Species diversity and environmental variability: patterns and processes of lacustrine fish community responses in a variable world

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Abstract

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Ecosystems are heterogeneous on multiple scales of space and time, and this variation in abiotic and biotic features confronts organisms with complex challenges. Climate change signals are also often heterogeneous across these scales, and it is important to understand how climate plays out over the landscape due fine-scale variability in habitat. In addition, the temporal scale over which species respond to environmental change may vary across taxa, presenting an opportunity for mismatches in ecological relationships. To date, much work has focused on climate change effects on primary and secondary production in lakes, but mechanisms and community-level processes for higher trophic level organisms remain less clear.

This dissertation aims to reveal patterns and processes of fish individual and community responses to environmental change on multiple time scales. In Chapter 1, I developed a bioenergetics model for the threespine stickleback to define ecological demands of this fish under a range of temperatures, indicating that this fish has a different thermal optimum than sympatric fishes. This physiological diversity has possible implications for community composition. Chapter 2 examined the intersection of seasonal variability and life history diversity, and showed that the timing of seasonal lake productivity varied widely across years and that sockeye salmon fry with more protracted migration experienced higher overall survival. Chapter 3 contributes to our understanding of how spatial variability can affect the way that fish communities change over time, and showed that, within a single lake, community change varied by fine-scale location and depended on species-specific responses to temperature. In Chapter 4, we asked how climate-driven changes in lakes can influence phenology and expression in a species trait. These results showed that reproduction in fish is closely linked to physical lake changes.

As a whole this research illustrates that lacustrine fishes can be highly susceptible to changes in the environment. However, the responses that we observed depended upon physiological or life history diversity among and within species and diversity within habitats, and upon the scale at which changes are observed in the environment. My hope is that this dissertation will contribute to the understanding of the role of biological diversity in explaining ecosystem processes and observed changes to the environment.

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DEDICATION

I dedicate this dissertation to my parents, Joe and Mary Hovel, who encouraged my interest in the natural world from an early age.

GENERAL INTRODUCTION

Ecosystems are heterogeneous on multiple scales of space and time, and this variation in abiotic and biotic features confronts resident organisms with complex challenges (Allen and Hoekstra 1992). Effects of climate change or the direct impacts of human disturbance or management further alter environments, and the biological responses can be complex and often unpredictable. The effects of disturbances can play out in systems in multiple ways and understanding these processes is an important goal in fundamental and applied ecology.

Ecological research examines patterns and processes in biological systems, and the complexity with which a system is described depends on which levels of organization are considered (Levin 1992). Diversity within biological communities is a central component of many ecosystems, and can dictate the ways that disturbances affect those systems and how organisms persist in variable environments (Chapin et al. 2000). Understanding the manner in which diversity is expressed in physiology, behavior, life histories, and ecological roles and on levels from species to biological communities can help explain the patterns of ecosystem responses to climate change or other perturbations (Bellard et al. 2012).

Processes and patterns in ecological communities function across a gradient of different scales in space and time, and the type of ecological question dictates the level of temporal variability examined in a system. With increased complexity in the question, more consideration must be paid to the temporal (and associated spatial and taxonomic) scales of how variation in the system is observed, as the scale at which we examine a system influence the patterns of variation that are detected (Allen and Hoekstra 1992). For example, the temporal scale over which a species responds to environmental change may vary across taxa, presenting an

opportunity for mismatches in ecological relationships. As taxa respond to environmental drivers on different time scales or with different temporal cycles, trophic linkages or other relationships might break down (Edwards and Richardson 2004; Winder and Schindler 2004; Satterthwaite et al. 2014).

Climate change signals are often heterogeneous in space (Stenseth and Mysterud 2002; Ashcroft et al. 2009), and in some cases are influenced by subtle landscape features over very small spatial distances (Ford et al. 2013). While some systems are assumed to operate as closed, homogenous units and may be strictly geographically defined (e.g. Parker et al. 2008), many systems include mobile organisms or encompass habitat heterogeneity that is less readily observed but that can influence ecosystem processes. This highlights a challenge in designing and carrying out research and emphasizes the importance of matching the scale of ecological observations to the true variation in the environment. For organisms reliant on multiple habitat types (e.g. migratory fishes), the strength of climate effects may vary across the geographic extent of their resource demands, especially because different habitat types may vary in response to climate (Parmesan 2007). In this way, it is important to understand the heterogeneous manner in which climate plays out over the landscape due fine-scale variability in habitat.

This dissertation uses fish communities in large lake systems to examine the role of species and community diversity in understanding how animals persist in variable environments and predicting the effects of habitat changes from climate warming. While lakes are sometimes considered a homogenous feature on the landscape, these systems can reflect a large amount of fine-scale variation in 2- and 3- dimensional habitat, temperature, and productivity (Benson and Magnuson 1992; Harrison and Hildrew 2001; Fragoso et al. 2008). In addition, lakes, especially

those at high latitude or high elevation, are highly susceptibility to physical effects from climate change (De Stasio et al. 1996; Magnuson 2000; Adrian et al. 2009; Schindler 2009). Mediated through changes to their habitat, lake-resident primary producers and consumers of all trophic levels show climate change effects (Smol et al. 2005). To date, much work has focused on climate change effects on primary and secondary production in lakes (i.e. phytoplankton and zooplankton) (e.g. Winder et al. 2009; Cantin et al. 2011; Carter and Schindler 2012), but mechanisms and community-levels processes for changes to higher trophic level organisms (e.g. fish) remain less clear.

This work aims to reveal patterns and processes of fish individual and community responses to environmental change on multiple time scales in large, Pacific-salmon rearing lakes in Washington and Alaska. In Chapter 1, we developed a bioenergetics model for a widespread, abundant fish, the threespine stickleback (*Gasterosteus aculeatus)* to define the performance (growth) and ecological demands (consumption) of this fish under a range of temperatures. Our model indicates that this fish experiences highest growth and consumption demands at temperatures higher than sympatric lake-rearing sockeye salmon (*Oncorhynchus nerka*) juveniles, and this physiological diversity has possible implications for community composition in the future. Chapter 2 examined the intersection of seasonal variability and life history diversity, and asked whether survival and growth of juvenile sockeye salmon depend on lake conditions during the time when they enter a lake and commence feeding. Results showed that the timing of seasonal lake productivity varied widely across years, and that fish with more protracted migration timing experienced higher overall survival. In addition, the effects of seasonally-variable zooplankton prey dynamics vary by specific life stage for juvenile sockeye salmon, with different time scales influencing survival or size when the fish migrate out of the

lake. Chapter 3 contributes to our understanding of how spatial variability can affect the way that fish communities change over time, and showed that, within a single lake, 50-year trends in temperature vary widely by location. Community change over time varied at each sample site, and depended on species-specific responses to temperature and on site location. In Chapter 4, we asked how climate-driven changes in lake habitat can influence phenology and expression in a species trait. These results showed that timing of reproduction and iterative breeding in fish is closely linked to physical lake changes, with earlier breeding occurring in years with early ice breakup and multiple breeding events observed in years where the growing season begins earlier.

As a whole this research illustrates that, through different mechanisms, lacustrine fishes can be highly susceptible to changes in the environment. However, the responses that we observed depended upon physiological or life history diversity among and within species as well as diversity within habitats, and upon the scale at which changes are observed in the environment. We found that fish community composition shifted with multi-decadal climate changes, but habitat heterogeneity explains fine-scale variability in community response within a habitat unit. Mechanistically, life history trait expression and physiological attributes can help predict climate effects on species abundance and community structure. In addition, we demonstrate that life history diversity within species may act as a buffer for organisms in changing or increasingly variable environments. As these examples illustrate, accounting for environmental and biological diversity is important in describing fish responses to habitats that change over time. My hope is that this dissertation will contribute to the understanding of the role of biological diversity in explaining ecosystem processes and observed changes to the environment. Especially when confronted with the pressures of climate change or other

anthropogenic impacts, maintaining this biological and habitat diversity may be a key component to protecting ecosystem functions in the future.

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Chapter 1. **Development of a bioenergetics model for the threespine stickleback *Gasterosteus aculeatus***

ABSTRACT

The Threespine Stickleback *Gasterosteus aculeatus* is widely distributed across northern hemisphere ecosystems, has ecological influence as an abundant planktivore, and is commonly used as a model organism, but the species lacks a comprehensive model to describe bioenergetic performance in response to varying environmental or ecological conditions. This study parameterized a bioenergetics model for Threespine Stickleback using laboratory measurements to determine mass- and temperature-dependent functions for maximum consumption and routine respiration costs. Maximum consumption experiments were conducted across a range of temperatures from 7.5ºC to 23ºC and a range of fish weights from 0.5 to 4.5 g. Respiration experiments were conducted across a range of temperatures from 8ºC to 28ºC. Model sensitivity was consistent with other comparable models, in that the mass-dependent parameters for maximum consumption were the most sensitive. Growth estimates based on the Threespine Stickleback bioenergetics model suggested that 22ºC is the optimal temperature for growth when food is not limiting. The bioenergetics model performed well when used to predict independent, paired measures of consumption and growth observed from a separate wild population of threespine stickleback. Predicted values for consumption and growth (expressed as % body weight per day) only deviated from observed values by 2.0%. Our model should provide insight into the physiological performance of this species across a range of environmental conditions, and be useful for quantifying the trophic impact of this species in food webs containing other ecological or economically important species.

INTRODUCTION

Bioenergetics models are valuable tools for estimating and comparing the growth and consumption demand of fish in response to changes in thermal regimes, diet, and body size (Hill and Magnuson 1990; Brandt and Hartman 1993; Hansen et al. 1993). Developed over the past several decades, these models incorporate size-dependent and temperature-dependent effects into a single equation to balance energetic losses and gains (Hanson et al. 1997). Bioenergetics models are frequently applied to understand growth or resource use by fishes under specified environmental conditions, and can be scaled up to the ecosystem or community level if informed by knowledge of population dynamics (Hansen et al. 1993). One application for bioenergetics methods on an ecosystem scale is the use of these models to quantify trophic interactions among dominant species in fish communities. Many of these model applications quantify a single trophic interaction, estimating consumption of a single predator on a prey base (Caut et al. 2006). Alternatively, bioenergetics models can help describe the potential for competition among species sharing a trophic level and prey resource, and therefore, inform the structure and function of food webs (Pazzia et al. 2002). The effective use of bioenergetics models on both species- and system-scales depends on accurate parameterization for the species of interest. Models for over 70 species have been successfully developed and widely applied in numerous systems (Kitchell et al. 1977; Jobling 1994; Hartman and Kitchell 2008).

Comparison of physiological performance and resource use among fishes often utilizes appropriately developed models specifically suited to the species in the system. Yet, some widely distributed and ecologically important species still lack a fully parameterized model. Among these is the Threespine Stickleback *Gasterosteus aculeatus*, a Holarctic species found in both marine and freshwater environments (Wootton 1984). Threespine Stickleback can play

important ecological roles by numerically dominating fish communities and influencing nutrient recycling and other ecosystem functions (Harmon et al. 2009). The Threespine Stickleback lacks commercial importance, but often co-occurs and shares prey with economically valuable species such as salmonids, especially juvenile Sockeye Salmon *Oncorhynchus nerka* in lakes around the North Pacific Rim (O'Neill and Hyatt 1987; Quinn 2005). Other juvenile salmonid species, and other fish taxa including cottids, overlap and share resources with Threespine Sticklebacks in lake, river and estuarine habitats (Maitland 1965; Bolnick et al. 2010; Spilseth and Simenstad 2011). Potential for competition in resource limited environments can therefore make Threespine Stickleback energetics relevant when discerning the mechanisms through which fish communities are structured, and the potential factors limiting the growth and production of economically important species like juvenile salmon. In addition to their ecological importance and broad distribution, Threespine Stickleback are intensively studied as a model organism in evolutionary ecology, behavior, and evolutionary genetics (Bell and Foster 1994; Kingsley and Peichel 2007; Huntingford and Ruiz-Gomez 2009). Knowledge of the energetic consequences of behavioral, morphological, or physiological changes could provide valuable insight into the underlying mechanisms of selection.

Previous physiological measurements conducted in laboratory and field settings have reported growth, prey consumption, and respiration relationships with body size and temperature for Threespine Stickleback, using populations from Russia, the United Kingdom and Sweden (Meakins 1975; Wootton et al. 1980; Allen and Wootton 1982; Lefebure et al. 2011). However, these relationships have not yet been combined to form a single comprehensive model. The Wisconsin-type bioenergetics model offers a standard and easily applied framework for integrating, implementing and comparing physiological parameters among species. Existing

parameters and additional data generated in this study were used to generate parameter values for a Wisconsin-type bioenergetics model for Threespine Stickleback (Kitchell et al. 1977; Hanson et al. 1997). The objectives of this study were to: (1) conduct a set of physiological experiments to inform the temperature-dependent and allometric relationships for maximum consumption of prey and for routine respiration rates, which are typically the most sensitive parameters in a bioenergetics model (Bartell et al. 1986); (2) use these data to parameterize a bioenergetics model for Threespine Stickleback under unlimited food conditions across a range of temperatures; and (3) compare predictions from the resulting model with growth and consumption data from the literature to corroborate the model. Developing a bioenergetics model for Threespine Stickleback following the standard framework used for species of economic interest will allow for more comprehensive management and for making predictions about species interactions under changing environmental conditions.

METHODS

We performed a series of feeding and respiration laboratory experiments across a range of temperatures and body sizes to parameterize mass- and temperature-dependent functions for maximum consumption (C_{max}) and routine metabolism for Threespine Stickleback. These experiments were designed to conform with the most commonly used and widely accessible Wisconsin bioenergetics model (Hanson et al. 1997).

Fish rearing and acclimation

All fish were low-plated, freshwater morphs originating from Lake Washington, Washington, USA, and were either wild-captured during the summer using unbaited minnow traps set in the littoral zone (those fish > 60 mm total length) or were first-generation lab-reared individuals (those fish < 60 mm total length). Individuals of wild origin were housed together in standard 110-L aquaria, and were held in the lab for a period of 6 months or longer before experiments were conducted. Lab-reared fish were housed in separate 110-L aquaria, grouped by brood. All fish were reared under summer lighting conditions (16 h light, 8 h dark) and were fed *ad libitum* with either brine shrimp (fish < 25 mm) or marine *Mysis* (fish > 25 mm). The fish used in the experiments were not gape limited for this prey and had been raised on a diet of mysids for two months or longer. Rearing tanks contained 3.5 g/L of Instant Ocean salt (Instant Ocean, Aquarium Systems, Mentor OH, USA) and 0.4 ml/L $NaHCO_3$ (3.5‰ salinity) to relieve osmoregulation stress. The fish experienced a stable thermal regime of 15.5 ± 0.5ºC while held in the lab prior to the experiments. All experimental subjects were reared and held in compliance of the Institutional Animal Care and Use Committees at the Fred Hutchinson Cancer Research Center (protocol no. 1575).

Fish used in consumption and respiration experiments with temperatures above or below rearing (for lab-reared) or holding (for wild-captured) conditions were slowly introduced to the new thermal environment at an increase of 1ºC every 24 hours. They were then acclimated to this temperature for a period of 96 hours before the experiment was conducted. Through this four-day period, oxygen consumption rates were measured twice daily, and this rate stabilized and remained consistent after 72 hours. Food was withheld from experimental subjects for a 24 h period before either respiration or consumption experiments began.

Maximum consumption experiment

After the acclimation period, maximum consumption experiments were conducted by holding fish individually in 1 L beakers placed in temperature control systems set to constant temperature treatments of 7.5, 13, 18, and 23°C for the duration of the 3-day trial. Water in the beakers was of the same salinity as in the rearing aquaria, and the 16L:8D photoperiod was maintained for these fish.

Maximum consumption was measured across a range of temperatures and body sizes of Threespine Stickleback. For each temperature treatment, two fish of each available size category (0.5-2.0g, 2.0-3.5g, and 3.5-4.5g) were used. Each experiment at a given temperature was conducted three times, with unique individuals (n=6 per temperature and size bin; n=18 per temperature), except for trials at 23°C, where unique individuals were only available for n=9 (one fish per size bin). The optimal consumption temperature was identified as that at which feeding rate was maximized. The relationship of C_{max} to body mass was determined only at this temperature (23.0°C). Pilot experiments for the temperature-dependence of maximum consumption were first conducted with 1.4-1.8 g fish over a range of 7.5-25.0°C. At near 25°C, multiple fish exhibited signals of stress, and consequently consumption experiments were not conducted with a maximum temperature of 23ºC.

During maximum consumption experiments, Threespine Sticklebacks were fed with previously-frozen marine *Mysis* (energy density = 2100 J/g wet weight (Chipps 2002)). Mysids averaged 7 mm long and were chopped into 1 mm pieces to remain below the gape limit of the smaller individuals and to allow more precise measurement of consumption rates. Fish were fed *ad libitum* throughout the 3-day trial, in quantities of approximately 70% of the body weight of each fish. The trial period was broken into three 24 h segments, with fresh food offered at the

beginning of each segment. Specific consumption per day ($g \cdot g^{-1} \cdot d^{-1}$) for each fish was measured by subtracting final from initial blotted wet weight of offered food for each 24 h segment, divided by the initial weight of the fish at the beginning of the trial. In trials soaking mysid prey for 24 hours without fish present, no significant weight change was observed before and after soaking (Student's t-test, $P = 0.67$). Mean daily specific consumption was calculated for all fish in a temperature category, and C_{max} was plotted as a function of temperature.

The mass-specific dependence of C_{max} ($g \cdot g^{-1} \cdot d^{-1}$) is typically represented as a power function, based on the regression of $\text{Log}_e(C_{max})$ versus Log_e (W, g), using the naming convention for parameters in the Wisconsin Bioenergetics model (Hanson et al. 1997):

$$\boldsymbol{C_{max} = CA \cdot W^{CB}}.$$

Initial attempts to estimate mass-dependent C_{max} at 23°C failed to determine a significant regression relationship, due to the small range of fish weights available for trials at 23°C. Therefore, sample size was increased by including temperature-adjusted C_{max} values from the 18°C trials. Based on the temperature-dependence trials described above, C_{max} values were 83.9 % lower at 18°C than at 23°C, so measured consumption values at 18°C were divided by 0.839 to generate the temperature-adjusted values. *CA* and *CB* parameter values were chosen using the slope and intercept from the regression of $\text{Log}_e(C_{max})$ versus Log_e (W). Specific consumption rate was calculated as

$$\boldsymbol{C = C_{max} \cdot p(C_{max}) \cdot f(T)},$$

where p is the proportion of C_{max} (between 0 and 1) where the fish is feeding and $f(T)$ is the function for temperature dependence. In this study, we parameterized for equation 2 in Hanson et al. (1997), the temperature dependence curve for warm-water species (Kitchell et al. 1977).

This equation takes the form of

$$f(T) = V^{x} \cdot e^{(X \cdot (1-V))},$$

where

$$V = (CTM - T) / (CTM - CTO),$$

$$X = Z^2 + 1 \cdot (1 + (1 + 40 / Y)^{0.5})^2) / 400,$$

$$Z = LN(CQ) \cdot (CTM - CTO),$$

$$Y = LN(CQ) \cdot (CTM - CTO + 2).$$

Using non-linear fitting and maximum likelihood estimation (nls package in statistical program R), we fit different forms of the consumption equation (Equation 2 and Equation 3 in Hanson et al. (1997)) to our data. Selecting that with the smallest residual standard error, we chose Equation 2 over Equation 3 (Thornton and Lessem 1978) as the best fit for these consumption data.

Respiration experiments

Respiration rates were measured in 50 min trials using an oxygen electrode (Eutech CyberScan 110 dissolved oxygen meter). The electrode was installed in a closed respirometer vessel containing 250 mL of magnetically-stirred water. All respiration rates were corrected for oxygen consumption of the probe, determined by measuring the average dissolved oxygen decline over ten 50 min trials. Before the trials, fish were placed in the respiration chamber for 30 min before the respiration trials were initiated. Each trial utilized a unique fish, separate from those used in consumption experiments, avoiding replication across temperatures or weights, and a total of 32 fish were used, with weights between 0.44g and 4.71g. All trials were completed at

or above 6.0 mg/L dissolved oxygen, across an approximately continuous temperature range from 8ºC to 28ºC.

The mass- and temperature-dependence of standard respiration (R, g $O_2 \cdot g^{-1} \cdot d^{-1}$) is typically represented as a power function of mass and an exponential function of temperature:

$$\boldsymbol{R = RA \cdot W^{RB} \cdot e^{(RQ \cdot T)}}.$$

Multiple regression was performed on a combination of body masses (0.5-4.5 g) and temperatures (8.0-28.1ºC) to examine the relationship of Log_e (R) to Log_e (W) and temperature. Slope and intercept values from this regression were used to parameterize the respiration equation.

Waste and digestion losses

Because waste losses have typically been reported as reasonably constant fractions of consumption and are relatively insensitive elements in bioenergetics formulations (Bartell et al. 1986; Ney 1993), this study adopted generic values of waste $W = F + U$. For egestion (fecal) losses (F), we assumed $F = FA \cdot C$, with $FA = 0.104$. For excretion losses, we assumed $U = UA \cdot (C\text{-}FA)$, with $UA = 0.068$. For specific dynamic action (SDA) the cost of processing food, we assumed $S = SDA \cdot (C\text{-}F)$, and used the widely-accepted value of $SDA = 0.172$. All equations and coefficients are from Hanson et al. (1997).

Energy density

Bomb calorimetry was performed on Threespine Sticklebacks sampled by seasonal midwater trawling in Lake Washington. Juveniles were collected in the limnetic zone in October (N = 10; 0.31-1.02 g) and adults were collected in March (N = 5; 2.8-3.4 g), during 2005-2006. Samples were frozen immediately upon capture and later thawed, weighed, measured, dried

(60ºC for 36 h until constant dry weight was achieved), and re-weighed. The dry specimens were ground to a fine powder with a mortar and pestle, homogenized, and pressed into 0.1g (range 0.5-0.15 g) pellets which were combusted in a Parr 1425 Semi-micro bomb calorimeter to measure the energy density (J/g dry weight) and were converted to wet weight energy density units (J/g wet weight) that were appropriate for use in the bioenergetics model. The energy density (J/g wet weight) was regressed against body mass (g wet mass) separately for juveniles during the growing season and for adults in late March.

Sensitivity analysis

All reported model parameters (Table 1) were tested by evaluating the sensitivity of the model estimates for growth of a 3.0 g fish for one year at 22ºC and with energy density of 3924 J/g. Nominal parameter values were increased or decreased by 10%, and temperature values for parameters were changed by ±1ºC (Kitchell et al. 1977). Individual parameters were tested by using 90% or 110% of the original value in the model and by calculating normalized sensitivities of growth as a response. Sensitivity values were reported in units where a value of 1.00 indicates that a 10% increase in the parameter value resulted in a 10% increase in the growth estimate, a value of 2.00 indicates that a 10% increase in the parameter value resulted in a 20% increase in growth, and so on.

