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Article

A multispecies, multiseason evaluation of body condition effects on fish survival in a coolwater stream

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ABSTRACT

Objective: Body condition is often used as a surrogate of individual fitness in fisheries ecology and management, but empirical data demonstrating this linkage are few. Here, we investigated whether weight at length (i.e., body condition) explained individual variation in survival.

Methods: We conducted a mark–recapture survey of three native fishes subseasonally (every 2 months) over 28 months in a coolwater Piedmont stream in South Carolina, United States. We used a Cormack–Jolly–Seber model in the Bayesian state–space framework to characterize whether survival was explained by body condition.

Results: Body condition changed subseasonally, with its peak in spring (May) and trough in fall (November) in all three species (Bluehead Chub *Nocomis leptocephalus*, Creek Chub *Semotilus atromaculatus*, and Mottled Sculpin *Cottus bairdii*). Survival decreased in warmer subseasons for all species. Additionally, individuals with higher body condition survived better than those with lower condition only in these warmer subseasons and only in the Mottled Sculpin, a species that is territorial and the most intolerant of warmer temperatures among the study species.

Conclusions: Our findings show that body condition is a predictor of survival only when populations undergo high mortalities in some but not all species, which are likely caused by a combination of factors, such as physiological stress, diminished food resources, and increased competition for resources.

KEYWORDS: apparent survival, Bayesian statistics, Cormack–Jolly–Seber models, PIT tags, Piedmont region

LAY SUMMARY

Fish body condition is often assumed to indicate the well-being of individuals. By linking body condition and survival, we show that this relationship depends on season and species in a coolwater stream and highlights the context dependency.

INTRODUCTION

Fish body condition (BC) is widely used as an index of physiological or nutritional states (Brosset et al., 2023) and consequently as a surrogate of fitness (Peig & Green, 2009; Wilder et al., 2016). Body condition is often measured based on weight-at-length indices in fisheries studies and is fundamentally an individual-level measurement, although it is also used to assess fish populations in management applications (Ney, 1999; Ogle, 2016). Individual variation in BC persists in local populations at a given time due to different life stages or intraspecific competition for food and habitat resources (Kanno, Locklear, et al., 2023; Poulos & McCormick, 2015). Some studies have

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documented positive associations between BC and survival (Evans et al., 2014; Pangle et al., 2004; Poulos & McCormick, 2015; Wilson et al., 2021), but others have found no such relationship (LaGory, 2017; Zabel & Achord, 2004), suggesting that BC effects on fish survival may be context dependent and species specific. However, our knowledge is limited as to when BC predicts survival.

We posit that temporal variation in water temperature may provide an environmental template in which context-dependent effects of BC on survival may arise. Seasonality is a defining trait of temperate streams, and temperature regulates the function and metabolic demand of aquatic ectotherms (e.g., fishes). In addition, the abundance of food resources (e.g., aquatic insects) changes seasonally (Kamimura et al., 2021; Kato et al., 2003; Marcarelli et al., 2020). As a result, fish BC changes seasonally (Kamimura et al., 2021; Kanno, Kim, & Pregler, 2023), along with metrics of fitness (e.g., survival; Evans et al., 2014; Poulos & McCormick, 2015; Xu et al., 2010). Although these seasonal patterns are adequately documented, much less is understood regarding whether individual variation in BC is associated with survival similarly or differently across seasons. It is plausible that (1) BC would be a more reliable predictor of survival during seasons in which overall BC decreases across individuals and (2) individuals with relatively better BC would have higher survival compared to individuals with worse BC (Schultz & Conover, 1997; Wang & Houde, 1994). For example, high temperatures increase metabolic rates in fish, and the failure to meet the increased demands for food and oxygen (Crozier et al., 2010) can impair BC and, consequently, survival (Myrick & Cech, 2004; Stevenson & Woods, 2006). Some stream fish species compete for food resources, including drift feeders (Fausch et al., 2021; Grossman, 2014) and benthic foragers (Petty & Grossman, 2007; Rueda et al., 2015). Such intraspecific competition during the season of resource limitation would result in uneven acquisition of food resources, leading to individual variation in BC. Multiseason investigations are needed to elucidate seasonal patterns in the relationship between BC and survival, but such work has remained elusive, partly due to logistical challenges in quantifying fish BC and demography seasonally in the wild.

Understanding the season-dependent association between BC and fish survival would also benefit from simultaneous evaluations of sympatric species with different thermal requirements. Coolwater streams are suitable for such investigations because these transitional habitats harbor coldwater species (e.g., salmonids and cottids) and warmwater species (e.g., leuciscids and centrarchids) in North America. With a summer temperature range of 18–22°C (Beauchene et al., 2014; Lyons et al., 2009), some members of the coolwater stream assemblages are more thermally stressed in summer than others, and individual variation in BC may be more likely related to the survival of thermally sensitive species than tolerant species in summer. However, previous studies of BC and fitness have targeted single species or those with similar ecological traits (Evans et al., 2014; Pangle et al., 2004; Poulos & McCormick, 2015). An evaluation of multiple species with different thermal requirements would provide a mechanistic understanding of how fish assemblages may shift under climate change (Chu et al., 2005; Lyons et al., 2010).

