overall, this analysis suggests that relative abundance metrics of the minnow community may act as an important mid-trophic level indicator that is easily collected and can capture both variation in lower food web availability for benthivorous species, as well as provide an indicator of food availability for piscivorous species (i.e., Lake Trout).

Optimal habitat for cold-water species was found to have a strong negative relationship with all species as well as community production, with production decreasing as optimal cold-water habitat increased. Declines in optimal cold-water habitat were driven by increases in total phosphorus that resulted in the formation of a large hypoxic zone in the hypolimnion (Bristow et al., 2008; Rennie et al., 2019). However, increases in fish production alongside decreases in habitat seems inconsistent with literature that supports positive relationships between habitat size and fish production (Minns, 1995; Prepas, 1983). By contrast, other work has shown that a loss of optimal cold-water habitat can lead to decreases in body size over time in Lake Trout (Guzzo et al., 2017). Initially, the loss of optimal cold-water habitat likely did not negatively influence production due to the sheer quantity of nutrients inputs during aquaculture that increased the abundance of prey items and provided a surplus of available energy to counteract any metabolic costs associated with a loss of optimal cold-water habitat (Guzzo et al., 2017; MacLeod et al., 2022). Near the end of the five-year aquaculture period, declines in body condition in both Lake Trout and White Sucker were reported (Rennie et al., 2019), potentially indicating density-dependent effects for Lake Trout (due to massive increases in the Lake Trout population during aquaculture), or a bottleneck where the metabolic costs associated with a loss of optimal habitat for cold-water species became too large to maintain body sizes of individuals. This was likely further conflated due to a large reduction in *Mysis* densities in 2007 and 2008 during the aquaculture experiment (Paterson et al., 2011) that led to diet shifts in Lake Trout during this time (Kennedy et al., 2019). However, this relationship does provide novel insight into population bioenergetics during disturbance and should be explored in future works, particularly as it relates to cold-water species like Lake Trout.

Total phosphorus was found to be highly correlated with several other predictors, indicating that total phosphorus is very likely the underlying driver of all significant correlates (predictors) of population and community production, as previous works have demonstrated that as total phosphorus increased and decreased with experimental aquaculture (Bristow et al., 2008), minnow CPUE, White Sucker life history traits, and optimal habitat for cold-water species followed changes in total phosphorus (Rennie et al., 2019). This is supported by empirical work that has clearly linked total phosphorus with overall ecosystem productivity as a limiting nutrient that mediates productivity through bottom-up controls (Mills, 1985; Mills & Chalanchuk, 1987; Schindler, 1974; Schindler et al., 1978; Wagner et al., 2011). However, while I recognize that changes in total phosphorus were the underlying mechanism of change temporally in this system, this study provided an opportunity to explore other ecosystem changes (as a result of total phosphorus changes) that also contributed to the observed changes in the fish populations and community over time.

Of the predictors identified in this study, total phosphorus and minnow CPUE are likely the most cost-and time-effective variables to collect as a possible surrogate of larger bodied fish production. Minnow CPUE can be quantified through deployment of minnow traps over a sampling period and CPUE can be estimated using simple calculations (Rennie et al., 2019). Total phosphorus can be quantified by collecting total dissolved phosphorus and suspended phosphorus from monthly epilimnion water samples during the open water season using analytical chemistry techniques (Bristow et al., 2008). However, of the two variables, minnow CPUE is the most accessible predictor as it is the most time- and cost-effective of the two based on material and time requirements. Particularly, since minnow traps can be easily set and are inexpensive, and counting minnows is easy to do and does not require specialized training or materials, although may require permits. Although, the use of minnow traps may have some limitations as they have shown to exclude young-of-year during fall sampling due to their small body size (Blanchfield et al., 2015; Kidd et al., 2007). If minnow CPUE is to be used as a surrogate for production, care will be necessary to ensure populations are well sampled to account for differences in location and behaviour. Lastly, White Sucker life history metrics are strong predictors, although, collecting population length and weight data can be expensive, time consuming, requires permitting and training, and usually access to nets and a boat, making it perhaps the least accessible of the predictors identified by this study. Although if your study area is not easily accessible for bi-weekly or monthly sampling, the immediate effort of sampling fish directly may be the most accessible means of data collection. Whereas, if the study area is easily accessible and there are barriers to sampling minnows, taking monthly water samples is likely a more accessible metric to monitor than handling large-bodied fish directly, especially with the recent use of drones for collecting water samples (Shelare et al., 2021).

In ecosystems where they are present, this work supports White Sucker as a potential indicator species for both community changes and top predator production in ecosystems. In this study, White Sucker production drove much of the community production and all major observed temporal community production changes. White Sucker were also a large portion of the total captured biomass for the fish community in the lake, contributing ~50% of the community biomass. Further, White Sucker production was correlated with Fathead Minnow production and had a significant relationship with Lake Trout production and was the only population in the lake 375 fish community that was significantly related to multiple life history metrics for the species (i.e., body condition, mean weight, mean fork length). Moreover, White Sucker (i) have a wide geographical distribution in North America, (ii) commonly occur in most lakes, and (iii) are generally not targeted in Canada by recreational or commercial fisheries (Becker, 1983); thus supporting their usefulness as an indicator species (Scott & Crossman, 1973). However, if White Sucker are to be used as an indicator species, it will likely be important that they are the main biomass contributing species in the system of interest.

These findings support empirical work within the literature that demonstrate both total phosphorus and body size to be drivers and predictors of fish production (Downing et al., 1990; Downing & Plante, 1993; Randall & Minns, 2000), as well as theoretical works that have reinforced the importance of physiochemical/limnological, and lower food web indices in shaping life history strategies and ultimately fish production (de Kerckhove, 2015; MacLeod et al., 2022; Smokorowski & Pratt, 2007). Most work to date has explored fish production across large spatial scales as opposed to temporal scales, with few exceptions (Mills et al., 2002). Here, I demonstrate that the main drivers of fish production from spatial comparisons were also found to be the main drivers of fish population and community production in Lake 375 over time. Further, I built on existing literature to provide additional support for previously identified drivers of freshwater fish productivity (i.e., total phosphorus), while identifying new potential predictors of production, such as minnow CPUE, and life-history metrics (i.e., White Sucker body condition, mean weight, mean fork length). Last, I demonstrate support for White Sucker as an indicator species in systems where they are found, as White Sucker population production was found to comprise the majority of community production over time and has a clear relationship with Lake Trout production (the top predator in the system). Overall, these findings support the hypothesis that bottom-up controls are the main drivers of population and community production and are stronger predictors of production than life-history metrics. Managing the impacts of development on freshwater fish productivity, or correlates of production, are legislated under the *Fisheries Act,* however, the existing level of understanding of drivers and correlates of production is not well understood due to time and monetary challenges associated with calculating production estimates. Here, I provide novel insights into mechanisms of population and community freshwater fish productivity, while identifying predictors of production that are potentially more time and cost effective than standard production estimation.

Table 3.1. Evaluation of predictors using Spearman's rank correlation coefficients of Lake Trout (LT), White Sucker (WS), and Fathead Minnow (FH) and community production predictors evaluated across different ecological time lags. Lag indicates the strongest ρ value. Only significant *p*-values* are noted and are false discovery rate corrected, uncorrected p-values can be found in supplemental correlation heat maps.

Taxa	**Predictor**	**Lag (yr)**	**ρ**	***p*-value**
LT	Max Fork Length	0	-0.35	
LT	Max Weight	3	-0.50	
LT	Mean Fork Length	3	0.66	
LT	Mean Weight	2	0.49	
LT	Zooplankton Biomass	2	0.64	
LT	Total Phosphorus	0	0.61	
LT	Optimal Habitat	2	-0.87	<0.05
LT	Body Condition	0	0.61	
LT	GDD	2	0.36	
LT	Minnow CPUE	0	0.90	<0.05
WS	Lake Trout Production	1	0.89	<0.01
WS	Max Fork Length	2	0.68	
WS	Max Weight	2	0.68	
WS	Mean Fork Length	2	0.97	<0.001
WS	Mean Weight	2	0.95	<0.01
WS	Zooplankton Biomass	3	0.52	
WS	Total Phosphorus	1	0.93	<0.01
WS	Optimal Habitat	3	-0.96	<0.001
WS	Body Condition	1	0.84	<0.05
WS	GDD	2	0.42	
WS	Minnow CPUE	1	0.90	<0.05
FH	Lake Trout Production	0	0.67	
FH	White Sucker Production	3	-0.68	
FH	Max Fork Length	0	0.58	
FH	Max Weight	0	0.52	
FH	Mean Fork Length	0	0.70	
FH	Mean Weight	0	0.70	
FH	Zooplankton Biomass	2	0.81	
FH	Total Phosphorus	0	0.73	
FH	Optimal Habitat	2	-0.59	
FH	GDD	2	0.53	
Community	Max Fork Length	0	-0.43	
Community	Max Weight	0	-0.17	
Community	Mean Fork Length	0	-0.38	
Community	Mean Weight	0	-0.32	
Community	Zooplankton Biomass	3	0.54	
Community	Total Phosphorus	2	0.87	<0.001
Community	Optimal Habitat	2	-0.95	<0.001
Community	GDD	2	0.20	
Community	Minnow CPUE	0	0.78	<0.05

Table 3.2. Model outputs from exploration of production predictors.

Predictor	Taxa	Lag (yr)	Coefficient Estimate	Intercept Estimate	Adjusted R^2	Residual df*	*F*-value	*p*-value
ln Total Phosphorus	Community	2	6.26 ± 1.62	-7.70 ± 3.17	0.52	12	14.86	<0.01
Total Phosphorus	Fathead Minnow	0	0.03 ± 0.01	-0.02 ± 0.09	0.44	7	7.24	<0.05
ln Total Phosphorus	Lake Trout	0	1.73 ± 0.54	-2.45 ± 1.03	0.38	14	10.39	<0.01
ln Total Phosphorus	White Sucker	1	6.99 ± 1.57	-10.88 ± 3.31	0.68	8	19.86	<0.01
Minnow CPUE	Community	0	0.02 ± 0.006	2.10 ± 1.22	0.57	8	12.71	<0.01
Minnow CPUE	Lake Trout	0	0.01 ± 0.001	-0.18 ± 0.36	0.69	8	21.01	<0.01
Minnow CPUE	White Sucker	1	0.02 ± 0.004	1.53 ± 0.91	0.70	6	17.16	<0.01
ln Optimal Habitat	Community	2	-7.62 ± 1.25	107.86 ± 16.88	0.80	8	37.05	<0.001
ln Optimal Habitat	Lake Trout	2	-2.28 ± 0.67	32.12 ± 8.97	0.54	8	11.67	<0.01
ln Optimal Habitat	White Sucker	3	-6.50 ± 24.13	90.91 ± 24.13	0.66	5	12.85	<0.05
Mean Fork Length	White Sucker	2	0.05 ± 0.01	-7.68 ± 1.50	0.86	7	63.11	<0.001
Mean Weight	White Sucker	2	0.01 ± 0.01	-1.34 ± 0.77	0.88	7	59.43	<0.001
Body Condition	White Sucker	1	34.97 ± 11.96	-25.60 ± 10.03	0.46	8	8.55	<0.05
Lake Trout Production	White Sucker	1	1.96 ± 0.37	1.60 ± 0.62	0.75	8	28.38	<0.001

* Regression degrees of freedom were one in all cases.

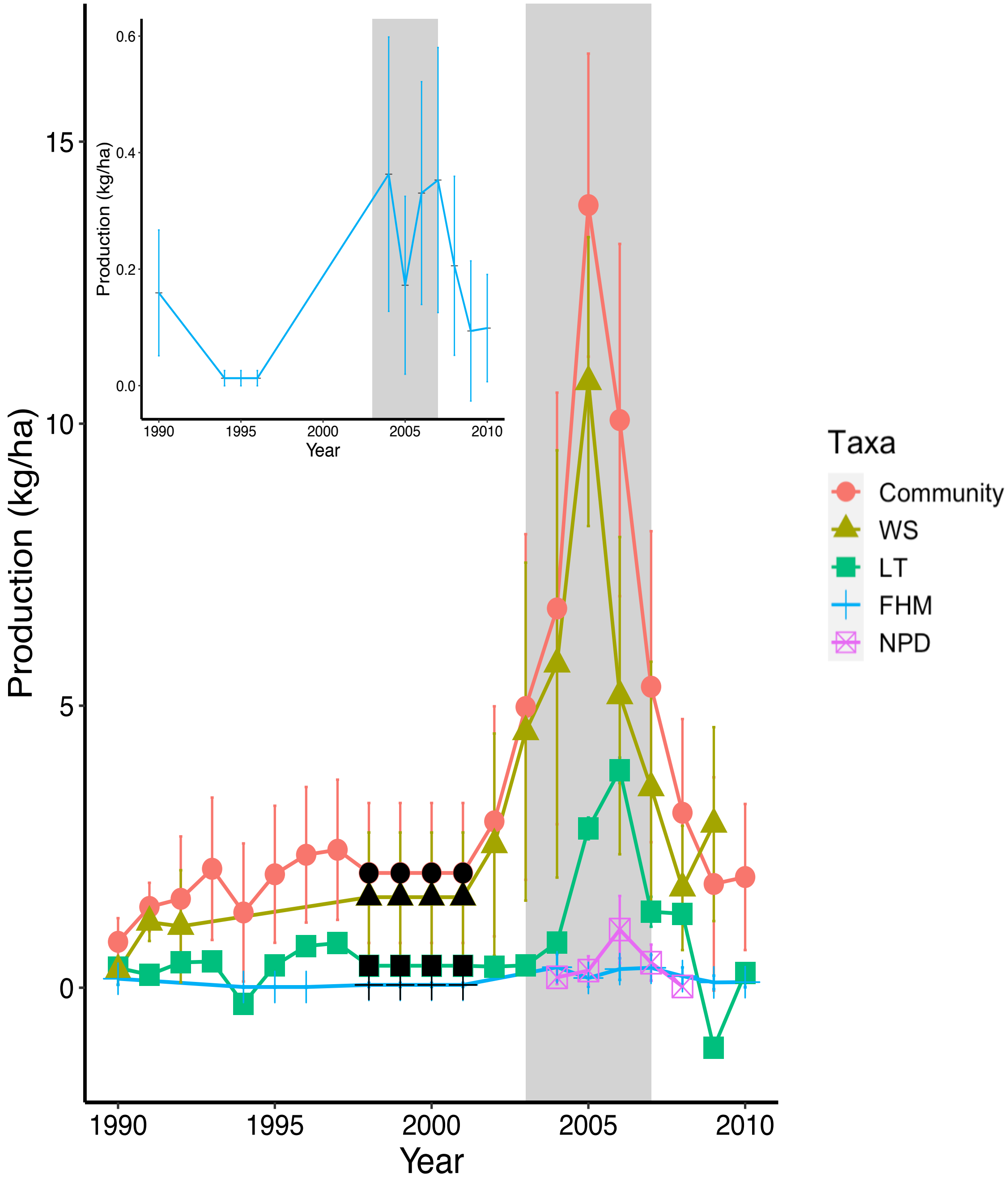


Figure 3.1. Species specific and community production estimates of Lake 375. Interpolated estimates are denoted by black points. Error bars represent standard deviation of the production estimates. Figure inlay in top left corner depicts Fathead Minnow production estimates.

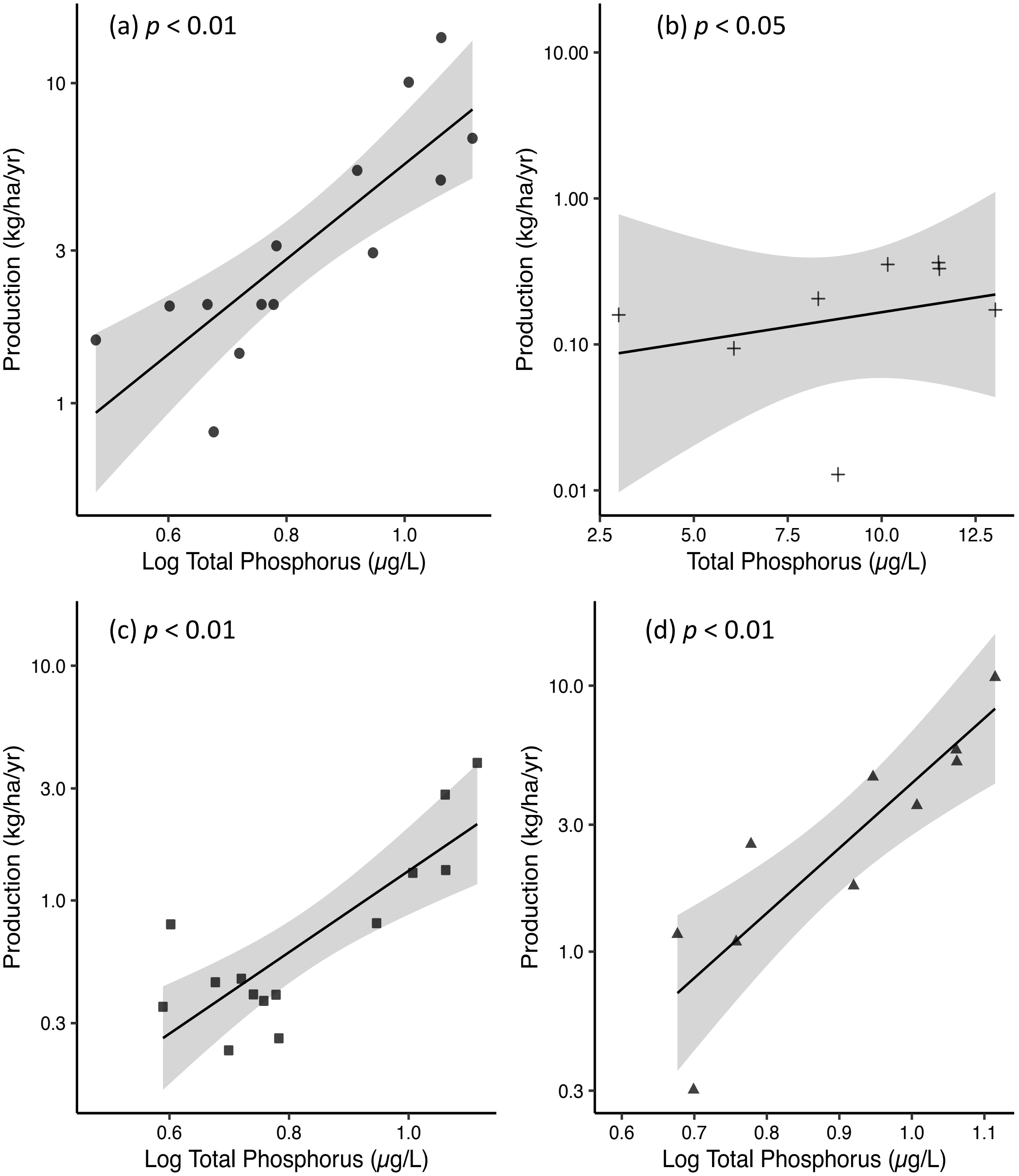


Figure 3.2. Relationships between epilimnetic total phosphorus estimates and (a) community (2 year lag; denoted by circles), (b) Fathead Minnow (0 year lag; denoted by crosses), (c) Lake Trout (0 year lag; denoted by squares), and (d) White Sucker (1 year lag; denoted by triangles) production estimates. Shaded regions represent 95% confidence intervals around the linear models. Model outputs can be found in Table 3.2.