Model corroboration

Because of logistic constraints, we were unable to complete a set of independent growth and consumption experiments to corroborate the bioenergetics model. Therefore, we compared predictions from the bioenergetics model to independent, paired measures of consumption and growth measured during laboratory experiments using fish from a separate wild population of

low-plated threespine sticklebacks (Ali and Wootton 2001). In this study, a control group of threespine stickleback ($N = 9$) were fed enchytraeids *ad libitum* daily for 56 days at 14°C. On average, these fish grew from 0.257 (95% CI = 0.198-0.318 g) to 0.964 g (95% CI = 0.766-1.162 g) over the 56 day trial period. We used the bioenergetics model to estimate the average total consumption needed to achieve this observed growth over the 56 day period, and compared predictions from the bioenergetics model to the average total consumption and growth (expressed as % body weight per day) measured directly by Ali and Wooten (2001). We selected 2,745 J/g as the energy density of enchytraeids (McCarthy 2004), but varied this value by ±20% and repeated the simulations since Ali and Wooten (2001) did not report the exact energy density of their prey.

RESULTS

Consumption

The *ad libitum* daily consumption rate increased rapidly with increasing temperature and was maximized at 23ºC at 0.42 $g \cdot g^{-1} \cdot d^{-1}$ for 1.4-2.0 g fish (Figure 1a). However, because fish started exhibiting thermal stress at near 25ºC, it was assumed that the proportion of C_{max} observed at 23ºC would decline to 0.10 of the maximum at 25ºC. After converting these data into proportions of the maximum daily *ad libitum* consumption at 23ºC, these results were incorporated into Equation 2 in Hanson et al. (1997), the temperature dependence equation for warm-water fishes (Kitchell et al. 1977), using the naming convention for the parameter values from the Wisconsin bioenergetics model (Table 1).

Parameterization of the model specified optimal temperature at the peak of *ad libitum* feeding rate as $CTO = 23.0\,^{\circ}C$. Maximum temperature, the upper limit at which consumption occurs, was set as $CTM = 25.0\,^{\circ}C$. A Q_{10} approximation was set as $CQ = 3.0$, to describe the rate of increase of the function at low water temperatures.

Mass-dependent C_{max} was estimated using the expanded data set of 23°C trials and the temperature-adjusted 18°C trials resulted in an improved relationship ($r^2 = 0.32$, N = 12, $P = 0.03$) with significant intercept ($P < 0.001$) and slope ($P = 0.03$) (Figure 1b):

$$\boldsymbol{C_{max}\,(\,g \cdot g^{-1} \cdot d^{-1}) = 0.4590 \cdot W^{-0.2675}}.$$

Error around *CA* and *CB* parameter values was produced while fitting Equation 2 (Hanson et al. (1997)) to our data using maximum likelihood estimation. For upper and lower 95% confidence intervals, this yielded values of $CA = 0.4590 \pm 0.0675$ and $CB = -0.2675 \pm 0.0238$.

Respiration

The mass- and temperature-dependent regression of respiration costs resulted in significant relationship ($r^2 = 0.36$, N = 25, $P = 0.0027$):

$$\boldsymbol{R\ (g\ O_2 \cdot g^{-1} \cdot d^{-1}) = 0.000994 \cdot W^{-0.5397} \cdot e^{(0.08392 \cdot T)}}\ .$$

This relationship resulted in significant slopes for the power function of body mass $RB = -0.53974$ ($P = 0.044$) and exponential function for temperature $RQ = 0.08392$ ($P = 0.016$), but no significant intercept ($RA = 0.000994$; $P = 0.061$). Predicted by the equation, metabolic (*R*) costs are most important for small-bodied fish at high temperatures (Figure 2). As this equation was parameterized via multiple regression, error around *RA*, *RB,* and *RQ* parameter values was determined with a likelihood function after fitting the curve with specified parameter values to the observed consumption data from the experiments. For 95% confidence intervals, this yielded values of $RA = 0.000994 \pm 0.000001$, $RB = -0.53974 \pm 0.0034$, and $RQ = -0.2675 \pm 0.0131$.

Energy density

Energy density was related to body mass during the growing season, but not after prolonged periods of poor feeding conditions (Figure 3). During the growing season, energy density (*ED*) was significantly correlated with body mass for juvenile Threespine Sticklebacks (0.3-1.0 g; $r^2 = 0.475$; N = 10; $P < 0.02$):

$$\boldsymbol{ED}\textbf{(J/g wet mass)} = \mathbf{4528 + 3756 \cdot} \boldsymbol{W}.$$

Thus, the intercept of mass-dependent energy density for smaller Threespine Sticklebacks was α_1 = 4,528 J/g, the slope $\beta_1 = 3{,}756\ g^{-1}$ for fish up to 1.0 g (Table 1). In the absence of data for larger Threespine Sticklebacks during the growing season, a conservative upper bound of a constant 8,284 J/g was chosen for fish above a cutoff weight of 1.0 g (i.e., α_2 = 9000 J/g and $\beta_2 = 0\ g^{-1}$; Table 1). No relationship existed between body mass and energy density for adult Threespine Sticklebacks at the end of winter ($r^2 = 0.01$; $N = 5$; $P > 0.85$); therefore, a simple constant mean (2 SE) energy density of *ED* = 6031 (502) J/g was considered a more appropriate measure of energy density following lower winter feeding conditions.

Sensitivity analysis

The sensitivity analysis indicated that growth estimates were quite robust to changes in model parameters (Table 2). Individual parameter perturbations indicated that the parameters for the allometric mass-dependent function for C_{max} have the greatest effect on growth estimates. Growth was most sensitive to perturbations of the intercept *CA* (±1.04) followed by the slope *CB* (±0.31). The parameters of the Threespine Stickleback model are somewhat less sensitive than are those for an equivalent Wisconsin bioenergetics model for Sockeye Salmon. However, *CA* and *CB* are two of the most sensitive parameters in both models, and for both Sockeye Salmon

and Threespine Stickleback, the consumption parameters are more sensitive than the respiration parameters (Beauchamp et al. 1989).

Model corroboration

The bioenergetics model performed well when used to predict independent, paired measures of consumption and growth (expressed as % body weight per day) observed from the separate wild population of threespine stickleback (Ali and Wootton 2001). Predicted values for consumption and growth only deviated from observed mean values by 2.0% when using the nominal prey energy density of 2,745 J/g (Table 3). Total predicted consumption was sensitive to a 20% increase (3,294 J/g) and 20% decrease (2,196 J/g) in prey energy density. However, predicted consumption using the higher and lower prey energy density remained within or near the bounds outlined by the 95% confidence interval computed for the mean observed consumption measured by Ali and Wooten (2001) (Table 3).

DISCUSSION

This study is the first to develop a bioenergetics model for Threespine Stickleback within a standardized, widely applied framework. We believe that the Wisconsin bioenergetics model will be useful when applied to physiological and ecological questions for this widely-distributed species, and feel comfortable with model performance as the consumption, respiration, and growth estimates generated by the model are consistent with previously conducted experimental work.

Using measured consumption and respiration parameters, the bioenergetics model suggested 22°C as the optimal temperature for growth. This agreed closely with a growth model

fit to other experimentally produced data (Lefebure et al. 2011), which found an optimal temperature of 21.7°C. The two models demonstrated less consistent results on the range of temperatures over which Threespine Stickleback experiences positive growth. We found 25 ºC as the near upper limit (e.g., 90% reduction in maximum feeding capacity) for positive growth in Threespine Stickleback, while the growth model from Lefebure et al. (2011) found an upper limit of 30 ºC. This could be attributed to the highly stable thermal regime for lab-reared fish used in this study, physiological differences between populations, or differences between freshwater and marine types.

Several studies have measured fish respiration and consumption for Threespine Stickleback under a range of conditions (Krokhin 1970; Meakins 1975; Allen and Wootton 1984). Our model integrates across the range of conditions evaluated in previous experiments, and is designed to handle variance across a broad range of conditions by specifying temperature and body size in the model inputs. The consumption measurements used in the development of this model (3.07-7.45% body weight consumed per day) correspond closely with the consumption rates of a Russian population (2.59-7.04% body weight consumed per day) (Krokhin 1970), suggesting that the consumption parameters developed for this model are broadly applicable. Across a range of fish sizes smaller than those used in our experiments, routine respiration values (0.0041-0.0068 g $O_2 \cdot g^{-1} \cdot d^{-1}$) at 15°C measured by Meakins (1975) during both February (winter season) and August (growing season) fell near to the values predicted for respiration in our model (0.0043-0.0066 g $O_2 \cdot g^{-1} \cdot d^{-1}$) (Figure 2). In addition, the *b* parameter reported by Meakins (1975), analogous to the *RB* parameter in the Wisconsin model, ranged between -0.3028 (maximum rate) and -0.8264 (minimum rate) in February and -0.4252 and -0.6478 in August. Our selected parameter value for *RB* fell at -0.5397. Thus, our respiration

parameters should successfully represent fish metabolic costs during both seasons of high productivity and warm temperatures and during cooler periods of the year.

Because of constraints that prohibited rearing fish for a sufficient duration to perform an experimental corroboration of this model, we turned to the literature to test the model performance against independent, paired observations of growth and consumption in Threespine Stickleback (Ali and Wootton 2001). Literature data were available for only young of year fish (mean initial mass of 0.257 g, 95% CI = 0.198-0.318 g), which represents a smaller range of sizes than those used in our experiments (initial mass ranged from 0.42-4.71 g). The corroboration was also limited in that only summary data were available, instead of individual measurements on starting and finishing weights and total prey consumption. However, our model outputs matched closely with the observed consumption and growth values in Ali and Wootton (2001) when using a reasonable value for the energy density of their experimental prey. Consumption estimates from our model under-predicted observed results by 2.0%, and growth estimates were over-predicted by 2.0%. After considering uncertainty in prey energy density, our model estimates still fell near or well within the 95% confidence interval reported for mean growth and mean total consumption by Ali and Wooten (2001).

While there is evidence that our bioenergetics model represents generalized physiological parameters for the Threespine Stickleback, this species is highly adaptive and can assume different morphological and ecological characteristics after few generations (e.g. Rundle et al. 2000; Hendry et al. 2002; Kitano et al. 2008). As a physiological trait, respiration rate seems to remain consistent across habitats and salinities (Grøtan et al. 2012), but some capacity for rapid selection for thermal regime and cold-adaptation has been observed in fish transplanted from marine to freshwater habitats (Barrett et al. 2011). Other parameters, such as energy density, may

be sensitive to physiological differences from different plating morphologies or freshwater versus marine habitats. While our experimental measurements are consistent with those published on fish from temperate bodies of water across the globe, caution is advised in applying this model to fish from populations established at the thermal extremes of their range.

Threespine Sticklebacks will continue to be an important model organism. Ecologically, these fish are frequently abundant throughout their natural Holarctic distribution and often share habitat and prey resources with ecologically and economically valued species such as salmonids. Bioenergetics models have been successfully used in the past to compare the physiological capacity of different fishes and evaluate their performance under varied environmental conditions (Bevelhimer et al. 1985; Yibo and Jiankang 1990; Essington 2003). By creating a standardized and comprehensive model for Threespine Stickleback, this species can now be more explicitly incorporated into community- or ecosystem-level evaluations of physiological performance or trophic impact in food webs. Having the capability to compare thermal optima and quantify the consumption demand and growth performance of key species is particularly important when trying to understand how different aquatic communities and ecosystems will respond to shifts in environmental conditions and to climate change.

The bioenergetics model presented here incorporates multiple experimentally derived physiological parameters for the Threespine Stickleback, and provides estimates that corroborate other laboratory measurements. While many of the direct measurements of consumption and respiration used in model development require a controlled laboratory setting, this environment may not always reflect *in situ* performance. We acknowledge that confidence is built through both laboratory and field corroboration of bioenergetics models (Ney 1993; Brandt and Hartman 1993). Therefore, we encourage the application and scrutiny of our model across a range of

habitats and morphs for the Threespine Stickleback. Future comparisons between model predictions and direct observations from different populations and under different environmental conditions will help identify model components in need of refining, and help reduce parameter uncertainty.

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Table 1.1. Threespine Stickleback bioenergetics model parameters, descriptions, and parameter values. Where it could be calculated, error around parameter values is shown in parentheses as the upper and lower bounds of a 95% CI. Values for SDA, FA, and UA are from Hanson et al. 1997. All others are from this study.

Parameter	Description	Value
	Consumption	
CA	Intercept: allometric function of C_{max} v. mass	0.459 (±0.0675)
CB	Slope: allometric function of C_{max} v. mass	-0.2675 (±0.0238)
CQ	Q_{10} approximation	3.0
CTO	Optimal temperature for growth in lab	23
CTM	Temperature above which consumption ceases	25
	Respiration	
RA	Intercept: allometric function of MO_2 v. mass	0.00099 (±0.00001)
RB	Slope: allometric function of MO_2 v. mass	-0.5397 (±0.0034)
RQ	Slope: MO_2 v. temperature	0.0839 (±0.0131)
RTO	Coefficient: respiration versus swimming speed	0
RTM	Maximum temperature	0
RTL	Temperature where activity relationship changes	0
RK1	Swimming speed intercept	1
RK4	Mass-dependence for swimming speed	0
ACT	Activity multiplier in respiration measurement	1
SDA	Specific dynamic action	0.172
	Egestion and Excretion	
FA	Intercept: egestion as proportion of consumption	0.104
UA	Intercept: excretion as proportion of consumption	0.068
	Predator Energy Density	
Energy density	For use as default constant: value for 2-3 g fish in winter	6,030
α_1	Intercept: allometric mass function (1)	4,528
β_1	Slope: allometric mass function (1)	3,756
Cutoff	Mass cutoff for energy density equations	1
α_2	Intercept: allometric mass function (2)	8,284
β_2	Slope: allometric mass function (2)	0

Table 1.2. Sensitivity of bioenergetics model estimates of Threespine Stickleback growth to 10% perturbations of the original parameter values. A value of 1.00 indicates that a 10% increase in the parameter value resulted in a 10% increase in the growth estimate.

	Deviation in growth	
Parameter	90% original value	110% original value
CA	-1.0416	1.0416
CB	0.3017	-0.3107
CQ	0.0054	-0.0046
CTO	0.0754	-0.0671
CTM	-0.0101	0.1984
CTL	0.0180	0.1506
RA	0.0416	-0.0416
RB	-0.0240	0.0254
RQ	0.0844	-0.0702

Table 1.3. Observed (from Ali and Wooten 2001) **and predicted** (from bioenergetics model) **values for total consumption (g) and growth in % body weight (BW) per day.** Predicted values were generated using a prey energy density of 2,745 J/g. Upper and lower values for observed mean consumption and growth are 95% confidence intervals computed by Ali and Wooten (2001). Upper and lower values for predicted growth and consumption reflect a 20% increase (3,294 J/g) and decrease (2,196 J/g) in prey energy density, respectively.

	Observed	Predicted	Percent difference from observed mean
Mean total observed consumption (g)	3.631	3.558	2.02
Upper 95% CI or 20% increase in prey ED	4.368	4.447	22.47
Lower 95% CI or 20% decrease in prey ED	2.918	2.965	18.35
Observed growth (% BW/day)	2.342	2.390	2.04
Upper 95% CI or 20% increase in prey ED	2.600	2.390	2.04
Lower 95% C Ior 20% decrease in prey ED	2.081	2.390	2.04

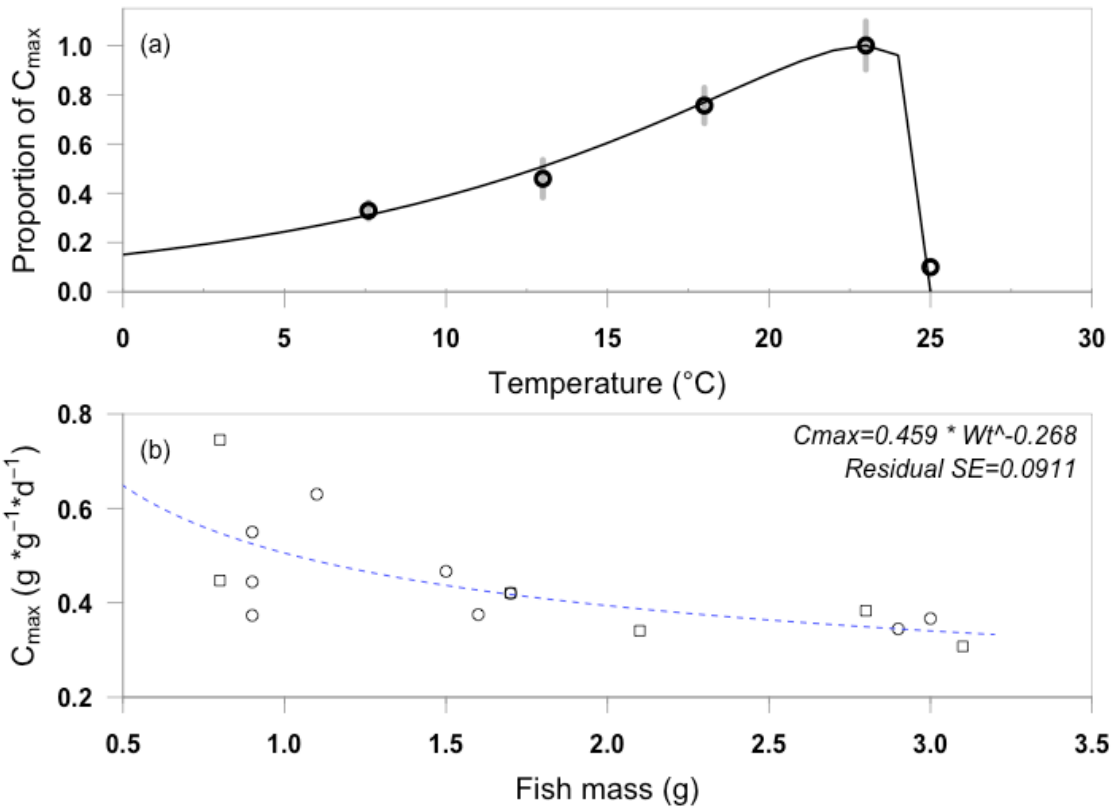

Figure 1.1. Effects of temperature-dependence (a) and mass-dependence (b) of maximum consumption for 1.4-2.0 g Threespine Sticklebacks. In the upper panel, C_{max} is displayed as unitless proportions (range 0.0-1.0) when referenced to the maximum daily consumption rate at 23ºC. Error bars represent 1 SE. In the lower panel, circles are consumption observations performed at 23ºC, and squares are temperature-adjusted C_{max} values from the 18ºC trials. Lines are model fits.

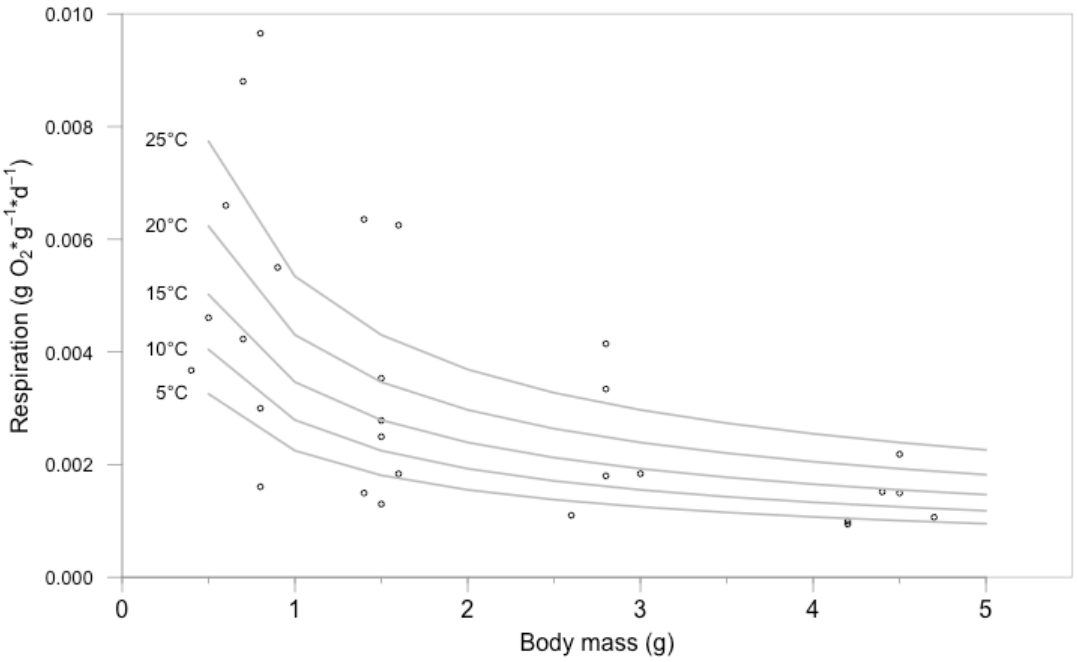

Figure 1.2. Routine respiration costs as functions of temperature and body mass. Open points are respiration data from Meakins (1975); circles are from February and squares are from August.

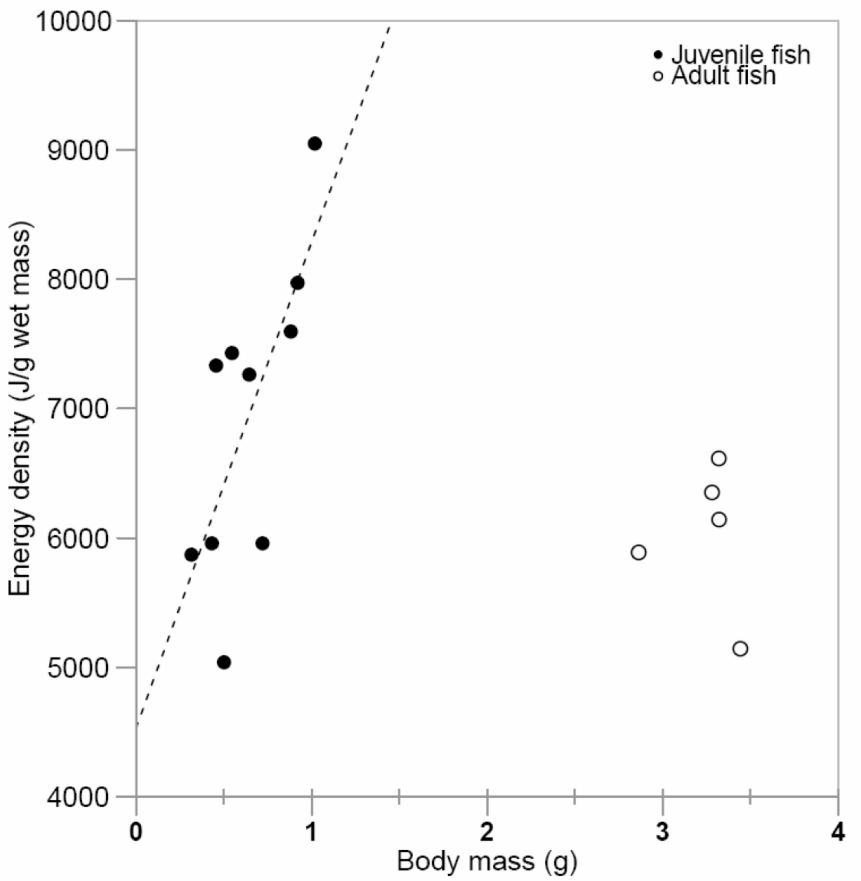

Figure 1.3. Mass-dependent energy density (ED) of Threespine Stickleback. Juveniles (closed circles) were sampled near the end of the growing season in October and larger adults (open circles) sampled at the end of winter in Lake Washington. The line indicates energy density v. body mass for juvenile fish ($r^2 = 0.475$; $N = 10$; $P < 0.02$).

