

Research article

Sub-seasonal correlation between growth and survival in three sympatric aquatic ectotherms

Yoichiro Kanno  ^{1,2}, Seoghyun Kim ^{1,2} and Kasey C. Pregler^{1,2} 

¹Dept of Fish, Wildlife and Conservation Biology, Colorado State Univ., Fort Collins, CO, USA

²Dept of Forestry and Environmental Conservation, Clemson Univ., Clemson, SC, USA

Correspondence: Yoichiro Kanno (yoichiro.kanno@colostate.edu)

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Animals experience seasonally changing conditions in temperate regions, thus population vital rates change seasonally. However, knowledge is lacking on patterns of seasonal correlation between growth and survival in sympatric ectotherms, and this knowledge gap limits our understanding of environmental change impacts on animal populations and communities. Here, we investigated sub-seasonal (two-month intervals) correlation between growth and survival in three stream fishes (bluehead chub *Nocomis leptoccephalus*, creek chub *Semotilus atromaculatus* and mottled sculpin *Cottus bairdii*) in South Carolina, USA, via a mark–recapture survey over 28 months. We found that patterns of temporal correlation between the population vital rates differed among the sympatric species. Growth increased and survival decreased with water temperature in two eurythermal species, resulting in negative correlation between growth and survival. Growth peaked in sub-seasons with an intermediate water temperature range in a third stenothermal species, while survival decreased with water temperature for this species too. Consequently, there was not significant negative or positive correlation between sub-seasonal growth and survival in the stenothermal species. Body condition (weight at given length) decreased from May through November in all three species, providing a potential physiological explanation for why survival rates were lower during this period. Negative correlation among population vital rates stabilizes population size over time and buffers animal populations from environmental change because the vital rates are not affected simultaneously in the same direction, indicating some degree of resiliency in the face of climate changes in the two eurythermal species. However, such a demographic mechanism of resiliency could be maintained so long as climate warming does not exceed optimal growth temperature, above which negative correlation between growth and survival may no longer be maintained.

Keywords: Bayesian analysis, Cormack–Jolly–Seber model, demography, mark–recapture, native fish

Introduction

Animals are subject to seasonally changing environments in temperate regions. This is characterized by temporally shifting temperature and precipitation patterns, which affect food resources (Svoboda et al. 2019), habitat availability (Froese et al. 2017) and competitive interactions (Saavedra et al. 2016). Consequently, population vital rates such as survival and growth change within a year (Vøllestad and Olsen 2008, Rockwell et al. 2017, Keevil et al. 2021). Much less is understood about how vital rates covary and what abiotic conditions determine the correlation (Fay et al. 2020, 2022, Paniw et al. 2020). Information on correlation between vital rates is scant in ectotherms (but see Letcher et al. 2015) despite their apparent sensitivity to seasonality, which is inherently characterized with changes in ambient temperature. Knowledge on seasonal correlation between vital rates is needed not only to understand dynamics of seasonally structured animal populations but also to predict population trajectories in a changing environment for conservation planning (Lachish et al. 2020, Paniw et al. 2020).

Several patterns of temporal correlation between survival and growth are conceivable in animals. Temporal correlation between survival and growth would be positive if one supports the other. For example, animals grow better in periods with abundant food resources, and consequently could survive better (Fay et al. 2020, Paniw et al. 2020). However, temporal correlation between survival and growth could decrease in some circumstances. Somatic body growth is minimal in unfavorable conditions (e.g. winter) (Olsen et al. 2006, Keevil et al. 2021), but animals may maintain survival rates comparable to or even higher than those in other periods via behavioral and physiological adaptation (Voituron et al. 2002, Turbill et al. 2011, Letcher et al. 2015). In ectotherms, optimal temperature ranges for growth are lower than upper lethal limits because their energetic demand increases with temperature and energy intake may not catch up with the metabolic demand (Hoffmann et al. 2013, Huey and Kingsolver 2019), which could decouple temporal correlation between growth and survival. These two vital rates could also covary negatively over time. For example, periods with active foraging for accelerated growth may be characterized with high mortality rates due to predation (Verdolin 2006, Urban 2007) or increased competition (Elliott 1994, Vincenzi et al. 2016). Characterizing the pattern of correlation between growth and survival and its environmental determinants is important for forecasting population vulnerability to environmental changes (van de Pol et al. 2010, Paniw et al. 2020, Fay et al. 2022). Positive correlation would amplify demographic effects of adverse conditions but expedite a population recovery after disturbances, leading to more volatile population trajectories over time. Conversely, negative correlation would stabilize population size over time because a negative effect on one vital rate is counteracted by a positive on another vital rate.

Patterns of correlation in population vital rates likely differ among sympatric species. Animal communities are typically

composed of species with different ecological characteristics, and the species may respond differently to seasonal environmental changes (Elmqvist et al. 2003). Animals are classified as stenothermal (species only capable of living with a narrow temperature range) or eurythermal (species capable of tolerating a wide range of temperatures) (Somero 2005, Logan and Buckley 2015). Water temperature regulates the function of stream fishes, the subject of this study, and warming climate will affect populations of a wide range of stream fishes but to different degrees (Lynch et al. 2016). In addition, stream fishes have different flow requirements, and some species are more sensitive to seasonality in flows than others (Freeman et al. 2022). However, comparisons of seasonal correlation in population vital rates among sympatric species have been hampered due partly to challenges of collecting demographic data on multiple species at seasonal intervals over a sufficiently long time period.