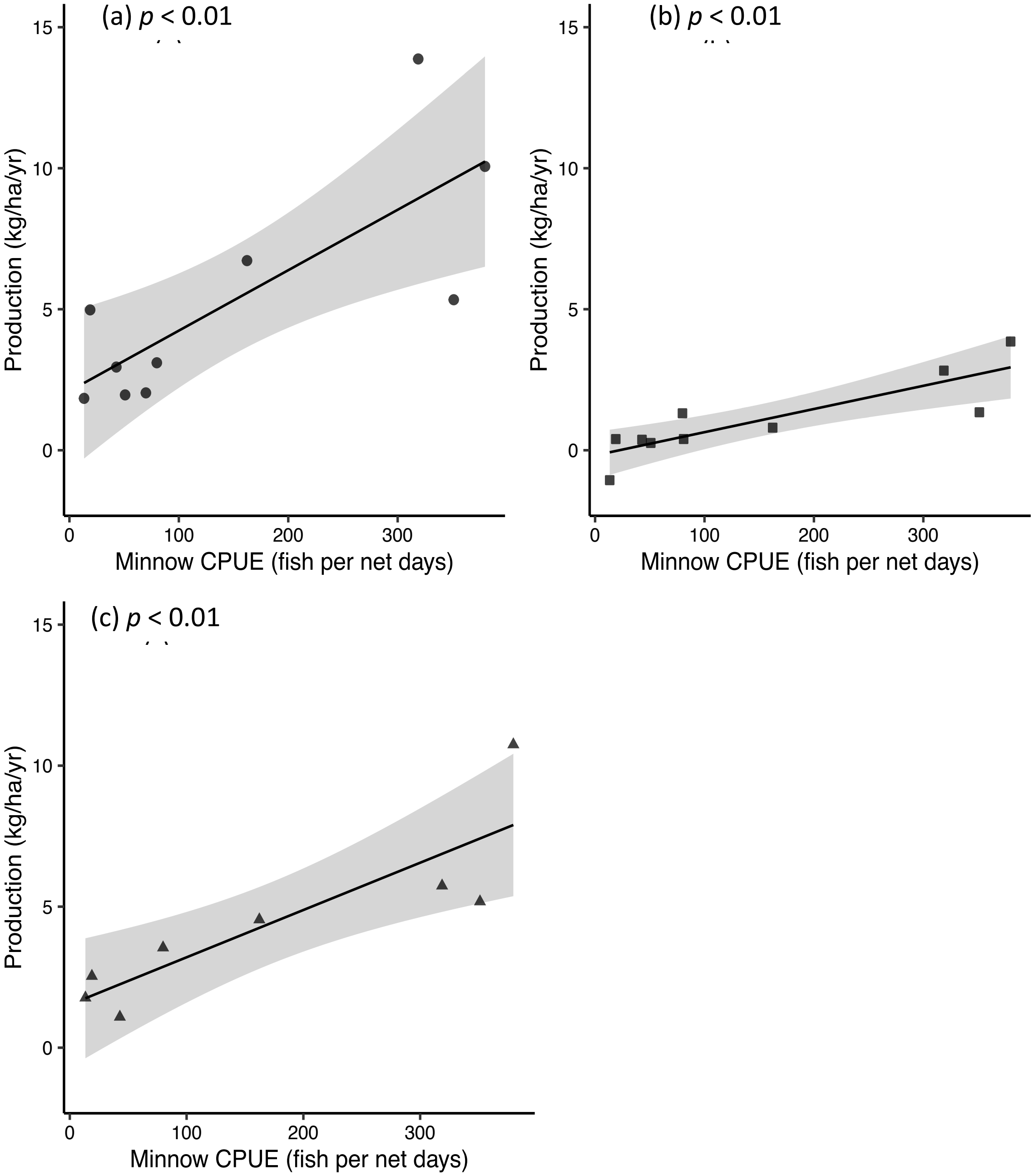


Figure 3.3. Relationship between minnow CPUE estimates and (a) community (0 year lag; denoted by circles), (b) Lake Trout (0 year lag; denoted by squares), and (c) White Sucker (1 year lag; denoted by triangles) production estimates. Shaded regions represent 95% confidence intervals around the linear models. Model outputs can be found in Table 3.2.

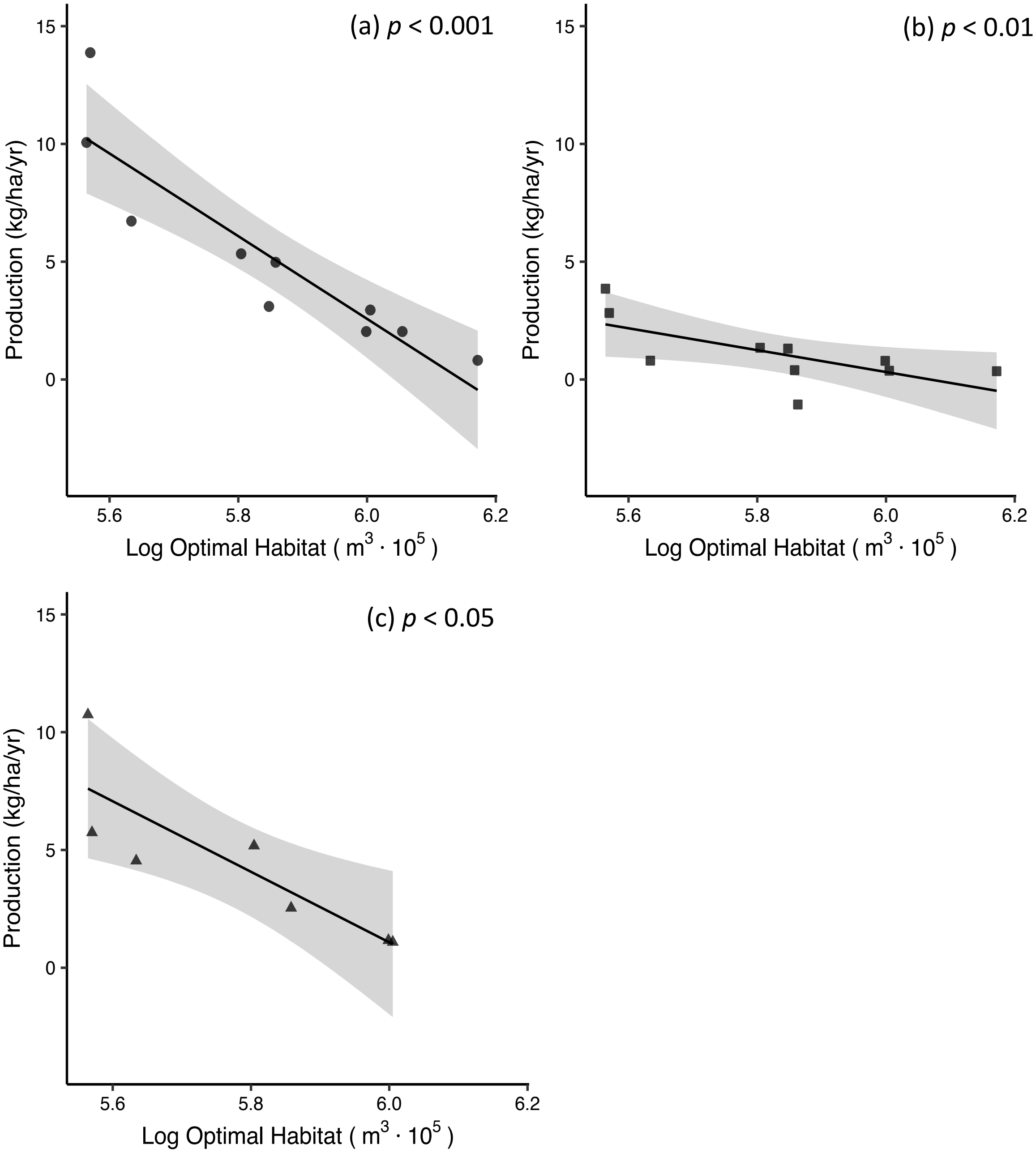


Figure 3.4. Relationship between annual volume of optimal habitat ($m^3 \bullet 10^5$) for cold-water species and (a) Community (2 year lag; denoted by circles), (b) Lake Trout (2 year lag; denoted by squares), and (c) White Sucker (3 year lag; denoted by triangles) production estimates. Shaded regions represent 95% confidence intervals around the linear models. Model outputs can be found in Table 3.2.

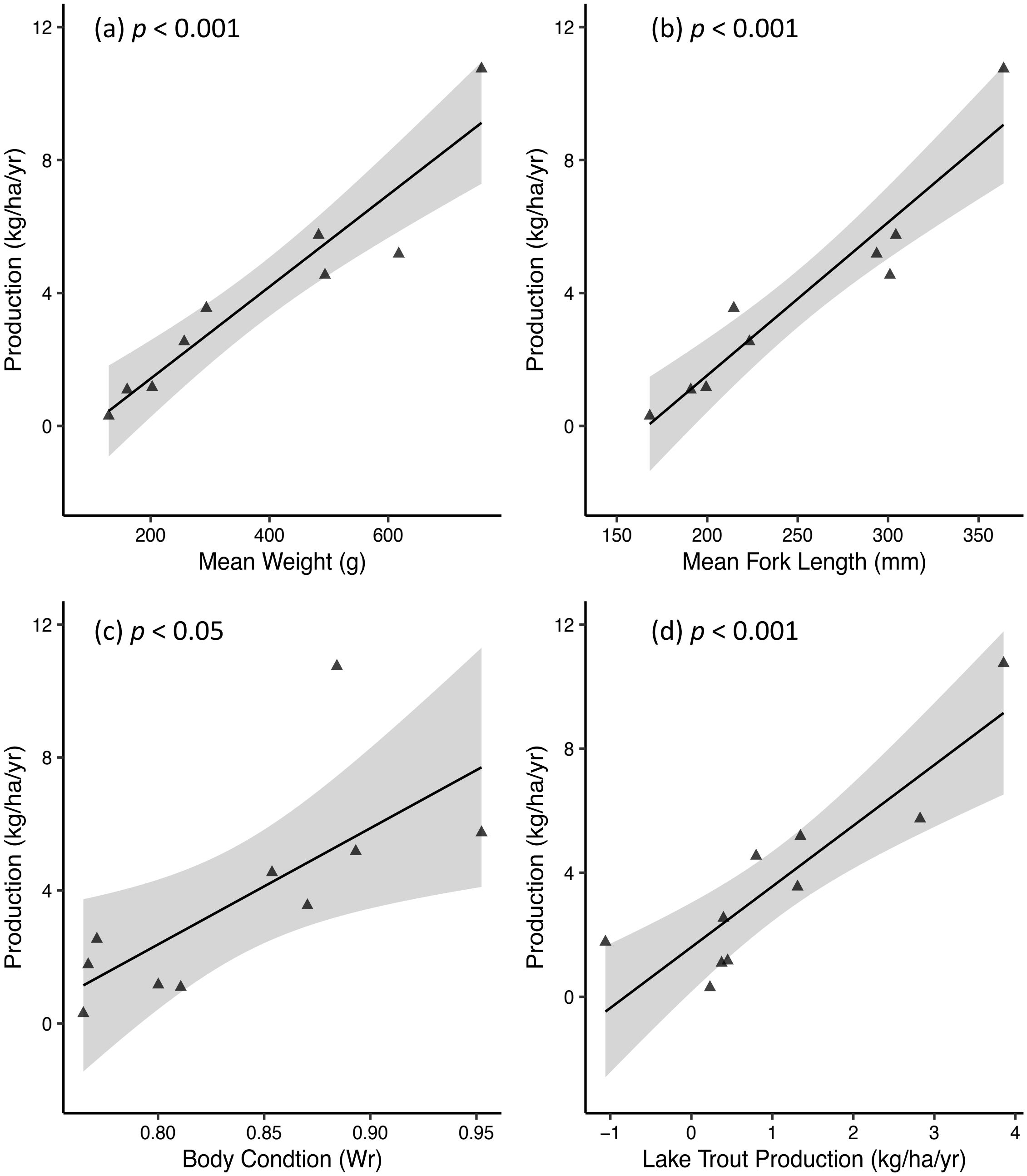


Figure 3.5. Relationships between White Sucker production and (a) annual estimates of mean weight (2 year lag), (b) annual estimates of mean fork length (2 year lag), (c) body condition (1 year lag), and (d) annual Lake Trout Production estimates (1 year lag). Shaded regions represent 95% confidence intervals around the linear models. Model outputs can be found in Table 3.2.

Chapter 3 Supplemental Information

Table S3.1. Percent total catch (as biomass) of each species in the lake 375 community across all years of sampling (1989-2011).

Taxa	**Total Catch (%)**
White Sucker	46.3
Lake Trout	53.2
Fathead Minnow	0.17
Northern Pearl Dace	0.14
Finescale Dace	0.15
Northern Redbelly Dace	0.06

Table S3.2. Length-weight regression information for minnow populations.

Species	**Year**	**Intercept Estimate**	**Coefficient Estimate**
Fathead Minnow	2003	-5.45 ± 0.18	3.31 ± 0.11
Fathead Minnow	2004	-5.83 ± 0.09	3.54 ± 0.05
Fathead Minnow	2005	-5.68 ± 0.10	3.42 ± 0.06
Fathead Minnow	2006	-5.06 ± 0.15	3.05 ± 0.09
Fathead Minnow	2007	-4.32 ± 0.21	2.64 ± 0.12
Fathead Minnow	2008	-4.87 ± 0.25	2.95 ± 0.15
Fathead Minnow	2009	-4.68 ± 0.19	2.85 ± 0.11
Fathead Minnow	2010 and 2011	-4.57 ± 0.06	2.77 ± 0.04

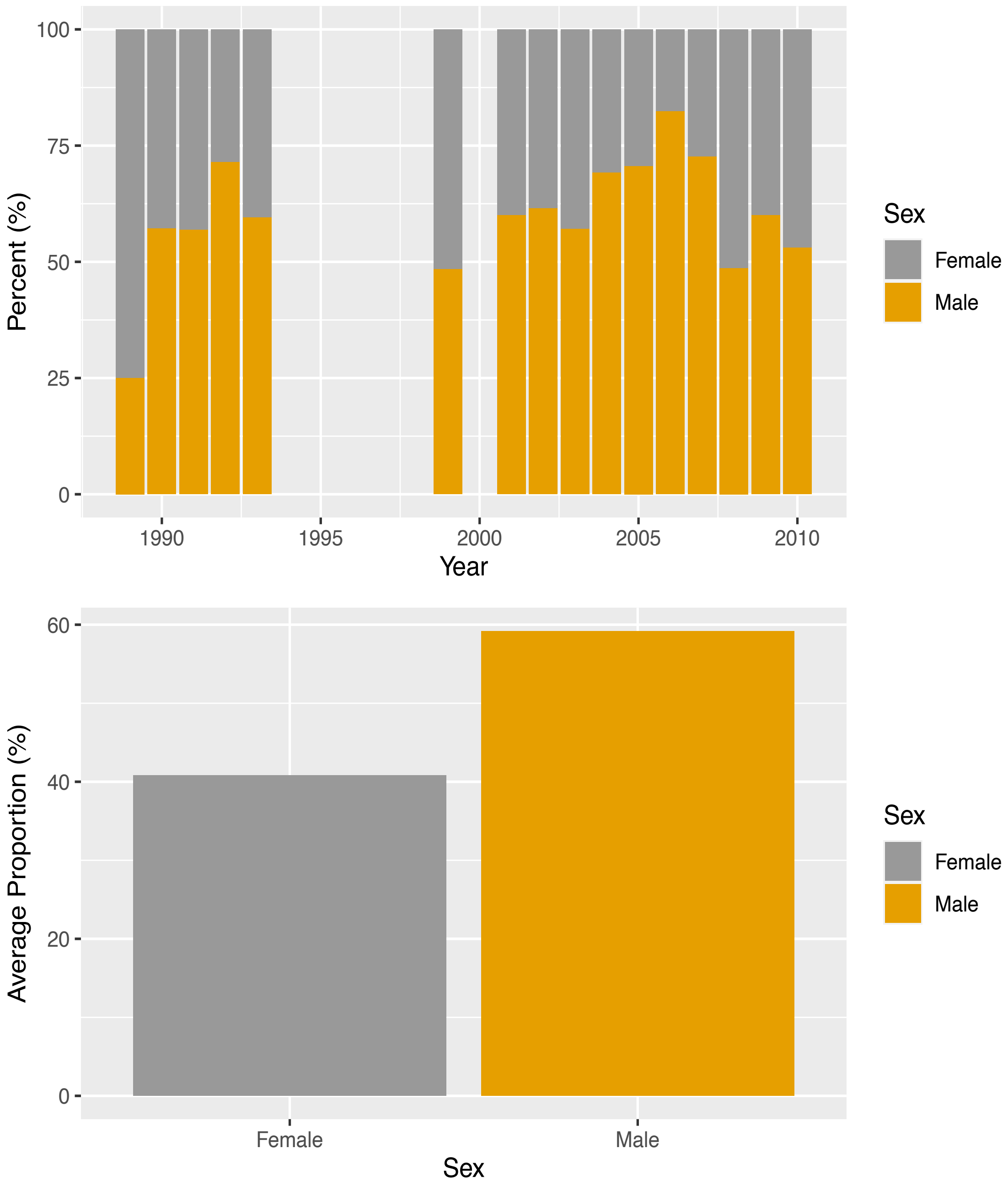


Figure S3.1. Percent proportion of White Sucker males to females in Lake 375.

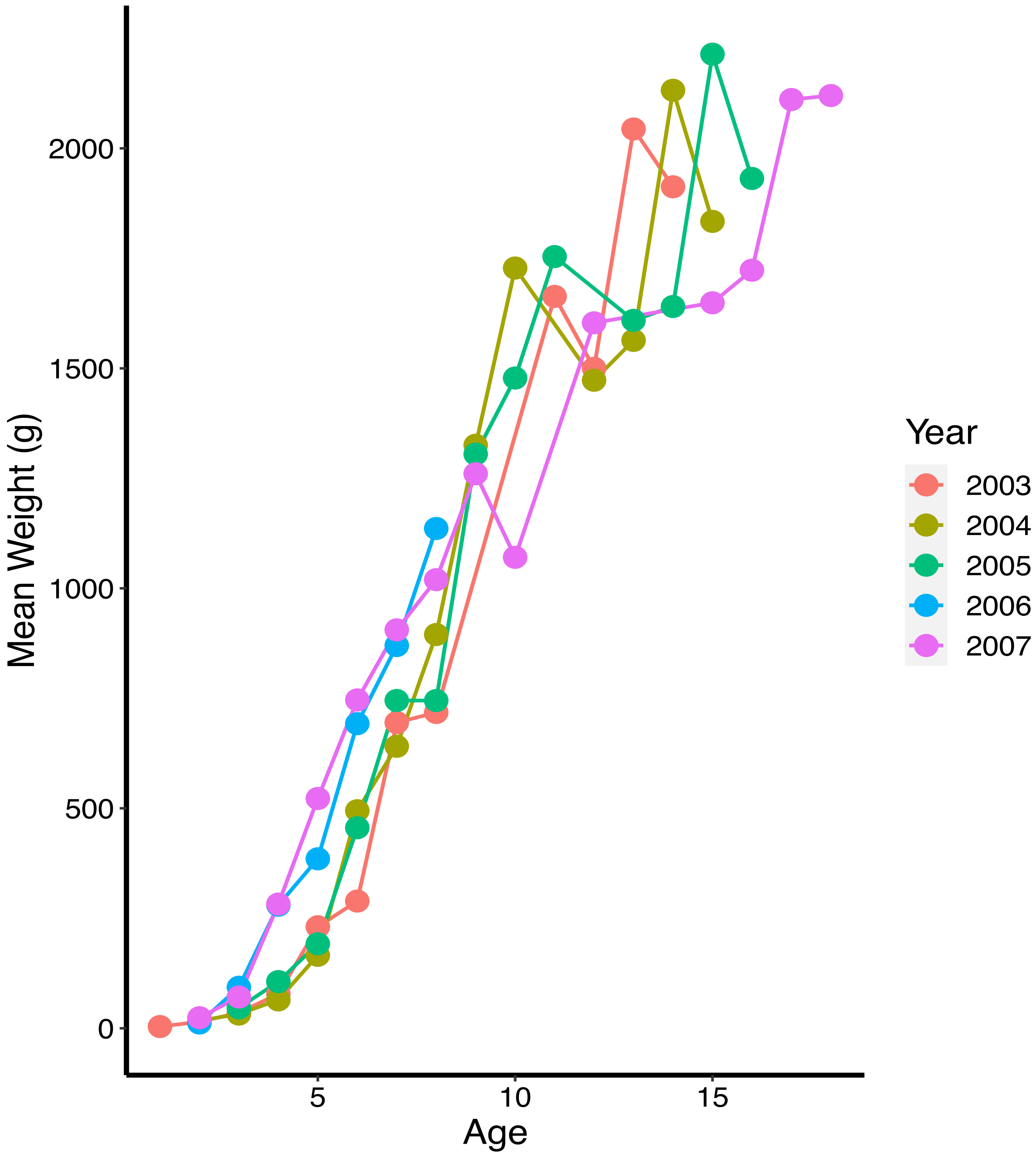


Figure S3.2. Comparison of age class mean weights of the White Sucker population over time.