To investigate the relationship between BC and survival, we conducted a mark–recapture survey of three native, nongame species at subseasonal (2-month) intervals spanning 28 months in a coolwater stream in South Carolina, United States. Our previous work in this system characterized survival and growth (Kanno, Kim, & Pregler, 2023; Pregler et al., 2023) and movement (Kanno et al., 2025; Terui et al., 2021) of our study species, which included Bluehead Chub *Nocomis leptocephalus*, Creek Chub *Semotilus atromaculatus*, and Mottled Sculpin *Cottus bairdii*. Body condition of these species changed subseasonally (Kanno, Kim, & Pregler, 2023), and survival depended on fish body size (Kanno, Kim, & Pregler, 2023; Pregler et al., 2023). Kanno, Kim, and Pregler (2023) evaluated temporal covariation between survival and growth averaged across individuals and found that periods of faster growth were associated with lower survival in Bluehead and Creek chubs but not in Mottled Sculpin (Kanno, Kim, & Pregler, 2023). However, we have not assessed whether individual variation in BC is associated with their survival and whether this pattern changes subseasonally. To address this knowledge gap, the current study aimed to fulfill three objectives. First, we evaluated whether BC was explained by subseasonal changes in temperature and fish abundance. Second, we tested our prediction that BC was associated with survival more significantly during subseasons in which overall condition was lower across individuals. We considered that the subseasons with low overall BC represent periods with low resource availability relative to their bioenergetic demand, when individual variation in BC may be most predictive of survival. Finally, we tested a second prediction that the relationship between BC and survival was not uniform across species in this coolwater fish assemblage due to their different thermal requirements and that individual variation in BC was a stronger predictor of summer survival in the most thermally sensitive species (i.e., Mottled Sculpin).

METHODS

Study area and species

This research was conducted in Indian Creek in the Clemson University Experimental Forest, which is located within the upper Piedmont region of South Carolina (34°44′32″N, 82°51′05″W). Indian Creek is a second-order perennial stream with an average wetted width of 2.6 m during base flow condition. Riffles and pools alternate to characterize its stream habitat, and the substrate is composed primarily of gravels, pebbles, and cobbles. The study area was 740 m long, and its lowermost boundary was upstream of Lake Hartwell to isolate this lotic habitat and the populations of our study species. Many individuals were sedentary, with limited records of long-distance movement, resulting in leptokurtic distributions of movement distances at 2-month sampling intervals (Kanno et al., 2025; Terui et al., 2021).

We conducted mark–recapture sampling to target three common species in Indian Creek, including Bluehead Chub, Creek Chub, and Mottled Sculpin. Bluehead and Creek chubs (family Leuciscidae) share more taxonomic and ecological similarities with each other than with Mottled Sculpin. Bluehead and Creek chubs are more commonly found in pools than in riffles and opportunistically consume a wide range of invertebrates

(McCormick et al., 2001). Creek Chub are habitat generalists, and among our study species, they are the most tolerant of environmental degradation and warm temperature (Kanno & Vokoun, 2010; McCormick et al., 2001), whereas Bluehead Chub and Mottled Sculpin are fluvial specialists (Freeman & Marcinek, 2006; McCormick et al., 2001). Mottled Sculpin primarily occupy riffles of clear streams and require cooler stream temperatures than Bluehead and Creek chubs (McCormick et al., 2001). The study stream is situated in the southernmost part of the Mottled Sculpin's native range. Mottled Sculpin are territorial, defending their benthic habitat near rocks (Petty & Grossman, 2007), but intraspecific antagonistic interactions are lesser known and likely weak in Bluehead and Creek chubs except during spawning and nesting periods (Kim, Peoples, & Kanno, 2020). Mottled Sculpin spawn during February and March in the study region (Y. Kanno, personal observation), whereas Bluehead and Creek chubs spawn later, between April and June (Kim & Kanno, 2020). Females were reported to reach sexual maturity at a minimum total length (TL) of 72 mm in Bluehead Chub (Kim, Pregler, et al., 2020), 65 mm in Creek Chub (Powles et al., 1977), and 41 mm in Mottled Sculpin (Grossman et al., 2002). However, pronounced secondary sexual characteristics were evident only for larger individuals—typically 120 mm or larger for Bluehead and Creek chubs (Kim, Peoples, & Kanno, 2020; Kim, Pregler, et al., 2020) and 70 mm for Mottled Sculpin (Kanno, personal observation). Male Bluehead Chub build and guard conspicuous nests composed of pebbles and gravels (Kim & Kanno, 2020), and Creek Chub spawn in small depressions in the substrate (Ross, 1976). Mottled Sculpin spawn on the underside of rocks, and the males guard the eggs (Grossman et al., 2002). In Indian Creek, Mottled Sculpin exhibited peak growth between 12°C and 16°C, whereas the growth of Bluehead and Creek chubs increased linearly with water temperature between 8.9°C and 22.6°C (Kanno, Kim, & Pregler, 2023). Additionally, Mottled Sculpin were likely the most movement-limited among the study species due to their smallest body size, benthic habitat requirement, and lack of an air bladder (Kanno et al., 2025). Accordingly, our study species included members of a coolwater assemblages with distinguishable ecological and behavioral characteristics.

Field sampling

We carried out a mark–recapture survey in a 740-m study area for 28 months from November 2015 to March 2018. Sampling was conducted at 2-month intervals (mean interval = 61 d, ranging from 48 to 70 d), and each sampling occasion was completed with an average window of 4 d (range = 1–10 d). We divided the study area into contiguous 20-m sections (±4 m; 37 sections in total) based on geomorphic breaks, and we sampled them upstream with a two-pass depletion method using backpack electrofishing units (Smith-Root Model LR-24 and Halltech Aquatic Research, Inc., Model HT-2000). Block nets were not used in this small creek because section boundaries were defined by mesohabitat types (pools and riffles). Upon capture, fish were separated by section and electrofishing pass and were held in buckets until processing.

Using 8-mm PIT tags, we marked all individuals with a TL of at least 60 mm for Bluehead and Creek chubs and at least 50 mm for Mottled Sculpin. The smaller minimum size was selected for Mottled Sculpin because this species was smaller overall than the chub species. We measured TL (nearest 1 mm) and weight (nearest 0.1 g) for all newly marked and recaptured fish on each occasion. Across 15 sampling occasions, we marked a total of 429 Bluehead Chub, 664 Creek Chub, and 928 Mottled Sculpin. Handling mortality was recorded for 13 (0.6%) of the 2,021 total individuals across the three species. Short-term tag loss was negligible in our pilot study (Cary et al., 2017). We recorded water temperature (°C) hourly using a remote logger (HOBO Model U20L-004; Onset Computer Corp.) and quantified the subseasonal mean temperatures between 2-month sampling occasions for statistical analysis.