In this paper, we investigated sub-seasonal (two-month intervals) correlation between growth and survival, and water temperature and flow effects on these population vital rates in three aquatic ectotherms (i.e. fishes) in a temperate stream by conducting a mark–recapture survey in a 28-month period. Although seasons are a convenient classification of months in a year, we chose to characterize growth and survival at two-month intervals because some key life events such as reproduction occur at a finer scale than a season (Kim and Kanno 2020). To understand the ecological mechanism of correlation between growth and survival, we also sub-seasonally characterized body condition, defined here as body weight at given length.

Material and methods

Study area and species

We conducted this study in Indian Creek in the Clemson University Experimental Forest located in the upper Piedmont region of South Carolina, USA (34°44'32"N, 82°51'05"W). Indian Creek is a second-order, perennial stream with a mean wetted width of 2.6 m under base flow condition and a well-forested riparian zone. Stream habitat was characterized by sequences of riffles and pools, and substrate was predominantly gravel, pebble and cobble. The study area was 740 m in stream length, with the downstream boundary located upstream of Lake Hartwell. Because our study species were primarily lotic, we considered that immigration and emigration was negligible and the study area was functionally isolated. In fact, fish movement is generally limited in our study area (Terui et al. 2021).

Our mark–capture study focused on bluehead chub *Nocomis leptcephalus*, creek chub *Semotilus atromaculatus* and mottled sculpin *Cottus bairdii*, based on their high abundance. Bluehead chub and creek chub (Leuciscidae) are more taxonomically and ecologically similar to each other than to mottled sculpin. Bluehead chub and creek chub are more abundant in pools than in riffles. Bluehead

chub require silt-free gravel and pebble substrate for spawning (Bolton et al. 2015). Creek chub is the most tolerant of environmental degradation among the three study species and are opportunistic feeders (i.e. insectivores–carnivores) (McCormick et al. 2001, Bramblett et al. 2005). Mottled sculpin (Cottidae) primarily occurs in riffles of clear streams and require cooler stream temperatures than bluehead chub and creek chub (McCormick et al. 2001). The study area is located at the southernmost limit of this species' native range. Based on their temperature requirements, mottled sculpin are stenothermal species, whereas bluehead chub and creek chub are eurythermal species (Lyons et al. 1996, McCormick et al. 2001). In Indian Creek, bluehead chub spawn between April and June (Kim and Kanno 2020) and its spawning season overlaps greatly with creek chub. Mottled sculpin spawn earlier than the other two study species, and their eggs were observed on the underside of rocks in March in Indian Creek. Based on ecological characteristics of our study species, we predicted that sub-seasonal patterns of survival and growth would be more similar between bluehead chub and creek chub, relative to mottled sculpin. Other species present in Indian Creek were yellowfin shiner *Notropis lutipinnis* (common), striped jumprock *Moxostoma rupicartes* (less common), northern hogsucker *Hypentelium nigricans* (rare) and redbreast sunfish *Lepomis auritus* (rare). No aquatic predators (e.g. trout and bass) were present in Indian Creek.

Field sampling

To characterize sub-seasonal patterns of survival and growth, we conducted mark–recapture sampling in the 740 m study area between November 2015 and March 2018 at an interval of two months (mean = 61 days (range = 48–70)). An average window of four days was required for each sampling occasion (range = 1–10 days). The study area was divided into 20-m sections, which were sampled in an upstream direction on each sampling occasion by backpack electrofishing units (Smith Root Model LR-24; and Halltech Aquatic Research Inc. Model HT-2000) using a two-pass depletion approach. We operated electrofishing with 300–400 V and 30–60 Hz with DC or pulsed-DC settings. Once captured, fish were held in a bucket separated by section and pass until processing.

We marked all captured fish ≥ 60 mm in total length (TL) for bluehead chub and creek chub and ≥ 50 mm TL for mottled sculpin with 8-mm passive integrated transponder (PIT) tags (Oregon RFID; Biomark), following the procedure described in Cary et al. (2017). We used different minimum TL among the species because mottled sculpin were smaller in body length than the other two species (Table 1). We measured TL (mm) and weight (g) of all marked and recaptured fish before they were returned to the section of capture alive. Across 15 sampling occasions between November 2015 and March 2018, we uniquely tagged a total of 429 individuals of bluehead chub, 664 individuals of creek chub and 928 individuals of mottled sculpin. We recorded water temperature (°C) hourly and level (m) daily in a shallow pool.

Table 1. Summary of mark–capture data collected between November 2015 and March 2018 in Indian Creek. Mark–recapture surveys were conducted every two months for a total of 15 sampling occasions; n = number of individuals uniquely marked with PIT tags.

	Total length (mm)				n	Total no. of captures
	Mean	SD	Min	Max		
Bluehead chub	91.65	23.45	60	185	429	986
Creek chub	93.23	24.01	60	190	664	1416
Mottled sculpin	64.36	9.30	50	90	928	1761

Data analysis

We investigated the direction and strength of temporal correlation between growth and survival in each study species. Growth and survival were individually analyzed in relation to mean water temperature and level to evaluate whether the abiotic factors explained temporal correlation between growth and survival. Finally, we examined relationships between growth, survival and body condition to elucidate ecological mechanisms to explain temporal variation in growth and survival.