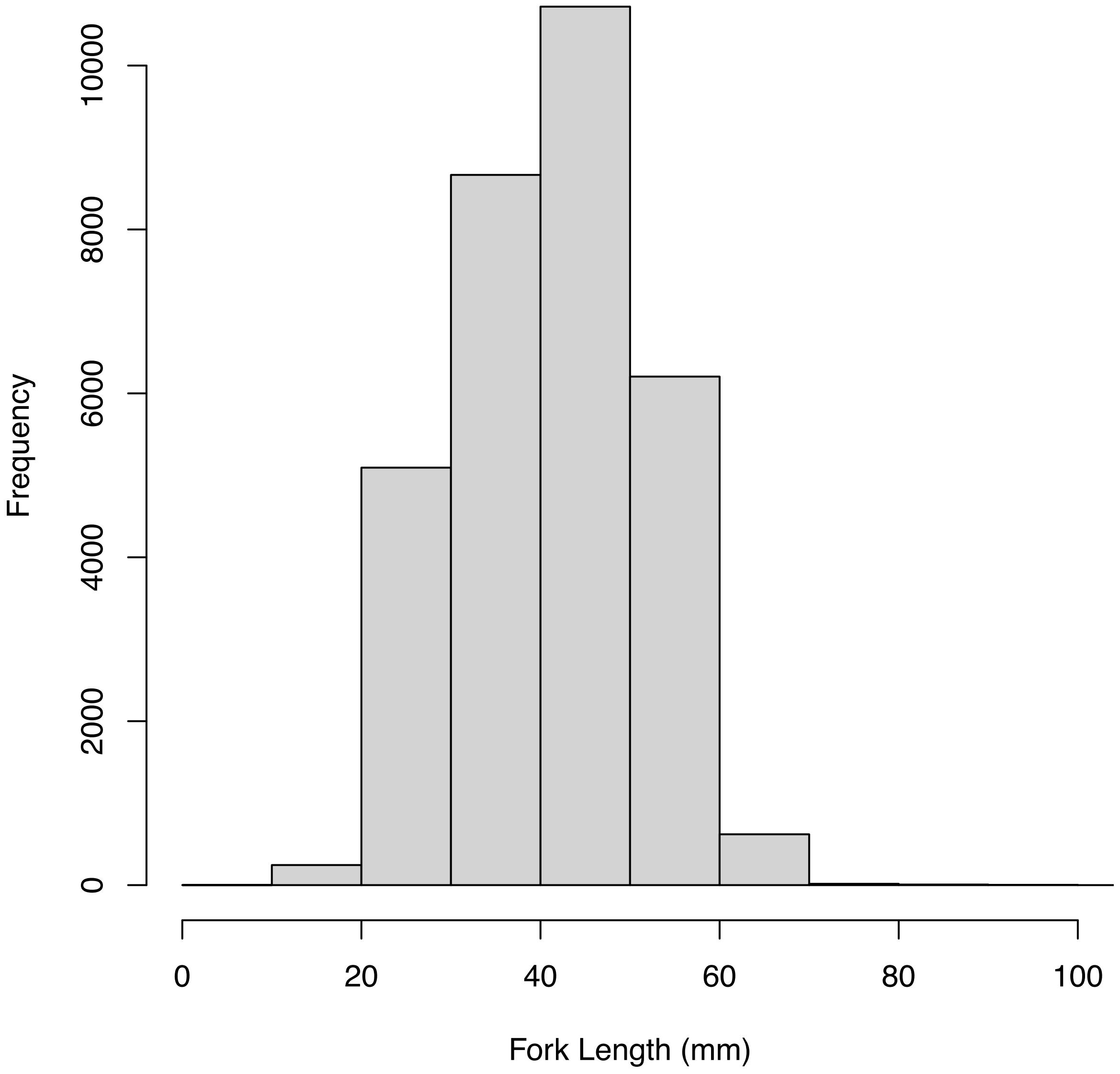


Figure S3.3. Comparison of length group mean weights of the Fathead Minnow population over time.

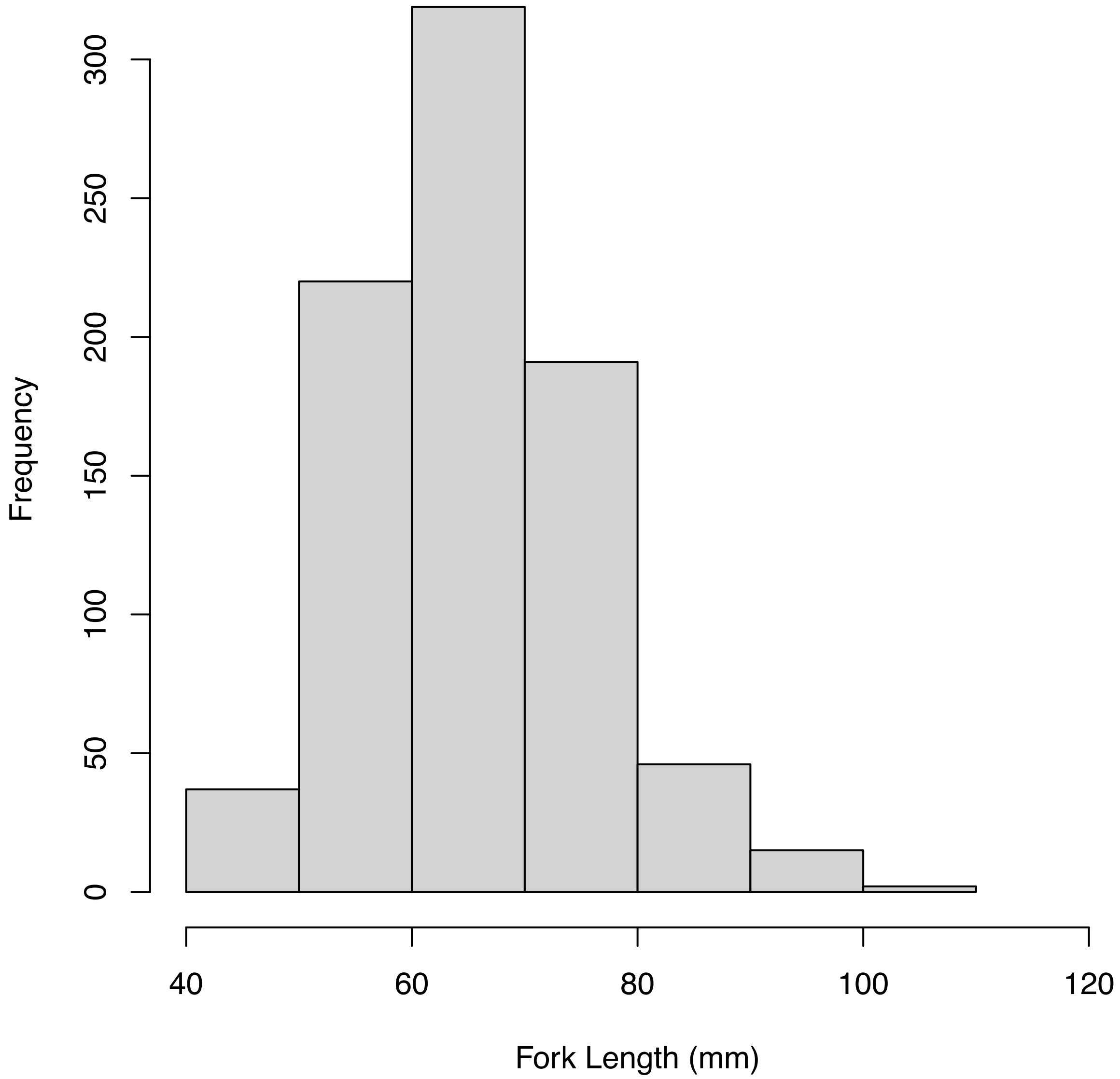


Figure S3.4. Histogram of individual fall sampled Northern Pearl Dace fork lengths.

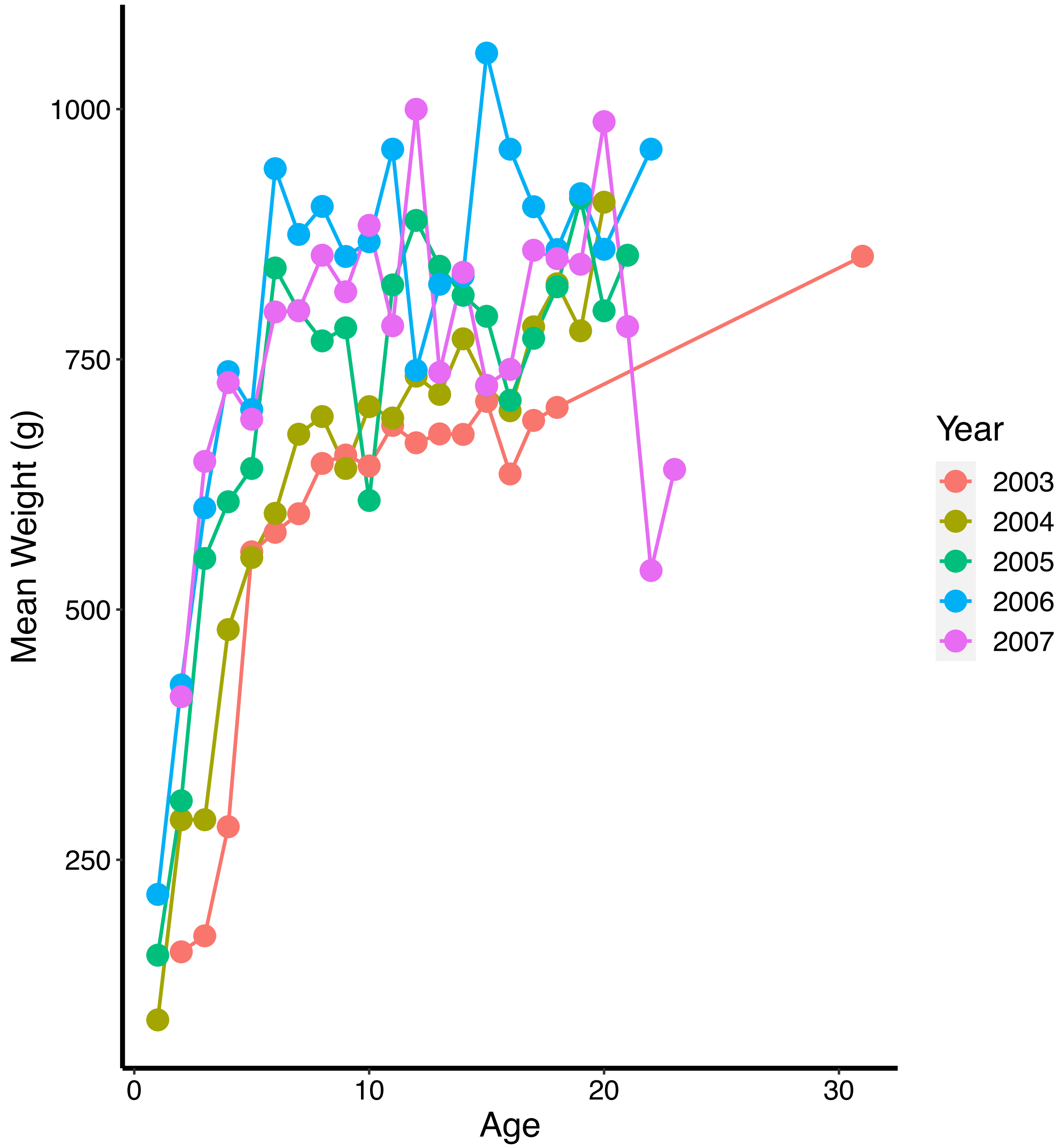


Figure S3.5. Comparison of age class mean weights of the Lake Trout population over time.

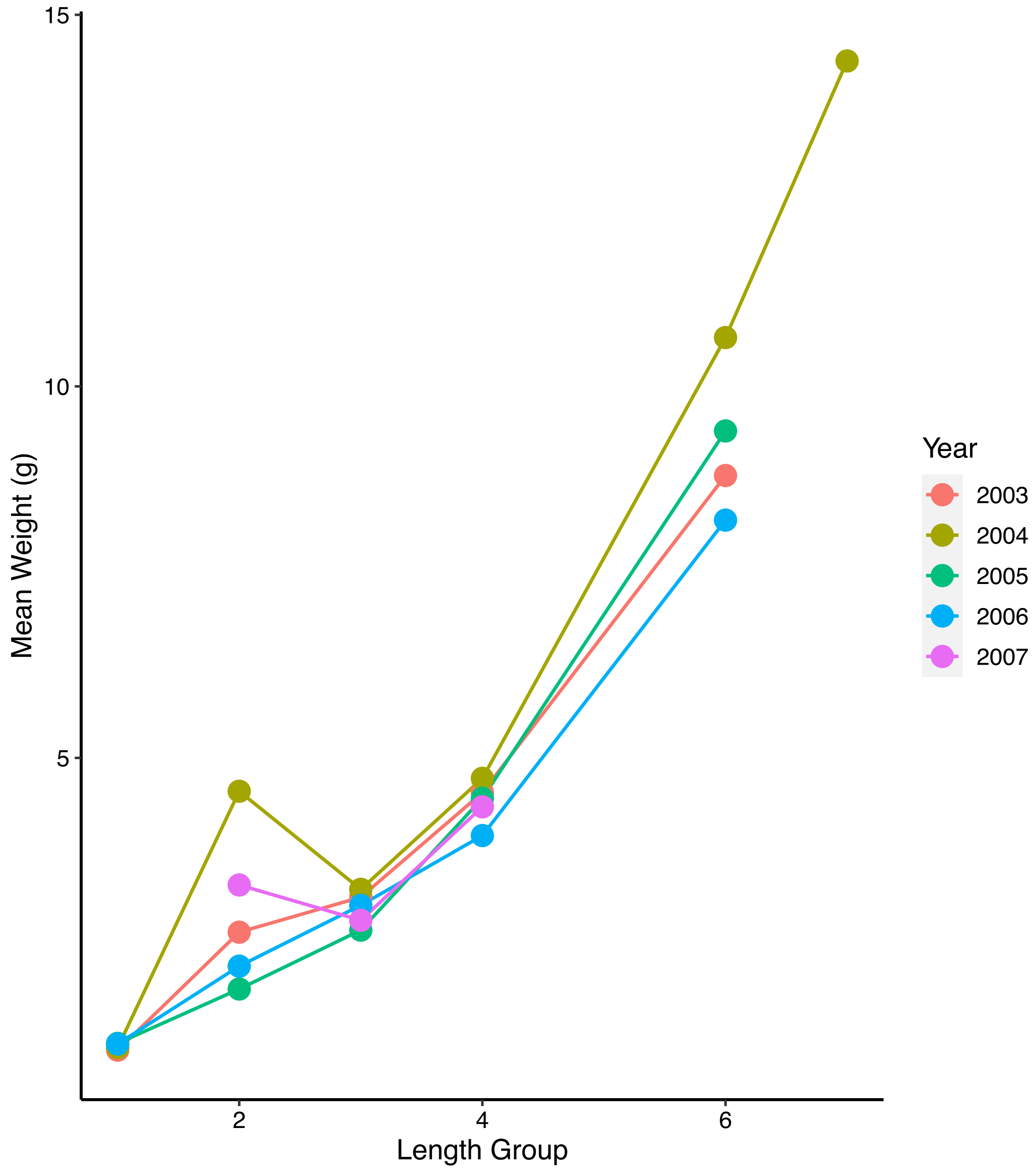


Figure S3.6. Comparison of length group mean weights of the Northern Pearl Dace population over time.

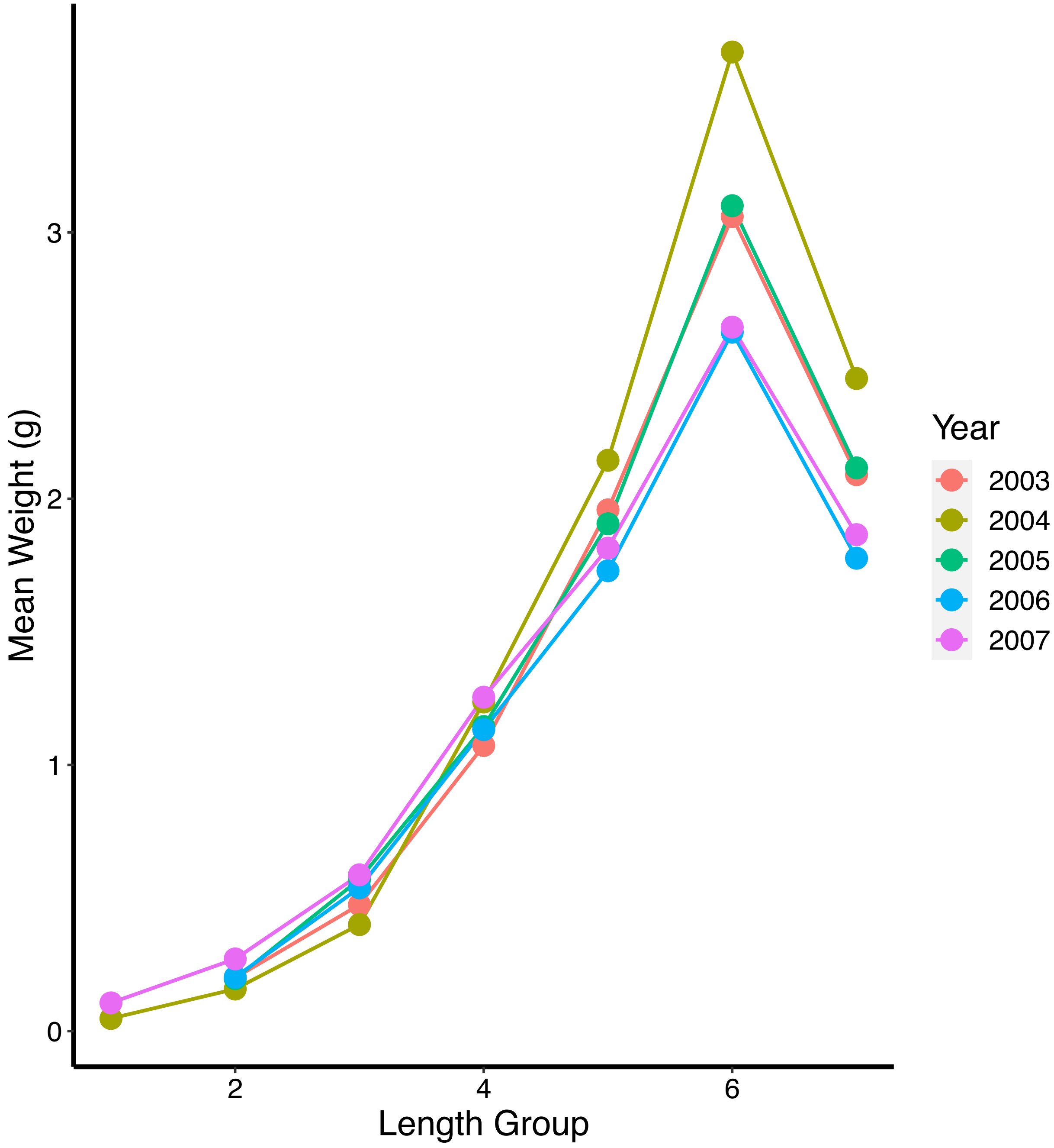
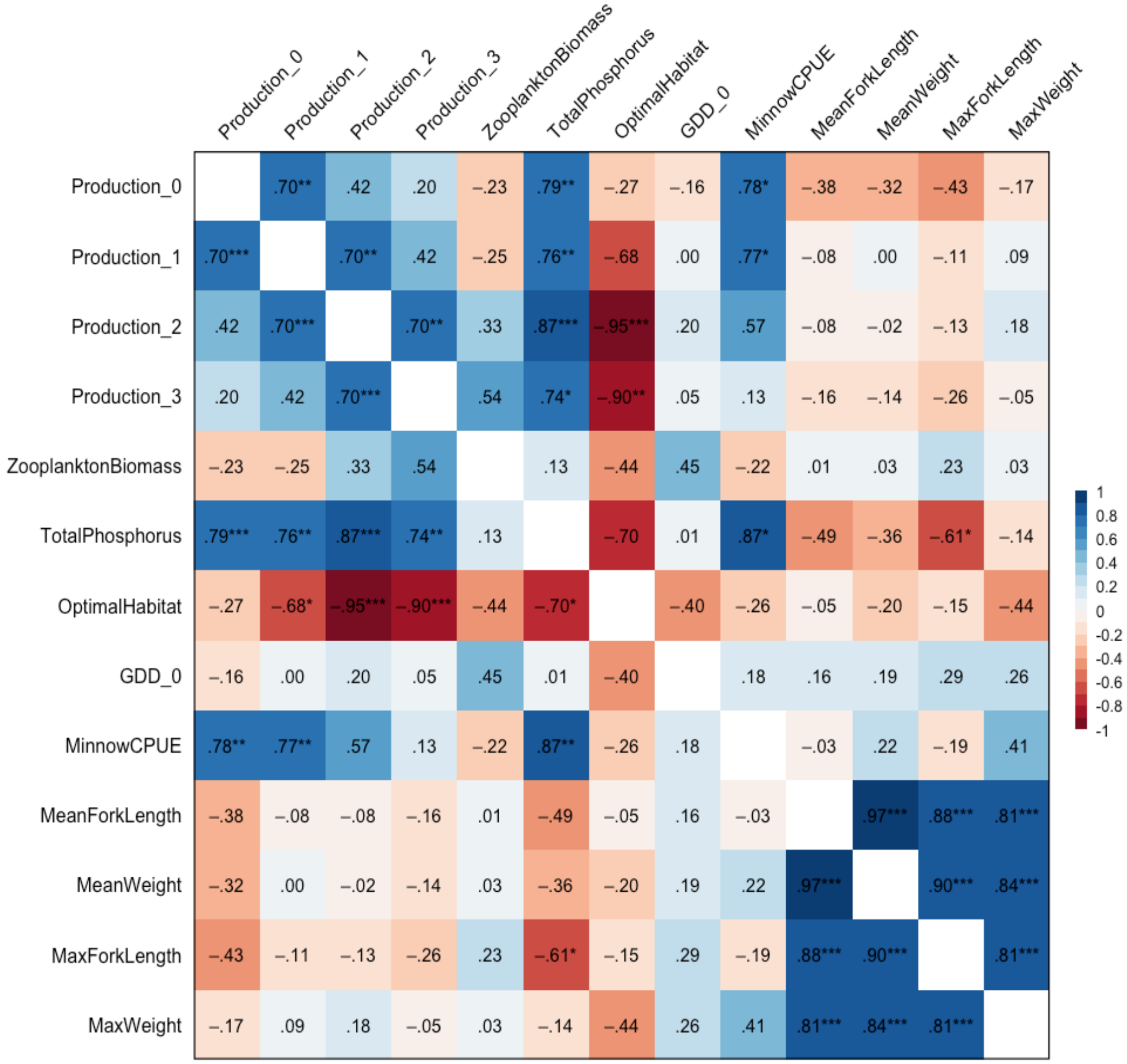
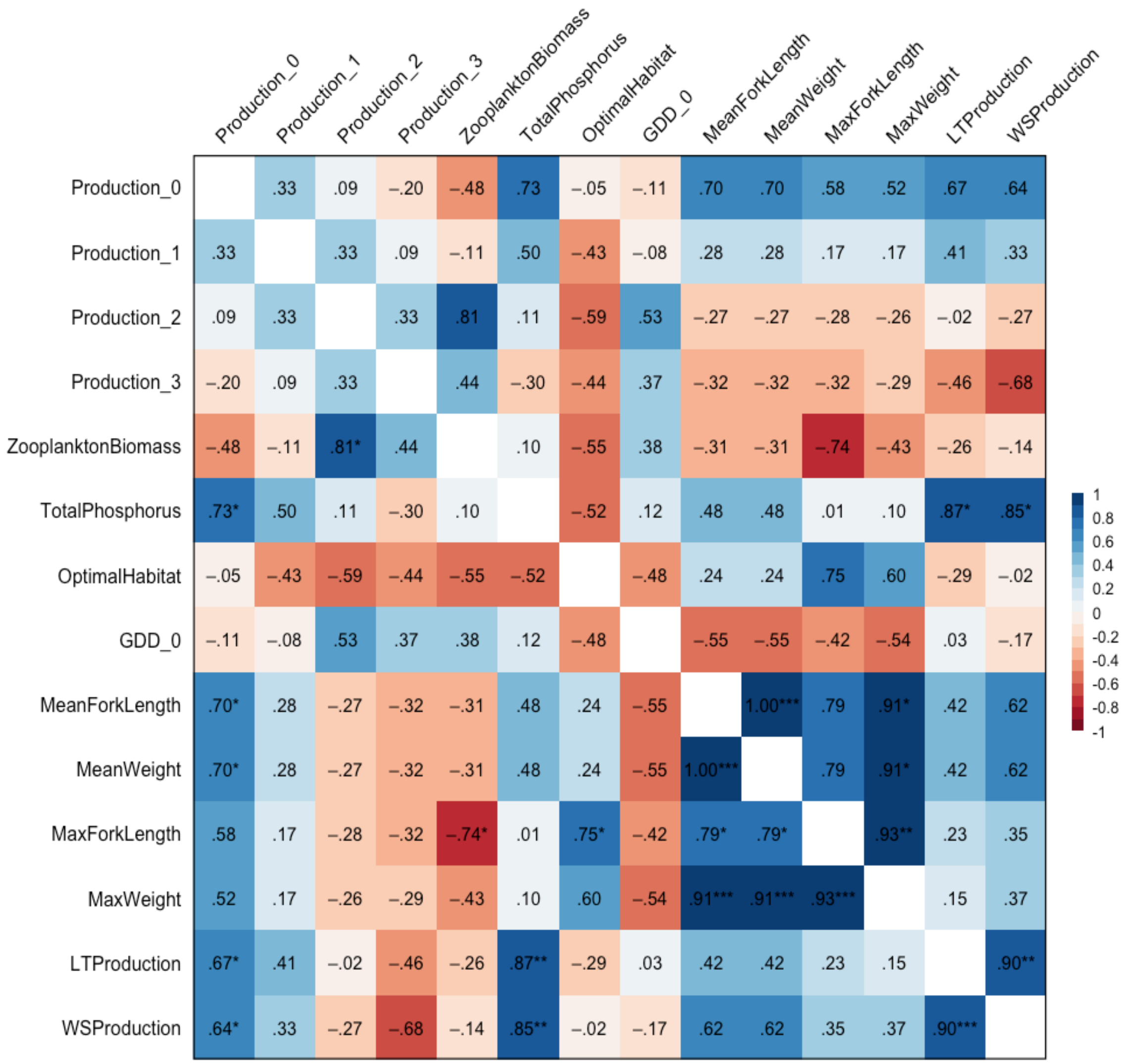