Data analysis

We analyzed the mark–recapture data to evaluate whether BC explained survival and whether this pattern changed by species and subseason in relation to water temperature. To this end, we inferred survival probability between 2-month sampling occasions while accounting for imperfect capture of individuals by using Cormack–Jolly–Seber (CJS) models (Lebreton et al., 1992). The CJS analysis and other inferential statistics were conducted in the Bayesian framework.

Body condition

Body condition of individuals was characterized as weight at length. For each species, we pooled data across all sampling occasions and fit $\log_{10}(\text{weight}) = a + (b \times \log_{10}[\text{TL}])$ to predict an average weight at a given TL (Blackwell et al., 2000). Body condition was quantified as the difference between the measured weight and the predicted weight, divided by the predicted weight. Therefore, a value of 0 indicated individuals with average BC, negative values indicated lower BC, and positive values indicated higher BC. We also used the scaled mass index as an alternative method for characterizing BC (Peig & Green, 2009) and found that the two indices of BC were highly correlated with each other for Bluehead Chub (Pearson's correlation coefficient $r = 0.997$), Creek Chub ($r = 0.997$), and Mottled Sculpin ($r = 0.992$). In addition, BC and TL were not correlated for Bluehead Chub ($r = -0.013$), Creek Chub ($r = -0.003$), or Mottled Sculpin ($r = -0.007$).

We examined whether temporal variation in BC was explained by water temperature and intraspecific abundance (i.e., density dependence). Because temperature and abundance were correlated with each other ($r > 0.50$) for Bluehead and Creek chubs, we fit hierarchical models (Equations 1 and 2) for each species by using temperature or abundance as a sampling occasion-level predictor of the BC of individual i on occasion j:

$$\text{Condition}_i \sim \text{Normal}\left(\mu_{j[i]}, \sigma_1^2\right), \tag{1}$$

$$\mu_j = \boldsymbol{x}_j \boldsymbol{\beta} + \varepsilon_j, \varepsilon_j \sim \text{Normal}\left(0, \sigma_2^2\right), \tag{2}$$

where σ_1^2 is the variance in individual BC within sampling occasions, $\boldsymbol{x}_j$ represents the intercept and an occasion-level predictor (temperature or abundance), β denotes their coefficients, and ε_j represents the residual after accounting for the occasion-level predictors with variance equal to σ_2^2. Abundance of each species on each sampling occasion was estimated by applying a Jolly–Seber model to mark–recapture data (Supplement 1 [see online Supplemental Material]). Temperature and abundance were standardized by z-score normalization prior to analysis so that their means were centered at 0 and a unit change corresponded to 1 SD. Abundance was highly correlated with biomass (sum of body weight across marked individuals on each occasion) for Bluehead Chub ($r = 0.79$), Creek Chub ($r = 0.83$), and Mottled Sculpin ($r = 0.78$).

Survival

We estimated survival probability between sampling occasions for each species independently in CJS models using the state-space approach (Kéry & 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 denoted by ϕ:

$$z_{i,t+1} \mid z_{i,t} \sim \text{Bernoulli}\left(z_{i,t}\phi_{i,t}\right), \tag{3}$$

$$\text{logit}\left(\phi_{i,t}\right) = \alpha0_{s[i],t} + \alpha1_{s[i],t}\text{BC}_{i,t} + \alpha2_{s[i]}\text{TL}_{i,t}. \tag{4}$$

The latent state variable denotes the fate of individuals, where $z_{i,t} = 1$ if individual i was alive on occasion t and $z_{i,t} = 0$ if the individual was dead. Survival probability was modeled for each individual from its first capture to the final sampling occasion or the known occasion of mortality (i.e., handling mortality)—that is, dead individuals were excluded in the analysis from the occasion on which mortality events were recorded. Individual variation in the survival probability was modeled by BC and TL, with $\alpha1_{s[i],t}$ representing the effect of BC on survival on occasion t and $\alpha2_{s[i]}$ indicating the effect of TL on survival for species s to which individual i belonged. Body condition and TL were standardized using z-score normalization before analysis (i.e., centered to a mean of 0, and a unit change corresponded to 1 SD). Body condition was standardized within each sampling occasion to account for its seasonality (see *Results*), and TL was standardized across all occasions. Thus, the intercept ($\alpha0_{s[i],t}$) of the logistic regression represented the predicted survival probability of an individual of species s with the average BC on that occasion and the average TL across all occasions. The TL effect on survival ($\alpha2_{s[i]}$) was set to be constant over time following Kanno, Kim, and Pregler (2023). We adjusted for varying sampling interval lengths by standardizing survival probability over 60 d between consecutive sampling occasions.

In addition, we tested whether temperature explained temporal variation in mean survival probability and, more importantly, the strength of BC association with survival, which may differ among sampling occasions:

$$\alpha0_{s[i],t} \sim \text{Normal}\left(\beta0_s + \beta1_s\text{Temp}_t, \sigma_\beta^2\right), \tag{5}$$

$$\alpha1_{s[i],t} \sim \text{Normal}\left(\gamma0_s + \gamma1_s\text{Temp}_t, \sigma_\gamma^2\right), \tag{6}$$

where $\beta0_s$ is an intercept, $\beta1_s$ is an effect of mean temperature (Temp_t) on mean survival of species s, σ_β^2 is a residual, $\gamma0_s$ is an intercept, $\gamma1_s$ quantifies whether the effect of BC on survival of species s was explained by temperature (Temp_t) during the sampling interval preceding the sampling occasion, and σ_γ^2 is a residual.