Chapter 2. **Environmental and phenological variability: match-mismatch effects of lake conditions and entry timing on the survival and growth of juvenile sockeye salmon**

ABSTRACT

Survival of post-larval and juvenile organisms can depend on multiple seasonally-fluctuating features, including suitability of thermal conditions and food availability. The fitness of consumers depends on spatial and temporal overlap with prey production and on physical conditions conducive to growth, and a modification in phenology of prey or consumers might decouple trophic relationships or reduce consumer growth and survival. The potential for mismatches might be especially pronounced in organisms that migrate, such as juvenile sockeye salmon. These individuals move from natal streams to lakes where they feed before migrating to sea, and rely on suitably-timed resources across habitats. This project compared growth and survival from fry to seaward migrant stage for sockeye salmon with different lake entry dates. Mixed effects models were used to test the hypothesis that the most successful entry times correspond to favorable prey densities and lake thermal conditions, and that a mis-match in either fish entry time or seasonal lake dynamics can have negative effects on fish growth and survival. Across years, fish entering the lake later in the season encountered higher productivity and warmer water, and experienced higher average rates of growth and survival. However, lake conditions varied, and the optimal date for lake entry ranged between years by up to a month. The relative effects of zooplankton abundance and timing and lake water temperature on sockeye salmon performance indicated that zooplankton dynamics were predictors, likely because they

integrated both temperature and productivity. These results suggest that maintaining a wide window of lake entry times preserves the biological variability in this life history event that is necessary to succeed in an unpredictable environment.

INTRODUCTION

Animal phenology, the timing of life history events in relation to the environment (Menzel and Fabian 1999), can be closely related to success of a population or species (Schwartz 2003). Survival can depend on multiple seasonally-fluctuating characteristics of the environment, including thermal dynamics and availability of food resources. The success of a consumer depends on spatial and temporal overlap with prey production, and the predator-prey relationship is only maintained through synchronous life history events of each trophic level (Cushing 1990). Posed as the "match-mismatch hypothesis" by D. H. Cushing, this phenomenon has been demonstrated primarily in marine systems where fishes rely on secondary productivity of zooplankton and other small pelagic prey (Sinclair and Tremblay 1984, Cushing 1990, Mertz and Myers 1994, Beaugrand et al. 2003). However, freshwater systems also experience dramatic seasonal fluctuations in primary and secondary productivity, and insect emergence or zooplankton bloom timing are often closely linked to physical conditions such as temperature, which can vary widely across years (Hampton et al. 2006a, Harper and Peckarsky 2006).

A modification in life history timing of either prey or consumer might confer a trophic decoupling and loss of ecological function. This has been observed in primary consumers in marine, freshwater, and terrestrial systems (Edwards and Richardson 2004, Winder and Schindler 2004, Post and Forchhammer 2008), but the strength of mismatch effects is less clear for secondary consumers and across different systems. Most studies on the match-mismatch

concept in freshwater systems examine the relationship between primary producers and primary consumers (Winder and Schindler 2004, de Senerpont Domis et al. 2007), but less work has addressed upper trophic level organisms with higher mobility (e.g. fish).

Such mismatches between organisms and the receiving environment might be especially pronounced in migratory species because they often initiate migration without direct information on conditions in the next habitat. In particular, post-larval and juvenile fishes, without the benefit of parental care, must forage on small organisms such as insects and zooplankton that have discrete seasonal fluctuations in availability and inter-annual variation in abundance. This variation can strongly affect growth, survival, and lifetime fitness of organisms commencing feeding at different times of the season. For example, the timing when juvenile Pacific salmon enter marine waters can have a strong effect on their survival (Cooney et al. 2001, Cross et al. 2008, Scheuerell et al. 2009, Satterthwaite et al. 2014).

Sockeye salmon (*Oncorhynchus nerka*) is an example of a species that undergoes habitat transitions early in the freshwater phase of life. Shortly after emergence, juvenile sockeye salmon migrate from stream habitats where they were spawned to lake systems where they rear for up to two years before migrating to the ocean as smolts (Quinn 2005). The timing of emergence depends on the date on which they were spawned (typically 5-6 months earlier), and the temperature regime that they experienced during development (Brannon 1987, Beacham and Murray 1990). Juvenile sockeye salmon feed in the lake for about one year, or two in environments less conducive to growth (Burgner 1987), consuming predominantly zooplankton (Quinn 2005). Their growth potential throughout this time is closely related to prey accessibility and abundance and thermal regime (Eggers 1978, Edmundson and Mazumder 2001). Sockeye salmon target *Daphnia* zooplankton as preferred prey, and will switch nearly exclusively to

Daphnia consumption even at low densities of this prey, supporting the close relationship between *Daphnia* abundance and sockeye salmon growth (Mazumder and Edmundson 2002, Beauchamp et al. 2004, Scheuerell et al. 2005). The period of time between entry into the lake by sockeye salmon and the seasonal increase in *Daphnia* abundance varies inter-annually, and might be an important factor affecting survival and growth of sockeye salmon rearing in a lake. Because growth is strongly related to seasonal changes in temperature and food resources, the dominant paradigm in studies of sockeye salmon has been the understanding that adult breeding date is largely adjusted to the local thermal regime such that fry emerge at a favorable time the following spring (Brannon 1987). However, in some populations breeding timing is compressed whereas in others it is protracted, suggesting that yearly variation in environmental conditions in some systems may prevent stabilizing selection on a narrow range of dates.

In this study we take advantage of both natural and artificial reproduction in sockeye salmon in Lake Washington (Washington State), to test hypotheses that the most successful entry times correspond to favorable zooplankton densities and lake temperature, and that a timing change in either fish entry time or seasonal lake dynamics can have negative effects on fish growth and survival. In Lake Washington, estimated survival rates for sockeye salmon from fry to smolt life stage vary widely from year to year (Beauchamp et al. 2004, Overman and Beauchamp 2007). Depending upon environmental conditions in a given year, fish of certain date of entry into a system times might experience greater feeding opportunity than later or earlier fish, potentially leading to higher rates of survival or growth. Fish growth and survival are closely tied to feeding opportunity (i.e., timing of the seasonal blooms of *Daphnia* and other zooplankton), but also subject to additional factors, such as metabolic costs of water temperature. Limitations imposed by these processes may persist, and where feeding opportunity is limited

because of predator-prey mismatches or density-dependent processes, growth and survival differences in fish with different lake entry dates might be amplified throughout the growing season as more successful fish continue to outcompete other individuals.

This project compared growth and relative survival from fry to smolt stage for hatchery and wild-origin sockeye salmon with different lake entry dates. Using physical and biological data collected in Lake Washington, including zooplankton abundance and timing and water temperature data, we identified lake conditions most influential to the success of juvenile sockeye salmon in the lake and demonstrated the interaction between lake entry timing and annual variations in environmental conditions. Variability in environmental conditions from year to year was found to determine relative size-at-smolting and survival of different entry times.

METHODS

Study system

Lake Washington, Washington, USA is surrounded by an primarily urban landscape dominated by the greater metropolitan area of Seattle, WA (Edmondson 1994), and drains into Puget Sound through a hydrologically-modified canal. The lake is large, with surface area of 87.6 km^2 and 33 m average depth, and mesotrophic after recovering from severe anthropogenic eutrophication in the 1960s (Edmondson 1994). The Cedar River (entering from the south) and the Sammamish River (entering from the north) account for nearly 90% of the annual hydraulic inputs to the lake (Arhonditsis et al. 2004) but the great majority (ca. 90% in most years) of sockeye salmon enter from the Cedar River, at the south end of the lake. Located in the

temperate Pacific Northwest at 47°N, Lake Washington is a monomictic lake that does not freeze and experiences thermal stratification between April and November (Winder and Schindler 2004), with average epilimnetic water temperatures exceeding 20°C in August.

Lake Washington's fish community includes over 30 native and non-native fishes (Eggers et al. 1978). The most abundant pelagic piscivores are cutthroat trout (*Oncorhynchus clarki)* and northern pikeminnow (*Ptychocheilus oregonensis)* (McIntyre et al. 2006). Pelagic planktivores include threespine stickleback (*Gasterosteus aculeatus*), longfin smelt (*Spirinchus thaleichthys),* which make up nearly 85% of the planktivore biomass (Chigbu 2000), and juvenile sockeye salmon (*Oncorhynchus nerka)* which reside in the lake for approximately one year before migrating to sea (Eggers 1980). The sockeye salmon population includes both wild and hatchery-origin fish (Fresh 1994); production is concentrated in two tributaries of Lake Washington: the Cedar River, which is supplemented by hatchery-origin fry, and Bear Creek, which is comprised of wild-origin fish (Beauchamp et al. 2004).

Timing of fry migration is an important difference between hatchery and natural origin fish (Seiler et al. 2005), as natural-origin eggs develop and hatch according to river water temperature, whereas embryos in the hatchery were reared on a stable, warmer ground-water source. In addition, hatchery adults were typically collected early in the sockeye run. The otoliths of all hatchery origin fry in the Cedar River were marked by exposure to brief fluctuations in temperature (Volk et al. 1994). In most years, hatchery fry were released at three locations in the river in three discrete time windows from early February through April, each of which could be distinguished by microscopic examination of the otoliths.

The pelagic zone invertebrate community is largely comprised of *Daphnia* spp., cyclopoid and calanoid copepods, and the freshwater shrimp *Neomysis mercedis* (Edmondson

and Litt 1982) but abundance of zooplankton taxa varies dramatically by season. *Daphnia,* the preferred prey of sockeye salmon, is moderately to highly abundant between May and November, and this genus is often not observed in winter or early spring (Scheuerell et al. 2005, Hampton et al. 2006b). Intra-annual fluctuations in abundance are observed in all of the dominant taxa, and timing of numerical increases for major taxa is tied to water temperatures and spatially-explicit in Lake Washington (Romare et al. 2005).

Data collection and processing

Hatchery origin and natural run sockeye salmon fry were counted using a weir trap at the mouths of Bear Creek (natural run fry only) and the Cedar River (hatchery origin and natural run fry, enumerated separately); traps were operated between January and the end of June from years 2003 to 2013 (Seiler et al. 2005, Kiyohara and Zimmerman 2012). These data were used to determine abundance of natural run and hatchery origin fish migrating into the lake, and describe the duration and median date of lake entry for each group. To assess the mean size and relative abundance a year later as the sockeye salmon migrated to sea, approximately 1000 smolts were captured each year via purse seine in the Ballard Locks ship canal over a four-week period in May of years 2004-2014. These samples are designed to take place throughout the distribution of the migration from the lake system to the ocean, reducing capture probability bias for any group. Fork length was recorded for each individual captured, and otoliths of each fish were dissected and read under microscopy to determine origin of sockeye salmon smolts, and release group for hatchery origin fish (Kiyohara 2012).

To assess environmental conditions in the lake, temperature and zooplankton data were collected on Lake Washington every two weeks between February and May. Sampling procedure and sample processing are described in Edmonson and Litt (1982). Epilimnetic temperature

recorded at the north-to-south midpoint of the lake was used as a measure for spring lake thermal conditions. The density of zooplankton was described using the mean density for all *Daphnia* species and all copepods for each month of February, March, April and May for years 2003-2014. Analyses focused on the February-May time period as the range that captures the majority of the fry entry and the seasonal increase in *Daphnia* abundance.

Statistical analyses

Only age-1 smolts (making up over 90% of the smolts in this system) were included in this analysis. Age was determined from the brood year hatchery code on the otolith or by using otolith annuli for natural run fish. A two-way ANOVA was performed on means of adjusted length at capture for smolts, using year and group as variables.

The number of sockeye salmon smolts captured from early-, middle- and late-entering hatchery origin and natural origin groups was divided by the number of fry of each group entering the lake system in the previous year, to represent relative survival of each group. Absolute survival could not be effectively determined in this system from fry to smolt stage because no quantitative estimate is generated for the total number of smolts as they migrate from the lake. To assess the effect of release group on survival in the lake, we calculated a log-odds ratio to compare survival of fish with different lake entry times (e.g. Fraser et al. 2011). This ratio is calculated by:

$$\text{effect size}_{LOR} = log_e\left[\frac{P_x}{1-P_x}\right] - log_e\left[\frac{P_y}{1-P_y}\right]$$

where *Px* is the number of captured smolts of group *x* divided by the number of fry entering the lake as group *x* and *Py* is the number of captured smolts of group *y* divided by the number of fry entering the lake as group *y*. The effect size was calculated for pairwise comparisions of early-to-middle, early-to-late, and middle-to-late releases, and for early-to-natural run, middle-to-natural run, and late-to-natural run smolts. Positive effects indicated that the the later group in the comparison survived at a higher rate than fish entering earlier (e.g., early vs late groups), and negative effects suggested that earlier entering fish survived at higher rate. To test whether magnitude and sign of effects were likely to occur by chance, we used a Pearson's chi-square test to compare an expected distribution of 50% positive and 50% negative effects to the observed number of negative outcomes.

To explain patterns in survival and in size at smolting, we used linear mixed-effects models on both the size and survival data sets with physical (temperature) and biological (zooplankton) predictors reflecting lake conditions from February to May. For both temperature and zooplankton density variables, each predictor was input into models for both the year that sockeye salmon entered the lake as fry ("fry year") and for the year that the fish left the lake as smolts ("smolt year"=fry year+1). We also included the median fry entry date for each group, and the duration of time over which each natural run and hatchery release occurred, tested as both interaction and additive terms. Our data were well suited to using mixed-effects models, as each year included many individual measurements for size and four (early, middle, and late hatchery release and natural run) survival estimates. We accounted for any year-to-year variation not captured by variables for lake conditions (temperature and zooplankton density) by testing year as a random instead of fixed effect.

To fit each model, we prioritized assigning variability in fixed effects and methodically determined inclusion of fixed and random effects (Zuur et al. 2009). In fitting the models, we used a stepwise approach for each dataset, where 1. linear models were fit with maximum likelihood ("ML") using different combinations of lake covariate and year, median entry day, and duration of fry lake entry, 2. the top models were selected via the Akaike Information Criteria, or AIC, for $\Delta AIC<5$ (Burnham and Anderson 2002), and 3. the covariates from these top models were incorporated into a single model, fit with restricted maximum likelihood ("REML") to determine significance and magnitude and direction of each predictor. Because of the large number of possible predictors to be used in these models in step 1, we first restricted the list of covariates using all-subsets regression and selected the predictor variable from the top three models with five covariates. Step 3 was performed iteratively, removing any predictor terms that were not significant. The final model, with only significant predictors, was reported with estimates, standard errors, and p-values.

To determine whether year should be included in the final model for each data set as a random effect, we performed model selection on models with year as fixed effect and as an intercept-varying random effect, using AIC to determine the most parsimonious fit to the data. These comparisons were conducted fitting models with ML. If the model including a random effect was chosen, the model was re-fit with REML to report the magnitude and direction of the coefficients.

Models for the size data set took the form of:

$$L_{iyd} = \beta_o + \beta_1 \mathrm{covar}_y + \beta_2 \mathrm{mig}_{yg} + \beta_1 \mathrm{covar}_y \, \mathrm{X} \, \beta_2 \mathrm{mig}_{yg} + \mathrm{b}_y + \varepsilon_i$$

where L is the length of individual *i* in year *y* with release date *d*. βs are coefficients for fixed effects, and covar was a lake condition predictor variable in year *y*. These lake predictor

variables were: day of the year when *Daphnia* reached 0.4 individuals/L, the density at which sockeye salmon pre-smolts selectively feed on *Daphnia* (Scheuerell et al. 2005); the difference between this *Daphnia* density date and the entry date for each group of fish; and the mean *Daphnia* density, mean copepod density, and mean water temperature for each of the months of February, March, April, and May. The mig_{yg} term included a descriptor of the migration for each group *g* in year *y*, either median date of fish entry or duration of the run. Residual errors in ε_i were assumed to be normally distributed, and the random effect variable of year was included in the b_y term. As these fish reside in the lake for one year only, no autocorrelation was included in the year term.

Models for the survival data set took the form of:

$$\ln (\mathrm{S})_{yg} = \beta_o + \beta_1 \mathrm{covar}_y + \beta_2 \mathrm{mig}_{yg} + \beta_1 \mathrm{covar}_y \, \mathrm{X} \, \beta_2 \mathrm{mig}_{yg} + \mathrm{b}_y + \varepsilon_g$$

where S is the survival metric (number of smolts captured from group *x* divided by number of fry entering the lake as group *x*) for each group *g* in year *y*. Other model components are as described above.

Each selected model reported here was examined to ensure that residuals were normally distributed and free of trends. All models were run using the R statistical program (R Core Team 2014) using functions from the package nlme (Pinheiro et al. 2014) and leaps . Prior to analysis, normality was confirmed for each covariate. The year predictor variable was adjusted to sequential integers with that the first year was assigned a value of 1, and the survival response variable was transformed with a natural logarithm to achieve normality.

RESULTS

Smolt abundance and lake variability

The period of time when natural run fish moved from Bear Creek or the Cedar River the lake varied across years, with natural run fry entering the lake between the months of January and June and the median migration date falling between 2 March and 25 March from fry years 2003-2013. Hatchery origin fry were released according to a schedule of three discrete times, with dates and duration of these releases varying by year (Figure 1); in the years of this study the peak release time for hatchery origin sockeye salmon fry occurred during the middle or late release time windows. Of the 10,990 sockeye salmon smolts analyzed in this data set, 72% of the captured individuals were not otolith marked (i.e., the fish were of natural origin). Of the remaining fish, 8.8% were assigned to groups released early in the season, 8.9% to middle groups, and 10.2 to late groups.

Dates when *Daphnia* reached a density of 0.4 individuals per liter ranged from April 1 to June 25 (Figure 1). Mean monthly epilimnion temperatures ranged across years between 6.2°C and 8.2°C for February, 6.5°C and 8.9°C for March, 8.1°C and 12.3°C for April, and 12.1°C and 15.5°C for May. Mean *Daphnia* density varied by up to a factor of 30 from year to year for some months (Figure 1).

Patterns in size at smolting—Sockeye salmon growth in the lake varied among years, as evidenced by the variation in mean size of smolts captured after a year of growth (Figure 2). Within years, hatchery origin fish of different release groups and natural run fish differed in size as smolts, but this variability was overwhelmed by the strong year effect that affected hatchery and natural run fish in a similar direction. While the difference among groups was significant across years, likely due to high sample sizes ($p=0.0112$), no single release was consistently

largest or smallest across the period of observations. Similarly, there was no consistent size difference between hatchery and natural run smolts, but natural run smolts demonstrated a broader size range than hatchery smolts. The strength of the interannual effect and the lack of consistent advantage of a release time or fish origin suggested that there was strong environmental control on growth, and that lake conditions favored different entrance times in different years.

Pairwise survival comparison

Relative survival of fish released at different times was calculated using a log-odds ratio test on proportions of fish of each group at release and capture, with survival values weighted by mean number of days in the lake for each release group. Comparing the early to middle and middle to late hatchery origin fry releases revealed no pattern that would not occur by chance in the relative survival of early-middle ($p=0.763$) and middle-late pairings ($p=0.366$), but the in the early-late comparison, later entering fish consistently survived at a higher rate ($p=0.034$) (Figure 3). In comparisons of all hatchery release times to the wild origin fry, hatchery origin fry experienced lower survival than the natural origin fish ($p=0.003$) (Figure 4).

Linear modeling with lake covariates

In models predicting size at smolting, the most parsimonious model selected via AIC included only fixed effects: year, the date when *Daphnia* reaches a density of 0.4 individuals/L in the spring that the fish leave the lake as smolts ("bloom day"), the density of April *Daphnia* in the spring that the fish leave as smolts, and interactions between year and the two prey density terms (Table 1). The preferred model had a ΔAIC value of 4.8. The *Daphnia* bloom day parameter had a negative value, indicating that a later bloom date in the spring that fish leave the

lake predicted smaller smolt size. April *Daphnia* density had a positive effect, where higher prey density predicted larger smolt size. The year effect was also positive, and interactions indicated that the relationship between prey density predictors and smolt size varied by year. The year lag in the prey density parameters (*Daphnia* bloom day and April *Daphnia* density) indicates that the length of sockeye salmon leaving the lake as smolts depends more on prey availability in spring when they out-migrate than on the prey availability in the spring when they enter the lake.

For models predicting survival of hatchery and natural origin sockeye salmon from fry to smolt stage, the most parsimonious model (with **Δ**AIC value of 6.1) included the date when *Daphnia* reaches a density of 0.4 individuals/L in the year that the fish enter the lake as fry, the density of all copepods in the year when fish enter the lake as fry, and the day of year representing the median migration date for each group of hatchery or natural origin fish (Table 2). The date of *Daphnia* density had a negative effect, where an earlier date of *Daphnia* bloom predicted higher survival. The density of copepods was also, suggesting that a higher density of this possible prey for the month of March predicted lower survival. Day has a positive effect, indicating higher survival for fish entering the lake later in the season. Year was included in this model as an intercept-varying random effect. In contrast to the smolt size model, the survival depended on *Daphnia* availability in the spring when the fish entered the lake.

DISCUSSION

Our results indicated that growth and survival of natural run fish and hatchery origin fish of all release times are strongly subject to changes in lake conditions from year to year, and that fish of all entry dates responded overall in a similar magnitude and direction to these inter-annual differences in the lake. Growth and survival of lake entry groups for both hatchery and natural

run fish do differ within years, with some years favoring early entry dates and some favoring later entry dates. However, the period in late winter and spring over which sockeye salmon fry enter the lake is highly dynamic in this system, and as such no date of lake entry is favored consistently across years.