Figure S3.7. Comparison of length group mean weights of the Fathead Minnow population over time.



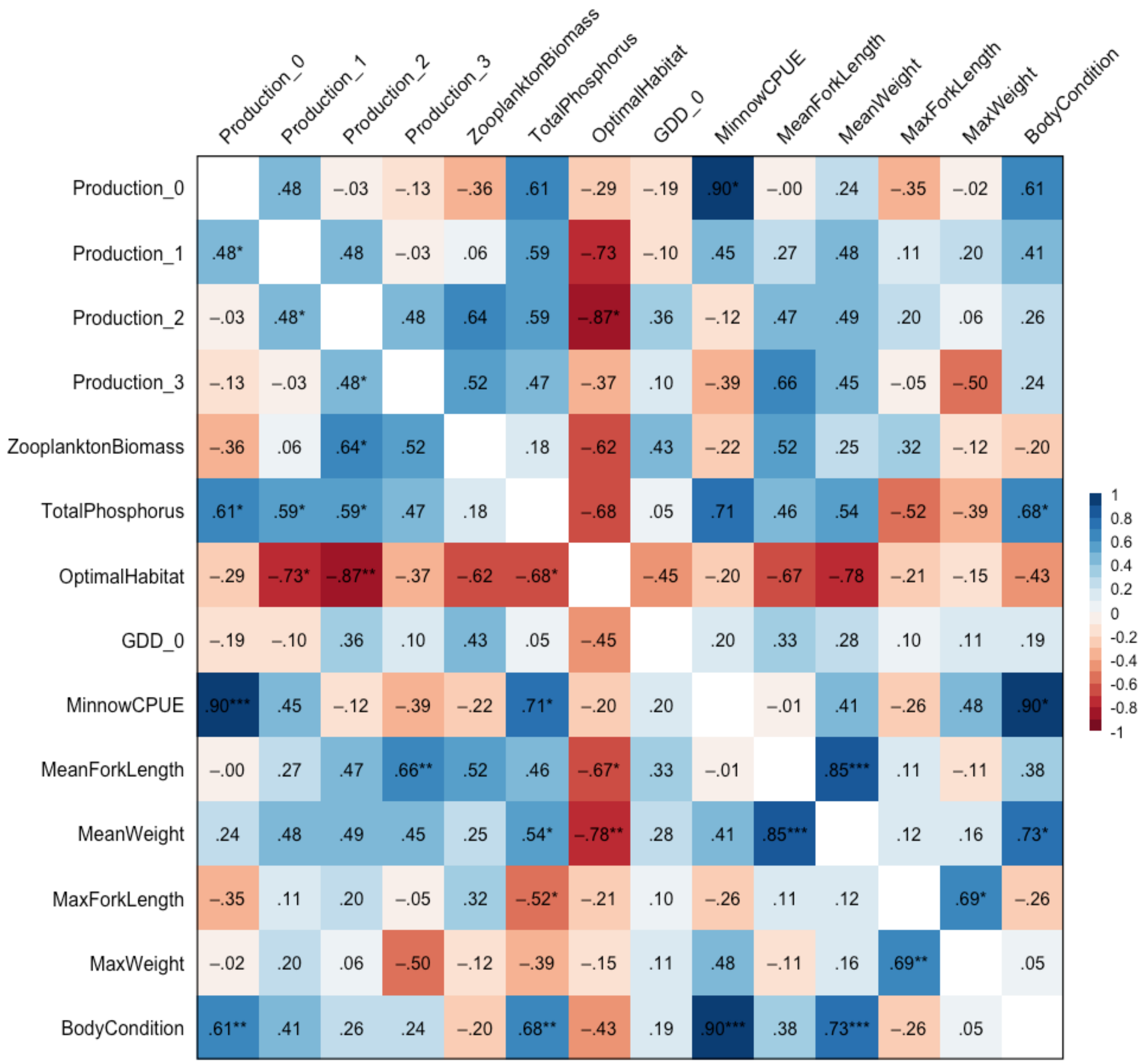
	Production_0	Production_1	Production_2	Production_3	ZooplanktonBiomass	TotalPhosphorus	OptimalHabitat	GDD_0	MinnowCPUE	MeanForkLength	MeanWeight	MaxForkLength	MaxWeight
Production_0		.70**	.42	.20	–.23	.79**	–.27	–.16	.78*	–.38	–.32	–.43	–.17
Production_1	.70***		.70**	.42	–.25	.76**	–.68	.00	.77*	–.08	.00	–.11	.09
Production_2	.42	.70***		.70**	.33	.87***	–.95***	.20	.57	–.08	–.02	–.13	.18
Production_3	.20	.42	.70***		.54	.74*	–.90**	.05	.13	–.16	–.14	–.26	–.05
ZooplanktonBiomass	–.23	–.25	.33	.54		.13	–.44	.45	–.22	.01	.03	.23	.03
TotalPhosphorus	.79***	.76**	.87***	.74**	.13		–.70	.01	.87*	–.49	–.36	–.61*	–.14
OptimalHabitat	–.27	–.68*	–.95***	–.90***	–.44	–.70*		–.40	–.26	–.05	–.20	–.15	–.44
GDD_0	–.16	.00	.20	.05	.45	.01	–.40		.18	.16	.19	.29	.26
MinnowCPUE	.78**	.77**	.57	.13	–.22	.87**	–.26	.18		–.03	.22	–.19	.41
MeanForkLength	–.38	–.08	–.08	–.16	.01	–.49	–.05	.16	–.03		.97***	.88***	.81***
MeanWeight	–.32	.00	–.02	–.14	.03	–.36	–.20	.19	.22	.97***		.90***	.84***
MaxForkLength	–.43	–.11	–.13	–.26	.23	–.61*	–.15	.29	–.19	.88***	.90***		.81***
MaxWeight	–.17	.09	.18	–.05	.03	–.14	–.44	.26	.41	.81***	.84***	.81***	

Figure S3.8. Heat map of spearman rank correlation coefficient community production predictors. The upper half of the heatmap reflects the FDR corrected *p*-values and the lower half depicts the uncorrected *p*-values. Numerical values and colour gradients depict the value and strength of the correlation coefficients, while asterisks denote significant correlations. The following are the abbreviation definitions: Production_0-Production_3 denote production (kg/ha) lag 0-3 years; ZooplanktonBiomass denotes Zooplankton Biomass (g/m^2); TotalPhosphorus denotes Total Epilimnetic Phosphorus (µg/L); OptimalHabitat denotes volume of cold-water habitat (i.e., volume of water that contains 4 mg/L O_2 and is 15°C); GDD_0 denotes Growing Degree Days above 0 º C; MeanForkLength denotes Mean Fork Length (mm); MeanWeight denotes Mean Weight (g); MaxForkLength denotes Max Fork Length (mm); MaxWeight denotes Max Weight (g).



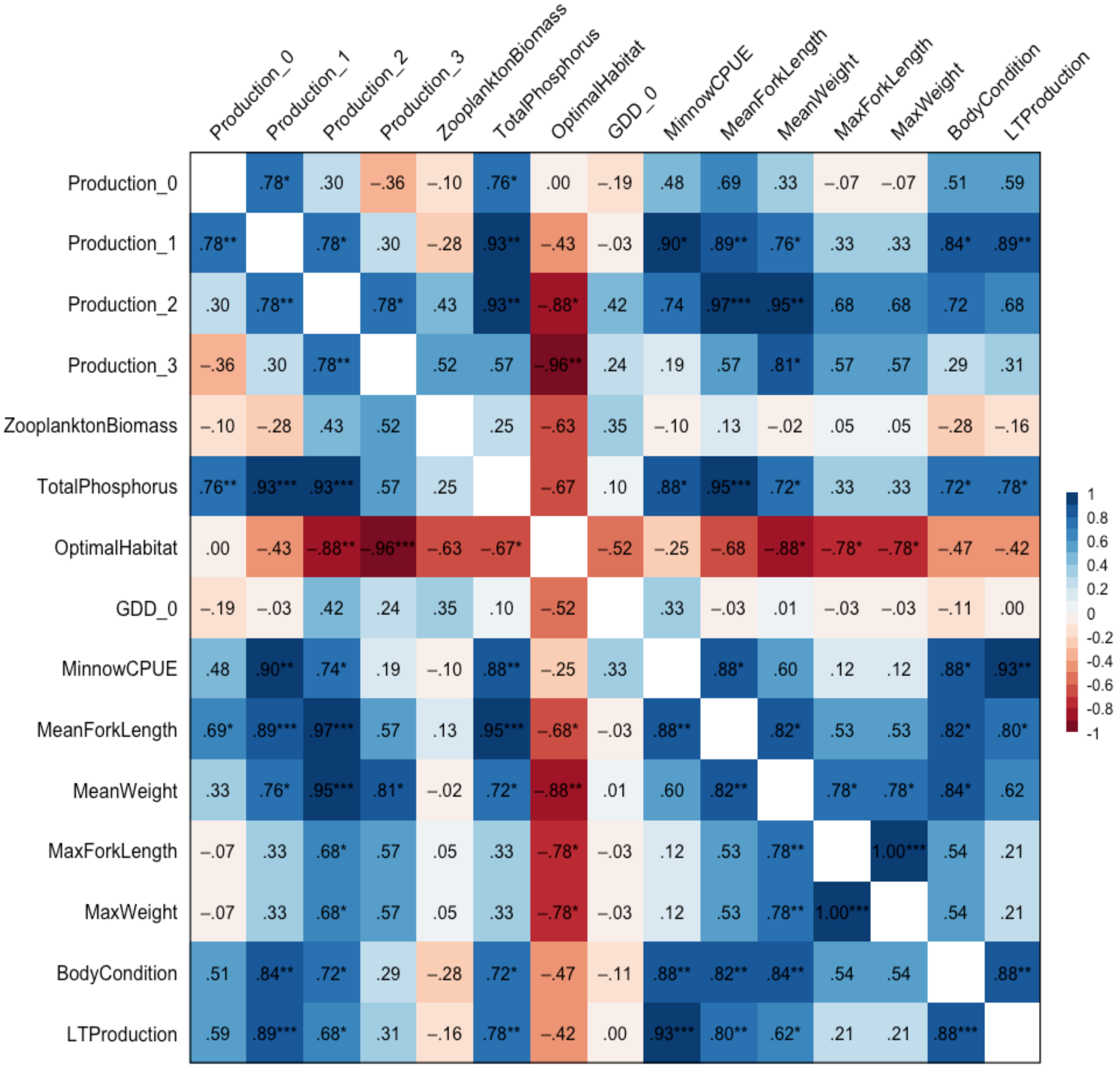
	Production_0	Production_1	Production_2	Production_3	ZooplanktonBiomass	TotalPhosphorus	OptimalHabitat	GDD_0	MeanForkLength	MeanWeight	MaxForkLength	MaxWeight	LTProduction	WSProduction
Production_0		.33	.09	–.20	–.48	.73	–.05	–.11	.70	.70	.58	.52	.67	.64
Production_1	.33		.33	.09	–.11	.50	–.43	–.08	.28	.28	.17	.17	.41	.33
Production_2	.09	.33		.33	.81	.11	–.59	.53	–.27	–.27	–.28	–.26	–.02	–.27
Production_3	–.20	.09	.33		.44	–.30	–.44	.37	–.32	–.32	–.32	–.29	–.46	–.68
ZooplanktonBiomass	–.48	–.11	.81*	.44		.10	–.55	.38	–.31	–.31	–.74	–.43	–.26	–.14
TotalPhosphorus	.73*	.50	.11	–.30	.10		–.52	.12	.48	.48	.01	.10	.87*	.85*
OptimalHabitat	–.05	–.43	–.59	–.44	–.55	–.52		–.48	.24	.24	.75	.60	–.29	–.02
GDD_0	–.11	–.08	.53	.37	.38	.12	–.48		–.55	–.55	–.42	–.54	.03	–.17
MeanForkLength	.70*	.28	–.27	–.32	–.31	.48	.24	–.55		1.00***	.79	.91*	.42	.62
MeanWeight	.70*	.28	–.27	–.32	–.31	.48	.24	–.55	1.00***		.79	.91*	.42	.62
MaxForkLength	.58	.17	–.28	–.32	–.74*	.01	.75*	–.42	.79*	.79*		.93**	.23	.35
MaxWeight	.52	.17	–.26	–.29	–.43	.10	.60	–.54	.91***	.91***	.93***		.15	.37
LTProduction	.67*	.41	–.02	–.46	–.26	.87**	–.29	.03	.42	.42	.23	.15		.90**
WSProduction	.64*	.33	–.27	–.68	–.14	.85**	–.02	–.17	.62	.62	.35	.37	.90***	

Figure S3.9. Heat map of spearman rank correlation coefficient Fathead Minnow production predictors. The upper half of the heatmap reflects the FDR corrected *p*-values and the lower half depicts the uncorrected *p*-values. Numerical values and colour gradients depict the value and strength of the correlation coefficients, while asterisks denote significant correlations. The following are the abbreviation definitions: Production_0-Production_3 denote production (kg/ha) lag 0-3 years; ZooplanktonBiomass denotes zooplankton biomass (g/m^2); TotalPhosphorus denotes total epilimnetic phosphorus (µg/L); OptimalHabitat denotes volume of cold-water habitat (i.e., volume of water that contains 4 mg/L O_2 and is 15°C); GDD_0 denotes growing degree days above 0 º C; MeanForkLength denotes mean fork length (mm); MeanWeight denotes mean weight (g); MaxForkLength denotes max fork length (mm); MaxWeight denotes max weight (g); LTProduction denotes Lake Trout production (kg/ha); WSProduction denotes White Sucker production (kg/ha).



	Production_0	Production_1	Production_2	Production_3	ZooplanktonBiomass	TotalPhosphorus	OptimalHabitat	GDD_0	MinnowCPUE	MeanForkLength	MeanWeight	MaxForkLength	MaxWeight	BodyCondition
Production_0		.48	–.03	–.13	–.36	.61	–.29	–.19	.90*	–.00	.24	–.35	–.02	.61
Production_1	.48*		.48	–.03	.06	.59	–.73	–.10	.45	.27	.48	.11	.20	.41
Production_2	–.03	.48*		.48	.64	.59	–.87*	.36	–.12	.47	.49	.20	.06	.26
Production_3	–.13	–.03	.48*		.52	.47	–.37	.10	–.39	.66	.45	–.05	–.50	.24
ZooplanktonBiomass	–.36	.06	.64*	.52		.18	–.62	.43	–.22	.52	.25	.32	–.12	–.20
TotalPhosphorus	.61*	.59*	.59*	.47	.18		–.68	.05	.71	.46	.54	–.52	–.39	.68*
OptimalHabitat	–.29	–.73*	–.87**	–.37	–.62	–.68*		–.45	–.20	–.67	–.78	–.21	–.15	–.43
GDD_0	–.19	–.10	.36	.10	.43	.05	–.45		.20	.33	.28	.10	.11	.19
MinnowCPUE	.90***	.45	–.12	–.39	–.22	.71*	–.20	.20		–.01	.41	–.26	.48	.90*
MeanForkLength	–.00	.27	.47	.66**	.52	.46	–.67*	.33	–.01		.85***	.11	–.11	.38
MeanWeight	.24	.48	.49	.45	.25	.54*	–.78**	.28	.41	.85***		.12	.16	.73*
MaxForkLength	–.35	.11	.20	–.05	.32	–.52*	–.21	.10	–.26	.11	.12		.69*	–.26
MaxWeight	–.02	.20	.06	–.50	–.12	–.39	–.15	.11	.48	–.11	.16	.69**		.05
BodyCondition	.61**	.41	.26	.24	–.20	.68**	–.43	.19	.90***	.38	.73***	–.26	.05	

Figure S3.10. Heat map of spearman rank correlation coefficient Lake Trout production predictors. The upper half of the heatmap reflects the FDR corrected *p*-values and the lower half depicts the uncorrected *p*-values. Numerical values and colour gradients depict the value and strength of the correlation coefficients, while asterisks denote significant correlations. The following are the abbreviation definitions: Production_0-Production_3 denote production (kg/ha) lag 0-3 years; ZooplanktonBiomass denotes zooplankton biomass (g/m^2); TotalPhosphorus denotes total epilimnetic phosphorus (µg/L); OptimalHabitat denotes volume of cold-water habitat (i.e., volume of water that contains 4 mg/L O_2 and is 15°C); GDD_0 denotes growing degree gays above 0 º C; MeanForkLength denotes mean fork length (mm); MeanWeight denotes mean weight (g); MaxForkLength denotes max fork length (mm); MaxWeight denotes max weight (g); BodyCondition denotes relative body condition (Wr).