Growth

Body growth was estimated based on TL between two consecutive occasions of capture. For species s and sampling interval t , we modeled TL of individual i of species s on occasion t ($TL_{i,t}$) as a function of its TL on occasion $t - 1$ ($TL_{i,t-1}$):

$$TL_{i,t} \sim Normal (\alpha 0_{s[i],t} + \alpha 1_{s[i],t} TL_{i,t-1}, \sigma^2) \quad (1)$$

where $\alpha 0_{s[i],t}$ is an intercept, $\alpha 1_{s[i],t}$ is a slope and σ^2 is a residual. Because $TL_{i,t-1}$ was centered by mean divided by standard deviation (SD) across occasions for each species (i.e. $TL_{i,t-1}$ of average-sized fish = 0), the intercept $\alpha 0_{s[i],t}$ was the predicted TL of an average-sized individual of species s on occasion t . Predicted growth of species s and occasion t was then $\alpha 0_{s[i],t}$ minus the average TL of each species (Table 1). Although we were primarily interested in growth rates in TL between sampling occasions, we did not directly use them as the response variable because $TL_{i,t-1}$ would then appear on both sides of the equation and this approach is known to induce spurious correlations between response and predictor variables (Kenney 1982, Brett 2004). We report predicted growth over 60 days to account for different sampling intervals and assumed that growth occurred linearly over days. We also considered a more parsimonious model in which the slope varied by species alone instead of species and time ($\alpha 1_{s[i]}$ instead of $\alpha 1_{s[i],t}$), but this model had a higher deviance information criteria (DIC) value (5470.04) than model 1 (5431.12) and thus was not selected.

We further investigated whether variation in growth among occasions would be explained by mean water temperature and level in a hierarchical model:

$$\alpha 0_{s[i],t} \sim Normal (\gamma 0_s + \gamma 1_s Temp_t + \gamma 2_s Temp_t^2 + \gamma 3_s Level_t, \varepsilon^2) \quad (2)$$

where γ_0 is an intercept, γ_1 is a linear effect of temperature ($Temp_t$), γ_2 is a quadratic effect of temperature ($Temp_t^2$) and γ_3 is a linear effect of water level ($Level_t$) for species s , and ϵ^2 is a residual. We included the quadratic term of temperature because exploratory analysis suggested that there would likely be a unimodal relationship between temperature and growth in mottled sculpin. Water temperature and level were standardized by mean divided by SD prior to analysis. From model 2, we sought a more parsimonious model for each species by dropping effects that were not statistically significant, one at a time. Statistical significance was based on 95% credible intervals (CRI) that did not overlap with 0. In this study, growth refers to somatic growth for the most part because the study species typically reach sexual maturity at body sizes larger than the mean TL recorded in this study and a majority of individuals were immature (Table 1) (Jenkins and Burkhead 1994, Grossman et al. 2006, Kim et al. 2020).

Growth models were analyzed using a Markov chain Monte Carlo (MCMC) method in Program JAGS (Plummer 2017) called from R program (www.r-project.org) with the jagsUI package. Regression coefficients (α 1, γ 's) were modeled as fixed effects, and diffuse priors were used in the Bayesian approach. Posterior distributions of model parameters were characterized by taking every 5th sample from 5000 iterations of three chains after a burn-in period of 5000 iterations. Model convergence was checked by visually examining plots of the MCMC chains for good mixture as well as confirming that the R-hat statistic was less than 1.1 for all model parameters (Gelman and Hill 2007).

Survival

We estimated survival probability between sampling occasions using Cormack–Jolly–Seber (CJS) models (Lebreton et al. 1992) in the Bayesian hierarchical approach (Kéry and Schaub 2012). We assumed that individual i of species s survived from occasion t to occasion $t+1$ with a species-specific, interval-specific survival probability, ϕ , for species s and occasion t :

$$z_{i,t+1} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} \phi_{i,t}) \quad (3)$$

$$\text{logit}(\phi_{i,t}) = \beta_0_{s[i],t} + \beta_1_{s[i]} TL_{i,t-1} \quad (4)$$

The latent state variable was binary, where $z_{i,t} = 1$ if individual i was alive on occasion t , and 0 if dead. For each individual, survival probability was modeled between its first capture occasion and the final sampling occasion (i.e. March 2018). We modeled survival probability as a function of TL, which was again standardized by mean, and $\beta_0_{s[i],t}$ was an intercept for species s on occasion t , and $\beta_1_{s[i]}$ was an effect of TL on survival probability for species s to which individual i belongs. Consequently, the intercept $\beta_0_{s[i],t}$ was the predicted survival probability of an average-sized individual of species s on occasion t on the logit scale. We did not include quadratic

effects of TL on survival because our preliminary analysis did not find evidence for these effects. We accounted for different sampling intervals by using $\phi_{i,t}^{60/n.days}$, where n.days refers to the number of days between two consecutive sampling occasions. We let the TL effect to be time constant ($\beta_1_{s[i]}$) because a model with a time-varying TL effect (i.e. $\beta_1_{s[i],t}$) had a higher DIC value (12 284.60) compared to model 4 (11 887.14).