Day of lake entry was not included in models predicting smolt length, and the effect of entry date is weak and inconsistent across years. While the ANOVA rsults suggested significant difference in size of fish of different entry times, the majority of variation in size in the mixed effects model is attributed to a year effect. Growth in the Lake Washington system is among the highest of sockeye salmon rearing lakes (Burgner 1991), and the effect of lake entry time appears to be overcome by the potential rapid growth in this system. Smaller fish are able to compensate for being small at lake entry by growing fast, and in some years late-entering fish are able to match or exceed the size of fish that are up to 4 months older by the time they leave the lake approximately one year after they entered. April *Daphnia* density in the spring of outmigration has the second-largest coefficient to describe smolt length, predicting larger smolt sizes with higher *Daphnia* densities. A larger smolt size predicted by a *Daphnia* bloom occurring earlier in the season suggests the importance of prey dynamics in the spring when fish outmigrate to the size when they enter the ocean. In many systems across the range of sockeye salmon, size at smolting and overwinter survival is largely dictated by growing conditions in the ice-free summer season, and many smolts may initiate their migration before the spring ice breakup (Hartman et al. 1967, Hyatt and Stockner 1985, Burgner 1991). This temperate system with less clearly defined productive periods may weaken selection for fast summer growth and high body condition entering the winter, and appears to provide a unique opportunity for substantial growth in the months before ocean migration.

The clear pattern in year-to-year size variation for fish of all entry dates suggests the strong effect of a predictor not included in these models. While density-dependence is not believed to be a strong dynamic of the pelagic planktivore community in this system (Beauchamp et al. 2004), density can strongly determine juvenile sockeye salmon growth in other lakes (Mazumder and Edmundson 2002, Schindler et al. 2005). Other pelagic fishes share prey resources with juvenile sockeye salmon in Lake Washington, with potential for competition in high abundance years. Threespine stickleback and longfin smelt target copepod and cladoceran zooplankters for all or part of their life cycle, and longfin smelt in particular exhibit large fluctuations in abundance from year to year. Especially with potential changes to the thermal environment or prey composition, density dependence might explain some component of fish length at smolting.

Day of entry was included in the final model for in-lake survival, and indicated that later entry days experienced higher survival. Pairwise comparisons of survival suggested that no single hatchery release date consistently experiences higher survival across years, but comparing the earliest to latest release groups reveals, consistent with the mixed effects model, that later entering fish experience higher survival. This is likely explained in part by increased prey availability during late spring (Hampton et al. 2006b) and more suitable matching of entry time to favorable lake conditions. In contrast to the smolt size model, which included prey density predictors of the year that fish leave as smolts, fry to smolt survival was best predicted by the date of *Daphnia* bloom in the year that fry enter the lake, with higher survival in years with an earlier bloom time. Across years, natural run fish experience higher survival than hatchery origin fish of all entry dates, especially when natural run fish are compared to hatchery early releases. Some component of this pattern is likely explained by the later median migration date for natural

run fish (occurring primarily during the late hatchery release period), however natural run fish can incur lower mortality even in years when early release hatchery fish survive at a higher rate than late release groups.

The longer period over which natural run fish enter the system may also contribute to their higher overall survival rate. As no single lake entry date has apparent advantage over the others, maintaining a diversity of entrance timing into the lake system allows fish to succeed despite physical and biological variability in lake conditions. Conditions in different years may favor later or earlier lake entry times, and a "portfolio" of phenological diversity in the trait of stream-to-lake migration stabilizes the population as a whole in an environment that may experience wide variability in conditions across years.

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Table 2.1. Coefficient estimates, standard error (SE), and P-values (P) for the best fitting model for sockeye salmon length model. The response variable is smolt fork length. DaphDay is the date when *Daphnia* density reached 0.4 ind/L, the density at which sockeye salmon prey selectively on *Daphnia*; AprDaph is the density of *Daphnia* in the lake for the month of April.

Model component	Estimate	SE	P
Fixed effects			
intercept	92.77	15.53	<0.001
DaphDay (year of smolting)	-0.11	0.04	<0.001
AprDaph (year of smolting)	14.49	3.23	<0.001
year	15.81	1.90	<0.001
DaphDay:year	-0.09	0.01	<0.001
AprDaph:year	2.81	0.69	<0.003

Table 2.2. Coefficient estimates, standard error (SE), and P-values (P) for the best fitting model for sockeye salmon survival. The response variable is smolt fork length. DaphDay is the date when *Daphnia* density reached 0.4 ind/L, the density at which sockeye salmon prey selectively on *Daphnia*, Day the day of the year when fry enter the lake, and MarCop is the density of all copepod species in the lake for the month of March for the year fish enter as fry.

Model component	Estimate	SE	P
Fixed effects			
intercept	-12.344	0.694	<0.001
DaphDay (year of fry entry)	-0.011	0.004	0.003
Day	0.014	0.004	0.002
MarCop (year of fry entry)	-0.032	0.011	0.021
Random effect			
Year	0.438	0.293	

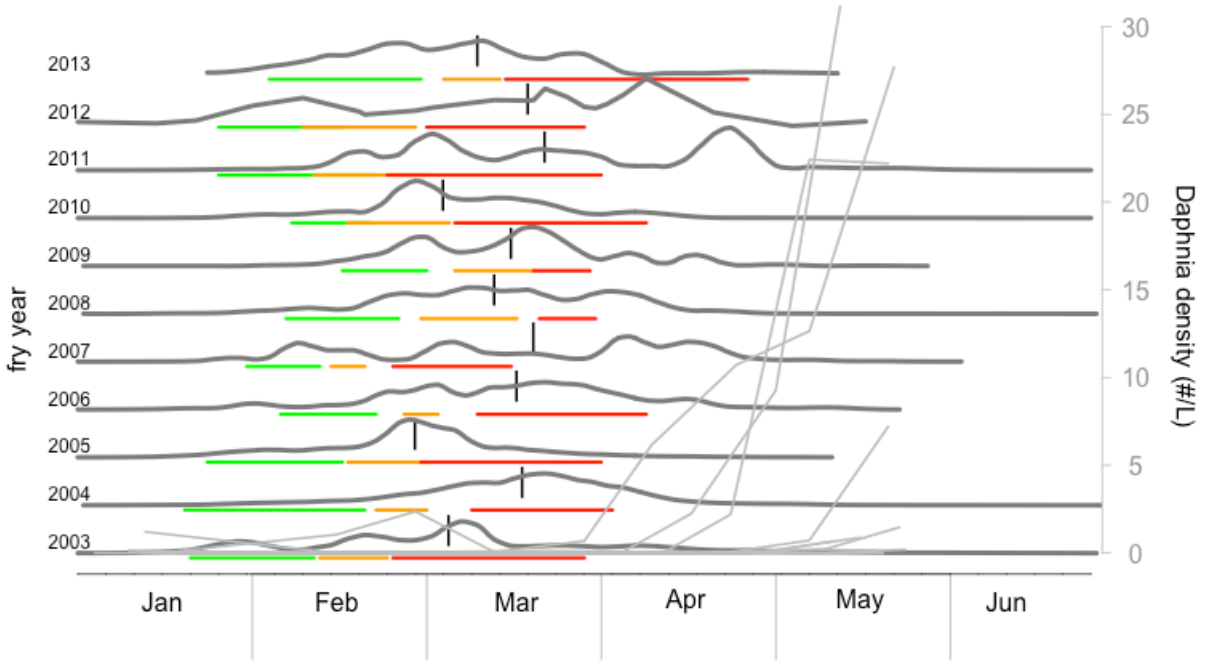

Figure 2.1. Natural origin and hatchery origin fry entry times into Lake Washington, with zooplankton density from January-June. The date ranges for hatchery fry release groups are depicted as colored lines (early=green, middle=orange, late=red), and natural origin fry outmigration is shown as grey lines with median date of natural origin fry outmigration as the dark vertical bar. Light gray lines depict Daphnia density from Feb 1 to May 30 for years 2003-2014.

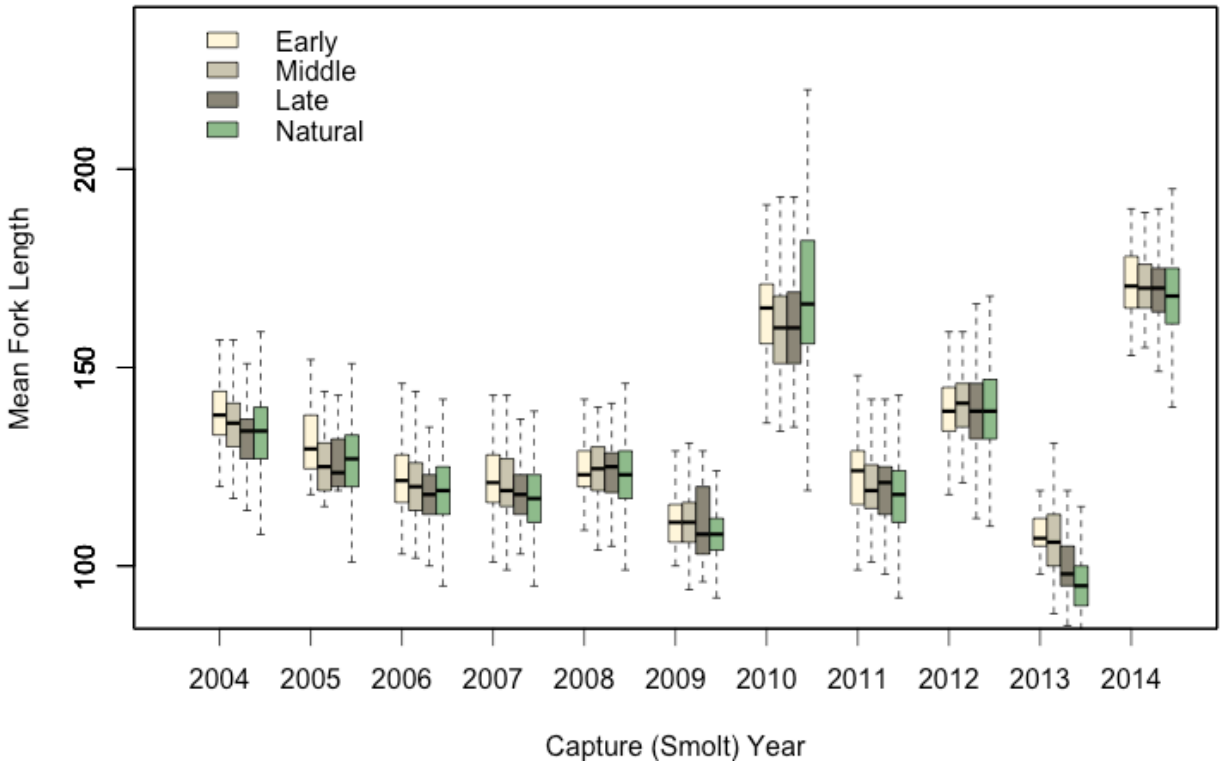

Figure 2.2. Median size of sockeye salmon smolts from natural run and hatchery origin groups. The horizontal black line indicates the location of the median, and the box bounds the first and third quartiles. Lengths were significantly different among years ($p<0.001$), release groups when nested within years ($p=0.011$) and there was an interaction between years and groups ($p<0.001$).

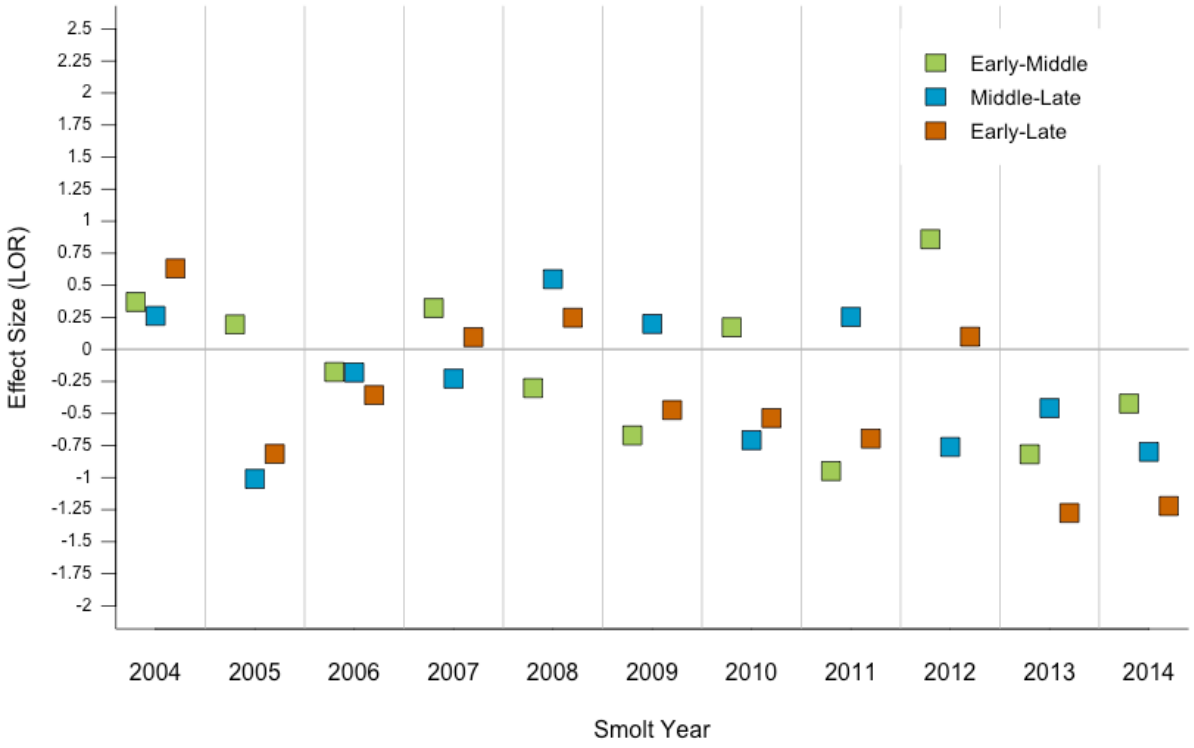

Figure 2.3. Pairwise log-odds ratio comparisons between early, middle, and late hatchery fry release groups. A negative effect size indicated that the earlier group in the comparison experienced lower survival than the group released later. Value of the effect size indicates the magnitude of the survival difference. Magnitude and sign of observed effect size did not occur by chance (p=0.031).

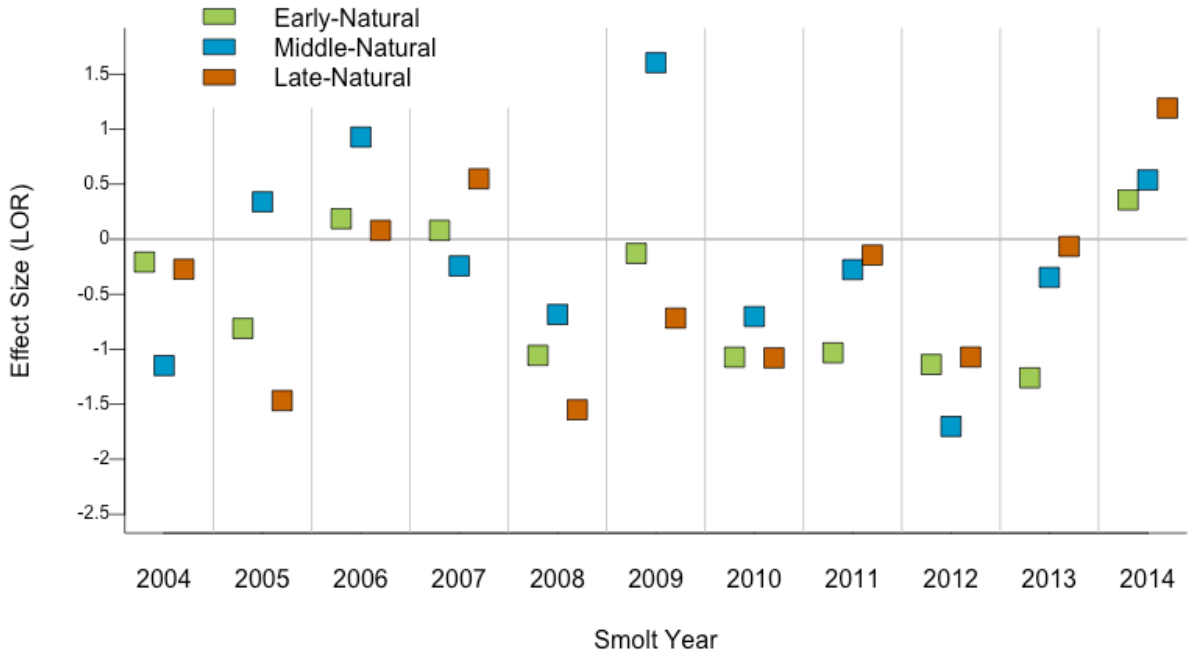

Figure 2.4. Pairwise log-odds ratio comparisons between natural run fish and early, middle, and late hatchery release groups. A negative effect size indicated that the designated hatchery release group experienced lower survival than natural run fry category. Value of the effect size indicates the magnitude of the survival difference. Magnitude and sign of observed effect size did not occur by chance (p=0.002).

Chapter 3. **Within-lake heterogeneity mediates fish community response to warming trends**

ABSTRACT

Climate changes are rapidly altering many aquatic systems, and evaluating community-level biological response captures diversity in organism response because of differences in life history traits and physiological limits. In addition to biological diversity, habitat heterogeneity can affect fish communities over small spatial scales, even within habitat units that are typically considered relatively homogenous such as lakes. Biological diversity and habitat heterogeneity are known to structure fish communities, but how these factors interact with changes in climate to alter species distribution and abundance is less clearly understood. It is therefore necessary to analyze climate impacts on fish communities while accounting for spatial and temporal patterns in community trends. This research used biological and environmental data from a northern-latitude lake to describe the role of temperature and spatial heterogeneity in predicting changes in community composition. For a 52 year period over which warming effects have been observed in the lake, weekly beach-seine sampling throughout the summer collected water temperature data and abundance for the 14 species captured in the littoral zone. We developed and applied a spatial dynamic factor analysis model to this time series, which estimates sensitivity to changing water temperature for each species and accounts for spatiotemporal variation by describing trends in the community composition for different locations in the lake. We then used the species temperature sensitivity estimates to predict future species abundance under climate projection scenarios. This analysis indicated difference in magnitude and direction of species responses to temperature, with some increasing and others decreasing in abundance. Our selected model

specified four “factors”, or unique trends associated with different sites in the lake described by unique species assemblages, indicating that different regions in the lake are experiencing different trajectories in community change associated with differences in rates of temperature change. These results highlight the importance of considering habitat heterogeneity in explaining and predicting future species abundances, and our model provides a means of visualizing spatiotemporal variation in species dynamics.

INTRODUCTION

Marked shifts in climate have been observed over the past several decades, varying in effect and severity depending on location, ecosystem characteristics, and time of year (Walther et al. 2002). These changes are expected to occur over a range of spatial and temporal scales, with far-reaching and complex ecological effects (Stenseth and Mysterud 2002). Climate warming has been linked to changes in species distributions, timing of ecological events and phenology, disruptions in food web dynamics, and species extinctions (Wiltshire and Manly 2004, Winder and Schindler 2004, Winder et al. 2009). The effects of climate changes include direct behavioral or physiological responses to warming as well as second-order responses of species interactions; a few studies have examined the system-wide effects of disruption of a key organism but most studies have observed responses and estimated future trajectories of only one or few species (Reist et al. 2006).

It is unlikely that all organisms will respond similarly to climate changes due to differences in habitat use, life span, breeding date and other life history traits, physiological limits, and other traits. Consequently, evaluating communities as a collection of species components may offer a framework for examining and predicting assemblage changes. Life

histories and physiological attributes (termed species traits below) have been used to predict individual species successes under environmental disturbances or habitat alterations, and trait variation among species can influence which species respond well or poorly to environmental and habitat impacts (Olden et al. 2006). In climate warming scenarios, life histories and physiological tolerances of individual species must be considered in efforts to predict winners and losers with respect to projected and presently-observed habitat changes (Mackenzie et al. 2007, Portner and Farrell 2008). A community-wide perspective can be effective in capturing the diversity of responses to climate change (Harley et al. 2006), but this approach is underrepresented in climate change literature and it remains uncertain how future communities might look. Community level analyses have indicated assemblage restructuring and idiosyncratic responses (Le et al. 2008). Some research has shown that changing climate conditions will lead to novel, no-analog communities, but if mobile species undergo range shifts together, communities as a whole might experience little change (Lyons 2003). Currently, predictive ability is largely lacking on an assemblage-wide level and little work has been done to assess the changes in community response on finer scales, in systems where species range shifts are restricted by physical limitations. In part, this is because many analytic approaches to date cannot effectively capture spatial and temporal variation for multivariate species abundance and community composition data. Moreover, a large proportion of terrestrial and aquatic communities have already been altered by non-native species, habitat modification, and other processes, making empirical studies of climate effects difficult to disentangle from the effects of anthropogenic changes.

Habitat heterogeneity maintains stability within ecosystem linkages, promotes life history diversity and can buffer fluctuations in population abundance, preserving system functions in

scenarios of landscape-level changes to the environment (Oliver et al. 2010, Schindler et al. 2010, Stirnemann et al. 2015). Benefits of heterogeneity have been recognized in terrestrial landscapes as functions of vegetation cover and small-scale topographical features (Ford et al. 2013) and in rivers due in part to dendritic structure and landscape gradients (Brown 2003, Thompson and Townsend 2005), but lakes have received less attention as systems that can display heterogeneity on spatial scales relevant to mobile organisms. Failure to recognize and account for this heterogeneity within lakes can mislead future predictions for species abundances and responses to changes in the environment (Luoto and Heikkinen 2008).

Recent research has illustrated that spatial heterogeneity in species abundance can cause biased estimates of abundance when analyzed using a model that integrates across spatial variation (Ray and Hastings 1996, Thorson et al. 2015b). Including spatial variation is likely to also affect estimates of environmental impacts when compared with non-spatial analyses (Legendre 1993). Nonspatial analysis of environmental impacts on communities have included linear (Ives et al. 2003, Zuur et al. 2003) and nonlinear (Deyle et al. 2015) multivariate dynamical models. Recent advances in statistical and computational methods now permit the development of spatial dynamical models for multivariate data (Cressie and Wikle 2011, Lindgren et al. 2011), by replacing all random variables representing population abundance with random fields that represent population density across the population's range (e.g., Thorson et al. 2015a). In this manner, dynamical models for communities could be fitted to observation-level data (i.e., species counts at each site and time) with associated environmental measures (i.e., water temperature). Spatial models for community dynamics would also follow Tobler's first law of geography and predict that nearby locations are more similar than distant locations.