	Production_0	Production_1	Production_2	Production_3	ZooplanktonBiomass	TotalPhosphorus	OptimalHabitat	GDD_0	MinnowCPUE	MeanForkLength	MeanWeight	MaxForkLength	MaxWeight	BodyCondition	LTProduction
Production_0		.78*	.30	−.36	−.10	.76*	.00	−.19	.48	.69	.33	−.07	−.07	.51	.59
Production_1	.78**		.78*	.30	−.28	.93**	−.43	−.03	.90*	.89**	.76*	.33	.33	.84*	.89**
Production_2	.30	.78**		.78*	.43	.93**	−.88*	.42	.74	.97***	.95**	.68	.68	.72	.68
Production_3	−.36	.30	.78**		.52	.57	−.96**	.24	.19	.57	.81*	.57	.57	.29	.31
ZooplanktonBiomass	−.10	−.28	.43	.52		.25	−.63	.35	−.10	.13	−.02	.05	.05	−.28	−.16
TotalPhosphorus	.76**	.93***	.93***	.57	.25		−.67	.10	.88*	.95***	.72*	.33	.33	.72*	.78*
OptimalHabitat	.00	−.43	−.88**	−.96***	−.63	−.67*		−.52	−.25	−.68	−.88*	−.78*	−.78*	−.47	−.42
GDD_0	−.19	−.03	.42	.24	.35	.10	−.52		.33	−.03	.01	−.03	−.03	−.11	.00
MinnowCPUE	.48	.90**	.74*	.19	−.10	.88**	−.25	.33		.88*	.60	.12	.12	.88*	.93**
MeanForkLength	.69*	.89***	.97***	.57	.13	.95***	−.68*	−.03	.88**		.82*	.53	.53	.82*	.80*
MeanWeight	.33	.76*	.95***	.81*	−.02	.72*	−.88**	.01	.60	.82**		.78*	.78*	.84*	.62
MaxForkLength	−.07	.33	.68*	.57	.05	.33	−.78*	−.03	.12	.53	.78**		1.00***	.54	.21
MaxWeight	−.07	.33	.68*	.57	.05	.33	−.78*	−.03	.12	.53	.78**	1.00***		.54	.21
BodyCondition	.51	.84**	.72*	.29	−.28	.72*	−.47	−.11	.88**	.82**	.84**	.54	.54		.88**
LTProduction	.59	.89***	.68*	.31	−.16	.78**	−.42	.00	.93***	.80**	.62*	.21	.21	.88***	

Figure S3.11. Heat map of spearman rank correlation coefficient White Sucker production predictors. The upper half of the heatmap reflects the FDR corrected *p*-values and the lower half depicts the uncorrected *p*-values. Numerical values and colour gradients depict the value and strength of the correlation coefficients, while asterisks denote significant correlations. The following are the abbreviation definitions: Production_0-Production_3 denote production (kg/ha) lag 0-3 years; ZooplanktonBiomass denotes zooplankton biomass (g/m^2); TotalPhosphorus denotes total epilimnetic phosphorus (µg/L); OptimalHabitat denotes volume of cold-water habitat (i.e., volume of water that contains 4 mg/L O_2 and is 15°C); GDD_0 denotes growing degree gays above 0 º C; MeanForkLength denotes mean fork length (mm); MeanWeight denotes mean weight (g); MaxForkLength denotes max fork length (mm); MaxWeight denotes max weight (g); BodyCondition denotes relative body condition (Wr); LTProduction denotes Lake Trout production (kg/ha).

CHAPTER 4

Mechanisms and predictors of freshwater fish population production across a spatial gradient of dissolved organic carbon

Abstract

Fish production is an ideal indicator of fish population fitness as it is the outcome of individual energetic processes that ultimately shape population production. Theoretical and empirical studies indicate various physiochemical and lower food web processes likely act to constrain fish production through altering life history strategies, however, few works have assessed these mechanisms of production spatially within a similar climatic region. It is supported that dissolved organic carbon (DOC) has been increasing in some freshwater ecosystems due to climate change and reductions in acid rain, with increasing evidence demonstrating the ability of DOC to alter ecosystem productivity. To identify spatial mechanisms and predictors of production, I assessed White Sucker *(Catostomus commersonii)* production in nine lakes across a gradient of DOC concentrations. I show here that White Sucker production declined with increasing DOC, which was primarily driven by DOC-mediated differences in population abundance and body size, but that neither DOC nor fish production were related to relative estimates of abundance or biomass. This work is consistent with literature demonstrating negative impacts of DOC on thermocline depth, light dynamics, and zooplankton biomass, which I observed across the nine lakes and appeared to be the main drivers of White Sucker production. I also report a possible top-down effect whereby declining White Sucker production (with increasing DOC) may explain increases in benthic invertebrate biomass across the same increasing DOC gradient. These findings emphasize that production in these systems is primarily driven by DOC, which at higher concentrations reduces available habitat by altering physiochemical and limnological dynamics (thermocline depth and light attenuation) to alter access to prey and prey availability, which in turn

shape life history traits (abundance and body size). Through the mechanistic exploration of drivers of production, I also present possible predictors of production for more cost- and time-effective monitoring opportunities of freshwater fish productivity as applied to this broadly distributed and ubiquitous North American species.

Introduction

Fish production is widely recognized as a dynamic measure of energetic processes that shape a population, and as such represents a strong measure of population fitness (Dolbeth, Cusson, Sousa, & Pardal, 2012; Lobón-Cerviá, 2003; Minns et al., 1996; Randall & Minns, 2000; Waters, 1977). Fish production can be defined as the amount of new biomass gained by a population or community over time and space (Randall & Minns, 2000; Waters, 1977). While estimates of fish production are widely recognized for best describing population and community change in aquatic ecosystems, direct estimates of fish production are time and cost-prohibitive in most situations, which has hindered our understanding of the drivers and predictors of fish production. With increasing pressures on freshwater fish populations (i.e., increasing fishing pressure, climate change, development, invasive species) there is a growing need to better understand underlying mechanisms that drive fish productivity and to identify potential predictors of fish production that are more time- and cost-effective to measure.

Seminal empirical studies that have shaped our understanding of landscape-level drivers of fish production have identified fish production to vary among lakes, specifically in response to habitat size (Kelso, 1985; Minns, 1995; Prepas, 1983), latitude, species richness (Downing & Plante, 1993; Rypel & David, 2017), temperature, total phosphorus, pH, chlorophyll-a, and primary production (Downing & Plante, 1993). Over large geographic ranges, latitude (i.e., temperature) is often the main driver of production as fish species have evolved different energetic strategies to be successful in cold, cool, and warm water habitats (McMeans et al., 2020). Latitude also constrains species richness and nutrient availability, where lower latitudes (i.e., warmer climates) are often dominated by eutrophic systems that support greater species richness and thus greater overall community production (Downing & Plante, 1993; Rypel & David, 2017). Whereas higher latitudes (i.e., colder habitats) are often dominated by more nutrient poor lakes (i.e., oligotrophic) and typically allow for greater population production but lower community production due to reduced species richness and competition for resources (Rypel & David, 2017). While there exists a general understanding of landscape-level mechanisms of production across large scales, mechanisms driving production across smaller spatial scales (i.e., areas within similar climatic regions) are not clearly defined. Latitude has been frequently identified as a main driver of fish production and is strongly correlated with climate. Therefore, assessing mechanisms of production within a more constrained or regional scale may help to disentangle latitude and climate from other mechanistic determinants.

Recently, substantial effort has been allocated towards ascertaining the impacts of dissolved organic carbon (DOC) on the productivity of freshwater ecosystems. In many parts of the globe, DOC has been increasing in freshwater ecosystems due to warming climates, reduced acid deposition, as well as changes in hydrological processes and land-use in a process referred to as 'brownification' (Evans et al., 2005b, 2006; Koizumi et al., 2018). DOC enters aquatic ecosystems through lake catchments like wetlands (Snucins & Gunn, 2000) and while some studies have expected DOC to act as an ecosystem subsidy, most work has demonstrated that DOC acts to dampen ecosystem productivity rather than subsidize it (Jones & Lennon, 2015; Sherbo et al., 2023; Tonin et al., 2022). This is because ecosystem increases in DOC can fundamentally change chemical and physical characteristics of lakes (Ask et al., 2009; Benoît et al., 2016; Craig et al., 2015, 2017b;

Karlsson, Bystrom, et al., 2009; Sherbo et al., 2023; Tonin et al., 2022; Zwart et al., 2016). Increases in DOC often results in shallower thermal stratification, modulating the amount of productive habitat within an ecosystem (Read & Rose, 2013; Snucins & John, 2000), so that primary production is more concentrated in shallower epilimnetic habitats (Sherbo et al., 2023). However, when expressed as depth-integrated estimates, primary production declines dramatically with increasing DOC, even as nutrient concentrations increase (Sherbo et al., 2023). This constraint of increasing DOC on primary productivity appears strong enough to override nutrient availability, including total phosphorus (Sherbo et al., 2023), which is typically considered a main driver of primary, secondary, and ecosystem productivity (Downing et al., 1990; Schindler, 1990). Work by Tonin et al. (2022) further demonstrates that high DOC influences nutrient and primary productivity dynamics through preventing the formation of deep chlorophyll peaks at higher DOC concentrations, reducing zooplankton biomass. While evidence supports the role of DOC in influencing fish production through modifying nutrients, primary production and usable habitat, DOC has only been evaluated against components of fish production (i.e., relative biomass (bCPUE), growth, biomass, yield; Craig et al., 2015, 2017; Finstad et al., 2014; Koizumi et al., 2018; Tonin, 2019) and has not yet been directly evaluated against estimates of fish production.

Relative estimates of biomass (biomass catch-per-unit-effort; bCPUE) and abundance (CPUE) are often employed for monitoring population and community changes under the assumption that catch is proportional to abundance (Hilborn & Walters, 1992; Kleiber & Maunder, 2008; Mosley et al., 2022). Several studies have assessed relationships between fish populations and DOC using relative estimates of biomass (bCPUE) and report declining (Koizumi et al., 2018; Tonin, 2019) or unimodal relationships of bCPUE with DOC (Finstad et al., 2014). However, relative estimates of biomass and abundance can suffer from biases relating specifically to catchability (i.e., hyperstability or hyperdepletion; Hilborn & Walters, 1992; Kleiber & Maunder, 2008; Mosley et al., 2022). Specifically, due to catch bias, relative estimates may deviate from proportionality by overestimating actual abundance (termed 'hyperstability'), or underestimating actual abundance measures (i.e., hyperdepletion; Hilborn & Walters, 1992; Kleiber & Maunder, 2008; Mosley et al., 2022).

To understand drivers of fish production not confounded by latitudinal/climatic variation, I examined White Sucker *(Catostomus commersonii)* production across nine lakes with varying concentrations of DOC at the IISD-Experimental Lakes Area (IISD-ELA). Theoretical work suggests that factors constraining usable habitat (i.e., temperature, nutrients, light) should affect fish productivity by modulating individual bioenergetics via temperature preferenda and access to prey quantity and size (MacLeod et al., 2022). If DOC alters nutrients, temperature, and light dynamics of ecosystems to modify usable habitat and overall ecosystem productivity and ultimately prey resources and access to prey, I expect fish production to respond accordingly. Specifically, I hypothesized that as DOC concentrations increased across the nine lakes, DOC would reduce the overall productivity of each lake and ultimately White Sucker production. I aimed to (1) evaluate the degree to which components of production (i.e., abundance, biomass) and relative estimates of biomass and abundance (i.e., bCPUE, CPUE) relate to direct estimates of production and DOC; (2) discern mechanisms driving fish production across regional spatial scales over which latitudinal and climate impacts are negligible (and therefore cannot contribute to patterns of production), and (3) identify possible predictors of fish production using this dataset, to potentially provide more time- and cost-effective means of estimating fish production (versus direct estimation).

Methods

Study Area

Nine boreal lakes were selected for this study to cover a range of DOC concentrations (3.5-11.5 mg/L) at the IISD-ELA (Table 4.1). All lakes support populations of White Sucker and are thermally stratified and dimictic, with the exception of lake 149 which does not stratify. All study lakes experience similar climatic variation and are within 30 km of the ELA research station and meteorological station. All lakes experienced minimum human disturbance and have catchments typical of the boreal landscape, with hydrology that is dominated by surface flow.

White Sucker were chosen for this study due to their abundance, wide geographic distribution, significant contributions to overall fish communities, and their lack of interest as a commercial, recreational or subsistence fish species (Scott & Crossman, 1973). Additionally, White Sucker have been shown to be a sensitive species to change as populations across Ontario have shown declines in growth in association with climate change induced reductions in cold-water habitat (Slongo, 2022), despite their broad thermal tolerance and being a cool-water species (Hasnain et al., 2010; Scott & Crossman, 1973).

Fish Collections

All White Sucker were sampled in spring during spawning (May-mid June) using Beamish-style trap nets (Beamish, 1973), with the exception of Lake 658 which was sampled primarily in the fall using short-set gillnets (Blanchfield et al., 2022). All White Sucker > 100mm in fork length had lengths (fork, total) and weights collected, and were given unique dorsal fin nicks. Of these, a subset of individuals were tagged with either Carlin sew-on or PIT tags below their dorsal fin on the left side. All newly tagged individuals as well as a subset of untagged individuals had fin rays collected on first sighting; fin rays were embedded in epoxy, cross-sectioned and mounted on slides to determine age using the marginal increment analysis (see Slongo, 2022; Campana, 2001). For tagged individuals, age was assigned upon recapture as the sum of determined age at first capture and time (in years) elapsed from this first capture. With the exception of two lakes (164, 149), the remaining seven lakes are part of the long-term monitoring program at IISD-ELA and have long-term White Sucker data (Table 4.1). Lakes 164 and 149 were only sampled for this study in 2019 and 2021 (due to the covid-19 pandemic in 2020 field work was unable to be completed). However, no individuals were captured in Lake 164 in 2021. It is assumed that the spawning event was missed due to high spring temperatures and the need to quarantine because of the pandemic prevented sampling immediately at ice-off. Additional size data from Lake 164 in 2017 was available from a previous study (Tonin, 2019) and was used in place of 2021 data.

Selection of Environmental Variables

Each lake in the study underwent standard limnological sampling bi-weekly or monthly from May to September, and water chemistry analyses followed standard analytical protocols consistent with IISD-ELA's long term monitoring program (Stainton et al., 1977; see also Sherbo et al., 2023 & Tonin et al., 2022). Physiochemical, limnological, and lower food web indices were selected based on previous analyses that demonstrated relationships between fish production or components of production (i.e., growth, biomass, abundance) across study lakes. Specifically, I assessed lake area (ha; Minns, 1995), mean lake depth (Z_{mean}; m), maximum lake depth (Z_{max}; m; Prepas, 1983); DOC (mg/L) and mean annual light attenuation (K_d m^{-1}); Finstad et al., 2014), mean annual thermocline depth (m; Tonin et al., 2022; Zwart et al., 2016), mean annual total epilimnetic phosphorus (Downing et al., 1990), mean annual estimates of total benthic invertebrate biomass and total chironomid biomass (g/m^2; i.e., main food resource for White Sucker), and mean annual zooplankton biomass (g/m^2; Tonin et al., 2022). Life history predictors were selected based on previously published and theoretical works indicating body size to be an important predictor (Downing et al., 1990; Downing & Plante, 1993; MacLeod et al., 2022), as well as results from the second data chapter of this thesis; these included mean annual weight, mean annual fork length, mean annual maximum weight, mean annual maximum fork length, and mean annual body condition. Since lake 149 is not a lake included in the long-term monitoring program, I did not have available data to calculate some predictors; specifically, no data were available to calculate benthic invertebrate estimates, or zooplankton biomass, and lake 149 does not stratify so there is no thermocline estimate for this lake. All predictors were calculated using available data from the IISD-ELA long term monitoring program, with the exception of estimates of benthic invertebrate and chironomid biomass which were from Tonin (2019). Water chemistry parameters were calculated as mean annual estimates, and a single mean value for each lake was estimated from annual means. Body condition was estimated using the relative weight method (Wege & Anderson, 1978) using an equation specific for White Sucker (Bister et al., 2000). As with water chemistry parameters, life history parameters were calculated as mean annual estimates, and a single mean value was estimated from annual means. Maximum fork length and maximum weight estimates were estimated using 95% quantiles based on all individuals collected from the lake across all sampling periods. To determine total lengths for body condition calculations for individuals sampled in Lake 658, I calculated total length for all White Sucker in the dataset across all lakes using fork length – total length regression analysis using length data from all White Sucker from the remaining eight lakes (Supplemental Table 4.1).

Production Estimation

For the lakes with sufficient age data (223, 224, 626, 239, 442, 373), I created year-specific age-length keys (Ogle, 2015) to assign ages to unaged fish. For lake 239, I only used a single age-length key for age assignment to individuals across all years due to too few annual observations from this lake to support annual age-length keys. To assign ages to populations with no age data (lakes 164, 149, and 658), I assessed size-frequency plots of unaged populations against populations with age data to find a population with ages that had a similar size distribution as these lakes (and therefore most likely to have similar growth patterns and age distributions as these lakes). Lake 239 was determined to have the most similar size distribution to lakes 164, 149, and 658 (specifically with regards to the right tails of the distributions characterizing large-bodied fish) compared to all other lakes with age data (Figure S4.1). Therefore, I used age-length keys produced from aged individuals in lake 239 to assign ages to individuals in lakes 164, 149, and 658. Lastly, I did not assign ages based on sex to account for sexual size dimorphism as not all lakes had age data.

Where annual White Sucker catches were sufficiently high, with a sufficient proportion of recaptures in each season (which was most of the lakes included in this study), abundance estimates were calculated using the Schnabel method (Schnabel, 1938) using available mark-recapture data from spring sampled individuals (Table 4.1). For lake 164, I only had sufficient mark-recapture data to calculate abundance in 2019, so the 2019 abundance estimate was used for both 2017 and 2019, under the assumption that 1) the spawning event was missed in 2021 due to lake sampling (preventing the collection of sufficient data to calculate production), and 2) that the system was stable and the population did not change significantly between sampling periods. Abundance for Lake 658 was modelled using the POPAN formulation of the Jolly-Seber model using mark-recapture data from tagged White Sucker. The top model used to estimate abundance (evaluated using AIC) was parameterized with time dependent survival and entry to the population and constant catchability.

Production estimates were calculated using the instantaneous growth rate (IGR) method (Hayes et al., 2007; Ryder, 1965). Following the IGR method, production is estimated using the following equations:

$$\hat{P} = \sum \hat{G}\bar{B} \tag{4.1}$$

where $\hat{P}$ is the sum of production for all population cohorts within a specified time interval, $\hat{G}$ is the instantaneous growth rate estimate for a cohort from time t to $t_{+1,}$ with $\bar{w}_t$ representing mean cohort weight at time t:

$$\hat{G} = \log_e \overline{w}_{t+1} - \log_e \overline{w}_t \tag{4.2}$$

where $\overline{B}$ is the mean cohort biomass from time t to t_{+1}:

$$\overline{B} = (\hat{B}_t + \hat{B}_{t+1})/2 \tag{4.3}$$

and $\hat{B}_t$ is based on the density (N_t) and mean weight of each age class at time t:

$$\hat{B}_t = N_t * \overline{w}_t \tag{4.4}$$

Lastly, N_t is calculated by apportioning abundance estimates to age-classes based on the proportion of individuals per age-class such that:

$$N_t = (n_{age\text{-}class} / n_{total}) * N_p \tag{4.5}$$

where $n_{age\text{-}class}$ is the number of individuals per age-class, n_{total} is the total number of individuals across all age classes caught in that sampling period, and N_p is the corresponding annual population abundance estimate.