To account for imperfect capture in electrofishing surveys, we modeled the capture probability ($p_{i,t}$) of individual i of species s on sampling occasion t using TL as a covariate:

$$y_{i,t} \mid z_{i,t} \sim \text{Bernoulli}\left(z_{i,t}p_{i,t}\right), \tag{7}$$

$$\text{logit}\left(p_{i,t}\right) = \delta0_{s[i],t} + \delta1_{s[i]}\text{TL}_{i,t}, \tag{8}$$

where $y_{i,t}$ is the capture history data (1 if captured, 0 if not) of individual i on occasion t, $\delta0_{s[i],t}$ is a species- and time-specific intercept, and $\delta1_{s[i]}$ is a species-specific effect of z-score-standardized TL on capture probability. Body size influenced capture probabilities of the study species in our previous investigations of the same data set (Kanno, Kim, & Pregler, 2023).

The CJS models and other hierarchical models were analyzed using a Markov chain–Monte Carlo method in JAGS (Plummer, 2017) called from R (R Core Team, 2024) with the jagsUI (Kellner, 2024) package. Regression coefficients in CJS models (the βs, γs, δs, and $\alpha2$) were modeled as fixed effects, and diffuse priors were used in the Bayesian approach. Posterior distributions of parameters were estimated using three parallel Markov chains, each with 30,000 samples after a burn-in period of 15,000 iterations, thinned by every fifth sample to reduce autocorrelation. Convergence was assessed by inspecting Markov chain–Monte Carlo trace plots for good mixing and by confirming that the Gelman–Rubin convergence statistic $\hat{R}$ was less than 1.1 for all parameters (Gelman & Rubin, 1992). Statistical significance was declared when the 95% credible interval (CRI) of a parameter did not overlap zero.

RESULTS

During the 28-month study period, 59% of released Bluehead Chub (254 of 429 individuals), 55% of Creek Chub (365 of 664 individuals), and 48% of Mottled Sculpin (444 of 928 individuals) were recaptured at least once. Across all sampling occasions, the average TL of individuals was 91.65 mm (range = 60–185 mm) for Bluehead Chub, 93.23 mm (range = 60–190 mm) for Creek Chub, and 64.36 mm (range = 50–90 mm) for Mottled Sculpin.

Body condition

Body condition of all three species exhibited subseasonal patterns (Figure 1), typically peaking in spring (May), declining through the fall (November), and improving again from November to May. The mean BC on sampling occasions ranged from −0.1035 (~10% lower than the overall mean across the sampling occasions) to 0.1583 (~16% higher) in Bluehead Chub, from −0.0791 (~8% lower) to 0.1554 (~16% higher) in Creek Chub, and from −0.0731 (~8% lower) to 0.0766 (~8% higher) in Mottled Sculpin. The mean temperature ranged from 8.9°C to 22.6°C during 2-month sampling intervals, with July and August being the warmest months and December and January being the coldest (Figure 2). Body