High-latitude lakes are very sensitive to the effects of climate change and warming temperatures, especially in regard to seasonal regulation of biological processes (De Stasio et al. 1996, Smol et al. 2005). In these systems, climate change has led to longer annual ice-free periods, warmer average and peak water temperatures, and higher productivity due to longer growing seasons and metabolic processes of primary producers (Schindler 2009). Biota of freshwater systems, including fishes, respond strongly to climate change (Parmesan 2006, Keller 2007, Adrian et al. 2009). Earlier ice breakup dates may induce altered timing in life history or reproductive cycles or influence species distribution and behavior, though temperature and competition are both important (Abrey 2005, Schindler et al. 2005, Rich et al. 2009). Increased water temperatures affect the distribution and phenology of fishes differently because the species differ in thermal preference and tolerance (Edwards and Cunjak 2007). Warmer temperature generally increases metabolic rates (Clarke and Johnston 1999) and, given a longer growing season and unrestricted availability of prey resources and thermal tolerance of the organism, many species will experience faster growth or maturation rates under higher temperature conditions (Magnuson et al. 1990, Schindler et al. 2005). However, physiological limits and thermal optima may be quite variable among taxa, and some species may undergo thermal stress and constraint in growth potential due to increasing metabolic costs (Beitinger and Fitzpatrick 1979). Destabilization trends have been observed in freshwater plankton communities with increased temperatures (Winder and Schindler 2004, Carter and Schindler 2012), and increased metabolic demands and shifts in niche exploitation may affect the behavior and ecological interactions of planktivorous fish and other organisms higher in trophic level (Beisner et al. 1997). Together, these species reactions ultimately shape community responses to climate change.

This project investigated the community-level effects of climate warming on littoral zone fishes in an oligotrophic, high-latitude Alaskan lake system, using a unique data set of methodologically consistent sampling conducted annually for over 50 years. This yearly sampling included repeated assessment of fish abundance and spatial distribution, as well as environmental data including water and air temperature. In contrast to studies in which biological responses to climate patterns are complicated by concurrent anthropogenic influences (Schindler 2011), this study offers a rare opportunity to examine long term changes in an entirely native freshwater fish community largely unaffected by direct human activity. These data are also well suited to applying a novel analytic method that explicitly accounts for spatiotemporal variation in multivariate species abundance data, while also estimating sensitivity to environmental covariates for each species. The goals of our analysis were to: 1. test whether within-lake spatial heterogeneity explains differences in abundance and community composition over time, and 2. use a newly-developed model to generate estimates for the effect of temperature on species abundance. We then combined these model outputs with 100-year air temperature projections to estimate species abundances. Our analyses indicate that community composition is shifting directionally over time, and that spatial heterogeneity within the lake is important both in describing trends in community change over the past 50 years and in predicting future abundance and species assemblage shifts.

METHODS

Study Site

The Bristol Bay region of Alaska is characterized by many large lakes used as rearing habitat for juvenile sockeye salmon (*Oncorhynchus nerka*), unique among Pacific salmon in their reliance on lakes during early stages of life. In most populations, adults breed in late summer and early fall, embryos incubate over the winter, and fry emerge from the gravel in spring and quickly move to lakes associated with their spawning habitat to rear for 1 or 2 years prior to seaward migration (Quinn 2005). The Wood River system of Bristol Bay is a complex of interconnected lakes that serves as a major tributary to the Nushagak River and annually accommodates up to 1 million or more returning adult sockeye salmon, after large-scale commercial fisheries catch approximately 50% of the run. Natural variation in abundance exceeds that related to fishing, such that there are often more salmon even after fishing in some years than would return without fishing in other years. Density-dependent competition for breeding space in streams plays an important role in determining the abundance of sockeye salmon fry entering the lake (Quinn 2005). Lake Aleknagik, a large oligotrophic lake averaging 43 m deep with an area of 83 km^2 (Hartman and Burgner 1972), is the farthest downstream of the five main lakes in the Wood River system (Figure 1). Located north of the 59^{th} parallel, this system has a short season of biotic productivity and growth and is ice-covered for up to eight months of the year (Hartman and Burgner 1972, Schindler et al. 2005). The lake experiences thermal stratification between mid-June and mid-September of most years, and average August water temperatures ranges between 10ºC and 12º C. Data collection has been standardized in this system since the early 1960s, and over this period significant trends have been observed in both

ice-out timing (average of 10 days earlier) and average lake water temperature, with taxa-specific effects on the zooplankton community (Carter and Schindler 2012). These changes have been attributed to the combined influences of global climate warming and the switch from a cool to warm phase of the Pacific Decadal Oscillation during the study period (Mantua et al. 1997, Schindler et al. 2005).

Lake Aleknagik supports an entirely native community of both anadromous and non-anadromous fish species, notably rainbow trout (*Oncorhynchus mykiss*), Arctic char (*Salvelinus alpinus*), northern pike (*Esox lucius*), threespine stickleback (*Gasterosteus aculeatus*), ninespine stickleback (*Pungitius pungitius*), sculpins (*Cottus* spp), Alaska blackfish (*Dallia pectoralis*) and whitefish species (Coregonidae). The numerically dominant anadromous fish, sockeye salmon, rear as juveniles in Lake Aleknagik from a few days after emergence in late spring until they migrate to sea, in late spring and early summer. Over 90% of the fry from Lake Aleknagik spend one full year in the lake (the remainder staying for two years), where they utilize primarily littoral prey and habitat resources during the summer after emergence (Rogers 1987) but move offshore by mid-late summer (Abrey 2005). Arctic char and whitefish speices rear in littoral habitats of the lake as juveniles, and threespine and ninespine sticklebacks and sculpin comprise the remainder of the numerically dominant members of the littoral community as both juveniles and adults. Other Pacific salmon, including coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*) and Chinook (*O. tshawytscha*) are present in the system in small numbers, as they migrate quickly to sea and do not represent a significant part of the lake community in relative abundance or duration of residence.

The Wood River lakes and rivers are largely unaffected by anthropogenic activities (e.g., no shoreline development, logging, agriculture, dams or water diversions), and habitat and fish

communities have remained largely intact. The commercial fisheries are well-regulated to meet biological escapement goals (Hilborn 2006) and the recreational fisheries on rainbow trout and Arctic char are predominantly catch-and-release.

Sample collection

Beach seining: The littoral zone fish community was sampled with beach seine nets at 10 locations in Lake Aleknagik, distributed along the north and south shores of the lake (Figure 1). The sites were chosen to not only encompass the entire circumference of the lake but they also differ in exposure to wind, gradient, substrate, vegetation, proximity to streams, and thermal regime. Sampling occurred every ~7 days each summer, between approximately the first week in June (shortly after ice-out) and the first week in August (Rogers et al. 2002), from years 1963 to 2014. After early August, catches diminish as sockeye salmon fry, Arctic char, and threespine stickleback move to the limnetic zone of the lake (Abrey 2005). Seining was carried out by deploying a 30 m beach seine (6 mm mesh size) using a boat, and returning the net manually to shore. All fish captured (or a random subset of the catch if prohibitively large) were identified to species (except for sculpins and whitefish, identified to genus) and enumerated.

Lake dynamics and limnology: Site-specific water temperature was recorded during each beach seine sample using a hand-held thermometer at a depth of approximately 10 cm. Limnological sampling was also conducted every 10 days from the end of June through early September at six fixed mid-lake locations, distributed along the length of the lake. At each site, vertical temperature profiles up to 30 m in depth were recorded using a YSI (Yellow Springs, Inc.) probe or, in earlier decades, at discrete depths with other electronic sensors or thermometer measurements from water bottle samples.

Statistical methods

Beach seine data were used from 1963-2014, reflecting the period over which standardized, consistent sampling occurred for these locations. Extremely rare species (observed in <5% of the samples) were removed from the data set to avoid overrepresentation of scarce taxa, leaving 14 species or species groups remaining: threespine stickleback, ninespine stickleback, sculpin, blackfish, sockeye salmon, Chinook salmon, coho salmon, chum salmon, pink salmon, rainbow trout, Arctic char, grayling, and whitefish. Sculpins (Cottidae) and whitefish (Coregonidae) were aggregated at a family level, to avoid discrepancies in identification over the years but two sculpins are present, coastrange (*C. aleuticus*) and slimy (*C. cognatus*). The lake has pygmy whitefish (*Prosopium coulteri*) and round whitefish (*P. cylindraceum*) and the latter seem to predominate.

Site-specific surface water temperatures were averaged over the season at each site and we fit a linear regression of surface water temperature versus year. Limnetic zone surface temperatures were averaged over the season and over all six limnology sites and plotted with linear model fit and p-values.

Temporal trends in assemblage composition: We develop a spatial dynamic factor analysis model as an extension of the spatial factor analysis (Thorson et al. 2015a) and the spatial Gompertz model (Thorson et al. 2015b). This model proceeds by calculating one or more dynamic factors, which each dynamic factor follows a spatial Gompertz dynamics over time:

$$\theta_p(n,t) = \sum_j L_{p,j} \psi_j(n,t)$$

where symbols are defined in Table 1. Dynamics for each individual species are then informed by all factors, as weighted by a loadings matrix **L**:

Finally, the expected count $\hat{c}_p(n,t)$ for species *p* at location *n* in time *t* also includes the effect of measured environmental variables:

$$\hat{c}_p(n,t) = \exp\left(\theta_p(n,t) + \sum_k \gamma_k x_k(n,t)\right)$$

where the set of covariates ***x(n,t)*** at location *n* in time *t* might include an intercept (controlling variation in average densities among species) as well as measured habitat variables (e.g., temperature). Observed counts $c_p(n,t)$ for species *p* at location *n* and time *t* are then assumed to arise from a Poisson count process that includes lognormal overdispersion:

$$c_p(n,t) \sim Poisson\left(\hat{c}_p(n,t)\exp(\delta_i)\right)$$

where overdispersion δ_i arises from a normal distribution with standard deviation σ_p that varies among species. In this model, spatial variation $\mathbf{\Omega}_k$ and spatiotemporal variation $\mathbf{E}_k$ for each dynamic factor *k* are approximated as Gaussian random fields:

$$\mathbf{\Omega}_k \sim MVN\left(0, \tau_{space}^{-1}\mathbf{\Sigma}_{k,space}\right)$$
$$\mathbf{E}_k \sim MVN\left(0, \tau_{time}^{-1}\mathbf{\Sigma}_{k,space} \otimes \mathbf{\Sigma}_{k,time}\right)$$

where we assume that the spatial range of correlation (represented by $\varkappa_j$ which in turn controls $\mathbf{\Sigma}_{k,space}$) is constant for spatial and spatiotemporal components (i.e., for $\mathbf{\Omega}_k$ and $\mathbf{E}_k$), and more details can be found in Thorson et al. (Thorson et al. 2015b). Details on identifiability conditions and rotation can be found in the appendix of this paper.

Using the species abundance data for each sample date at each site across the years from 1963-2014, we ran a suite of SDFA models with the number of specified factors ranging from 1 to 8. The factors are latent variables that vary over time and space while including water temperature as a covariate in each model and estimating a separate effect of temperature on

population density for each species (i.e., γ_k is different for each species). Estimated factors represent groupings in the way that species abundance vary across sites and over time. The Bayesian Information Criterion was used to select the most parsimonious model from the suite of from 1 to 8 factors. Models were run in statistical program R (R Core Team 2014), using TMB model package and the R-INLA package.

To evaluate how fish assemblage composition might respond to continuing warming in Lake Aleknagik, we used baseline air temperature and site-specific water temperature, future air temperature projections, and SDFA model-generated estimates for effect of temperature on species abundance. Air temperature (NOAA Climate Data Online average air temperature from months of June, July and August for Dillingham, AK) and site-specific water temperature data (mean from months of June, July, and August) from years 1980-1999 were used to develop regressions of water temperature versus air temperature for each sample site. The median regional air temperature projection for Alaska from the IPCC's Fourth Assessment Report predicts an increase in air temperature of 2.3°C between a baseline period of 1980-1999 and the projection range of 2080-2099 (Christensen et al. 2007). We used this predicted value for air temperature in the water temperature versus air temperature regressions to predict the change in water temperature over the same time period for each sample site. In the SDFA model, the temperature covariate is additive in log-space, so to predict future species densities we used the formula

$$\mathrm{d}_{ij} = \exp\left(\mathrm{t}_i \gamma_j\right)$$

where d_{ij} is the change in density of species j at site i, t_i is the projected water temperature increase of site i, and γ_j is the model generated temperature effect for species j. To report species

density change in percent per 1°C temperature increase, values were converted back into log-space.

RESULTS

Summer limnetic surface water temperatures have increased significantly over time (Figure 1) at the six index limnology sites in Lake Aleknagik. However, site-specific surface temperature trends were heterogeneous (Figure 1). All sites increased significantly over time, with different slope values, except for sites 5S and 7S, located on at the southeast end of the lake. Sites 2N, 5N, and 6N, located on the north shore of the lake, experienced the highest rate of temperature increase.

From 1963-2014, a total of 2,720,954 fish were captured of the eight species retained in SDFA analysis. The total catch was numerically dominated by threespine stickleback (45%) and juvenile sockeye salmon (44%). Ninespine sticklebacks (5%), sculpin (3%), and Arctic char (2%) were the next most abundant species, and the remaining 1% was composed of less frequently captured species, including whitefish species and Alaska blackfish.

Temporal trends in community structure

Bayesian Information Criterion model selection chose the model with 4 factors as the most parsimonious (Δ BIC=11.4). Of these, two factors (1 and 4) described the majority of variation in species loadings. Species grouped into sub-assemblages based on estimates corresponding with different factors (Figure 2). Most of the variation was explained by factor 1, comprised of a threespine stickleback-ninespine stickleback-sockeye salmon assemblage, and by factor 4, comprised of a sculpin-Arctic char-whitefish assemblage. Plotting the factor values for

each site in each year of Factor 4 versus Factor 1 revealed a trend in factor values over time (Figure 3). Years before 1980, shown in shades of blue, had higher factor values for both Factor 1 and Factor 4; years after 1995, shown in shades of yellow to red, had lower values for both factors, indicating a directional shift in community structure over time.

Factor values varied by sample location and over time (Figure 4). Factor 1 had highest values at sites on the north shore and east end of the lake, at sites 5N, 6N, 8N and 8S. Factor 2 had highest values at the far northwest end of the lake at site 1S; factor 4 had highest values at sites 2N, 2S, and 7S. Factor 4 had highest values at the south shore and east end of the lake, at sites 5S, 7S, and 8S. The overall direction of the trend in each factor is plotted in the right column of the figure; all sites share the overall trend described by each factor (black line), but site-specific factor values vary (gray lines).

An advantage to using time series models is the ability to generate estimates of the effect of covariates. Site-specific surface water temperature used as a model covariate predicted changes in species abundance (Table 2), and estimate values indicated percent change in abundance predicted by a 1°C increase in temperatures. Changes in density were significantly associated changes in with surface temperature for three- and ninespine stickleback, Arctic char, sockeye salmon, and sculpin species. Sculpin, whitefish species, rainbow trout and sockeye, pink, chum and coho salmon were predicted to decrease in abundance in the lake with temperature increases; all other species were predicted to increase in abundance.

Predictions for future species densities indicated decreased abundances of sculpin, whitefish species and sockeye salmon at all sample locations, and increased abundances of threespine and ninespine stickleback, pink salmon, Arctic char, and blackfish (Table 3). Threespine and ninespine stickleback and blackfish were predicted to experience greatest

increases in abundance, with over 20% increase in abundance projected at some sites. The values of predicted abundance increase were highest in sites experiencing faster warming and for species with the strongest water temperature effect.

Discussion

Temperature variability

From the 1963 to 2014, surface water temperatures have consistently increased in Lake Aleknagik, but the rates of temperature change varied among sites, with and some decreased in average temperature across years (Figure 1). The sites that have become cooler, 5S and 7S, are located at the south and east end of the lake, where they are subject to wind and wave action and limnetic habitat might be increasingly exposed to water from below the thermocline due to vertical mixing in the lake. Other sites vary in beach slope and substrate, but sites 5N and 6N are shallow and protected and have been rapidly warming.

Temporal patterns in community structure

To explicitly test the variability in space and time for species assemblage composition, we developed and applied a new model as an extension of the recently developed spatial factor analysis model (Thorson et al. 2015a). This model offers a new informative and predictive approach to multivariate species abundance data that are hierarchical in space and time. The model both estimates species-specific sensitivity to environmental covariates (in our study, temperature) and partitions remaining spatiotemporal variability into categories, or "factors", that represent positive or negative associations in population growth rate among species within the community. Our most parsimonious model explained most of the variation with two factors, and

the crossplot of Factors 1 and 4 demonstrate a consistent trend over time (Figure 3). The Lake Aleknagik temperature observations are consistent with the noted switch from the cool to warm phase Pacific Decadal Oscillation (PDO) in the mid-1970s and the marked warming trends observed in the Bristol Bay region over the last decade (Mantua and Hare 2002, Rich et al. 2009, Carter and Schindler 2012). These climate trends also correspond with temporal patterns in fish assemblages, showing a clear trend with separation between years before the mid-1970s (dark through light blue points) and the years post-1976 (teal through red points) (Figure 3).

The first of the dominant factors (factor 1) associated with a threespine stickleback-ninespine stickleback-sockeye salmon species grouping and the second (factor 4) associated with a sculpin-Arctic char species grouping. These species values for factors are supported by cross-correlation estimates for trends in species abundance; the stickleback species and sockeye salmon are strongly correlated, and correlation values for Arctic char and sculpin also support this sub-assemblage. Values for factor 1 fluctuated across years, but the highest values for the factor occurred in the at the east end of the lake along the north shore, at warmer, more protected sample sites. Values for factor 4 varied widely across years, but the highest values concentrate on the south shore of the lake, at sample sites on rockier beaches (Figure 4).

Threespine and ninespine stickleback, Alaska blackfish, and sculpins are all small-bodied lake resident fish, with lake distributions largely regulated by breeding dynamics (McPhail and Lindsey 1970). While threespine stickleback do move offshore and feed in the limnetic zone of the lake in schools (Wootton 1976), these low-plated, small sticklebacks are not believed to be migratory or undergo large movements (McPhail and Lindsey 1970). Sculpin and blackfish are demseral or benthic fishes believed to have limited ranges (McPhail and Lindsey 1970). Distributions of these fish in the lake are likely not attributed to systematic movements or

redistribution. All Pacific salmon species are spawned in tributary streams and rivers on the north and south shores of Lake Aleknagik, and their distributions are likely influenced in part by the proximity of these sites to the stream mouth (Quinn 2005). During the time that pink and chum salmon are captured in beach seine samples, these fish have recently emerged from the gravel (within 3 months of capture) and are migrating to the ocean (Robins et al. 2005); sockeye salmon have recently emerged from the gravel and the dominant life history strategy will remain in the lake for a period of one year, moving from the littoral zone to the pelagic within their first season of growth (Burgner 1987). Rainbow trout and grayling (freshwater resident) and juvenile coho and Chinook salmon (anadromous after freshwater rearing for up to two years) are primarily stream- and river-oriented, and the in-lake distributions for these fishes are correlated and likely influenced by lotic conditions. Arctic char and whitefish species are captured as juveniles in beach seine samples (primarily young of year for Arctic char), and their distributions are likely driven in part by breeding location; Arctic char and most whitefish species persist largely in the pelagic zone of the lake as adults (McPhail and Lindsey 1970), though juvenile Arctic char also move into streams in this system.

Threespine and ninespine sticklebacks were among the most positively associated with temperature increases, with predictions of over 5% and 9% increases in abundance with increases of 1°C water temperature. These species can tolerate warmer water temperatures than salmonids or other cold water fishes (Lefebure et al. 2011), and with a sufficiently long and warm growing season threespine sticklebacks will breed iteratively, producing additional broods (Brown-Peterson and Heins 2009). Alaska blackfish, predicted to increase almost 6% with a water temperature increase of 1°C, are unique in their ability to tolerate warm water and hypoxic conditions for breeding locations (Lefevre et al. 2014).

Pink salmon abundance increases are likely attributed to dynamics outside of the lake system as they spawn in streams and rear in marine habitats (Quinn 2005), and lake temperature dynamics may be correlated with favorable ocean conditions. Pink salmon are among the least sensitive species to temperature, with 0.4% abundance increase predicted with water temperature increase of 1°C. Sockeye salmon are also subject to stream and marine dynamics outside of the lake possibly co-varying with lake temperature trends (Quinn 2005), but the approximately 5% decline with every 1°C increase in temperature might also be explained by in-lake conditions. Sockeye salmon move from the littoral zone, where they are vulnerable to capture in our sample gear, to the pelagic zone of the lake, and this transition is predicted in part by a size threshold (Abrey 2005); in warmer years or locations, more rapid growth might lead to earlier off-shore migration and lower catches. To the extent that this is true, the abundance projection based on littoral zone catches is somewhat paradoxical as it could occur with increasing actual abundance. This type of interaction highlights the complex ways in which the life history patterns of species must be considered when interpreting trends and projections. Predictions for changes to future species abundances also must incorporate both individual species sensitivity to the temperature covariate and the change in water temperature with air temperature for each sample location. The largest abundance increases are projected for threespine and ninespine stickleback species in rapidly warming, sheltered locations within the lake.

Developing a method to capture both environmental predictors and variability in time and space offers a novel way of assessing the trajectory of fish assemblage shifts in the future, and represents an important component in understanding the complexity and nuance of biological responses to climate. In particular, spatial dynamic factor analysis represents a compromise between mechanistic and phenomenological approaches to analyzing community dynamics. For

example, a spatial version of the Ives et al. (2003) model would include an estimate of interaction strength between every species in the community. This requires estimating an *n* by *n* matrix of interactions, and is not likely to be parsimonious (or even computationally feasible) or a large number of species, or when analyzing data from infrequent community components such as whitefish. By contrast, nonmetric multidimensional scaling provides insight regarding community dynamics and environmental drivers only by performing post-hoc comparisons, and such comparisons risk doing "statistics on statistics". We note, however, that there are many other ways to construct parsimonious representations of community associations and interactions (Kissling et al. 2012), and recommend that future research expand the range of available options for spatiotemporal analysis of communities.

This work highlights the importance of approaching biological responses to climate change in a manner that incorporates inherent dynamics of ecological complexity while suggesting methods to assess the future trends in these community responses. Further developing and implementing these techniques will have important implications for conservation concerns, as well as our understanding of the role that ecological interactions play in shaping the ecosystem responses to large scale disturbances.

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Table 3.1. List of symbols used in the spatial dynamic factor analysis model

Symbol	Description	Dimension
Variables		
$\boldsymbol{\Psi}$	Dynamic factor	$n \times j \times t$
$\boldsymbol{\Theta}$	Expected density from dynamic factors	$n \times p \times t$
$\mathbf{E}$	Spatiotemporal variation	$n \times j \times t$
$\boldsymbol{\Omega}$	Spatial variation	$n \times j$
$\mathbf{L}$	Loadings matrix	$p \times j$
$\mathbf{H}$	Varimax rotation matrix	$j \times j$
$\mathbf{X}$	Measured environmental variables	$i \times k$
c	Count data for all species, sites, and time periods	i
ϱ	Autocorrelation in spatiotemporal variation	j
λ	Ratio of spatiotemporal and spatial variance	j
δ	Lognormal overdispersion	i
γ	Effect of covariates	k
σ_{δ}	Standard deviation of overdispersion	p
ϕ	Ratio of initial and median value for dynamic factors	k
τ_{space}	Magnitude of spatial variation	k
τ_{time}	Magnitude of spatiotemporal variation	k
$\varkappa$	Distance of spatial correlation	k
Indices		
t	Number of time periods	1
p	Number of species	1
s	Number of sites with available data	1
n	Number of knots used to approximate spatial variation	1
j	Number of factors	1
k	Number of covariates	1
i	Number of observations	1

Table 3.2. Effect for water temperature as a covariate for each species in the SDFA. Estimate values indicate percent change in abundance for each species per 1°C increase in temperature (e.g. threespine stickleback increase by 5.3% for each 1°C temperature increase).