We used the growth models ('Growth' section) to predict TL on occasions when individuals were not captured, because CJS models did not allow missing TL values as a predictor. Missing TL values were imputed in two ways. When data were missing between two capture occasions, TL were linearly interpolated by using average sub-seasonal growth rates as a weight for each species. For example, assume that an individual of a species was 70 mm in TL on the first occasion, was not detected on the second occasion, and was 100 mm in TL on the third occasion. Further assume that this species grew, on average, twice as long between the first and second occasions, relative the interval between the second and third occasions. Then the predicted TL of this individual on the second occasion would be 90 mm. From the last capture occasion onward, we used the growth models to predict TL on subsequent occasions because CJS models survival probability of individuals from their first capture occasions until the final sampling occasion, unless mortality of individuals was known from electrofishing and handling. Predicted TL was capped at the maximum TL observed in each species (Table 1).

In addition, we modeled temporal variation in survival as a function of water temperature and level:

$$\beta_0_{s[i],t} \sim \text{Normal}(\delta_0_s + \delta_1_s Temp_t + \delta_2_s Level_t, \eta^2) \quad (5)$$

where δ_0_s is an intercept, δ_1_s is an effect of temperature ($Temp_t$) and δ_2_s is an effect of water level ($Level_t$) for species s , and η^2 is a residual. Water temperature and level were standardized by mean divided by SD. From model 5, we dropped covariate effects that were not statistically significant (95% CRI not overlapping with 0) to develop a more parsimonious model for each species.

Because capture is imperfect in electrofishing surveys, we modeled capture probability ($p_{i,t}$) of individual i of species s on occasion t using TL again as a covariate:

$$y_{i,t} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} p_{i,t}) \quad (6)$$

$$\text{logit}(p_{i,t}) = \omega_0_{s[i],t} + \omega_1_{s[i]} TL_{i,t} \quad (7)$$

where $y_{i,t}$ is the capture-history data (1 if captured, 0 if not) of individual i on occasion t , $\omega_0_{s[i],t}$ is a species- and time-specific intercept, and $\omega_1_{s[i]}$ is a species-specific effect of TL on capture probability. Total length was standardized by

mean divided by SD, so that $\omega_{0,s|t}$ is the capture probability of average-sized individuals of species s on occasion t on the logit scale. Similar to growth models, we fit survival models in Program JAGS by specifying regression coefficients (β_1 , δ 's, ω 's) as fixed effects and using diffuse priors.

Relationships among growth, survival and body condition

We used a simple linear regression to examine the relationship between predicted mean sub-seasonal growth and survival for each species, and whether body condition explained temporal patterns of growth and survival. Body condition of individuals was inferred as weight at length, and for each species we fit $\log_{10}(\text{weight}) = a + b \times \log_{10}(\text{TL})$ to predict weight at given total length (Blackwell et al. 2000). Body condition

was $\frac{\text{measured weight} - \text{predicted weight}}{\text{predicted weight}}$, so that individuals of the average body condition would have a value of 0, with negative values indicative of poorer body condition and positive values indicative of better body condition. We used an analysis of variance (ANOVA) to test whether body condition differed by sampling occasion in each species. Finally, we regressed sub-seasonal mean growth rate and survival probability against changes in mean body condition in the same sampling intervals. Statistical significance was set at $\alpha = 0.05$ in simple linear regression and ANOVA analysis.

Results

During the 28-month study period, we recaptured at least once 254 out of 429 individuals (59%) released in bluehead chub, 365 of 664 individuals (55%) in creek chub and 444 of

928 individuals in mottled sculpin (48%). Individuals were recaptured up to 10 times in bluehead chub, 9 times in creek chub and 8 times in mottled sculpin. Average TL of individuals across the sampling occasions was 91.65 mm in bluehead chub, 93.23 mm in creek chub and 64.36 mm in mottled sculpin (Table 1).

Water temperature and level

Water temperature showed seasonal patterns with its peak in July and August and trough in December and January (Fig. 1). Daily mean temperature ranged 1.4–23.6°C. Sub-seasonal mean temperature between two-month sampling occasions ranged 8.9–22.6°C (mean = 15.1). Water level did not clearly show seasonal patterns and was relatively stable over time (Fig. 1). Short-term increases in water level were due to high precipitation events and lasted a few days. Sub-seasonal mean water level ranged 15.4–20.4 cm (mean = 17.6). Sub-seasonal water temperature and level were weakly negatively correlated with each other (Pearson's $r = -0.39$).

Growth

Sub-seasonal patterns of growth were similar between bluehead chub and creek chub, which differed markedly from mottled sculpin (Fig. 2). Body growth was high between March and September in bluehead chub and creek chub, with negligible growth rates between November and March. Growth rate was highest between May and July 2017, when an average-sized bluehead chub (91.65 mm TL) grew to attain a mean TL of 101.82 mm (95% CRI: 98.99–104.54) and an average-sized creek chub (93.23 mm TL) attained a mean TL of 106.27 mm (95% CRI: 104.45–108.00). In