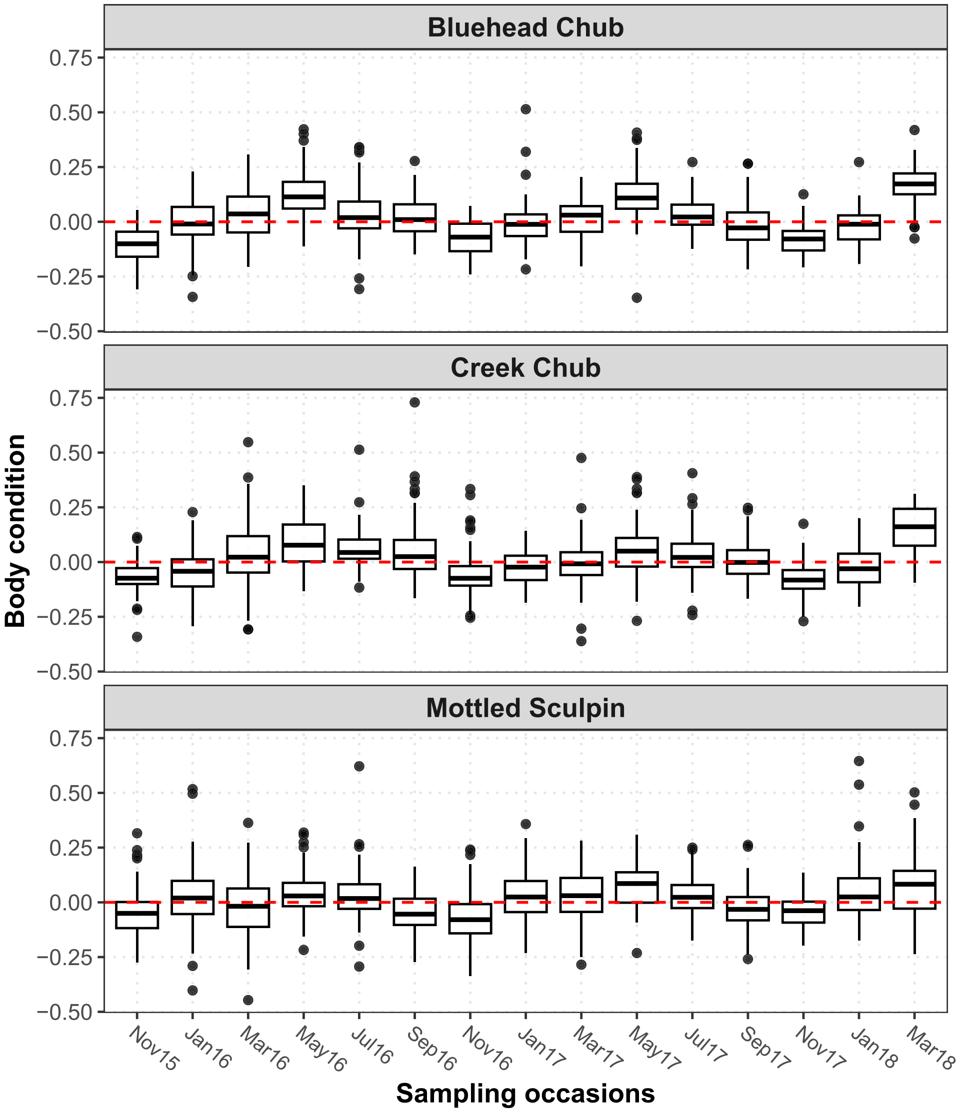

Figure 1. Subseasonal variation in body condition of Bluehead Chub, Creek Chub, and Mottled Sculpin in Indian Creek, South Carolina (November 2015–March 2018). The horizontal line within each box represents the median; the upper and lower edges of the box represent the 75th and 25th percentiles, respectively; and the whiskers extend to 1.5 times the interquartile range. Points beyond the whiskers indicate outliers. Body condition was calculated as the relative difference between an individual's observed weight and its predicted weight based on species-specific length–weight relationships, normalized by the predicted weight. A value of 0 (red dashed horizontal line) represents average body condition, negative values indicate lower condition, and positive values indicate higher condition.

condition was not explained by temperature for Bluehead Chub (mean = −0.001; 95% CRI = [−0.009, 0.009]), Creek Chub (mean = −0.0007; 95% CRI = [−0.0095, 0.0093]), or Mottled Sculpin (mean = −0.0041; 95% CRI = [−0.0098, 0.0075]). In addition, BC was not associated with density dependence in Bluehead Chub (mean = −0.026; 95% CRI = [−0.069, 0.022]), Creek Chub (mean = −0.012; 95% CRI = [−0.049, 0.026]), or Mottled Sculpin (mean = −0.009; 95% CRI = [−0.036, 0.019]).

Survival

Subseasonal survival patterns were similar among the three species (Figure 3; Supplement 2). During cooler subseasons (November–May), the posterior mean probabilities of survival were high, ranging from 0.76 to 0.97 across the three species. Throughout warmer subseasons (May–November), mean survival probabilities across the three species were lower, ranging from 0.65 to 0.86 for Bluehead Chub, from 0.68 to 0.84 for Creek Chub, and from 0.71 to 0.78 for Mottled Sculpin. Fish were less likely to survive during warmer sampling intervals for Bluehead Chub ($\beta 1 = -1.25$; 95% CRI = [−3.03, −0.46] on the logit scale), Creek Chub ($\beta 1 = -0.60$; 95% CRI = [−1.52, −0.02]), and Mottled Sculpin ($\beta 1 = -0.48$; 95% CRI = [−0.85, −0.16]). The odds ratios of these posterior mean estimates ($\exp[\beta 1]$) indicated that with a unit increase in the stream temperature (4.77°C), Bluehead Chub were 3.49 times less likely to survive, Creek Chub were 1.82 times less likely, and Mottled Sculpin were 1.61 times less likely. Larger individuals were less likely to survive for Bluehead Chub ($\alpha 2 = -0.29$; 95% CRI = [−0.49, −0.12]), Creek Chub ($\alpha 2 = -0.23$; 95% CRI = [−0.38, −0.08]),

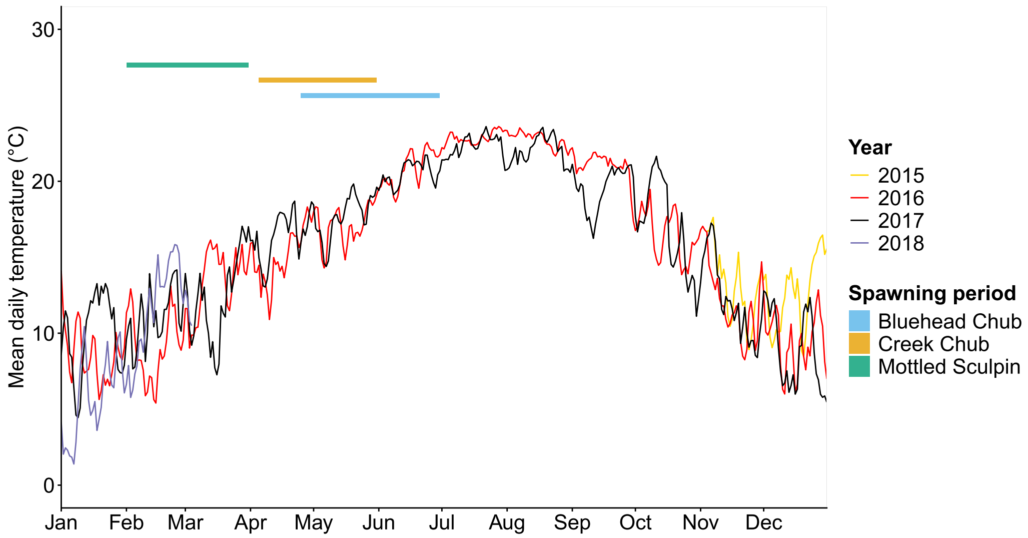

Figure 2. Daily mean water temperature in Indian Creek, South Carolina, during the study period (November 2015–March 2018). Horizontal bars approximate the spawning period of each study species: Bluehead Chub (late April–late June; blue), Creek Chub (April–May; orange), and Mottled Sculpin (February–March; green).