Species	Estimate	Standard error	p-value
Threespine stickleback	0.053	0.009	<0.001
Ninespine stickleback	0.099	0.008	<0.001
Sockeye salmon	-0.058	0.011	<0.001
Arctic char	0.028	0.008	<0.001
Sculpin	-0.031	0.006	<0.001
Blackfish	0.026	0.025	0.304
Whitefish spp	-0.036	0.023	0.116
Pink salmon	-0.005	0.032	0.887
Chinook salmon	0.017	0.032	0.603
Chum salmon	-0.026	0.083	0.752
Coho salmon	-0.068	0.064	0.288
Grayling	0.016	0.062	0.799
Rainbow trout	-0.085	0.058	0.146

Table 3.3. Predicted change in abundance by sample location for each species with a significant response to temperature (from Table 1). These changes in species abundance are predicted for the IPCC median temperature projection of a 2.3°C air temperature increase between 1980-1999 and 2080-2099.

Site	Threespine stickleback	Ninespine stickleback	Arctic char	Sockeye salmon	Sculpin
1S	0.097	0.180	0.050	-0.099	-0.06
2N	0.084	0.156	0.044	-0.086	-0.052
2S	0.058	0.108	0.030	-0.060	-0.036
4S	0.101	0.189	0.053	-0.104	-0.063
5N	0.208	0.387	0.108	-0.213	-0.13
5S	0.124	0.231	0.064	-0.127	-0.077
6N	0.215	0.400	0.112	-0.220	-0.134
7S	0.085	0.158	0.044	-0.087	-0.053
8N	0.191	0.355	0.099	-0.196	-0.119
8S	0.105	0.196	0.055	-0.108	-0.066

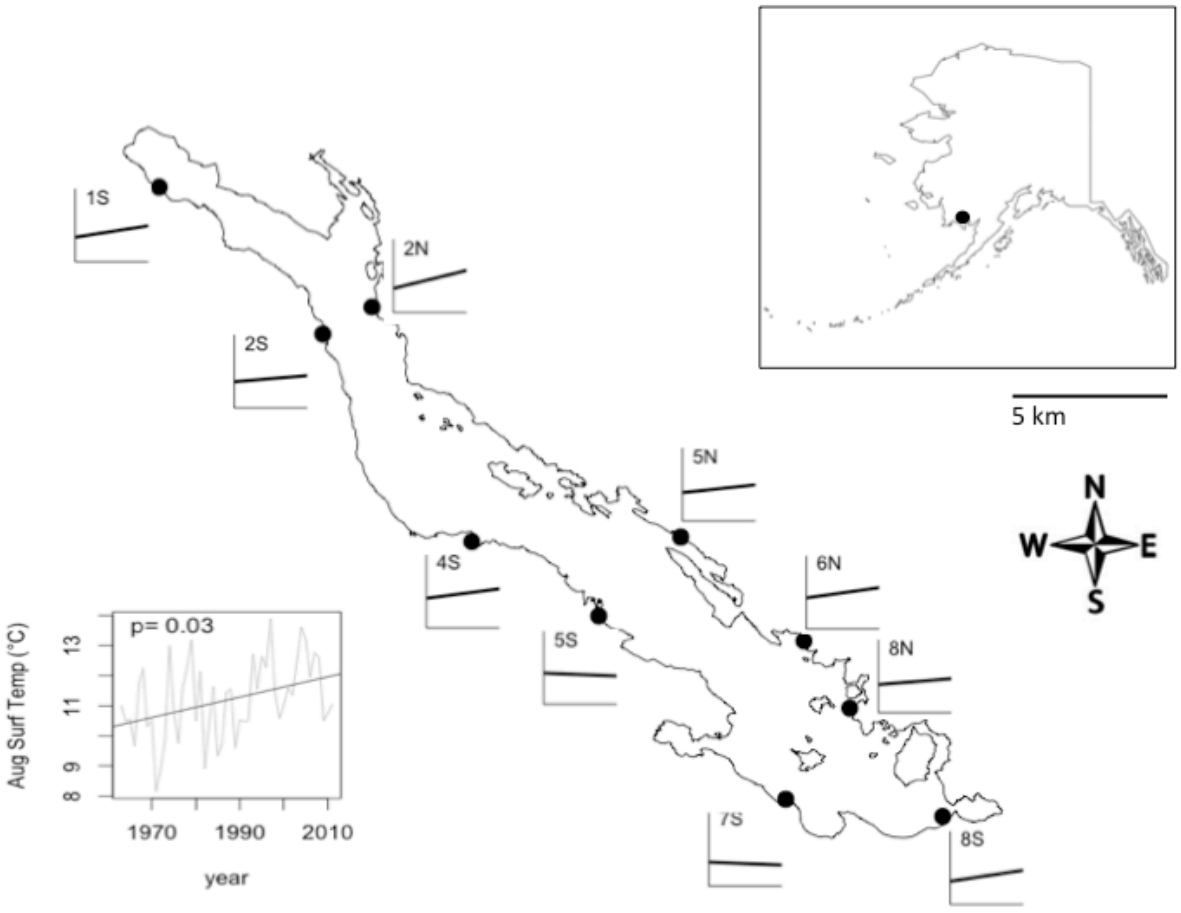

Figure 3.1. Lake Aleknagik, Alaska. Black dots indicate beach seine sample locations, and plots display line of linear model fit for mean August surface water temperature across years at each beach seine sample location. Bottom left inset shows trend, line of linear model fit, and linear model p-value for mean August limnetic surface water temperature across years for Lake Aleknagik.

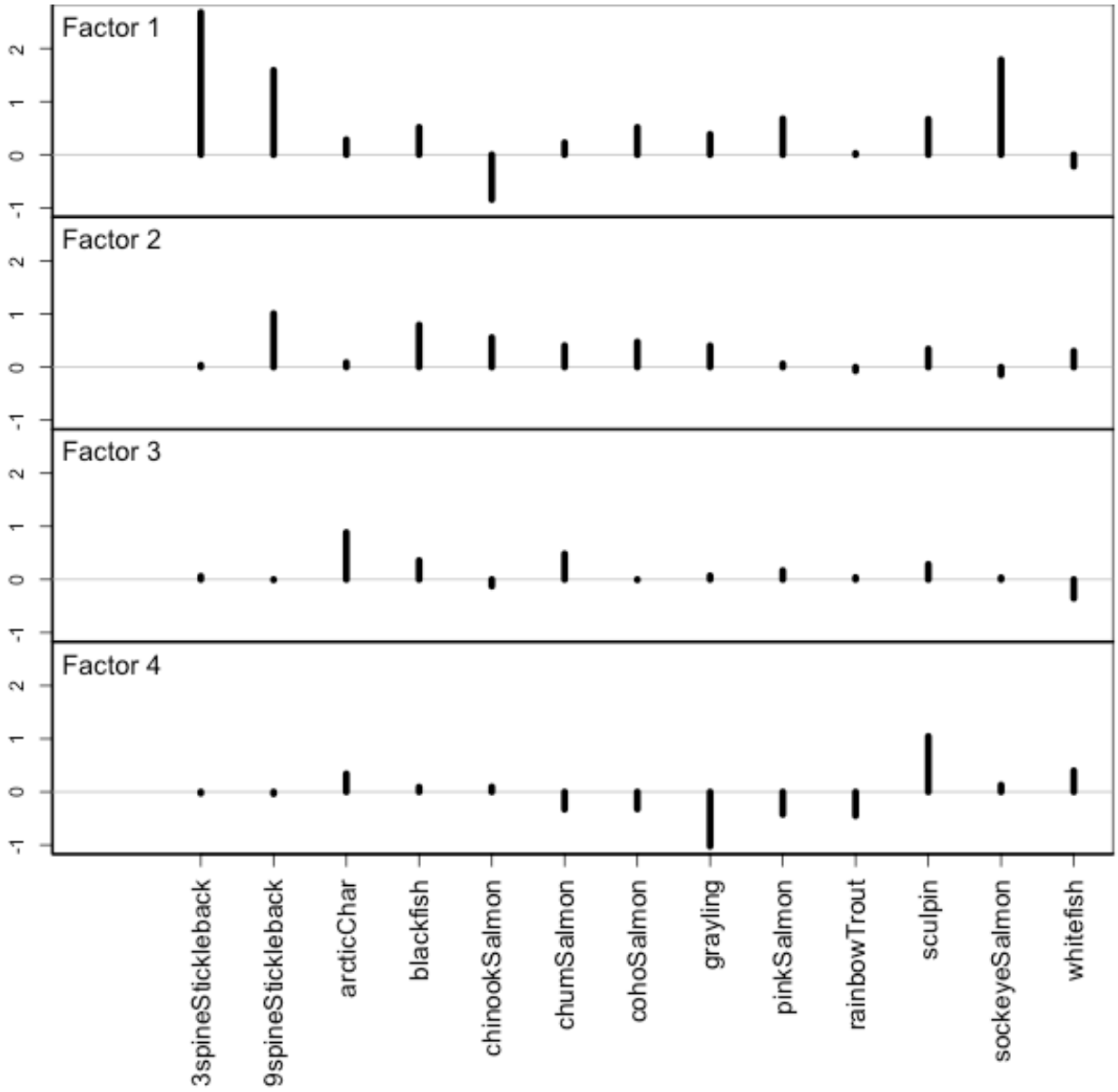

Figure 3.2. Species estimates for each of the five factors in the SDFA. Values are after varimax rotation in the SDFA model.

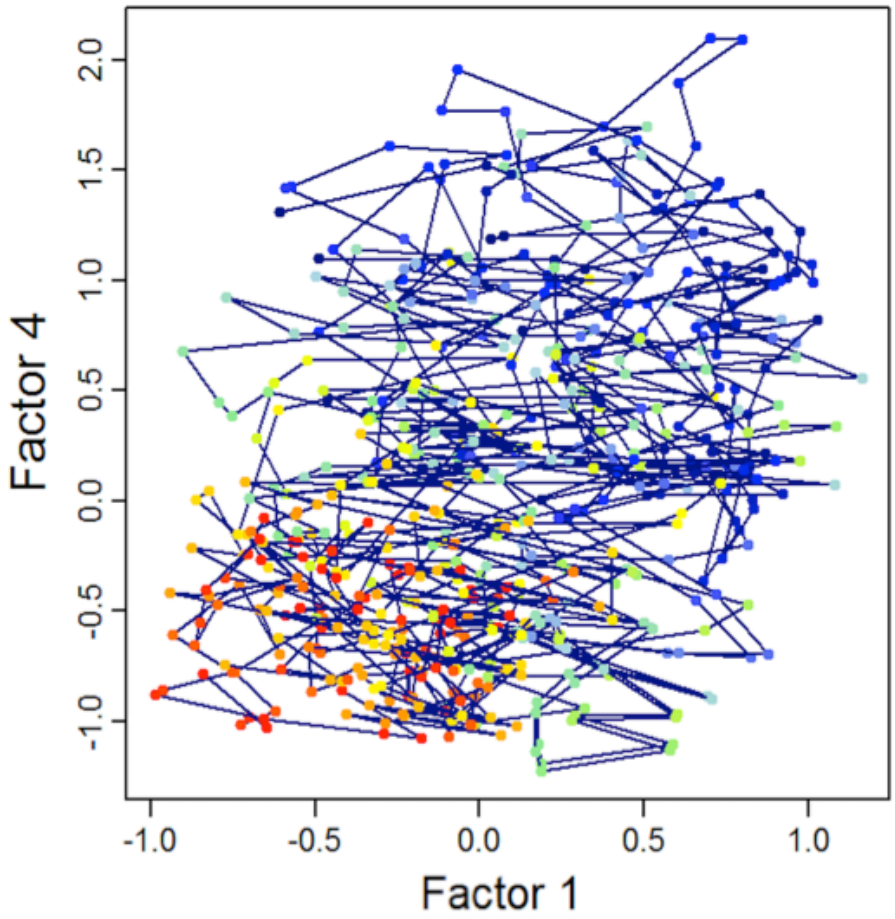

Figure 3.3. Bi-plot of Factor 1 and Factor 4, the two factors describing the majority of the species loadings. Each point represents the factor values for each year from 1963-2014 for each site; sites are connected by black lines. Points are colored with more recent years in red and earlier years in blue.

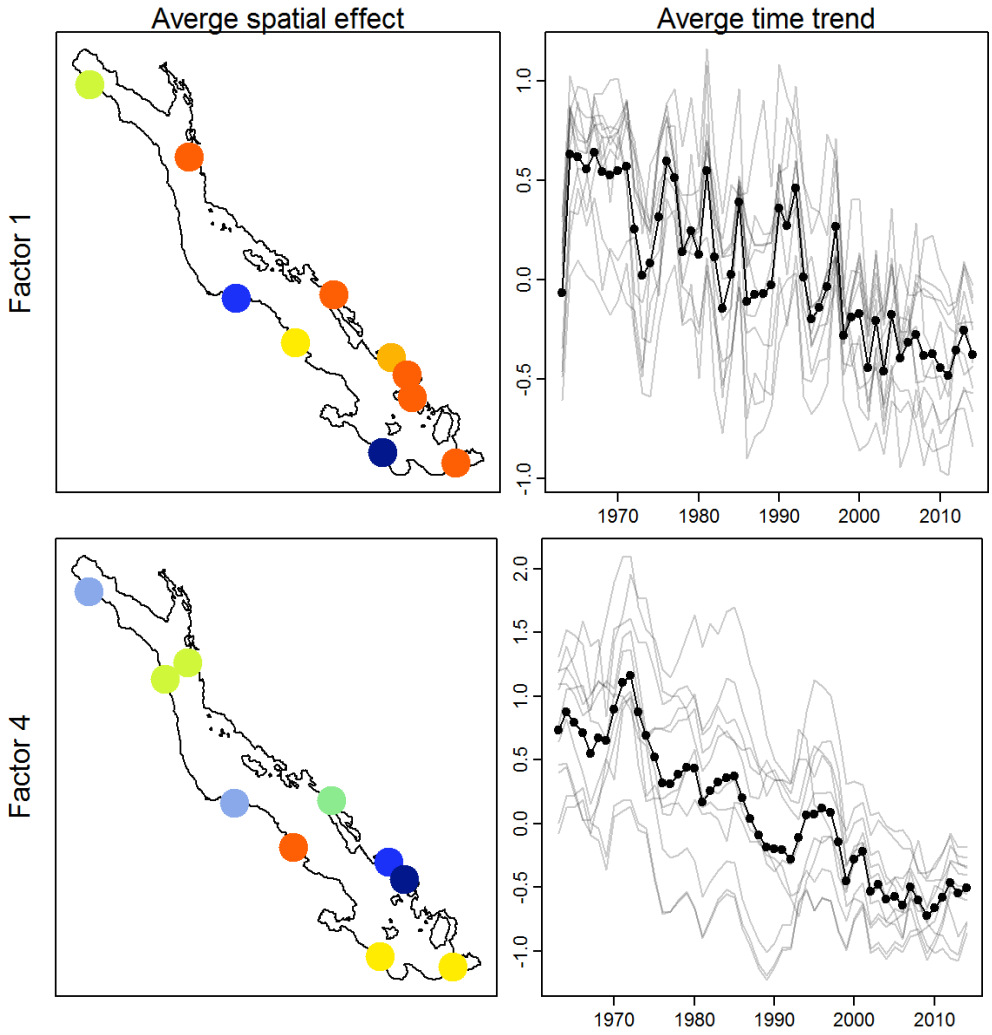

Figure 3.4. Spatial and temporal trends for the two dominant factors in the SDFA model. Mean factor value estimates for each seine sample site (left panels); red points are high values and blue points are low values. Right panels indicate trend over time for factor values for each site (grey lines) and the mean trend across sites (black line). See Table 2 for species associations with each factor.

CHAPTER 3 APPENDIX

Identifiability conditions—The spatial dynamic factor analysis model requires that some parameters be fixed to ensure that the remaining parameters are all uniquely identifiable. We follow Thorson et al. (Thorson et al. 2015a) in imposing the following two constraints:

1. *Loadings matrix* – We specify that the upper-right corner of the loadings matrix **L** is fixed at zero. This constraint is analogous to a similar constraint in dynamic factor analysis (Harvey 1990, Zuur et al. 2003).
2. *Marginal variance of dynamic factors* – We also specify that the variance Var[$\boldsymbol{\Psi}_j$] = 1 for each dynamic factor *j* (Eq. 1), following an analogous constraint for spatial factor analysis (Thorson et al. 2015a) and dynamic factor analysis (Harvey 1990, Zuur et al. 2003). The variance for each dynamic factor can be calculated as follows:

$$\mathrm{Var}[\boldsymbol{\Psi}_j] = \mathrm{Var}\left[\phi_k \rho_j^t + \boldsymbol{\Sigma}_j + \frac{\boldsymbol{\Omega}_j}{1-\rho_j}\right] = \mathrm{Var}\left[\phi_k \rho_j^t\right] + \mathrm{Var}\left[\boldsymbol{\Sigma}_j\right] \mathrm{Var}\left[\frac{\boldsymbol{\Omega}_j}{1-\rho_j}\right]$$

where this reduces to:

$$\mathrm{Var}[\boldsymbol{\Psi}_j] = 0 + \frac{1}{4\pi\tau_{space,j}^2 \kappa_j^{\,2}} + \frac{1}{4\pi\tau_{time,j}^2 \kappa_j^{\,2}(1-\rho_j^{\,2})}$$

We additionally define a parameter $\lambda_j \equiv \frac{\sigma_{time,j}^2}{\sigma_{space,j}^2}$, such that:

$$\tau_{space,j} = \left(\frac{1+\lambda_j}{4\pi\kappa_j^{\,2}}\right)^{1/2}$$

$$\tau_{time,j} = \frac{\tau_{space,j}}{\sqrt{\lambda_j(1-\rho_j^{\,2})}}$$

In summary, we calculate a parameter λ_j for each dynamic factor *j*, which represents the relative magnitude of spatiotemporal and spatial variance, and other parameters representing the magnitude of spatial and temporal variation are uniquely defined given the constraint that the marginal variance of each dynamic factor is one.

Rotation and interpretation—Given these identifiability conditions, the dynamic factors **Ψ** and the loadings matrix **L** are uniquely identifiable. However, any non-singular linear transformation **H** can be used to rotate dynamic factors **Ψ** and the loadings matrix **L**:

$$\psi_j'(n,t) = \sum_{j^*} H_{j,j^*}\psi_{j^*}(n,t)$$
$$L_{p,j}' = \sum_{j^*} L_{p,j^*}(\mathbf{H}^{-1})_{j^*,j}$$

such that rotated factors **Ψ'** and the rotated loadings matrix **L**' will generate the same predicted dynamics **Θ** as the un-rotated ones. We therefore use varimax rotation to calculate rotation matrix **H**. This rotation ensures that **L'** is composed of a few large values and many small values, such that each dynamic factor **Ψ**$_k$**'** can be interpreted as representing a small number of observed species.

Conditions imposed to improve easy of interpretation—We also impose several constraints that are intended to improve interpretability, but which are not generally necessary to ensure that parameters are uniquely identifiable. Specifically, we impose the three additional constraints:

1. *Spatial scale* – We assume that the spatial scale of each dynamic factor is identical (i.e., $\varkappa_j = \varkappa$ for all dynamic factors *j*).
2. *Magnitude of density dependence* – We assume that the magnitude of density dependence is identical among dynamic factors (i.e., $\varrho_j = \varrho$ for all dynamic factors *j*).
3. *Ratio of spatial and spatiotemporal variance* – Finally, we assume that the relative magnitude of spatial and spatiotemporal variance is identical among factors (i.e., $\lambda_j = \lambda$ for all dynamic factors *j*).

These three assumptions collectively ensure that the rotated dynamic factors **Ψ'** can be interpreted similarly to the un-rotated factors **Ψ**:

$$\psi_j'(n,t) = \sum_{j^*} H_{j,j^*}\psi_{j^*}(n,t) = \sum_{j^*} H_{j,j^*}\left(\phi_{j^*}\rho^t + \varepsilon_{j^*}(n,t) + \frac{\omega_{j^*}(n)}{1-\rho}\right)$$

which implies that:

$$\psi_j'(n,t) = \rho^t\phi_j' + \varepsilon_j'(n,t) + \frac{\omega_j'(n)}{1-\rho}$$

where

$$\phi_j' = \rho^t \sum_{j^*} H_{j,j^*} \phi_{j^*}$$

$$\varepsilon_j'(n,t) = \sum_{j^*} H_{j,j^*} \varepsilon_{j^*}(n,t)$$

$$\omega_j'(n) = \frac{1}{1-\rho} \sum_{j^*} H_{j,j^*} \omega_{j^*}(n)$$

where ϕ_j' is the deviation of rotated factor *j* away from the median of its stationary distribution, and where $\mathbf{E}_j$' and $\mathbf{\Omega}_j$' are still distributed as Gaussian Markov random fields that have correlation following a Matérn distribution as a function of distance (where the correlation distance is controlled by parameter $\varkappa$).

Chapter 4. **Climate-driven conditions control reproductive phenology and investment in a lacustrine fish**

ABSTRACT

Temperature governs many physiological and ecosystem processes, suggesting that these processes are vulnerable to effects of climate change such as earlier timing of ice breakup and warmer water temperatures. An extended productive season lengthens the duration for growth and might result in altered reproductive strategies. Here, we examined effects of changing climate on the threespine stickleback in large Alaskan lakes. We sought to determine if spring water temperature and date of ice breakup influence fish size and age structure at the end of the growing season, and whether stickleback reproduction has shifted earlier in the season to track the earlier ice breakup. Results supported our hypotheses that early ice breakup and warmer temperatures correspond to larger individual size at the end of the growing season as well as more complex size structure. This latter result is due to earlier breeding and the longer ice-free period, which allows for multiple reproductive events in some years. Our results highlight multiple phenotypic modifications due to climate changes, and emphasize the importance of understanding life history shifts for predicting population responses to environmental change. Organisms respond to environmental changes though many mechanisms, and life history modifications may play an important but often overlooked role.