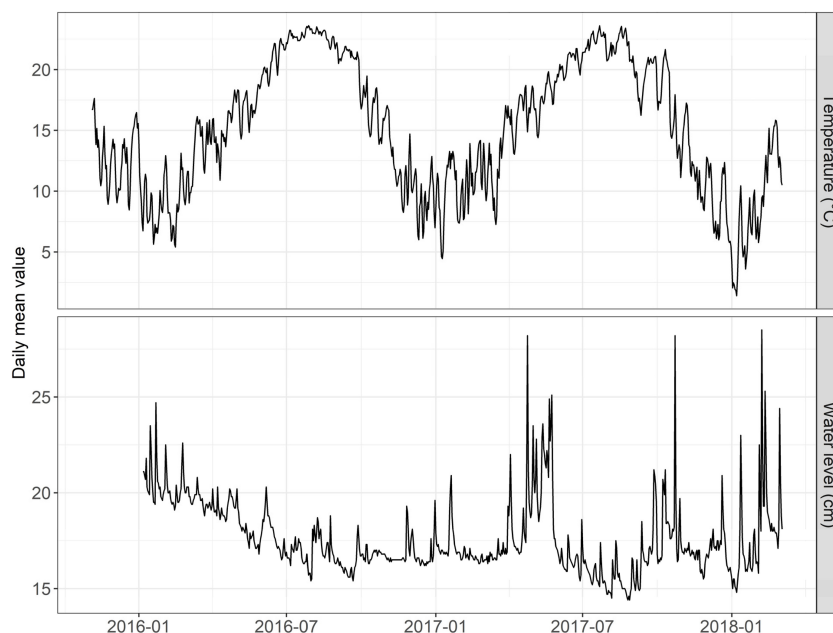


Figure 1. Mean daily water temperature and level during the project period (11 November 2015–4 March 2018). A water level logger was installed between the first and second sampling occasion, and data were not available until 5 January 2016.

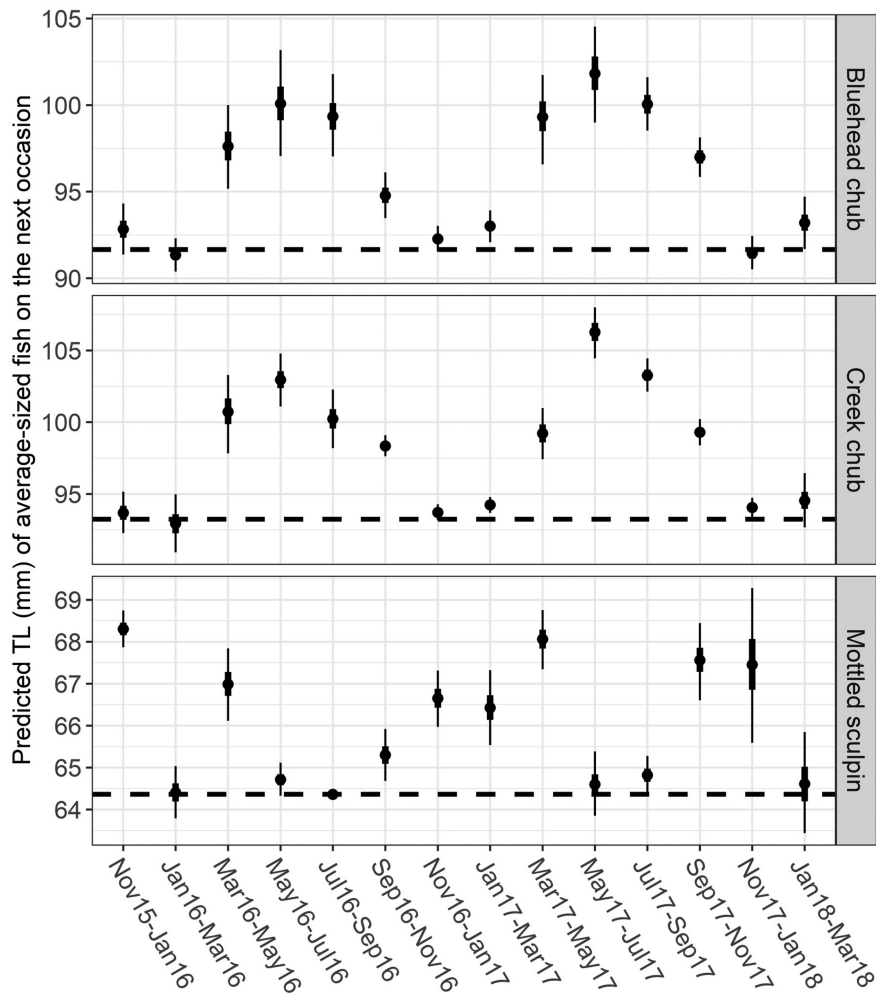


Figure 2. Model-predicted total length (TL in mm) of average-sized fish on the next sampling occasion in bluehead chub (average = 91.65 mm), creek chub (average = 93.23 mm) and mottled sculpin (64.36 mm). Horizontal dashed lines indicate average body size. Posterior mean values are shown by dots with 50% (thick lines) and 95% (thin lines) credible intervals.

mottled sculpin, growth was negligible between May and September, and high growth occurred in November–January and March–May. The highest growth occurred between November 2015 and January 2016, when an average-sized mottled sculpin (64.36 mm TL) grew to attain 68.30 mm (95% CRI: 67.87–68.74).

Body growth increased linearly with water temperature in bluehead chub and creek chub, and there was a quadratic relationship between growth and temperature in mottled sculpin (Fig. 3). The effect of water temperature on mean growth (γ_1 in model 2) was significantly positive in bluehead chub (mean = 3.26; 95% CRI = [1.90, 4.69]) and creek chub (mean = 3.77; 95% CRI = [2.27, 5.29]). The quadratic term of water temperature (γ_2 in model 2) was significant in mottled sculpin (mean = -1.36; 95% CRI = [-2.45, -0.28]), resulting in the highest growth rates occurring when sub-seasonal mean water temperature ranged 12–16°C (Fig. 3). The effect of water level on growth was not significant in any species.