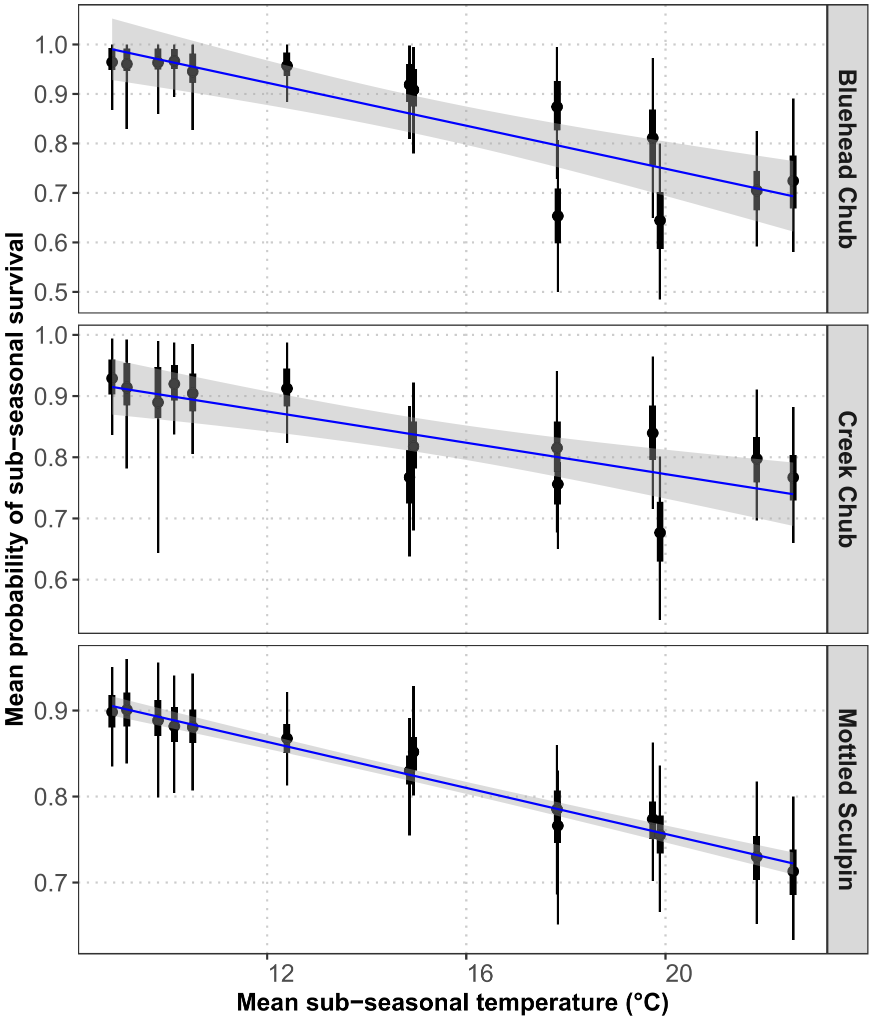

Figure 3. Predicted survival probability for the three study species based on the Cormack–Jolly–Seber model and mean water temperature (°C) over 2-month intervals leading up to sampling occasions. Points represent posterior mean survival probabilities, with thick lines indicating 50% credible intervals and thin lines representing 95% credible intervals. Statistically significant relationships between mean water temperature and survival probability are illustrated by the solid blue regression fit, with 95% prediction intervals shown in gray shading.

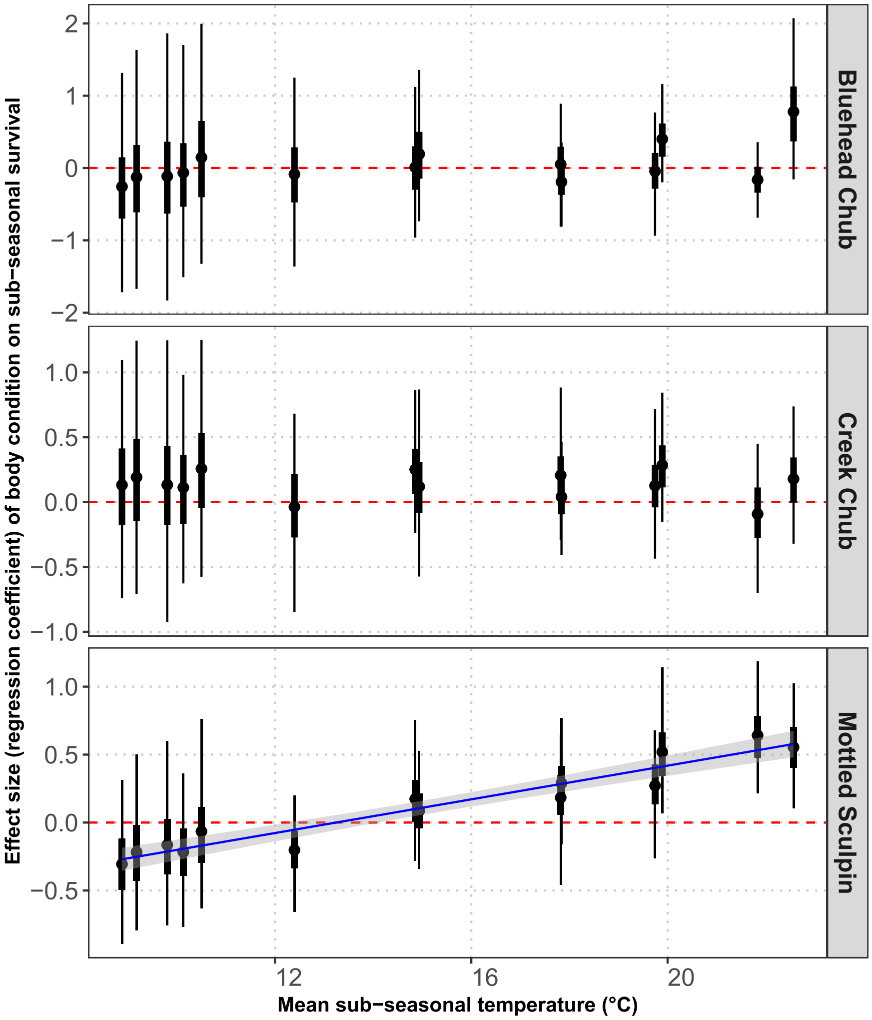

Figure 4. Posterior effect sizes (α1 on the logit scale) of body condition on subseasonal survival for the three study species based on the Cormack–Jolly–Seber model along the temperature gradient. Posterior mean values are shown by points, presented with 50% credible intervals (thick lines) and 95% credible intervals (thin lines). A statistically significant relationship between temperature and effect size of body condition on survival in Mottled Sculpin is illustrated by the solid blue regression fit, with 95% prediction intervals shown in gray shading.

and Mottled Sculpin ($\alpha 2 = -0.27$; 95% CRI = [−0.40, −0.14]). Larger individuals were more readily captured by electrofishing in Bluehead Chub ($\delta 1 = 0.15$; 95% CRI = [0.02, 0.30]), Creek Chub ($\delta 1 = 0.20$; 95% CRI = [0.06, 0.33]), and Mottled Sculpin ($\delta 1 = 0.50$; 95% CRI = [0.38, 0.62]).