INTRODUCTION

Life history traits evolved to maximize fitness across a landscape of selective regimes imposed by the environment (Stearns 1992, Winemiller and Rose 1992). As such, life history traits are often highly sensitive to changes in the environment (Gotthard and Nylin 1995), including those associated with global climate change. Traits such as size at age, age of first reproduction, fecundity, development rate, and migrations respond to thermal cues across a range of taxa, from insects to birds and mammals (Walther et al. 2002, Parmesan and Yohe 2003). Physiological transitions associated with reproduction might be especially sensitive (Pankhurst and Munday 2011). By influencing metabolic rate and gonad development, temperature affects the timing of clutch laying in birds (Crick et al. 1997, Crick and Sparks 1999), and reproductive changes can have demographic and population dynamic consequences, such as longer and more stable reproductive periods in rabbits allowing additional broods and increases in abundance (Tablado and Revilla 2012). The physiological effects of temperature are especially pronounced in heterotherms; temperature governs diapause and breeding timing in many insects (Musolin 2007), and can affect both egg-laying timing and sex ratio in lizards (Telemeco et al. 2009).

While terrestrial systems experience direct effects of warming air temperatures, freshwater systems, especially high-latitude lakes, are highly sensitive to atmospheric temperature changes and have been described as "sentinels" of climate change (Adrian et al. 2009, Schindler 2009). Warming trends in boreal lakes are evident in increasing surface water temperatures, increased duration of thermal stratification, and longer ice-free seasons (Magnuson 2000, Smol et al. 2005). Freshwater biota respond to these effects, with possible consequences for reproduction and abundance. Organisms with short generation times appear particularly sensitive to these changes, and shifts in primary and secondary productivity have been observed

in zooplankton and phytoplankton corresponding with physical changes to the lake (De Stasio et al. 1996, Adrian et al. 2006, Winder et al. 2009, Cantin et al. 2011, Carter and Schindler 2012).

Changes to the physical lake environment and to lake productivity can affect fish and their life history traits in numerous ways. In cold lakes with discrete, temperature-limited growing seasons, increasing temperatures and duration of ice-free period can increase fish growth rates (Magnuson et al. 1990, Shuter and Post 1990). Growth reflects prey availability as well as temperature, and so intra-specific and inter-specific competition can also be important as density increases (Beverton and Holt 1957, Jenkins et al. 1999, Lorenzen and Enberg 2002, Amundsen et al. 2007). Strong competition can lead to reduced resource acquisition, higher mortality rates, and lower growth rates (Bohlin et al. 1994, Jenkins et al. 1999). In addition to the effects on growth, changing climate can also affect the timing of life history events such as migration, breeding, and larval hatching. Timing of reproduction is often mediated through physiological changes that are cued by temperature, and the relationship between temperature and spawning time has been observed across fishes (Vlaming 1972, Genner et al. 2009, Pankhurst and Munday 2011, Webb and McLay 2011). Spawning plasticity has been observed in bluegills related to environmental conditions (Kaemingk et al. 2014), and walleye egg maturity and spawning timing have been shown to track date of ice breakup (Schneider et al. 2010).To date, most research has focused on timing of spawning in fishes, and less work has been conducted on iterative breeding or the number of breeding bouts for individuals or populations within a single season.

In lakes around the North Pacific Rim, juvenile sockeye salmon (*Oncorhynchus nerka*) are typically the numerically dominant lacustrine planktivore, and their growth in freshwater has been linked to the combined effects of climate (date of ice out and temperature) and density of

conspecifics (Schindler et al. 2005, Rich et al. 2009). Sockeye salmon often co-occur with threespine stickleback (*Gasterosteus aculeatus*) in many of these lakes. The diets of these species overlap (Rogers 1968, Jaenicke et al. 1987, O'Neill and Hyatt 1987) and densities of both can be very high, suggesting possible inter-specific competition. In contrast to the large literature on the ecology of sockeye salmon (Burgner 1991, Quinn 2005), the population dynamics of sticklebacks are less well known. However, their life history makes them very suitable for studies on the effects of climate and density on growth, and interactions with breeding date. Specifically, they breed in the littoral zone in spring and so might be affected by the date of ice out, they are short-lived, and are not subject to artificial enhancement or any fisheries, so their abundance and growth are entirely influenced by natural processes (Wootton 1984). A longer ice-free growing season (Magnuson 2000) suggests that stickleback may be larger going into the winter now than in the past when the ice-free season was shorter. Moreover, Rogers (1977) reported that interannual variation in timing of stickleback reproduction was correlated with ice break up. Because the date of lake ice breakup in many north temperate systems is earlier now than in the past (Magnuson 2000, Schindler et al. 2005), the timing of stickleback reproduction may also be earlier. Threespine stickleback are capable of iteratively breeding, and if energetic and thermal conditions are suitable individuals may produce multiple broods of eggs in a season (Wootton 1977, Brown-Peterson and Heins 2009)

Given these indications of effects of climate on breeding timing and breeding frequency, our objectives were: (1) to determine if summer water temperature and date of ice breakup control threespine stickleback size structure at the end of the growing season, alone or in combination with their density or the density of their competitors, and (2) to determine whether the timing of stickleback reproduction has become earlier in the season corresponding with a

shift in the timing of lake ice break up. We predicted that early ice breakup and warm temperatures would be associated with earlier breeding and larger size at the end of the growing season, and that competition would depress growth. To test these predictions, we used size-frequency data collected in an Alaskan lake during the summer over five decades, revealing important effects of climate on breeding patterns and demographics.

METHODS

Study site

The Wood River system is a major tributary of the Nushagak River that flows into Bristol Bay in southwestern Alaska (59°20' N, 158°40' W) (Figure 1). Lake Aleknagik, the farthest downstream lake in a chain of five large, interconnected lakes composing the Wood River system, averages 43 m deep with an area of 83 km^2 and is oligotrophic with a short period of productivity during the summer (June-September), followed by ice cover from November through May (Hartman and Burgner 1972). The fish community is comprised of entirely native species. Resident threespine stickleback and juvenile anadromous sockeye salmon are the numerically dominant fishes in the littoral zone; these two species were 45% and 46% of all fish caught in beach seine sampling from 1963-2013, respectively (sampling details below). Other important but less abundant fishes include ninespine stickleback (*Pungitius pugitius*), coastrange and slimy sculpins (*Cottus aleuticus* and *C. cognatus*), and multiple species of whitefish (Coregonidae) in the littoral zone. The primary species of mobile piscivores in the lake are northern pike (*Esox lucius*), rainbow trout (*Oncorhynchus mykiss*), and Arctic char (*Salvelinus alpinus*).

Study organism

Threespine sticklebacks are widely distributed and can be highly abundant, and often express variation in phenotypic and life history traits between freshwater and marine habitats or among locations within a habitat type (Wootton 1984). In the Wood River system, sticklebacks generally mature at age-3, although some large individuals mature at age-2 (Rogers 1977). In Lake Aleknagik, previous observations indicated that sticklebacks spawned in June and July along the lake shoreline on sandy or muddy substrate (Rogers 1977). Male fish build and guard a nest constructed of detritus and macrophyte, and attract females through courtship behavior and spawning coloration. The cycle of nest building and egg guarding may take up to 4 weeks, at which point the male can construct a new nest (Whoriskey and FitzGerald 1994). Young of the year are approximately 6 mm in length at hatching and are first caught in beach seine nets at about 12 mm (Rogers 1977). By mid-July, immature age-1 and most of the age-2 fish migrate to the pelagic areas of the lake, but young of the year stickleback tend to remain in the nearshore environment through August. Most annual growth occurs during July and August, determining their pre-winter size (Rogers 1977). During this time, sticklebacks prey primarily on zooplankton in the limnetic zone, and zooplankton and aquatic and terrestrial insects in the littoral zone (Hovel and Stapleton, *unpublished data*). There are four dominant age classes observed in the lake (ages- 0+, 1+, 2+, and 3+), with a few observed individuals up to 4 years old (Figure 2). Observed movements from onshore (breeding areas) to offshore (feeding area) suggest that fish in both littoral and limnetic zones likely compose a single population, and little to no stream-to-lake migration has been observed in this system. Fish captured in both habitat types demonstrate similar size classes, size at age and plating structure morphology, with fish displaying almost exclusively a partially plated freshwater morph (Rogers 1977). The mean plate number for

littoral zone fish was 12.7 (SD=1.8, n=49), and mean plate number for limnetic fish was 12.1 (SD=1.4, n=51) (Hovel, *unpublished data*).

Fish collection and sample processing

Littoral zone fishes were sampled in Lake Aleknagik using a 30 m beach seine (mesh size = 6 mm) deployed from a boat and manually returned to shore. Ten sites, distributed along the north and south shores of the lake, were sampled approximately every 7 days between June and September from 1963 to 2012. All fishes captured were identified to species, enumerated and measured for fork length (mm) unless the catch was very large, in which case it was randomly subsampled in the field (to retain approximately100 or more sticklebacks for a length distribution) and the remainder was released. Total abundance for each species in the catches was calculated either by the number of fish counted and measured, or by extrapolating the number counted by the percent of the catch retained for a subsample. The sampling was not designed to yield a quantitative population estimate but the catches provided annual indices of abundance when summed across sample locations and dates for the month of July. This month was chosen as the period of the most stable littoral zone abundance; catches included a new cohort of fish, and the seasonal off-shore movement had not occurred.

The otoliths were removed from a subset of individuals spanning the range of fish lengths collected in years 2010, 2011 and 2012, and the number of rings was recorded to determine the age of each fish. Along with the length of each aged fish, these data were used to verify that observed breakpoints in fish size modes correspond to age classes (Figure 2).

Environmental indices

The timing of ice breakup is an indicator of spring warming rates (Magnuson 2000) and the beginning of productivity in the lake (Schindler et al. 2005, Carter and Schindler 2012). The date of lake ice breakup was recorded annually since 1964 at the southeast end of Lake Aleknagik (Figure 3). Vertical profiles of the lake temperature were recorded at six locations distributed longitudinally from the north to the south end of the lake. The temperatures were recorded at 1- m intervals at depths from 60 m to the surface approximately every 10 days between June and early September, using either a bathythermograph or an electronic thermistor (YSI, Yellow Springs, OH). We used the average temperatures from the surface to 20 m depth for June, July and August, as these months capture the range of temperatures during the early, middle, and late summer growing season.

Statistical analyses

Resolving multi-modality—The size structure of threespine sticklebacks in Lake Aleknagik is multi-modal, so it is necessary to distinguish the size classes and treat them individually instead of calculating catch-wide mean lengths. For each sampling date throughout the summer each year, length-frequency distributions for all threespine sticklebacks collected across all sites in the lake were used to describe the dominant size modes for the captured fish. To extract the mean size of each stickleback size mode (location of the peak of the mode, in mm total length) in a statistically robust manner, the mixing model features in statistical program R was applied to each of the length frequency distributions (Varadhan et al. 2011, R Core Team 2014). These models fit a curve to the distributions and identified the location (length, in mm) of the peak the curve for each mode. Each of these modes is interpreted to be an age class or cohort, and the locations of the curve maxima are used as the mean fork length for each size mode.

Trends and predictors for size mode means— Multivariate autoregressive state-space (MARSS) models (Holmes et al. 2013) were used to describe trends in the mean length of multiple size modes for fish captured near the end of the sampling season, on or within a 5-day period of August 10. Environmental (monthly water temperature and ice breakup date) and biological (density of threespine stickleback or juvenile sockeye salmon) covariates were incorporated into the model to test whether they explain variation in mean size over time. Water temperature and day of ice breakup were log-transformed prior to including in the model, and the indices of abundance for threespine stickleback and for juvenile sockeye salmon were obtained by calculating mean abundance for each species in beach seine catches for all sites for the month of July. MARSS models for group processes assume the general equation form of:

$$X_t = X_{t-1} + u + w_t$$

where $w_t \sim \text{MVN}(0, Q)$; the process error in the model, described by term w_t, is drawn from a multivariate normal distribution with a mean of 0. The X matrix is composed of vectors of mean length for age-0 and age-1 size classes of sticklebacks for each year *t*, and in this matrix all size modes can be specified as a single group combining both age classes, or modes can be distinguished as unique for a multivariate response. The *u* term describes the direction and magnitude of the trends over time for either a single trajectory (both groups treated as one) or for two trajectories (treating age-0 and adult sticklebacks as independent trends).

When including covariates, the general form of this model is:

$$X_t = X_{t-1} + C_t c_t + u + w_t$$

where C is a matrix describing covariation between the trends in fish size and the biological and environmental predictors, and c is a matrix of vectors of biological and environmental "predictors" used as model covariates.

We composed a suite of models, with the X matrix specified as either a single group or two groups and with the trends over time, *u,* as either a single trajectory or two. We also included combinations of environmental and biological covariates. Models were run with 2000 independent simulations using randomly selected starting points. Best-fit models were selected using Akaike's Information Criterion (AIC). In ranking model performance, a difference of two or greater units indicated support of one model over competing models. Before implementing these time series models, the threespine stickleback size mode data were confirmed to be appropriate for this model format, as the data were normally distributed and free of trends in residuals, uncorrelated from year to year, and stationary.

Growth rate and cohort recruitment to sampling gear—We calculated growth rates for threespine sticklebacks to test the hypothesis that size at the end of the growing season is driven by rate of growth during the ice free season. Specific growth rate for the age-1 cohort (mean size between 28 and 38 mm in the last week of June) of threespine sticklebacks was calculated by the equation:

$$SGR = \frac{\ln(s_1 - s_0) * 100}{d}$$

where s_0 and s_1 are the initial (first sample of the year) and final (last sample of the year) mean lengths for the age-1 cohort size class, and *d* is the number of days between the first and last sample (Ricker 1979). We used linear models and model selection via AIC to determine whether relationships are present between fish growth rate and fish size at the end of the season, and whether fish growth rate is predicted by environmental or biological covariates. These covariates

include lake water temperature, ice breakup date, and threespine stickleback and sockeye salmon abundance indices.

The sample date where the young of the year cohort first appears in the beach seine nets was calculated for each year. This sample date was used in linear models to determine whether water temperature or ice breakup date predict the timing when age-0 fish are large enough to be captured with the sampling gear.

RESULTS

Each year sampled had at least 4 sample events throughout the summer, and some years had up to 8 beach seine samples collected approximately 7 days apart, yielding 50 – 300 or more fish used to create length frequency distributions. Catch < 50 fish were insufficient to generate length frequency histograms that distinguished size modes, and in these cases we used the most proximate earlier or later sample date to perform mixing model size mode classifications.

The results of the otolith ageing closely matched the locations of the size mode breakpoints; fish determined to be age-0 were 31 mm or below, age-1 fish were between 29 and 50 mm, age-2 fish were between 47 and 72 mm, and fish age-3 and older were > 66 mm (Figure 2). Of the 112 fish aged by examining the otolith, 7 appeared to be age-4, and one age-5. Between 1963 and 2012, Lake Aleknagik exhibited significant trends over time in ice breakup date and water temperature ($p<0.001$) (Figure 3). Over these years, the mean date of ice breakup in the spring advanced by 13 days, and the mean summer epilimnetic temperature increased by 2.3°C (Schindler et al. 2005, Carter and Schindler 2012). In addition to July epilimnetic temperatures (included in Figure 3), mean water temperature also increased significantly over time in June ($p=0.013$) and August ($p<0.001$).

The MARSS model chosen to best describe trends in mean length for threespine stickleback size modes had age-0 and adult (age- and age-2) fish modeled separately and had two uniquely-varying trajectories in the data (Table 1). Over five decades, mean length of the adult cohort has been increasing but mean length of the age-0 cohort has been declining (Figure 4). This model also included the full suite of environmental and biological covariates, though the effects of some, reflected in the estimate values, were small (Table 2). Ice breakup date had a positive effect on the smallest cohort (i.e., an earlier breakup date predicted a smaller mean cohort size), and negative for the adult cohort of age-1 and age-2 fish (an earlier date predicted a larger mean cohort size). Mean June and July epilimnetic water temperature had positive effects on both cohorts, with a stronger effect on the age-0 size class than the adult fish. Indices for juvenile sockeye salmon and for threespine stickleback density had negative effects on mean stickleback size, with a much stronger effect from sockeye salmon density.

To explore the paradoxical decrease in mean size of young of the year fish in warmer years, we visually examined length-frequency histograms in years spanning a range of dates of ice breakup. For example, in consecutive years (1984 and 1985) when ice breakup occurred approximately three weeks apart (May 17 in 1984 and June 8 in 1985), and the age-0 fish first recruited to the sampling gear 16 days earlier in the year with earlier ice breakup (Figure 4). In addition, the cohort of fish below 30 mm in size had a more complex size structure in the year with earlier ice breakup, with an additional size mode present. Thus in the years when the ice left earlier, there was an additional young of year cohort, and this second cohort accounted for the shorter mean length in the age 0 fish. In a logistic regression, ice breakup day significantly predicted whether two young of year size modes were detected in the last sample of the season (1) or whether one size mode was detected (0) ($p<0.003$) (Figure 5). The date when the first age-

0 cohort was captured depended significantly on the date of ice breakup; young of year threespine stickleback were captured earlier in the season in years with an earlier ice breakup date (Figure 6).

In contrast to the trends in size, no significant change was observed in threespine stickleback growth rate between 1963 and 2012 (Figure 7). Linear models poorly fit the data when growth rate was predicted by year (r^2=0.023, p=0.908), and there was also no significant relationship between specific growth rate and ice breakup date (r^2=0.002, p=0.336) or between specific growth rate and July mean epilimnion temperature (r^2=0.006, p=0.268).

DISCUSSION

These analyses revealed changes over time in the size structure of threespine stickleback on August 10 between 1963 and 2012. The multi-modal length-frequency size distributions exhibited two trends in the data: across years, adult fish (age-1 and older, with mean length over 45 mm) were larger in size at the end of the season, while the mean size for the smallest age-0 cohort declined over time. The strongest effects of environmental or biological conditions on both the young of year and adult trends were from date of ice breakup and a competitive effect of juvenile sockeye salmon abundance, with weaker effects of temperature and threespine stickleback abundance. These patterns suggest that the late summer size structure for threespine stickleback is more influenced by the date when the productive period begins in these seasonally-regulated systems than by physiological effects of temperature increases across the range observed here. In this system, juvenile sockeye salmon density depresses conspecific growth in the lake (Schindler et al. 2005), but it is unclear why the effect of juvenile sockeye salmon density was stronger by orders of magnitude than the density effect of threespine stickleback on

stickleback size because they are captured in roughly equal proportions in the littoral zone of the lake. Sockeye salmon productivity is regulated in part by stream/river and ocean conditions as well as lake conditions (Quinn 2005), so it is possible that their per-capita demands on lake resources are unequal to those of the freshwater-resident stickleback.

Young of year cohorts appear earlier in years with early date of ice breakup, suggesting earlier breeding date; as these fish spawn in habitats affected by ice cover, access to these near-shore areas may be one cue to initiate spawning. For these fish, and others in systems with discrete productive periods, a longer growing season with earlier breeding can lead to larger size at the end of the season and greater overwinter survival. However, modifications to the timing of stickleback spawning and larval fish emergence might induce mismatches with other phenological events such as zooplankton blooms or piscivore migrations, and mismatches in predator and prey phenology can lead to poor survival of the predator (Cushing 1982, Gotceitas et al. 1996). The additional cohorts of young of year fish that appear in years with early ice breakup suggest that these fish produce multiple broods when conditions are suitable or the duration of the productive season is long enough to accommodate the inter-spawning interval for these fish. This interval is between 3 and 8 days for female freshwater sticklebacks in Alaska (Brown-Peterson and Heins 2009) and for male sticklebacks the interval may be up to 28 days (Whoriskey and FitzGerald 1994).

Growth rate did not account for increasing mean length for adult sticklebacks sampled at the end of the season, as specific growth rate for adult sticklebacks has not changed over time and has shown no relationship with water temperature. Bioenergetics models predict increases in growth rate with the observed temperature increases in the lake given adequate rations (Hovel et al. *in review*), it is likely that density effects or other processes are masking any temperature

effects on growth. Thus the larger mean size for late-season adult sticklebacks appears to result from extension of the growing season and not from physiological compensations such as increased growth rate.

With their reproductive strategy of seasonal spawning, male nest guarding, and moderately large clutch size, freshwater threespine stickleback fall within an "intermediate" life history strategy (Winemiller and Rose 1992). However, improving understanding of iterative spawning events and the conditions under which threespine sticklebacks can reproduce multiple times, trading off clutch size for spawning frequency, might move this species closer to an "opportunistic" categorization. Species in this category have high potential for population increases, especially if individuals mature early (Winemiller 1989, Winemiller and Rose 1992). Some evidence suggests that warmer temperatures and higher productivity decreases age at maturity for sticklebacks; near the lower latitudinal extent of their range (e.g. Lake Washington), threespine stickleback mature at age 1, and they mature primarily at age 3 in higher latitude lakes like Lake Aleknagik (Rogers 1977, Eggers et al. 1978).

Environmentally-induced changes in the number of breeding events in a season, along with potential effects of body size for over-winter survival, have implications for species abundance, community composition, and trophic relationships over time (Rijnsdorp et al. 2009). Threespine stickleback are the numerically dominant planktivorous fish in many holoarctic lakes, and can make important contributions to an ecosystem through nutrient recycling and other functions (Harmon et al. 2009). They are important prey species for piscivorous fishes, including Arctic char, brown trout (*Salmo trutta*) and cutthroat trout (*Oncorhynchus clarki*), in oligotrophic lakes with simple fish communities (Reimchen 1990, L'Abee-Lund et al. 1992). Threespine stickleback have no direct commercial value, but the species widely overlaps with commercially

exploited Pacific salmon species in habitat and diet in lakes and estuaries (O'Neill and Hyatt 1987, Spilseth and Simenstad 2011). While threespine stickleback are widely used as a model organism in evolutionary ecology, genetics, and behavior (Bell and Foster 1994, Kingsley and Peichel 2007, Huntingford and Ruiz-Gomez 2009), much about their ecological role remains unstudied.

These results also suggest the utility of size-distribution data in making inferences about demographics and life history expression. While work on breeding timing in fishes often demands lethal sampling of either gravid adults or larval fish (Genner et al. 2009, Schneider et al. 2010), length-frequency data may offer a non-lethal method for observing direct effects of modified reproductive strategies. However, meaningfully interpreting the size structures assumes no changes in growth or any recruitment or loss to the population.

We have presented evidence that threespine stickleback modify spawning timing and frequency with corresponding with date of ice breakup, and that end of the season size structure is predicted by ice breakup date, water temperature to a lesser degree, and density effects of sockeye salmon, an abundant competitor of threespine stickleback. Mechanistically understanding the manner in which effects of global climate change might affect species life histories can be as important as the physiological thermal tolerances that are presently often used in landscape-level projections of species range shifts or extirpations (Portner and Farrell 2008, Calosi et al. 2008). We encourage further investigation of flexibility in life history trait expression both for this species across its range and for other abundant fishes.

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Table 4.1. A subset of the full suite of MARSS models run to determine how many unique groups and trajectories, and what environmental and biological covariates, are the most parsimonious and best-fitting models to describe mean size of threespine stickleback size modes on or near August 10 from years 1963-2012. AIC values from model selection are shown.