Survival

Sub-seasonal patterns of survival were similar among the three species (Fig. 4). The posterior mean probability of survival was < 0.80 between May and November in both years across all three species, whereas it ranged between 0.80 and 0.95 in cooler sub-seasons. The effect of water temperature on mean survival (δ_1 in model 5) was significantly negative in bluehead chub (mean = -1.00; 95% CRI = [-1.91, -0.35]), creek chub (mean = -0.56; 95% CRI = [-1.35, -0.06]) and mottled sculpin (mean = -0.50; 95% CRI = [-0.88, -0.18]) (Fig. 5). Water level did not significantly affect survival probability in any species.

Survival probability decreased significantly with TL in bluehead chub ($\beta_1 = -0.25$; 95% CRI = [-0.42, -0.18]), creek chub ($\beta_1 = -0.24$; 95% CRI = [-0.39, -0.10]) and mottled sculpin ($\beta_1 = -0.30$; 95% CRI = [-0.43, -0.17]). Capture probability increased significantly with TL in bluehead chub ($\omega_1 = 0.16$; 95% CRI = [0.01, 0.30]), creek chub

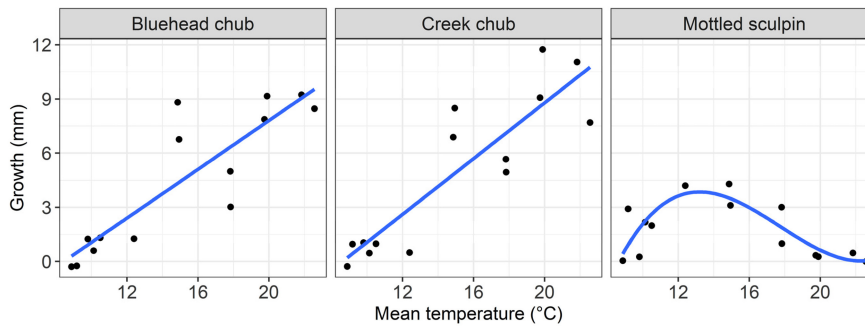


Figure 3. Model-predicted mean growth rate in total length (mm) of averaged-sized fish and mean water temperature (°C) over two months. Average total length was 91.65 mm in bluehead chub, 93.23 mm in creek chub and 64.36 mm in mottled sculpin. Growth increased significantly with water temperature in bluehead chub and creek chub, and a quadratic term of water temperature affected growth significantly with peak growth in an intermediate temperature range in mottled sculpin.

($\omega_1 = 0.21$; 95% CRI = [0.08, 0.35]) and mottled sculpin ($\omega_1 = 0.51$; 95% CRI = [0.39, 0.63]).

Relationships among growth, survival and body condition

There was a significantly negative relationship between sub-seasonal growth and survival in bluehead chub ($p = 0.003$) and creek chub ($p < 0.001$), but not in mottled sculpin ($p = 0.179$) (Fig. 6). This species-specific pattern was because temperature affected growth positively and survival negatively

in bluehead chub and creek chub, but growth of mottled sculpin had a unimodal relationship with temperature (Fig. 3, 5).

Body condition of fish differed significantly among sampling occasions in all three species (ANOVA: $p < 0.001$). Body condition of all species was typically best in May and declined through November, and improved from November to May (Supporting information). In mottled sculpin, both growth and survival were higher in sub-seasonal intervals in which their body condition improved ($p < 0.01$) (Fig. 7). Survival of bluehead chub was also higher when body condition improved ($p < 0.001$), suggesting that body condition was a predictor of these vital rates in some but not all cases. Changes in body condition did not significantly affect growth or survival of creek chub.

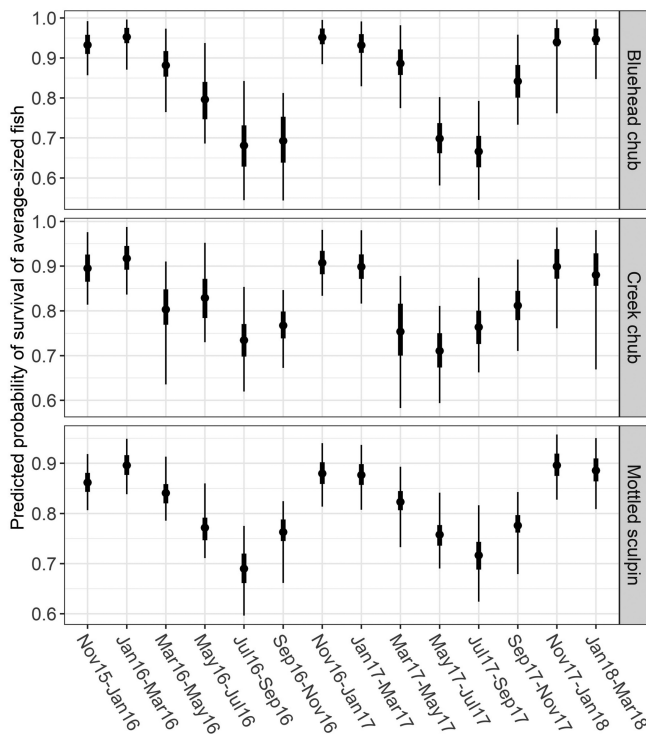


Figure 4. Predicted survival probability of average-sized fish in bluehead chub (average = 91.65 mm), creek chub (average = 93.23 mm) and mottled sculpin (64.36 mm) based on a Cormack–Jolly–Seber model. Posterior mean values are shown by dots with 50% (thick lines) and 95% (thin lines) credible intervals.