Analyses of Components of Production

Estimates of abundance, biomass (equation 4.3), and production were calculated as described above, with a single mean estimate calculated using all available annual estimates. My estimate of relative biomass, bCPUE, was estimated by determining the sum of the mass of White Sucker caught each spring divided by the total effort of that season (as in Tonin, 2019). A mean estimate was taken across all annual bCPUE estimates to calculate a single mean estimate for each lake. Estimates of lake 658 bCPUE were obtained from Tonin et al. (2019). Estimates of relative abundance (CPUE) were calculated by determining the total number of individuals caught per net days per sampling period, and a mean was taken of annual estimates to generate a single mean for each lake. CPUE estimates were not reported in Tonin (2019) and therefore not available for lake 658.

Statistical Analyses

Estimates of White Sucker production, biomass, abundance, bCPUE, and CPUE were assessed via Spearman's (rank order) correlation, and all estimates were assessed using linear regression against DOC. I used Spearman's correlation to assess correlates of production since it is a nonparametric measure of rank correlation. Potential environmental correlates of White Sucker production were also identified using Spearman's rank correlation coefficients (rank order). A false-discovery-rate (FDR) correction was initially applied to correlates following a Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995). However, this procedure was highly conservative and returned very few significant correlates (i.e., zooplankton biomass and body condition) despite a number of very strong correlations ($\rho > 0.7$). Given the small number of observations (lakes) used in my analysis, it was determined that FDR corrections were ultimately too conservative to assess relationships in this analysis. Instead, significance was assessed at an alpha of 0.05. Linear regression analyses were applied to all variables significantly correlated with White Sucker production. For linear regression analyses, all data were assessed for normality and heterogeneity using residuals plots and the Shapiro-Wilk's test for normality, and data were log transformed to meet linear model assumptions of normality and heterogeneity if required. Because total phosphorus is a known and well-established driver of fish production (Downing et al., 1990; Downing &

Plante, 1993), it was included in linear regressions regardless of significance in Spearman rank correlations.

Results

Assessment of Relative and Direct Components of Production

Estimation of White Sucker production across all nine lakes determined White Sucker production ranged from 0.04 – 2.39 kg/ha. Comparisons between relative and direct measures of White Sucker production and components of fish production identified varying relationships among components and with DOC. Spearman's (rank order) correlation assessment identified abundance as significantly correlated with production ($\rho = 0.72$; $p > 0.05$; Table 4.2; Figure 4.1), and CPUE was correlated with production ($\rho = 0.62$), although not significantly so. Estimates of biomass, relative biomass, and relative abundance were also not significantly correlated with production, although biomass and abundance were significantly positively correlated with one another ($\rho = 0.75$, $p > 0.05$; Table 4.2; Figure 4.1). Relative biomass (bCPUE) and biomass estimates were not strongly correlated with each other, ($\rho = 0.28$), neither were CPUE and abundance ($\rho = 0.5$; Table 4.2). Linear regression analyses of relative and direct measures of White Sucker production found White Sucker production ($F_{1,7} = 6.1$, $p < 0.05$) and abundance ($F_{1,7} = 8.36$, $p < 0.05$) both decreased with increasing DOC concentrations, while standing biomass, bCPUE, and CPUE were found to have no significant relationship with DOC (Figure 4.2).

Analyses of Potential Drivers of Production

Spearman’s rank correlations identified DOC, K_d, and thermocline depth to be significantly correlated with production (Figure 4.3). Based on linear regression, White Sucker production was not significantly related with K_d, although a negative association was visually apparent (Figure 4.4a). Thermocline depth was significantly and positively related with White Sucker production **(**$F_{1,6} = 7.24$, $p < 0.05$; Figure 4.4b). Although total phosphorus was not identified as a significant correlate, it had a strong rank-based correlation coefficient ($\rho = -0.64$). There was also no significant linear relationship between epilimnetic total phosphorus and White Sucker production, although a negative association was visually apparent, with White Sucker production declining as total phosphorus increased (Figure 4.4c).

Assessment of lower food web predictors (benthic invertebrate and zooplankton biomass) demonstrated opposite relationships with White Sucker production, where fish production decreased as benthic invertebrate biomass increased ($F_{1,6} = 10.86$, $p < 0.05$; Figure 4.5a), but fish production increased with increasing zooplankton biomass ($F_{1,7} = 7.819$, $p < 0.05$; Figure 4.5b).

Analyses of life history predictors identified that mean fork length ($F_{1,7} = 11.42$, $p < 0.05$; Figure 4.6a), mean weight ($F_{1,7} = 11.97$, $p < 0.05$; Figure 4.6b), maximum fork length ($F_{1,7} = 7.04$, $p < 0.05$; Figure 4.6c), maximum weight ($F_{1,7} = 6.33$, $p < 0.05$; Figure 4.6d), and body condition ($F_{1,7} = 14.43$, $p < 0.01$; Figure 4.6e) were all negatively related to production, with production decreasing as all life history metrics increased.

Correlative assessments identified several significant ($p > 0.05$) correlations between DOC and putative predictors (Figure 4.3). Negative correlations were observed between DOC and Z_{mean} ($\rho = - 0.71$), thermocline depth ($\rho = - 0.97$), and zooplankton biomass (ρ = - 0.89), as well as positive correlations between DOC with K_d (ρ = 0.90), total phosphorus (ρ = 0.80), mean weight (ρ = 0.70), mean fork length (ρ = 0.67), maximum fork length (ρ = 0.76), and body condition (ρ = 0.70). Zooplankton biomass was also found to be significantly ($p > 0.05$) correlated with K_d (ρ = - 0.83), thermocline depth (ρ = 0.90), total phosphorus (ρ = - 0.67), mean weight (ρ = - 0.75), and mean fork length (ρ = - 0.68). Lastly, all life history variables (i.e., mean weight, mean fork length, maximum weight, maximum fork length, body condition) were significantly and strongly correlated with one another ($\rho > 0.70$; $p > 0.05$).

Discussion

Here, I demonstrate that DOC has an inhibitory effect on fish production (in lakes ranging from 3.5-11.5 mg/L), where increases in DOC led to clear and significant reductions in White Sucker production to near-zero values at the highest DOC concentrations observed. Similarly, White Sucker abundance declined significantly with increasing DOC, but White Sucker life history traits (i.e., mean weight, mean fork length, maximum weight, maximum fork length, body condition) all increased with DOC and declined with production. Combined, these observations explain why patterns of standing biomass did not change with DOC or production. Specifically, my results indicate DOC alters how biomass is allocated in populations (i.e., greater abundance and smaller body size; lower abundance and larger body size), which was also observed in previous work with bCPUE estimates among the same lakes (Tonin, 2019). Standing biomass is a large component of estimates of production, so it is surprising that these estimates are not correlated with either production or DOC in the current study. This may potentially indicate that individuals in from higher DOC lakes are experiencing slower growth, particularly as estimates of production in these lakes was close to 0 kg/ha. This is consistent with general concepts of life history theory which expects slower growth to result in larger and fewer individuals (Andersen & Beyer, 2006). Further, while there were clear trends with total epilimnetic phosphorus and fish production, the relationship was not significant. In fact, total phosphorus seemed to increase as production decreased, which is contradictory to relationships described in the literature that fish production should increase with total phosphorus (Downing et al., 1990; Downing & Plante, 1993; Mills, 1985). Together, these findings strongly establish DOC as the main driver of White Sucker production across the nine lakes evaluated in this study, such that DOC reduces White Sucker production through physiochemical and limnological bottom-up controls (i.e., light attenuation) and not through nutrient availability.

My results suggest that increasing DOC likely also reduced available habitat for White Sucker through decreasing both K_d (light attenuation) and thermocline depth. Thermal preferenda for White Sucker across several studies has been reported to be 23.4°C (Hasnain et al. 2010), temperatures which are only available in epilimnetic waters during the summer stratification period. Thus, shallower thermoclines in higher DOC lakes would place significant constraints on habitat availability for this species as DOC increases. These results are also in line with the literature that has identified light and heat as mechanistic limnological characteristics related to epilimnetic habitat availability in association with DOC (Ask et al., 2009; Craig et al., 2015, 2017; Karlsson et al., 2009; Sherbo et al., 2023; Tonin et al., 2022; Zwart et al., 2016).

Theoretical frameworks dictate that reduced available habitat should result in reduced food availability to fishes occupying the reduced available habitat (MacLeod et al., 2022). While I found support for this with regards to zooplankton biomass, which declined with increasing DOC, benthic invertebrate biomass increased with DOC, which is in contrast to theoretical expectations. Previous work has found benthic invertebrate biomass to be lower in high DOC lakes as a function of oxygen-mediated habitat limitation due to low dissolved oxygen in high DOC lakes (Craig et al., 2015). However, previous work did not identify reductions in dissolved oxygen with increasing DOC in the same lakes (Tonin, 2019), which my results support since benthic invertebrate biomass increased with DOC concentrations. Rather, these results are more consistent with a top-down effect where high densities of White Sucker in low DOC lakes leads to higher rates of benthic predation (and therefore reduced benthic invertebrate biomass in low DOC lakes). Benthic invertebrates are a main prey item for White Sucker (Chen & Harvey, 1995; Trippel & Harvey, 1987), but have also been found to selectively forage on zooplankton species (Saint-Jacques et al., 2000). Isotopic evidence from the same lakes found that the degree of allochthony among all three of these food web components—White Sucker, benthic invertebrates and zooplankton—increased with DOC, reflecting increased allochthony with DOC across the whole ecosystem (Tonin, 2019). This could explain the top-down effect observed; if White Sucker forage primarily within their thermal preferenda, then declines in zooplankton biomass as DOC increases may also reflect an element of top-down effects. Particularly as it is likely more energetically advantageous for White Sucker to predate predominantly on zooplankton species within their optimal habitat than pursue benthic invertebrates in less optimal (cooler) habitats in high DOC lakes.

There is limited empirical work evaluating drivers of fish production, with most work pointing towards total phosphorus and/or primary production as being the main driver of fish productivity (Downing et al., 1990; Downing & Plante, 1993). However, I demonstrate here that within a similar climatic region, variation in DOC played a larger role in dictating fish production than nutrient availability, despite higher total phosphorus present in high DOC lakes. Even though epilimnetic chlorophyll-*a* increased with DOC in this same set of lakes (Sherbo et al., 2022), primary production (integrated over the water column) was reduced as DOC increased. Similarly, in these same lakes it has been previously shown that deep chlorophyll maxima (DCM) do not form in high DOC lakes, which is an important resource for zooplankton (Tonin et al., 2022). Interestingly, my results indicate a strong significant correlative relationship between DOC and total phosphorus, as well as demonstrate that fish production in fact decreases as total epilimnetic phosphorus increases. It is likely that while high concentrations of epilimnetic total phosphorus were available in high DOC lakes, high light attenuation and shallower thermocline depths inhibit the utilization and integration of these nutrient sources by the food web. This all suggests that there may be a switch-point in freshwater ecosystems where total phosphorus ceases to be the main ecosystem driver and where DOC-induced increases in light attenuation becomes the main driver of primary production.

To date, no other study has directly assessed the relationship between fish production and DOC, however, a number of studies have assessed components of production (i.e., growth, biomass, yield) or relative estimates of biomass and abundance (i.e., bCPUE, CPUE; Benoît et al., 2016; Craig et al., 2017; Finstad et al., 2014; Karlsson et al., 2009; Koizumi et al., 2018). Tonin et al. (2019) found that White Sucker bCPUE increased with DOC, while Finstad et al. (2014) report a unimodal relationship where Brown Trout (*Salmo trutta*) bCPUE was low at low DOC concentrations and increased to an optima (~ 1-3 mg/L) before declining as DOC increased. The DOC concentrations reported by Finstad et al. (2014) range from just above 0 to ~ 8 mg/L and Tonin et al. (2019) assessed concentrations ranging from 3.5-9.2 mg/L, whereas the concentrations in this study ranged from 3.5-11.5 mg/L. Clearly, the DOC concentrations assessed in this thesis are equivalent to those in the descending arm of the unimodal relationship described by Finstad et al. (2014), with the lowest DOC concentrations reported here being similar to the tail end of the optima DOC range of the unimodal relationship.

It is well documented that relative estimates of biomass and abundance (i.e., bCPUE and CPUE, respectively) often suffer from catchability biases where estimates can overestimate (i.e., hyperstability) or underestimate abundance (i.e., hyperdepletion; Hilborn & Walters, 1992; Kleiber & Maunder, 2008; Mosley et al., 2022). Further, my results found no relationship between bCPUE, CPUE, or standing biomass with DOC, although I did show that mean size of individuals increased with DOC while abundance decreased. This supports the unreliability of estimates of relative abundance and biomass and that it is more appropriate to estimate absolute measures when available to directly capture population changes.

While this study aimed to understand drivers of fish production regionally among lakes, a second aim was to identify time- and cost-effective predictors of fish productivity. My study identified possible landscape-level predictors of production within similar climatic regions, such as DOC, thermocline depth, zooplankton biomass, as well as a number of life history predictors such as mean weight and length, maximum weight and length, and body condition. While there are barriers to sampling fish populations and communities (i.e., training, specialized gear, permitting), fish sampling will likely always provide the most accurate information if this is a feasible option. Particularly as fish production is an informative metric, but understanding the underlying life histories (i.e., body size, abundance) in the population and/or community is highly beneficial for interpreting estimates of production. However, depending on sampling locations (i.e., remote vs easily accessible areas) and personnel time, some predictors may be more accessible than others.

Overall, my analyses indicate that DOC mediates available habitat for White Sucker, ultimately shaping fish production through individual adaptations to optimal life history strategies (i.e., body size and abundance) within constraints set by habitat limitations, following theoretical bioenergetic expectations of production (MacLeod et al., 2022). This work here demonstrates that DOC modifies available habitat within lakes through changes in K_d and thermocline depth; these habitat changes result in changes in prey quantity (i.e., zooplankton) and access to prey within optimal habitat (i.e., benthic invertebrates). These limitations shape growth, body size and ultimately population abundance to influence estimates of White Sucker production. This work provides a strong mechanistic description of the role of DOC in modifying freshwater fish production spatially within a similar climatic region. Further, I provide strong mechanistic evidence to support that total phosphorus is not a universal driver of fish production, rather this work supports that there is a switch point where DOC mediated light limitation becomes the main constraint of fish production rather than nutrient availability. Fish production is considered an important metric for understanding the state of fish populations and communities yet remains understudied and challenging to estimate. Here I have made contributions to the understanding of mechanisms of freshwater fish production and have identified direct estimates of fish abundance and production may be the best possible predictors for monitoring fish production despite associated monetary and time challenges.

Table 4.1. Lake characteristics and data availability.

Lake	Area (ha)	Z_{mean} (m)	Z_{max} (m)	DOC (mg/L)	K_d (m^{-1})	Total Phosphorus (µg/L)	Thermocline Depth (m)	Data Availability
149	26.9	2	4.1	11.5	0.75	9	NA	2019, 2021
164	38.7	4.94	7.1	9.2	1.22	9.8	4.6	2017, 2019
223	37.3	7.15	14.4	4.8	0.43	6.7	6	1988-2013
224	25.9	27.4	27.4	3.5	0.31	5.8	7.8	1989-2018
239	56.1	10.5	30.4	7.4	0.65	6	5.6	1981-2019
373	27.3	10.8	20.8	4.3	0.37	6.2	7.6	1988-2013
442	16	8.1	17.8	6.8	0.75	6.9	5.7	1990-2005
626	25.9	6.8	11.2	5.1	0.48	6.7	6.4	2013-2018
658	8.4	7.4	13.2	9.2	1.01	8	5	2000-2021

Table 4.2. Spearman's (rank order) correlation coefficients (ρ) of White Sucker production estimates, components of production, and relative abundance. Significance is denoted by * ($p < 0.05$).

	Production (kg/ha)	Biomass (kg)	bCPUE (kg/net/day)	CPUE (fish per net days)
Biomass (kg)	0.37			
Log bCPUE (kg/net/day)	0.37	0.28		
CPUE (fish per net days)	0.62	0.10	0.64	
Log Abundance	0.72*	0.75*	0.27	0.50

Table 4.3. Model outputs of significant predictors of White Sucker production.

Predictor	Slope	Intercept	Adjusted R^2	df	*F*-value	*p*-value
DOC	-0.24 ± 0.10	2.69 ± 0.70	0.39	1, 7	6.10	< 0.05
Thermocline Depth	0.62 ± 1.42	-2.61 ± 0.62	0.47	1, 6	7.24	< 0.05
Log Total Benthic Invertebrate Biomass	-1.34 ± 0.41	-0.15 ± 0.45	0.58	1, 6	10.86	< 0.05
Zooplankton Biomass	3.35 ± 1.20	-0.26 ± 0.53	0.46	1, 7	7.82	< 0.05
Mean Weight	-0.001 ± 0.0004	2.09 ± 0.38	0.54	1, 7	10.54	< 0.05
Mean Fork Length	-0.007 ± 0.002	3.37 ± 0.71	0.57	1, 7	11.42	< 0.05
Max Fork Length	-0.01 ± 0.004	6.44 ± 2.03	0.43	1, 7	7.05	< 0.05
Max Weight	-0.001 ± 0.004	2.62 ± 0.66	0.40	1, 7	6.33	< 0.05
Body Condition	-6.76 ± 1.78	7.04 ± 1.58	0.63	1, 7	14.43	< 0.01

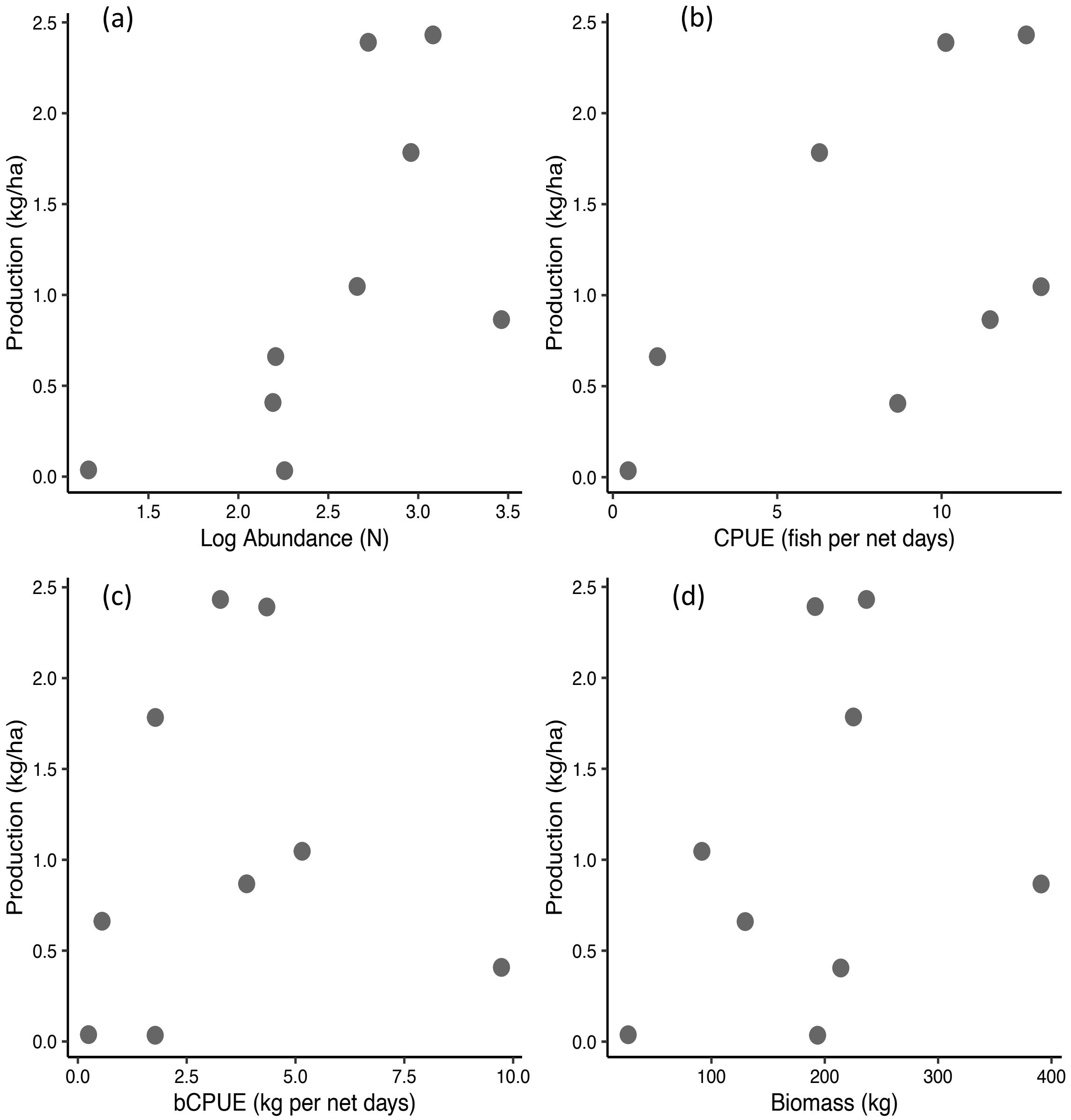


Figure 4.1. Relationships between components of production and estimates of relative abundance and biomass (a) abundance (N), (b) relative abundance, CPUE (fish per net days), (c) relative biomass, log bCPUE (kg per net days), (d) biomass (kg). Only the correlation shown in panel (a) was statistically significant.