Relationship between body condition and survival

Individuals with higher BC on a given occasion were more likely to survive during warmer subseasonal intervals in Mottled Sculpin, the most coldwater-adapted species among three study species ($\gamma 1 = 0.31$; 95% CRI = [0.00, 0.59]), but not in Bluehead Chub ($\gamma 1 = 0.15$; 95% CRI = [−0.50, 0.78]) or Creek Chub ($\gamma 1 = -0.01$; 95% CRI = [−0.46, 0.40]). In Mottled Sculpin, survival was positively associated with BC during the three warmest sampling intervals (19–23°C), and odds ratios (exp[α1]) indicated that individuals were, on average, 1.75, 1.68, and 1.90 times more likely to survive with a 1-SD increase in BC between July and September 2016, May and July 2017, and July and September 2017, respectively (Figure 4). Although not significant, 70% of the posterior samples of γ1 values were positive for Bluehead Chub, indicating weak evidence that temperature explained the magnitude of BC effects on survival. However, only 50% of posterior samples were positive for Creek Chub, showing that survival was not explained by BC regardless of temperature. Overall, our analysis revealed strong (Mottled Sculpin) to no (Creek Chub) evidence that BC effects on survival were temperature dependent in this coolwater fish assemblage. Given this finding, we further evaluated whether mortality was more likely to occur for individuals below a threshold value of BC across the subseasons. However, no such threshold was discernable in any of the three species (Supplement 3).

DISCUSSION

We found subseasonal variation in fish BC, and this was not related to stream temperature or fish abundance. Our prediction that individual variation in BC would more strongly explain survival during subseasons with lower overall condition was weakly supported because the pattern was found only in Mottled Sculpin. Survival decreased with increased temperature in all three study species. During these warmer periods (i.e., summer), Mottled Sculpin with higher BC were more likely to survive than those with lower condition. This finding supports our other prediction that the relationship between BC and survival differs among species, being strongest in the most thermally sensitive species (e.g., Mottled Sculpin), where individual variation in BC more strongly predicted survival in summer. Albeit a different seasonal context, our results corroborate studies that have reported the importance of BC as a predictor of overwinter survival in coldwater species (Pangle et al., 2004), with winter being a period of high mortality rates in these species. Overall, accounting for seasonal variation in BC observed in this and other studies can yield improved insights when using BC as a surrogate of fitness in fish management and ecology (Balcombe et al., 2012; Guy & Willis, 1991; Heim et al., 2016). Body condition can be a more reliable predictor of seasonal survival among individuals for species within a local fish assemblage.

Heterogeneous responses among the members of this coolwater assemblage highlight the importance of our multispecies investigation and contribute to a mechanistic understanding of fish assemblage dynamics. The stronger temperature-dependent association between BC and survival in Mottled Sculpin relative to the chub species can be attributed to two factors. First, the Mottled Sculpin is the most intolerant of warm temperature among our three study species (McCormick et al., 2001). The body growth of Mottled Sculpin was maximized at 12–16°C in the study creek, but growth rates increased with warming up to 22.6°C in Bluehead and Creek chubs (Kanno, Kim, & Pregler, 2023). Additionally, the Creek Chub is the most tolerant of environmental degradation among the three species, it is classified as a habitat generalist and omnivore (Colby et al., 2022; Jordan et al., 2013; Nagrodski et al., 2013; Palić et al., 2007; Quist et al., 2006), and BC showed the weakest association with survival in this species. Second, Mottled Sculpin are territorial and interact behaviorally with conspecifics (Petty & Grossman, 2007). This suggests that resource acquisition was less even among individuals of Mottled Sculpin when they underwent warmer and physiologically stressful subseasons compared to individuals of Bluehead and Creek chubs, although BC was not density dependent in any of the study species. Importantly, coolwater stream assemblages occupy a relatively narrow summer temperature range (18–22°C; Beauchene et al., 2014; Lyons et al., 2009), and some of current coolwater assemblages will likely shift to warmwater assemblages in a warming climate (Lyons et al., 2010). Our study suggests that such a shift could be facilitated by species-specific demographic responses to thermal tolerances in summer, during which climate change winners and losers (de Visser et al., 2023; Yousefi et al., 2020) become distinguishable.

Our earlier study (Kanno, Kim, & Pregler, 2023) and the current study build upon each other to quantify how BC affects the survival of sympatric stream fish species. Both studies used CJS models for survival estimation at 2-month intervals, but our current work uniquely evaluated BC as a predictor of survival among individuals at different times of the year. The inclusion of individual BC did not change the association between survival and other predictors; specifically, survival decreased with increased water temperature, and for all three species in both studies, larger individuals were less likely to survive. This consistency in results showed that the inferences of these predictors on survival were not sensitive to the presence of the additional predictor (i.e., BC). More importantly, Kanno, Kim, and Pregler (2023) assessed temporal covariation between growth and survival averaged across individuals on each sampling occasion, whereas our current study focused on how individual BC explained survival. Intriguingly, patterns observed for Mottled Sculpin were different from those for Bluehead and Creek chubs in both studies. Kanno, Kim, and Pregler (2023) reported that survival and growth were not temporally correlated, but each of them was positively related to mean BC across individuals only for Mottled Sculpin. In addition, our current work demonstrated, only in Mottled Sculpin, that individuals with higher BC survived better than those with lower BC in warmer seasons. Taken together, our studies show that sympatric species have different demographic responses to environmental variation, showcasing the value of multispecies investigations. We could not detect a threshold of BC below which mortalities are likely to occur when viewed across subseasons (Supplement 3). Body condition based on length and weight (i.e., standard weight equations) is often used to identify the need for management intervention or to monitor individual and population responses to management action. Some arbitrary threshold of BC is typically used for such assessments without considering the fitness consequences (Blackwell et al., 2000; Gabelhouse, 1987; Murphy et al., 1991). Additional research is needed to evaluate how BC affects other fitness metrics, including reproductive success and growth (Wilder et al., 2016), and how such information can be used to derive species-specific target thresholds of BC in fisheries monitoring. Body condition can be measured by using other nonlethal options, such as body composition and physiology, which may more accurately characterize BC than morphological condition indices (e.g., length–weight relationships; Stevenson & Woods, 2006).