Discussion

We found negative correlation between growth and survival in two eurythermal species (bluehead chub and creek chub), where individuals grew more but had lower survival in warmer sub-seasons. The similar patterns of correlation between the two eurythermal species were expected based on taxonomic and ecological characteristics, which differed from a third stenothermal species (mottled sculpin). In the stenothermal species, growth was maximized at an intermediate temperature range and this response decoupled seasonal correlation between survival and growth. Different patterns of correlation between population vital rates among species triggered by their responses to water temperature indicate that climate warming will affect sympatric species differently with consequences on community composition and dynamics.

Sub-seasonal changes in body condition of fish offer an insight into temporal variation in growth and survival. Individuals grew better (mottled sculpin) or were more likely to survive (bluehead chub and mottled sculpin) when mean body condition improved from one sub-seasonal to the next (November through May). These results are likely due to sub-seasonal food availability and bioenergetic demand of ectotherms. Stream benthic macroinvertebrate production increases from winter to spring in temperate streams

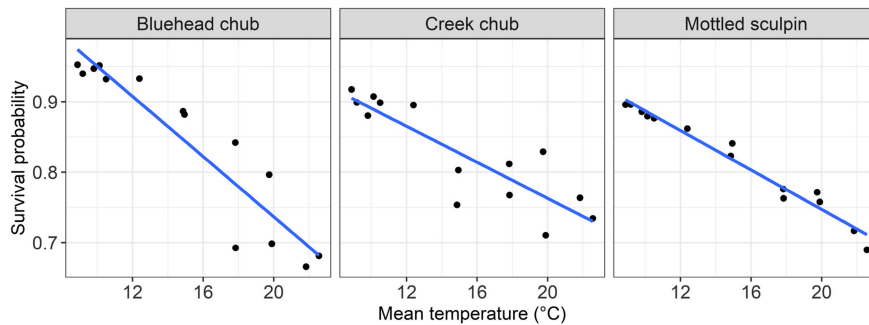


Figure 5. Predicted survival probability of averaged-sized fish and mean water temperature (°C) over two months. Average total length is 91.65 mm in bluehead chub, 93.23 mm in creek chub and 64.36 mm in mottled sculpin. Survival probability increased significantly with water temperature in three species based on a Cormack–Jolly–Seber model.

([Marcarelli et al. 2020](#)) and bioenergetic demand of ectotherms is low at these cooler temperatures. Intriguingly, growth and survival were explained by sub-seasonal changes in body condition in one species (mottled sculpin), but growth and survival did not depend on changes in body condition in another species (creek chub). This finding demonstrates that the utility of body condition as a proxy for fitness may be species-specific even when they occur in sympatry.

Negative temporal correlation between population vital rates generated by an abiotic condition (e.g. temperature) can make animal populations resilient in the face of environmental changes because a negative effect on a vital rate by the abiotic condition is offset by a positive effect on the other vital rate ([Fay et al. 2020, 2022, Paniw et al. 2020](#)). In our study species, negative correlation was observed in bluehead chub and creek chub (eurythermal species), but not in mottled sculpin. Along with their cooler thermal requirements, the lack of a negative temporal correlation would make mottled sculpin the most vulnerable species among the three species in a warming climate. This result is not surprising for a population of the stenothermal species located at the southernmost range of its native distribution. However, populations of eurythermal species are not indefinitely immune to warming climate. Similar to mottled sculpin, growth rates would start declining at some temperature threshold if warming accelerates. Reduced growth rates and consequently shrinking body sizes have been reported and projected for a wide range of animals in a warming climate ([Gardner et al. 2011,](#)

[Sheridan and Bickford 2011](#)). Additionally, a unimodal growth response to temperature would eventually result in a summer where body growth is minimal and survival is low, where negative temporal correlation between population vital rates no longer exists. Identifying this tipping point is important for species conservation and an early indicator would be slowed growth in summer because it occurs at a temperature below the lethal limit.

Water level did not explain sub-seasonal variation in growth or survival in any species. Stream flow is a key variable that affects population vital rates of stream fishes, in which survival and growth respond positively to an increase in flow ([Vøllestad and Olsen 2008, Letcher et al. 2015, Freeman et al. 2022](#)). We attribute lack of flow effects to the temporally stable flow condition in the study stream. Indian Creek was small in size located in a well-forested landscape and lacked a seasonally punctuated flow regime such as a snowmelt-driven peak flow. In addition, the study region experienced a dry condition throughout much of 2016 and 2017 ([Williams et al. 2017](#)), which resulted in the less variable water level over time in Indian Creek. We acknowledge that water level was used as a surrogate for stream flow and we lack stream flow measurements in Indian Creek. However, the same water level data were used to discover that fish movement distance depended on sub-seasonal variation in water level ([Terui et al. 2021](#)), and we think that water level data sufficiently characterized sub-seasonal variation in stream flow. Relative importance of stream temperature and