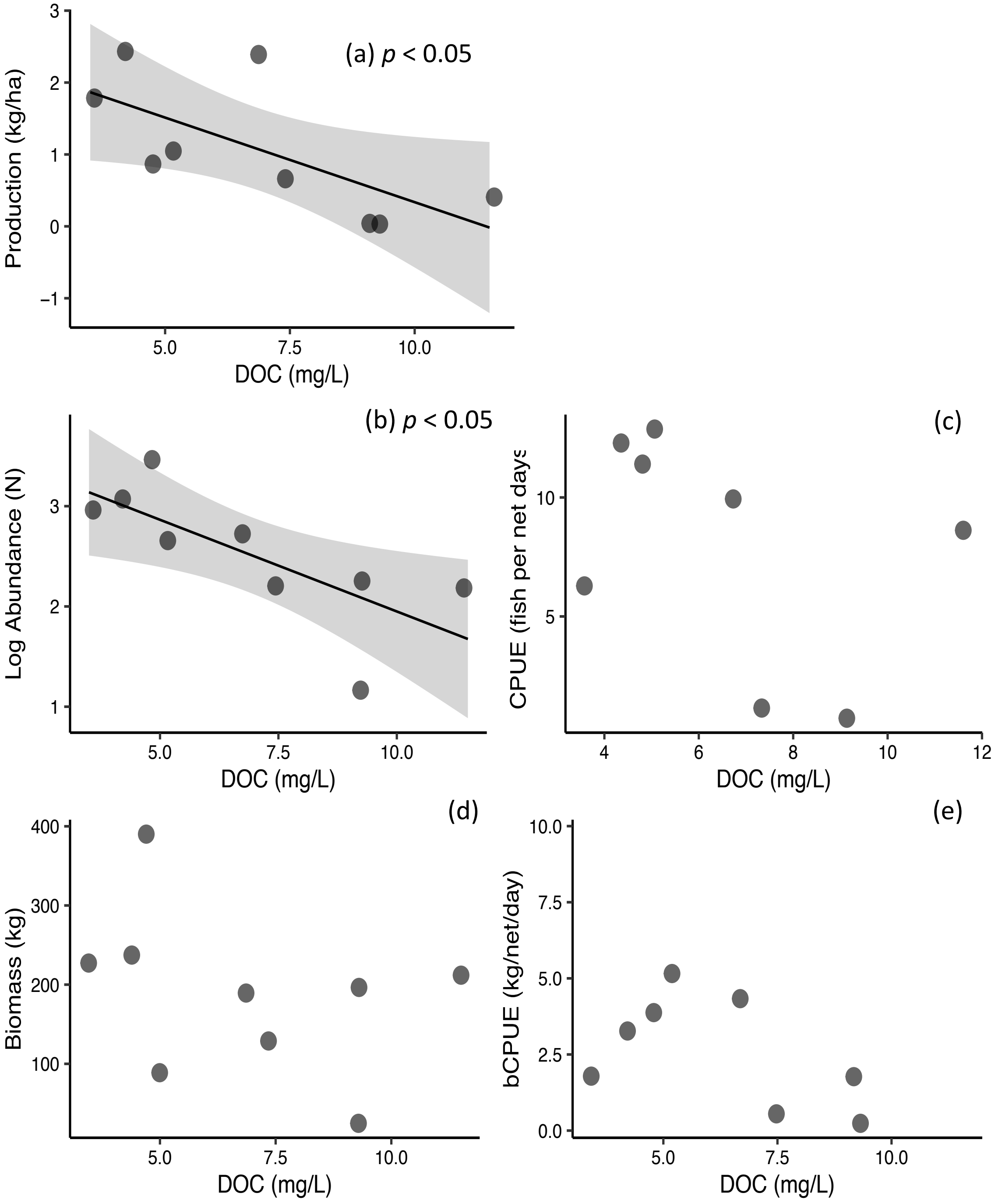
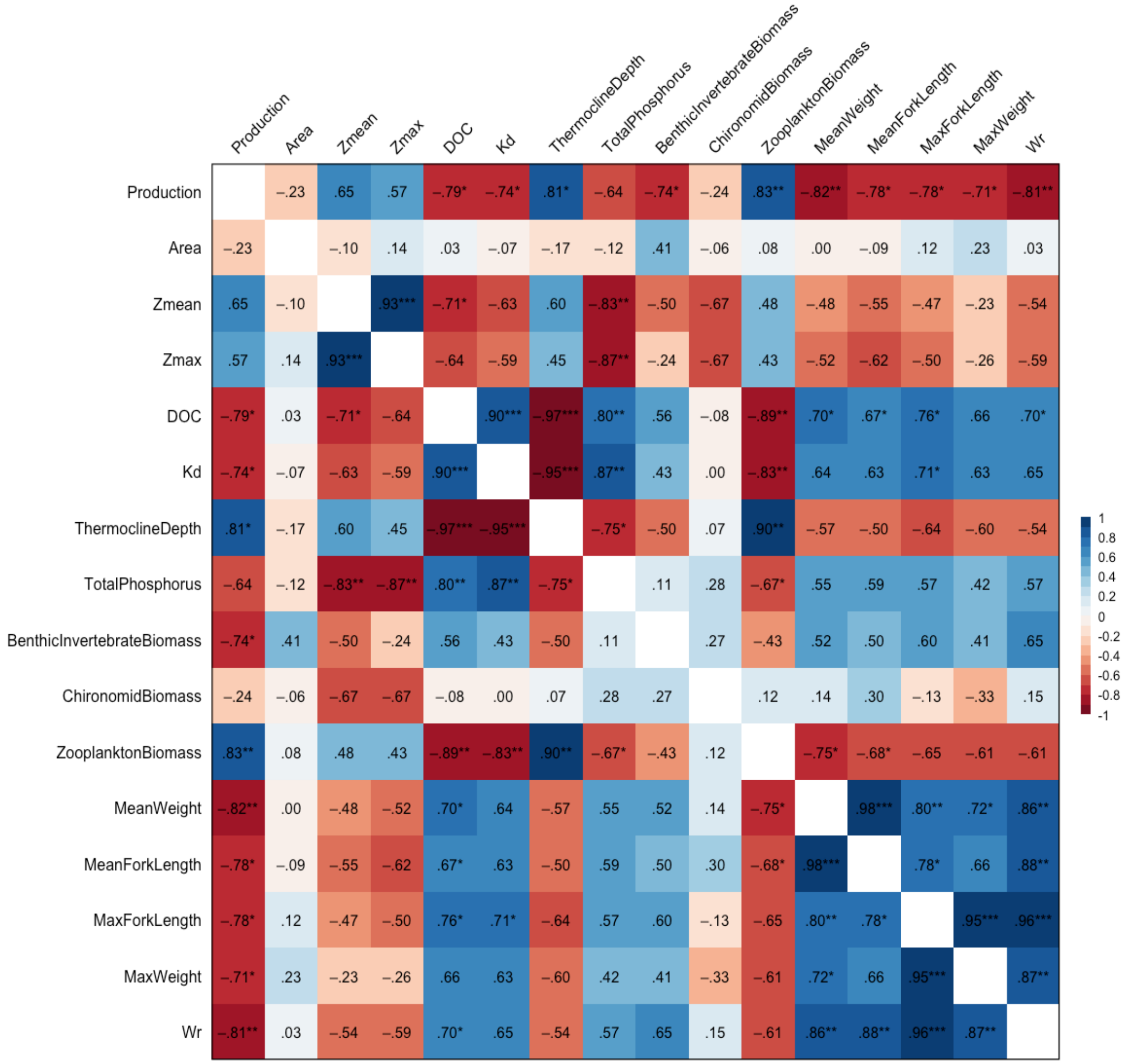


Figure 4.2. Relationships between DOC, (a) White Sucker production (kg/ha), components of White Sucker production, (b) log abundance and (c) CPUE (fish per net days), (d) biomass (kg), (e) bCPUE (kg/net/day). Shaded regions represent 95% confidence intervals around linear models.



	Production	Area	Zmean	Zmax	DOC	Kd	ThermoclineDepth	TotalPhosphorus	BenthicInvertebrateBiomass	ChironomidBiomass	ZooplanktonBiomass	MeanWeight	MeanForkLength	MaxForkLength	MaxWeight	Wr
Production		−.23	.65	.57	−.79*	−.74*	.81*	−.64	−.74*	−.24	.83**	−.82**	−.78*	−.78*	−.71*	−.81**
Area	−.23		−.10	.14	.03	−.07	−.17	−.12	.41	−.06	.08	.00	−.09	.12	.23	.03
Zmean	.65	−.10		.93***	−.71*	−.63	.60	−.83**	−.50	−.67	.48	−.48	−.55	−.47	−.23	−.54
Zmax	.57	.14	.93***		−.64	−.59	.45	−.87**	−.24	−.67	.43	−.52	−.62	−.50	−.26	−.59
DOC	−.79*	.03	−.71*	−.64		.90***	−.97***	.80**	.56	−.08	−.89**	.70*	.67*	.76*	.66	.70*
Kd	−.74*	−.07	−.63	−.59	.90***		−.95***	.87**	.43	.00	−.83**	.64	.63	.71*	.63	.65
ThermoclineDepth	.81*	−.17	.60	.45	−.97***	−.95***		−.75*	−.50	.07	.90**	−.57	−.50	−.64	−.60	−.54
TotalPhosphorus	−.64	−.12	−.83**	−.87**	.80**	.87**	−.75*		.11	.28	−.67*	.55	.59	.57	.42	.57
BenthicInvertebrateBiomass	−.74*	.41	−.50	−.24	.56	.43	−.50	.11		.27	−.43	.52	.50	.60	.41	.65
ChironomidBiomass	−.24	−.06	−.67	−.67	−.08	.00	.07	.28	.27		.12	.14	.30	−.13	−.33	.15
ZooplanktonBiomass	.83**	.08	.48	.43	−.89**	−.83**	.90**	−.67*	−.43	.12		−.75*	−.68*	−.65	−.61	−.61
MeanWeight	−.82**	.00	−.48	−.52	.70*	.64	−.57	.55	.52	.14	−.75*		.98***	.80**	.72*	.86**
MeanForkLength	−.78*	−.09	−.55	−.62	.67*	.63	−.50	.59	.50	.30	−.68*	.98***		.78*	.66	.88**
MaxForkLength	−.78*	.12	−.47	−.50	.76*	.71*	−.64	.57	.60	−.13	−.65	.80**	.78*		.95***	.96***
MaxWeight	−.71*	.23	−.23	−.26	.66	.63	−.60	.42	.41	−.33	−.61	.72*	.66	.95***		.87**
Wr	−.81**	.03	−.54	−.59	.70*	.65	−.54	.57	.65	.15	−.61	.86**	.88**	.96***	.87**	

Figure 4.3. Heat map of physiochemical and biological predictors against estimates of mean White Sucker production using Spearman's rank correlation. Asterisks denote varying levels of significance ($p < 0.5$). Numerical values and colour gradients depict the value and strength of the correlation coefficients. Abbreviation definitions are as follows: Production denotes White Sucker production (kg/ha); Area denotes lake area (ha); Zmean and Zmax denote mean and max depth (m); DOC denotes dissolved organic carbon (mg/L); K_d denotes light attenuation (m^{-1}); ThermoclineDepth denotes thermocline depth (m); TotalPhosphorus denotes total epilimnetic phosphorus (µg/L); BenthicInvertebrateBiomass denotes benthic invertebrate biomass (g/m^2); ChironomidBiomass denotes chironomid biomass (g/m^2); ZooplanktonBiomass denotes zooplankton biomass (g/m^2); MeanWeight and MaxWeight denote mean weight and max weight (g), respectively; MeanForkLength and MaxForkLength denote mean and max fork length (mm), respectively; Wr denotes relative body condition.

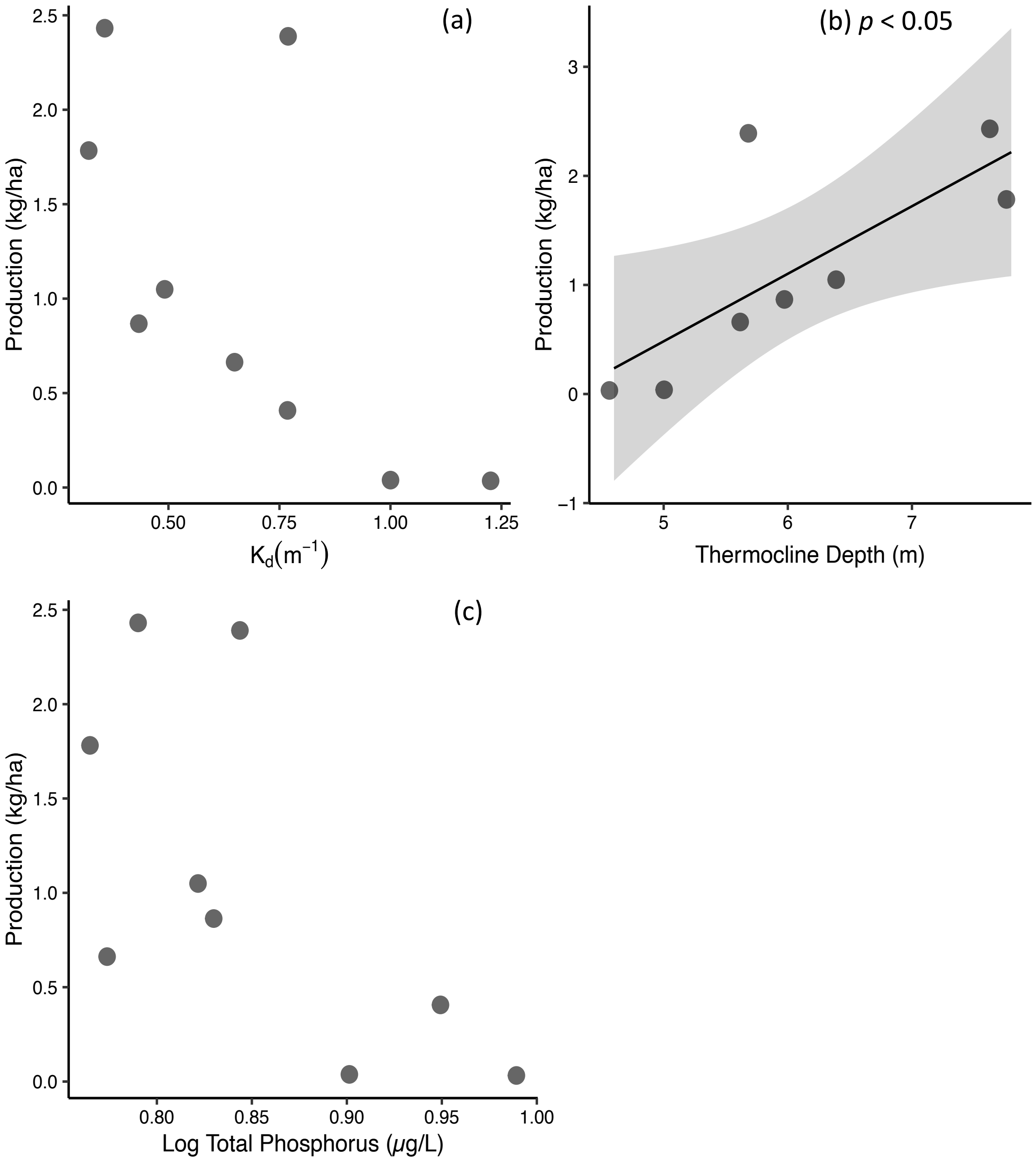


Figure 4.4. Relationships between physiochemical and limnological predictors K_d (m^{-1}), thermocline depth (m), and log total phosphorus (μg/L) with mean White Sucker production across nine lakes. Shaded regions indicate 95% confidence intervals around the linear model. Rank-based Spearman's correlation coefficient was significant for panl (a), but not for panel (c).

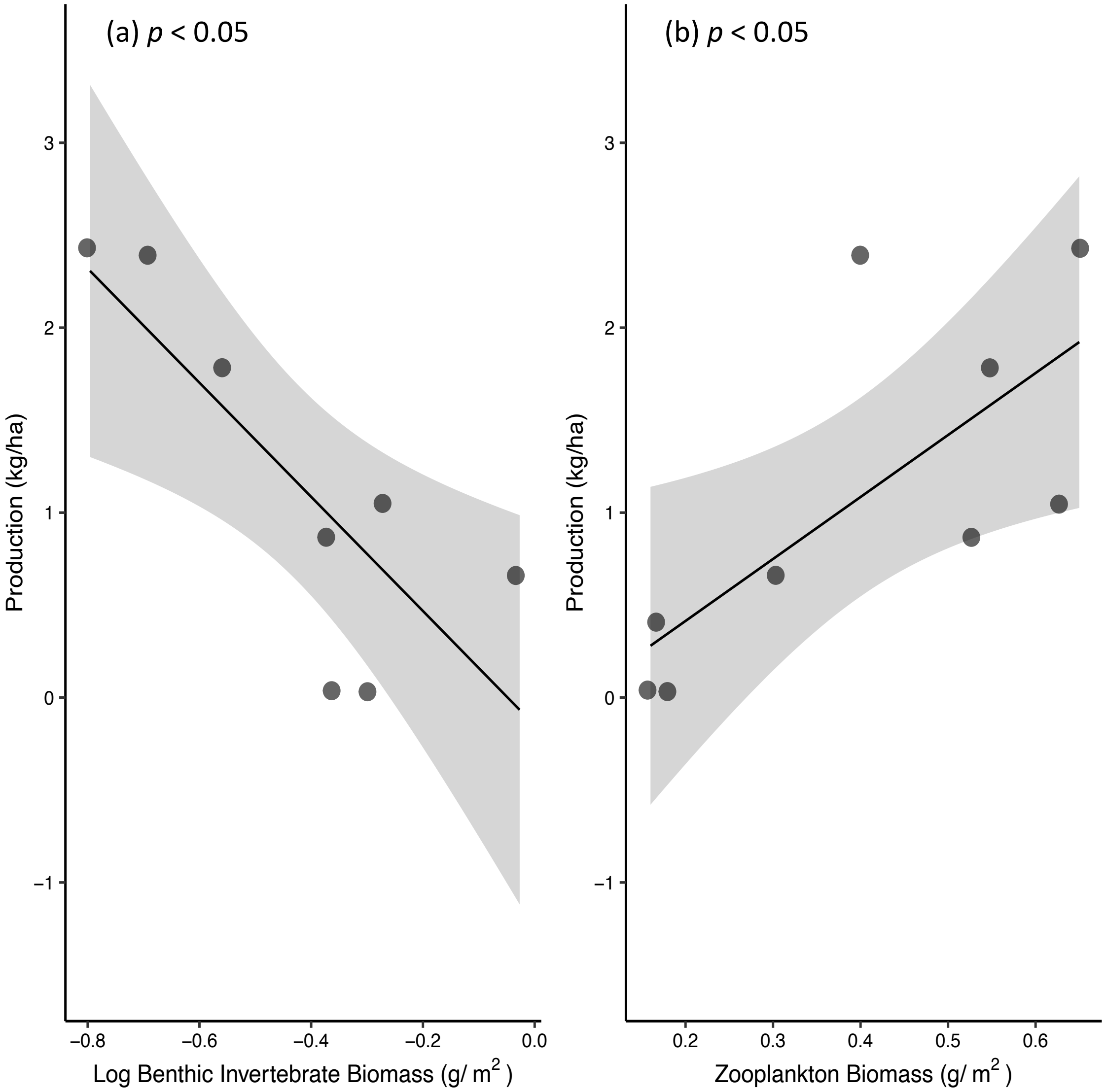


Figure 4.5. Relationships between lower food web indices, ln benthic invertebrate biomass (g/m^2) and zooplankton biomass (g/m^2) with White Sucker production across nine lakes of varying ecosystem productivity. Shaded regions indicate 95% confidence intervals around the linear model.