Number of groups	Number of trajectories	Covariates included	Δ AIC
1	1	None	51.6
1	2	None	46.7
2	1	None	10.2
2	2	None	6.8
2	2	Ice breakup, June temp, July temp, sockeye density	2.1
2	2	Ice breakup, June temp, July temp, sockeye density, threespine stickleback density	0

Table 4.2. Estimate values for environmental or density-dependent covariates included in the MARSS model for two modes of threespine stickleback size.

Covariate	<20 mm size mode	35-50 mm size mode
Ice breakup date	0.587	-0.219
Mean June water temperature	0.277	0.030
Mean July water temperature	0.152	0.089
Sockeye density index	-0.512	-0.311
Threespine stickleback density index	-0.003	-0.017

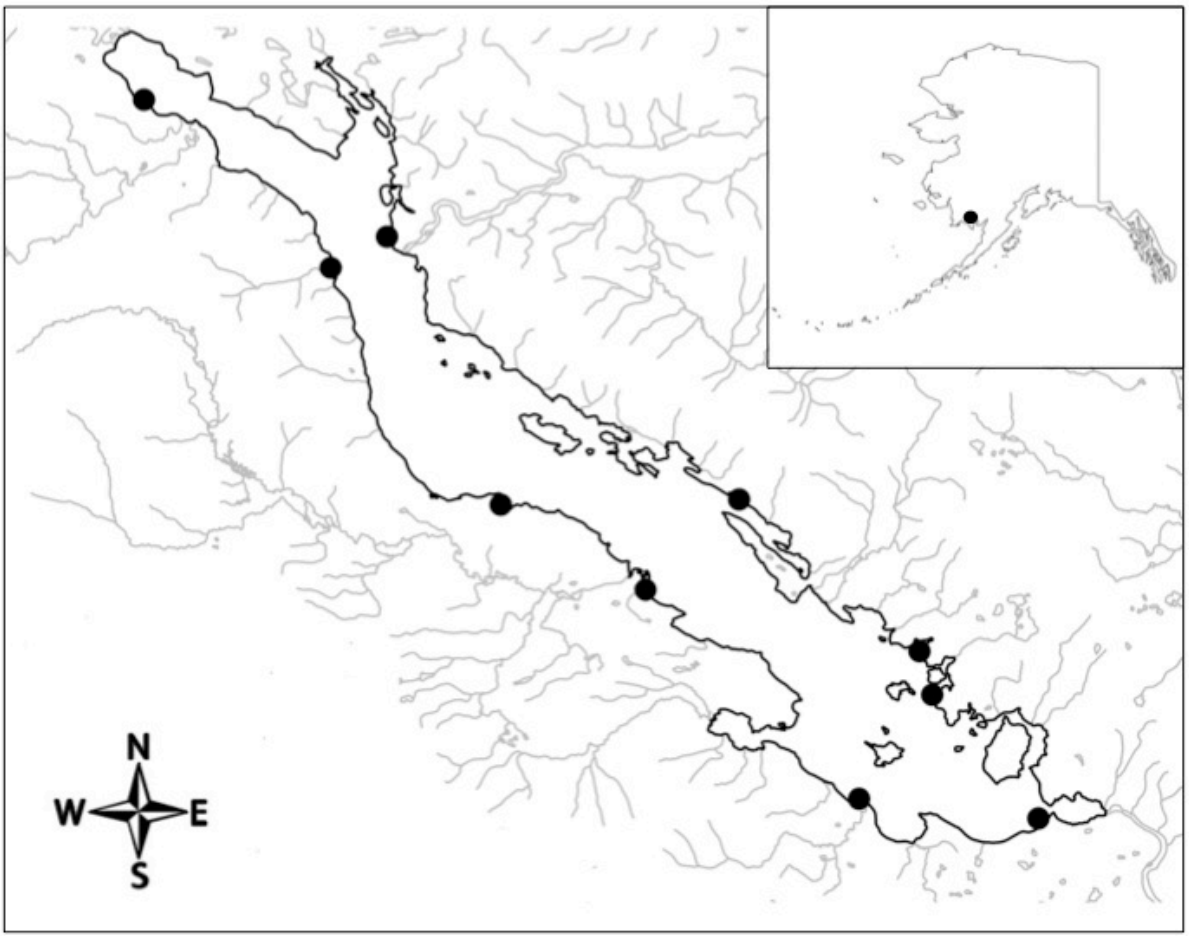

Figure 4.1. Map of study location of Lake Aleknagik, Bristol Bay, Alaska. Black points are sample locations for beach seine collections.

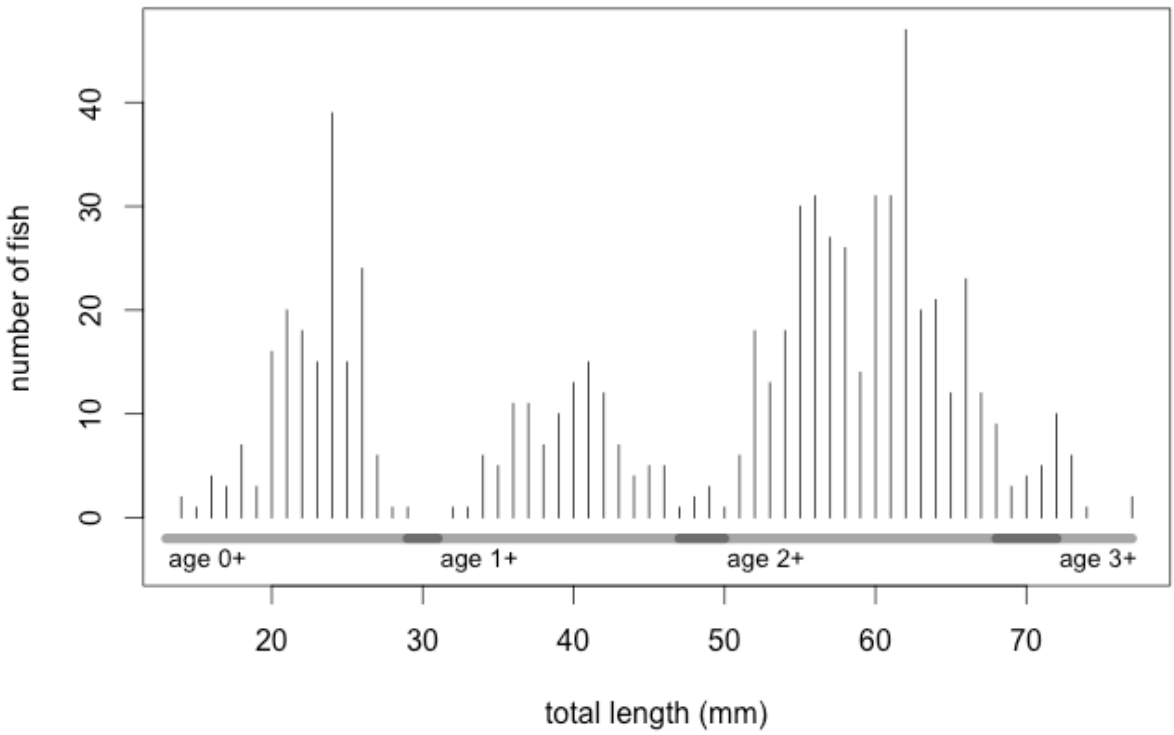

Figure 4.2. Length-frequency histogram of littoral zone threespine stickleback, showing size mode breaks and, beneath, length intervals for stickleback age classes as determined by otolith analysis.

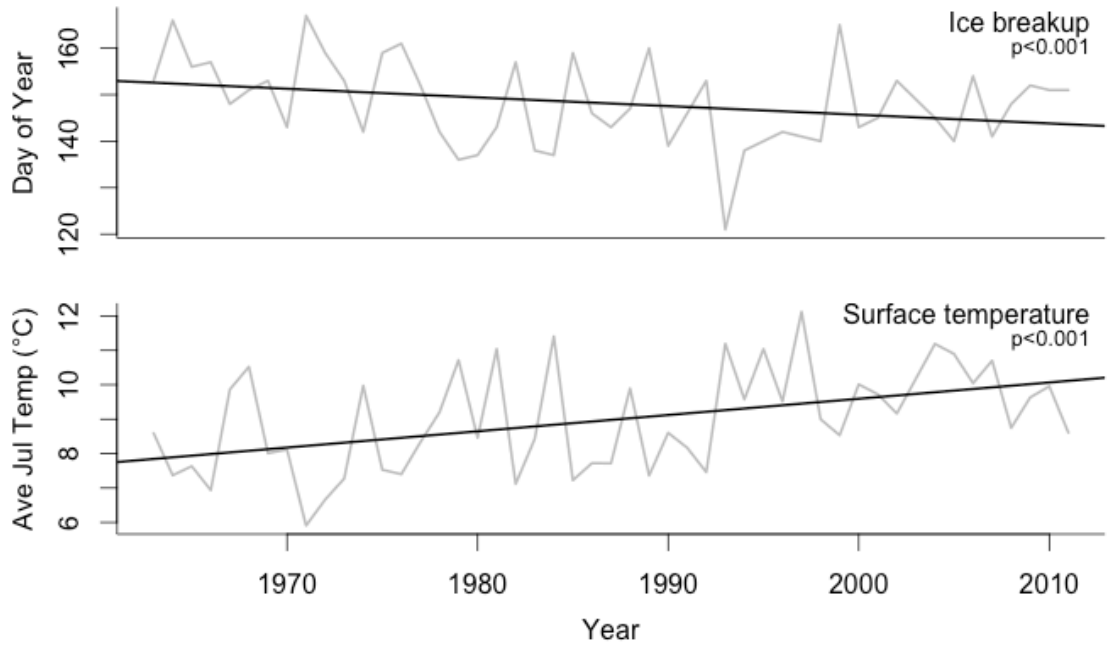

Figure 4.3. Trends over time for date of ice breakup in Lake Aleknagik (top) **and trend over time for mean July epilimnion water temperature** (bottom). Both are significant for linear regression.

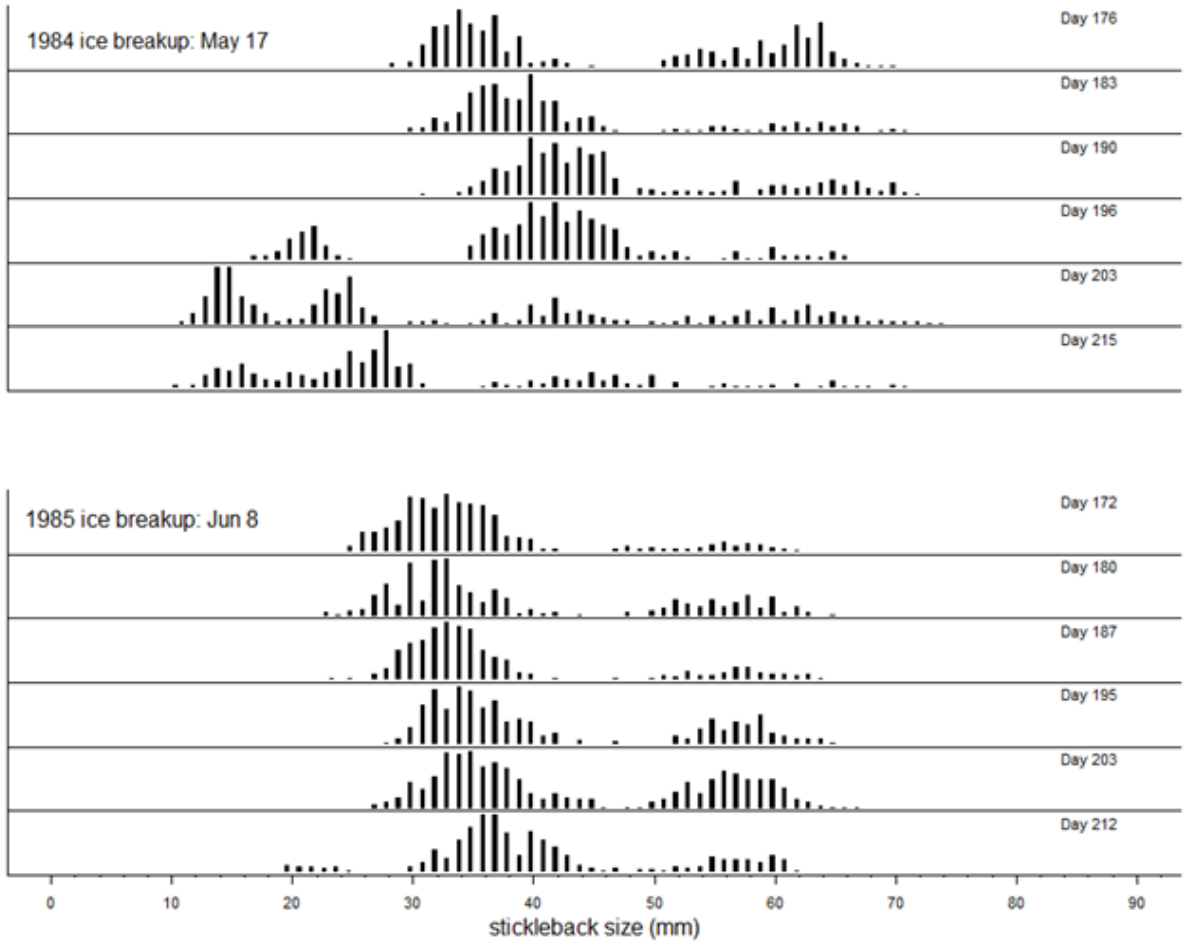

Figure 4.4. Length-frequency histograms for two years selected as representative of years with early and late dates of ice breakup. Two young of year age-0 size modes are evident during the last two samples of the year with early breakup date (top). The age-0 size mode appears in the last sample week of the year with late ice breakup, and no second size mode within this cohort is present (bottom).

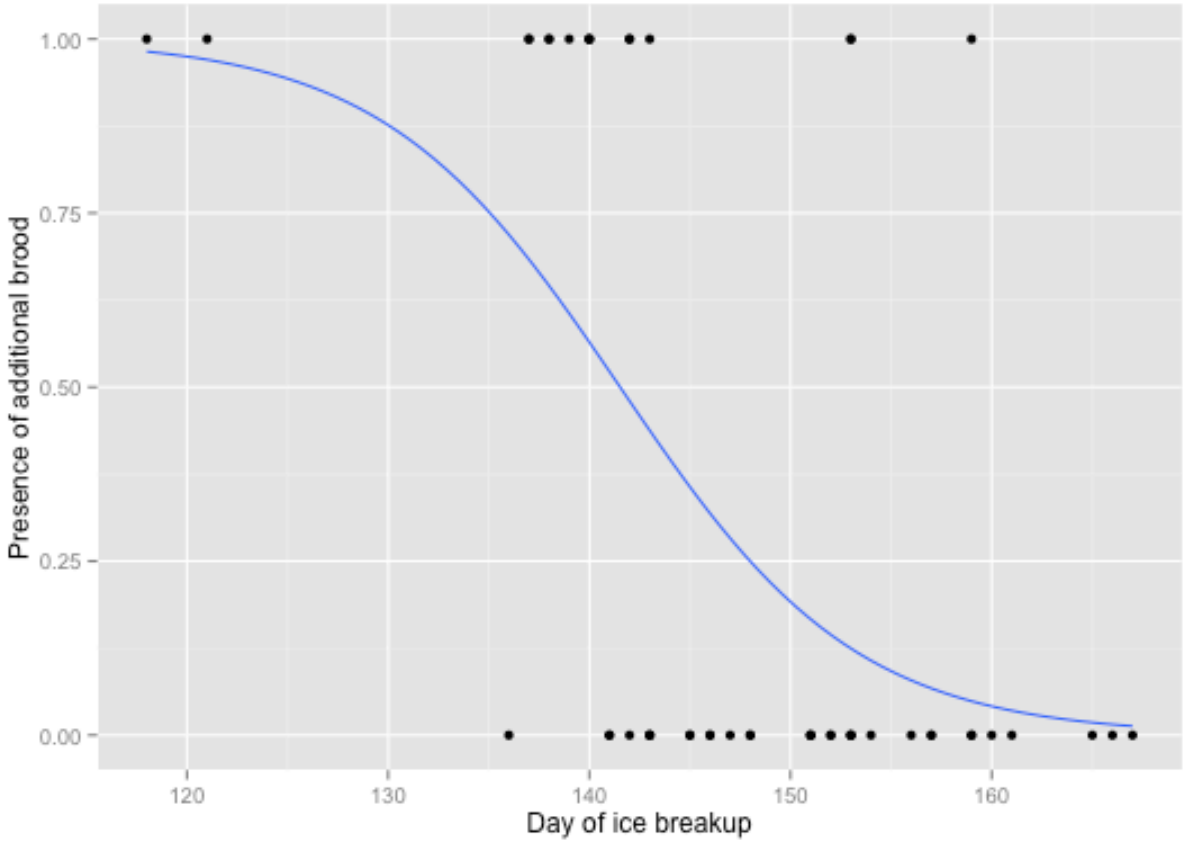

Figure 4.5. Logistic regression of presence (1) or absence (0) of multiple modes of young of year stickleback at end of the season. The relationship is significant ($p<0.003$).

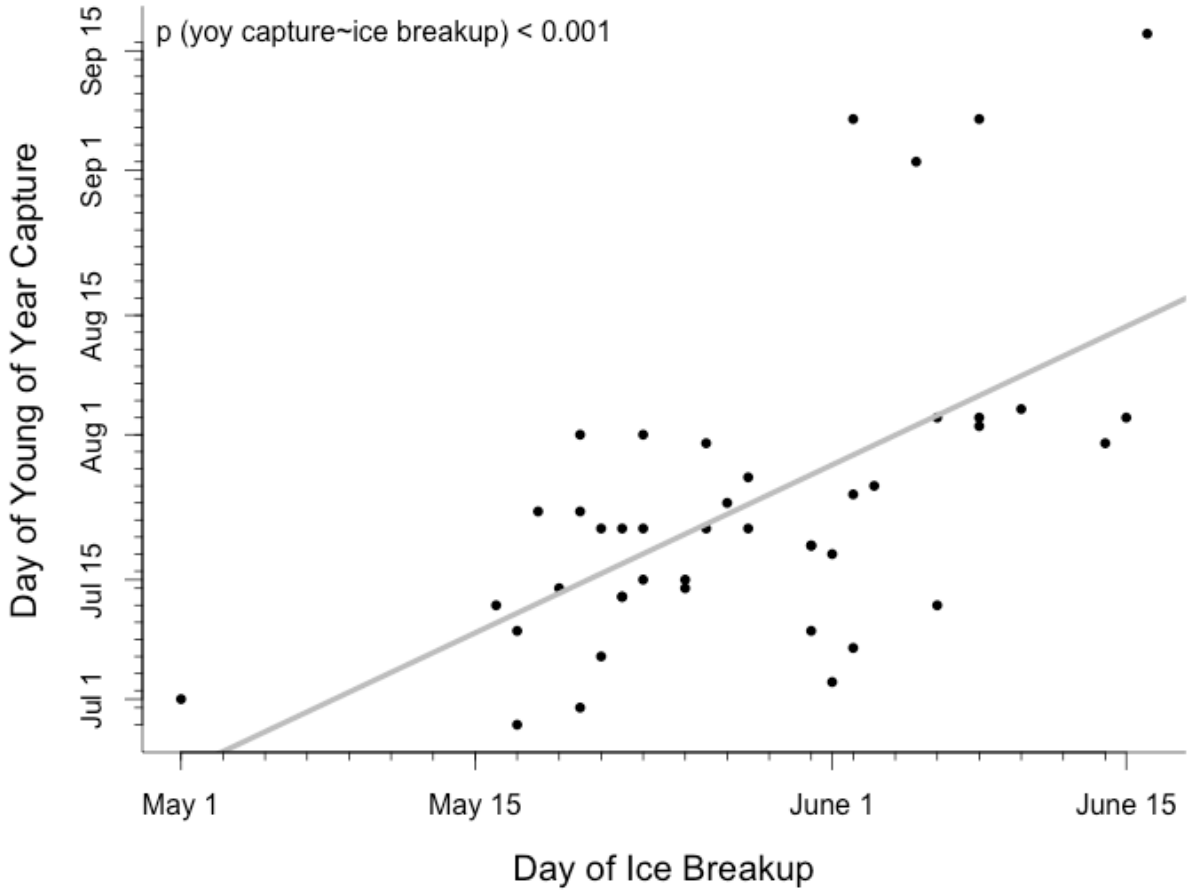

Figure 4.6. Relationship between day when the age-0 cohort first appears in sampling each year and the date of ice breakup. The linear model fitting the data is significant.

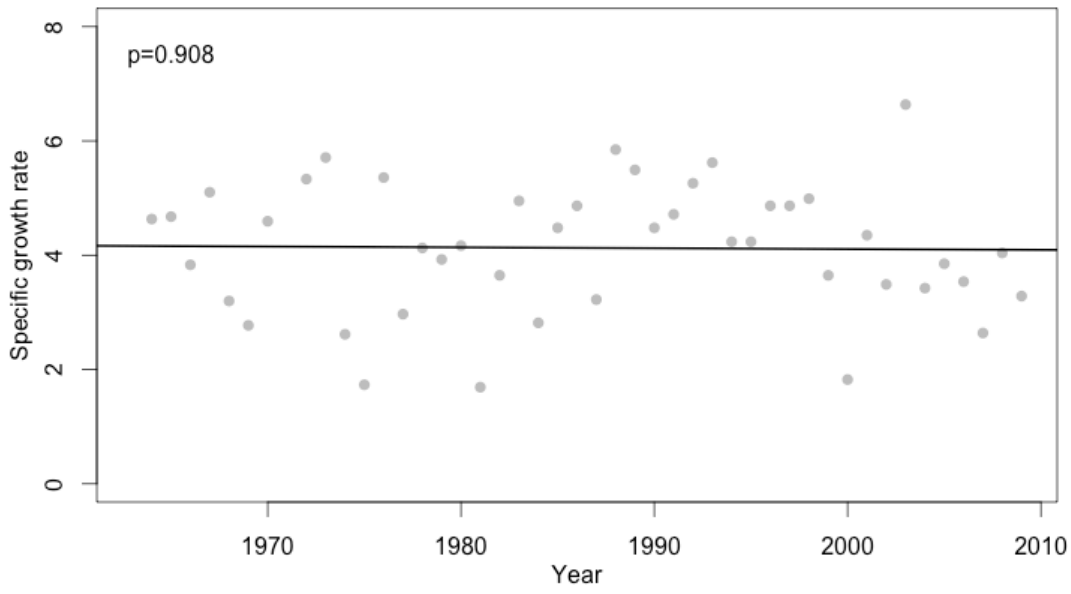

Figure 4.7. Trend over time for specific growth rate for the adult size mode for threespine stickleback. The linear regression is not significant.

APPENDIX A: COLLABORATIONS AND ACKNOWLEDGEMENTS

Chapter 1

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Chapter 2

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Chapter 3

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Chapter 4

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