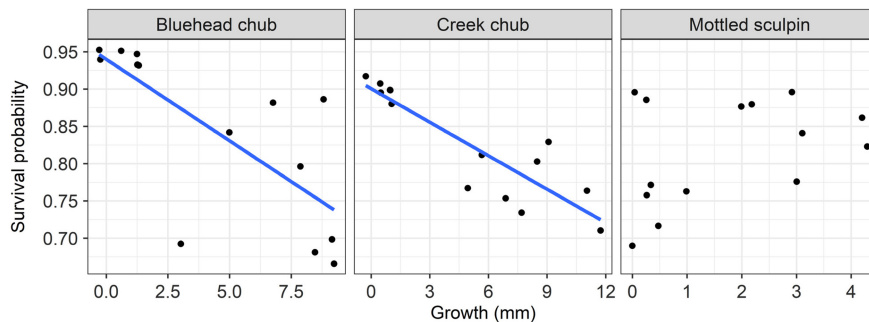


Figure 6. Relationship between posterior mean survival probability and growth in total length (mm) over two months. There was a significant relationship between survival and growth in bluehead chub ($p=0.003$) and creek chub ($p < 0.001$).

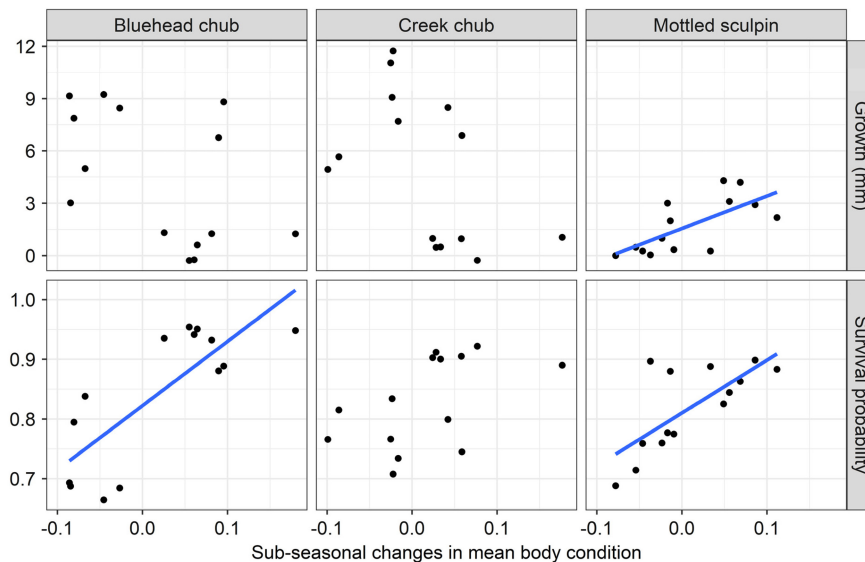


Figure 7. Relationship between changes in mean body condition versus mean growth rate in total length (mm) and survival probability between occasion t and $t+1$. There was a significantly positive relationship between changes in body condition and survival probability in bluehead chub ($p < 0.001$) and mottled sculpin ($p = 0.004$). In addition, there was a significantly positive relationship between changes in body condition and growth rate in mottled sculpin ($p = 0.007$).

flow, two key variables affected by climate change, may shift over time and space, and additional seasonal and sub-seasonal investigations on population vital rates need to be synthesized for understanding context-dependent patterns of correlation between growth and survival.

Sub-seasonal variation in growth and survival informs environmental temperature criteria designed to protect aquatic life. Temperature criteria rely rarely on field data on population vital rates of fish. Instead, they use fish distribution and abundance patterns in relation to temperature (Eaton et al. 1995, Beauchene et al. 2014), bioenergetic models (Bevelhimer and Bennett 2000, Petersen and Paukert 2005) and laboratory tests such as critical thermal maxima (Todd et al. 2008, Selong et al. 2011). However, adequacy of these temperature criteria for protecting fish in the wild has not been rigorously tested. Kowalski et al. (1978) reported that the critical thermal maxima of mottled sculpin was 30.9°C. This value is much higher than the optimal growth range of mottled sculpin in this study (12–16°C). Our study shows that population vital rate data based on mark–recapture surveys in the wild provide more ecologically meaningful temperature criteria and highlights the importance of collecting more data of this kind particularly for non-game species such as our study species for which data on seasonal vital rates are lacking.

In summary, growth and survival of three sympatric ectotherms were sub-seasonally structured. Growth and survival covaried over time in two eurythermal species but not in one stenothermal species, demonstrating additional demographic complexity that varies among species. Investigating population vital rates of sympatric species at the sub-seasonal resolution (two-month intervals) is logistically challenging, and we are not aware of any previous study of sympatric ectotherms with a similar temporal resolution. That said, this study

shows that rich information on demography could be gained from an intensive mark–recapture study, and this information assists us understand environmental change impacts on ectotherms more fully. Animal population vital rates are often correlated spatially (Tsuboi et al. 2020) and spatiotemporal correlations between animal population vital rates warrant additional investigations.

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Ethics statement – The fieldwork was conducted in accordance with protocols approved by the Clemson University Institutional Animal Care and Use Committee (IACUC Protocol Number 2014-047 and 2017-039).

Conflict of interest – There is no conflict of interest to declare.

Author contributions

Yoichiro Kanno: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Seoghyun Kim:** Conceptualization (supporting); Data curation (equal); Investigation (supporting); Resources (equal); Validation (supporting). **Kasey Pregler:** Conceptualization (supporting); Data curation

(equal); Investigation (supporting); Resources (supporting); Validation (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.np5hqbzxx> (Kanno et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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