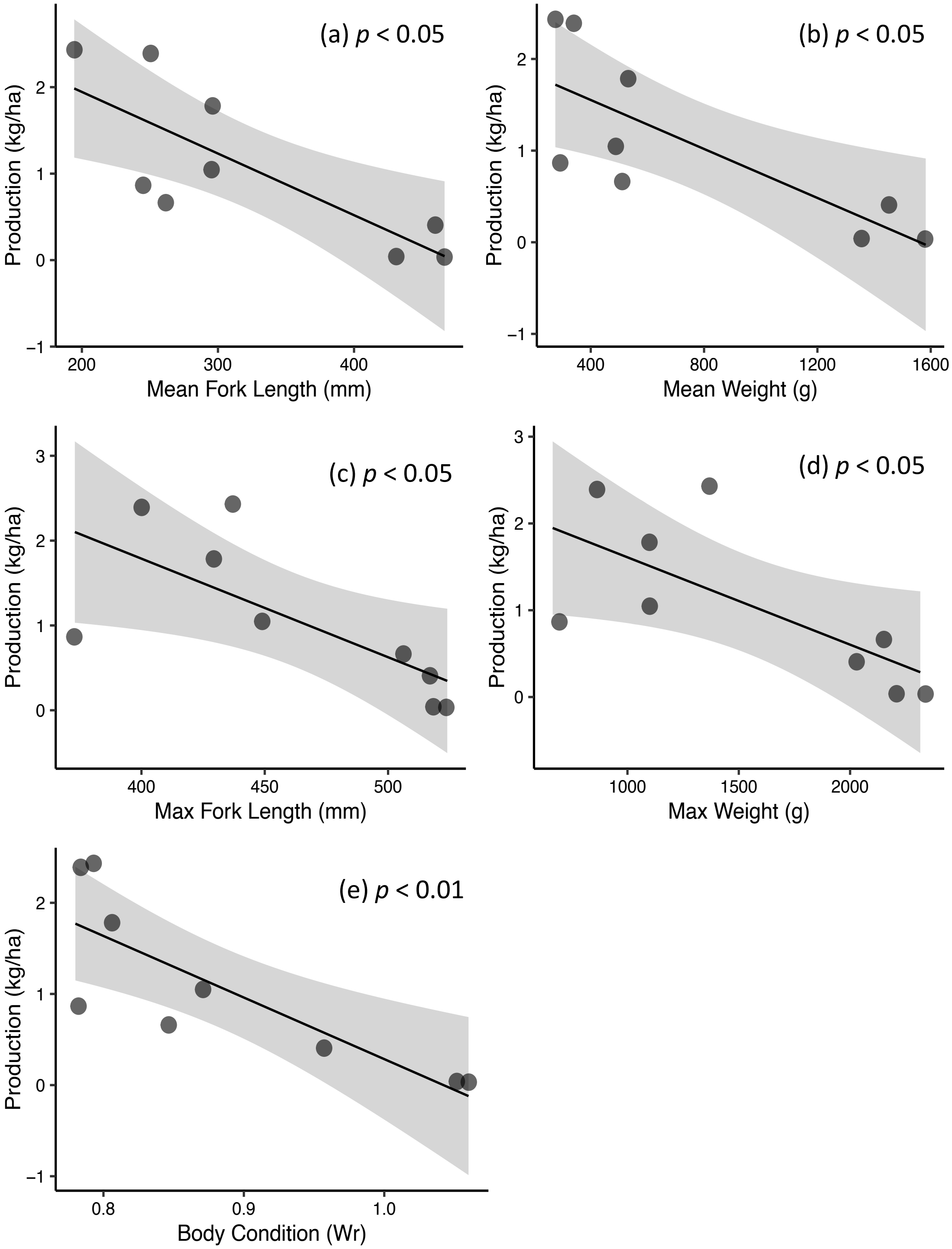


Figure 4.6. Relationships between life history predictors, mean fork length, mean weight, max fork length, max weight, and body condition with White Sucker production across nine lakes of varying ecosystem productivity. Shaded regions indicate 95% confidence intervals around the linear model.

Supplemental Information

Table S4.1. Fork length – total length regression equation based on White Sucker across nine Boreal lakes.

Coefficient Estimate	**Intercept Estimate**	**Adjusted R^2**	**df**	***F*-value**	***p*-value**
1.08 ± 0.0002	-1.24 ± 0.04	0.99	1, 76613	$4.67e^{07}$	< 0.0001

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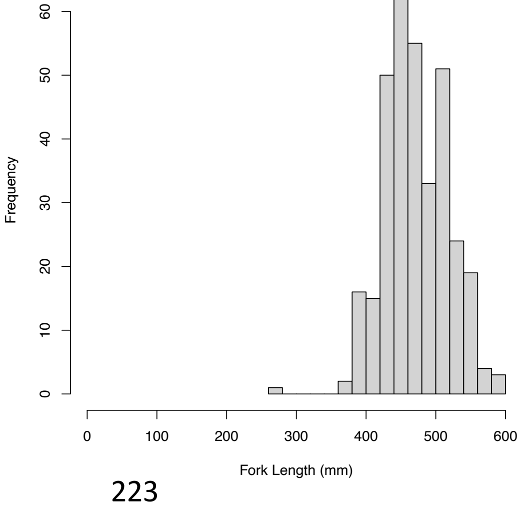

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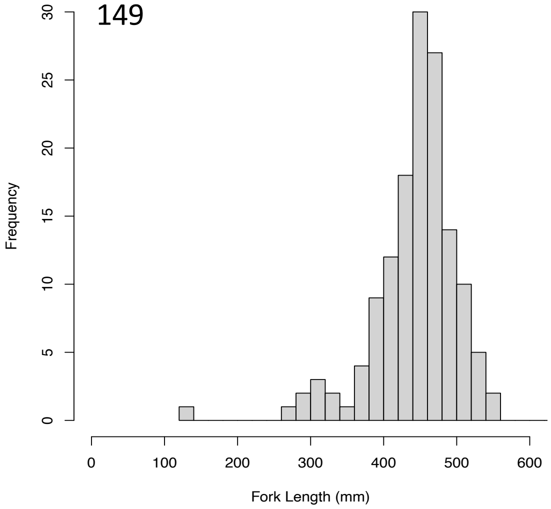

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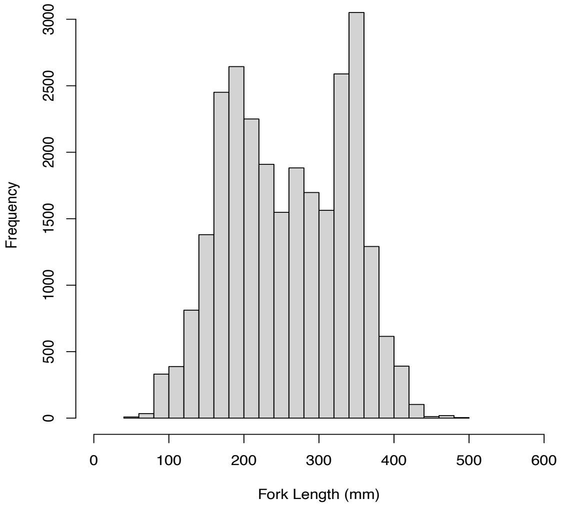

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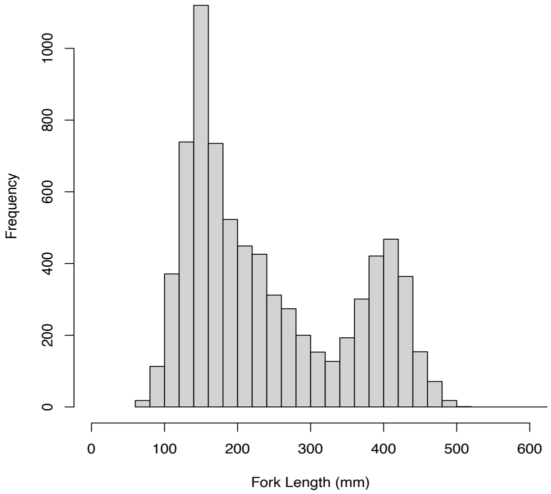

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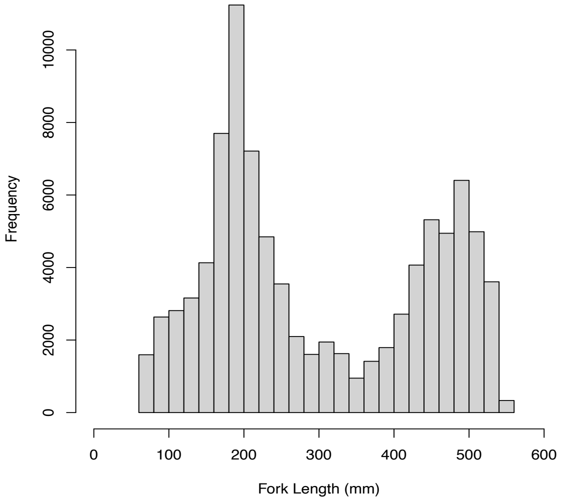

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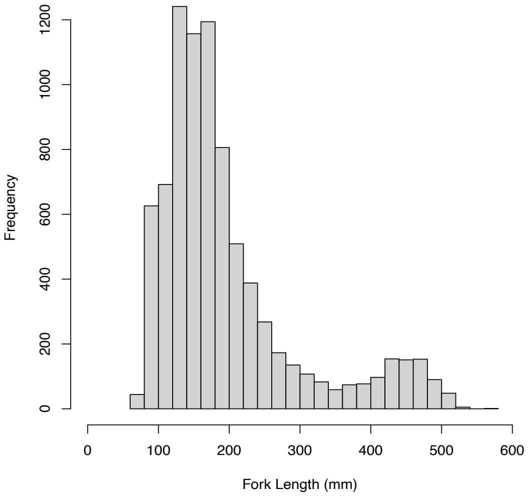

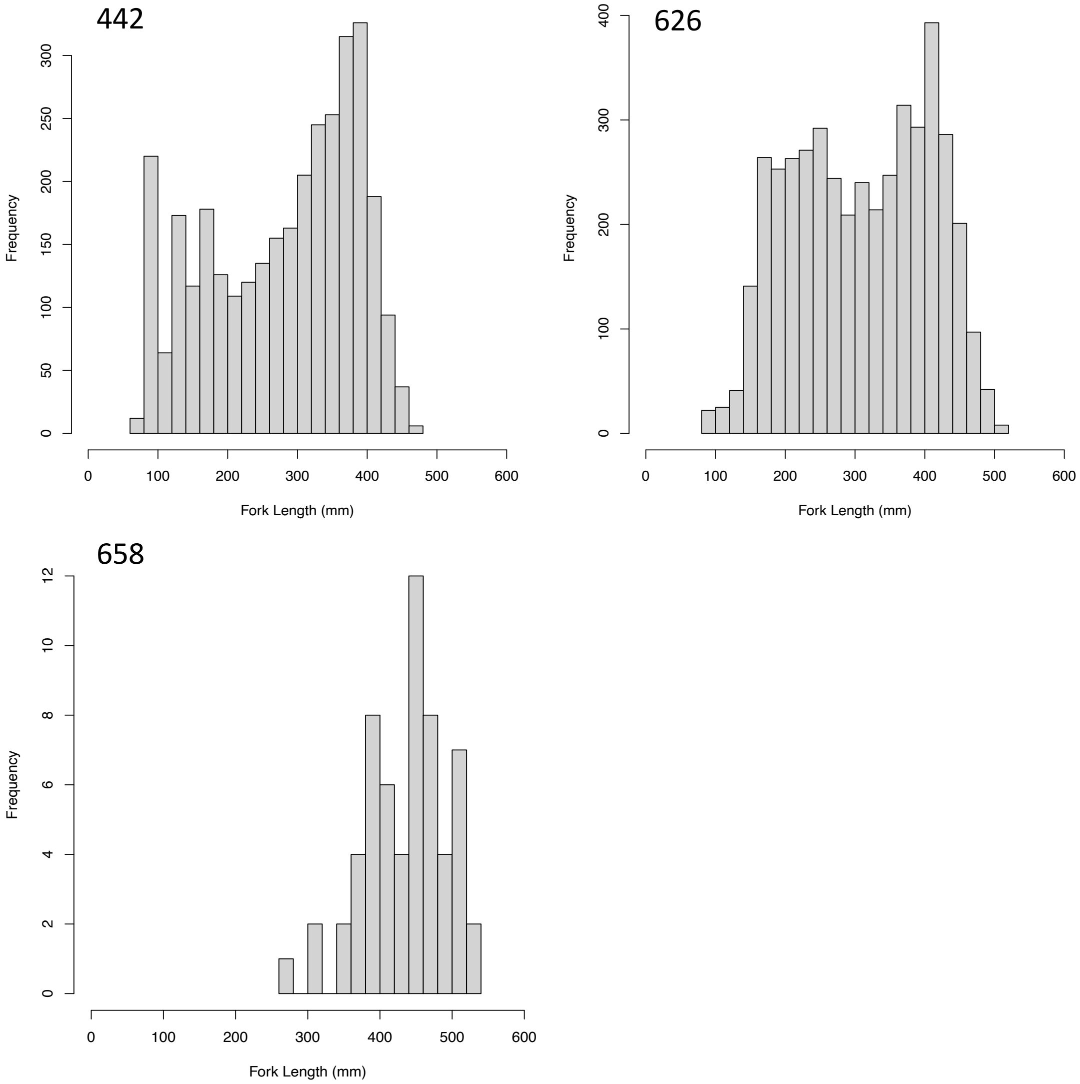

Figure S4.1. Frequency of fork lengths (mm) of individuals sampled across all nine lakes.

CHAPTER 5

General Conclusions

The work presented in this thesis provides empirical support for recent theoretical frameworks demonstrating how individual bioenergetics shape population and community dynamics. Here I provide clear insight into the correlates and dynamics of population- and community-level estimates of freshwater fish productivity over long-term and regional scales. This work also provides strong support for the recommendation of potential predictors of fish production and demonstrates that components of production commonly used to make inferences on fish productivity can in fact have no relationship with direct estimates of fish production (i.e., standing biomass, relative biomass, relative abundance), apart from abundance which scaled significantly with production in my dataset.

Prior to the results presented in this thesis, most work has identified temperature (climate), total phosphorus, and body size over large latitudinal gradients to be the main predictors of freshwater fish production (Downing et al., 1990; Downing & Plante, 1993; Rypel & David, 2017). These direct relationships consisted of fish production increasing with (i) total phosphorus, (ii) and temperature, and decreasing with (iii) body size. Rypel and David (2017) identified more nuanced relationships where community production is higher in warmer climates, versus population production that is greater in colder climates (due to reduced competition). I build on these initial large landscape-level relationships (Downing et al., 1990; Downing & Plante, 1993; Rypel & David, 2017) by providing insights into fine-scale dynamics and identified contradictory relationships between body size and production, as well as total phosphorus and production. Specifically, Chapter 3 of this thesis reports that population- and community-level production increased as total phosphorus increased (despite reductions in oxythermal habitat as a result of the formation of hypoxic zone), until a switch point where fish production began to decline even with continued nutrient inputs. This suggests that increases in prey availability can offset bioenergetic consequences of reductions in optimal habitat to a point, before habitat constraints become too energetically costly despite high prey availability. These findings demonstrate that nutrient availability is the main the driver of population and community production when habitat conditions are ideal, until habitat availability becomes the main constraint of fish production despite high nutrient availability.

These findings are further supported in Chapter 4, where I show that habitat availability is the main driver of fish production regionally among lakes with varying DOC concentrations. Specifically, I found that as DOC concentrations increased, White Sucker production decreased, as DOC led to shallower thermocline depths and increased light attenuation (Tonin et al., 2022; Sherbo et al., 2023). I also found that total epilimnetic phosphorus increased as DOC increased (and fish production decreased), once again supporting that habitat availability is the main mechanism driving fish production when acting as a constraint.

Interestingly, when assessing production among lakes experiencing the same climate, body size was an important predictor of production, although in the opposite direction as previously reported (Downing et al., 1990; Downing & Plante, 1993). In this dataset, decreases in fish production were associated with decreased abundance and increasing body size. While this does follow theoretical expectations of life history theory (Andersen & Beyer, 2006), it does not follow theoretical expectations of production, as it is anticipated for body size to increase with increasing habitat size and prey availability. In Chapter 3, I found that body size increased with increasing production over time during a nutrient manipulation, but in Chapter 4 I found that body size increased as production declined across lakes with varying DOC concentrations. This highlights the need to exercise caution when relying on body size as a predictor of production and the need to better understand other models of production based on body size (i.e., P/B ratios, body size-based models of production by Downing and Plante, 1993).

Similarly, standing biomass did not scale with production in Chapter 4; rather, biomass was maintained across all lakes despite changing DOC concentrations. The analyses presented in Chapter 4 demonstrate that while standing biomass is maintained, abundance decreased with increasing DOC, indicating that growth is likely the main factor leading to population changes at higher DOC concentrations. This finding is supported by fish production theory that suggests that life history strategies are optimized according to habitat constraints, and therefore, growth rates are altered accordingly (MacLeod et al., 2022). While in Chapter 4, abundance seems to be a large contributing factor to differences in production across lakes regionally, in Chapter 3, both changes in cohort weight and abundance over time are driving changes in production. Where Lake Trout production in Lake 375 was driven by a combination of changes in abundance and cohort mean weight, increases in White Sucker production in the same lake was driven exclusively by changes in cohort mean weight as abundance did not change over time. This highlights that while the production estimates presented in this thesis are capturing population changes in abundance and biomass both temporally and spatially, estimates of production are clearly challenging to interpret without additional insight into further population responses (i.e., changes in body size and abundance). So, while estimates of fish production are legislatively required through the *Fisheries Act* to understand impacts of development, estimates of production alone may not provide sufficient fine-scale insight into population responses to disturbance.

Through the exploration of mechanisms of fish production across both temporal (Chapter 3) and spatial gradients (Chapter 4), I identified a number of potential predictors of production. As previously discussed in these general conclusions, habitat availability seems to be the most important overall constraint on fish production. However, when available habitat is not being altered through extensive nutrient inputs or high DOC concentrations, fish production is relatively unimpeded and driven primarily by nutrient availability. Under conditions where habitat availability is not the main constraint, this work supports total phosphorus, body size, and minnow CPUE as good predictors of fish production. However, under conditions of habitat constraint, thermocline depth, light attenuation and abundance may be more accurate predictors of production. The results of this thesis do indicate however that multiple predictors are likely necessary to fully ascertain the state of a fish population or community. There is a strong indication that certain constraints alter body size in contradictory ways, as well as abundance, since abundance does increase with increasing estimates of production in Lake Trout, but not White Sucker in Chapter 3. This then suggests that to truly comprehend the state of a population or community, collecting direct fisheries data will be the most useful for monitoring fishes. Though, understanding how development is altering productive habitat in an ecosystem will be beneficial as an indirect indicator as I show that reductions in optimal habitat had the largest negative impact on fish production.

Our theoretical understanding of fish production suggests that food availability plays a large role in determining fish production, yet my results suggest habitat is a stronger driver rather than prey size and availability. In Chapter 3 Lake Trout production initially increased with minnow CPUE (a main prey item for the species) during aquaculture before reductions in optimal cold-water habitat ultimately overshadowed any bioenergetic benefit of high prey availability. While in Chapter 4, White Sucker production declined with zooplankton biomass, despite benthic invertebrate biomass increasing with DOC. Again, supporting that habitat availability was the greatest constraint on fish production assessed in this thesis. However, in ecosystems where habitat is not acting as the main constraint, it is likely that prey size and availability would be more important in dictating production dynamics. This would be the case in ecosystems with typical oxythermal dynamics and at the mid-lower end of the DOC concentration range evaluated.

Lastly, I demonstrate that White Sucker may be an ideal indicator species for assessing changes in community and top predator production. This species comprised the majority of the community production in the lakes examined here, was strongly tied to top predator production, and responded predictably to physiochemical/limnological and lower food web changes among lakes. Additionally, White Sucker are generally not targeted through recreational or commercial fisheries and are ubiquitous within their North American distribution range (Scott & Crossman, 1973). Other works have suggested the use of White Sucker as an indicator species, and the findings in this thesis further support their ability to respond to spatiotemporal ecosystem differences and ecosystem change (Doherty et al., 2010; McMaster et al., 2020; Munkittrick, 2000; Slongo, 2022).

This thesis provides empirical support for many theoretical expectations of fish production, and provides important insight into the application and interpretation of fish production. Particularly with the contributions made in Chapter 2, where I clearly demonstrate the application of growth models in improving production estimates by (a) addressing introduced biases through small sample sizes, and (b) provide a means of identifying legitimate instances where fish can lose weight over time when faced with disturbance, allowing for legitimate instances of negative production to be identified and interpreted. While predictors of production were assessed throughout this thesis, collecting fish data directly still remains the best way to understand population and community dynamics, as no predictors evaluated here maintained the same relationship across both time or space. While the application of estimates of fish production are clearly useful in capturing major population and community changes, the role of physiochemical and limnological processes in shaping both the lower food web and ultimately life history strategies would benefit from further characterization. The work presented here provides comprehensive insights into the dynamics of freshwater fish production both over long-term time scales, as well as within regional spatial scales. Further, the results presented here indicate that changes to habitat availability due to development or climate change will likely impact fish production, especially cold-water species. As such, further advancement of empirical estimates of fish production should be encouraged; however, a lack of long-term data will be a major deterrent to the application of these estimates.

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