Length–weight relationships are most commonly characterized for large-bodied game species because it is less accurate to measure weights of smaller fish in the field due to their higher surface area : volume ratios. Minimum TLs are defined for the application of standard weight equations and often range from 100 to 200 mm (Blackwell et al., 2000). Standard weight equations have not been developed for the Bluehead Chub or Creek Chub, but information exists for Mottled Sculpin in some regions (Bailey, 1952; Kinziger, 1998). We marked Bluehead and Creek Chub individuals that were over 60 mm TL and Mottled Sculpin that were over 50 mm TL, and our BC metric might have been less accurately approximated for these small-bodied individuals. Despite this potential caveat, we inferred that BC was a predictor of survival in some seasons for Mottled Sculpin, suggesting that our finding was likely a strong ecological pattern. In addition, the temporal variability in BC suggests that it is important to collect temporally replicated length–weight data, in addition to spatial replicates, to develop standard weight equations for freshwater fishes in the temperate region.

Body condition measured as weight at length is influenced by the maturation status of individuals, such as gonad development (Encina & Granado-Lorencio, 1997; Mozsár et al., 2015), but we could not collect data on the maturation status of our marked individuals. Recording accurate data on maturity would have required sacrificing the individuals. Secondary sexual characteristics were evident only for large individuals in our study (>120 mm TL for Bluehead and Creek chubs; >70 mm TL for Mottled Sculpin). These body size thresholds are larger than the mean TLs of marked Bluehead Chub (92 mm), Creek Chub (93 mm), and Mottled Sculpin (64 mm), suggesting that a majority of the individuals marked in our study were likely immature. In addition, the spawning period of our study species spanned approximately 2 months, which coincided with one sampling interval or two intervals at the most. Importantly, the BC of Mottled Sculpin was a predictor of survival during the warmest sampling intervals, which occurred a few months after this species' spawning season in February and March. Therefore, we think that this season-dependent association between BC and survival in Mottled Sculpin was not influenced by their reproduction.

Mark–recapture studies like ours are labor-intensive, and spatial replication is challenging. Our study was spatially limited (740 m long) and was conducted in a single creek, although the same sampling protocol was used simultaneously in a nearby creek that did not harbor Mottled Sculpin (Pregler et al., 2023). Lack of spatial replication prevents us from assessing the generality of our findings, and this warrants additional studies in coolwater streams that are geographically dispersed in North America (Beauchene et al., 2014; Lyons et al., 2009). Such investigations would be most meaningful when carefully designed to allocate sampling effort along temporal and spatial dimensions. Although our sampling was conducted every 2 months, time-varying effects of BC on survival could be quantified with a minimum of two surveys annually. Study streams should be large enough to allow for recaptures of many individuals, and in cases with connected habitats (e.g., tributary–main-stem networks), an understanding of whether time-dependent BC effects on survival are spatially consistent would contribute to spatial ecology and watershed-scale conservation of stream fishes. Individual-scale marked data are irreplaceable for this type of demographic investigation.

In the CJS analysis, we estimated the probability of apparent survival, which is a product of true survival and fidelity of individuals to the 740-m study area. Based on our mark–recapture data, we cannot quantify how frequently individuals emigrated from the study area over 2-month sampling intervals. However, population-scale movement of our study species in Indian Creek was characterized by many individuals moving short distances (<40–60 m) and a few individuals moving long distances (Kanno et al., 2025; Terui et al., 2021). Similar leptokurtic distributions of movement distances have been reported for our study species elsewhere (Albanese et al., 2004; Petty & Grossman, 2004). Although we believe that emigration was not frequent and thus that our estimates of apparent survival do not deviate greatly from true survival, BC can affect the movement behavior of stream fishes (Gowan & Fausch, 1996; Kanno, Locklear, et al., 2023). Future research is warranted to characterize season- and context-dependent BC effects on true survival and emigration via additional data collection, such as the installation of PIT antennas at study area boundaries to monitor emigration (Horton et al., 2011; Kanno et al., 2020).

In conclusion, our multispecies, multiseason evaluation showed that BC was a predictor of survival during some seasons (above ~20°C) but not in other seasons, and the strength of this pattern differed among the members of this coolwater assemblage. Our work is unique by linking BC as a surrogate of fitness (i.e., survival) for nongame stream fishes via an intensive mark–recapture approach. Two key lessons from this study can inform future studies and fisheries management. First, considering the seasonality of BC can help to identify the period of the year in which individual variation in BC is likely a predictor of survival. Second, sympatric species do not necessarily show similar associations between BC and survival. These considerations are equally applicable to game and nongame species and encourage fisheries biologists and managers to think carefully about the utility of this common fisheries tool (i.e., BC).

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Transactions of the American Fisheries Society* online.

DATA AVAILABILITY

The data are available from the corresponding author on reasonable request. The JAGS code for the CJS model is provided in Supplement 4.

ETHICS STATEMENT

The fieldwork was conducted in accordance with protocols approved by the Institutional Animal Care and Use Committee at Clemson University (protocol numbers 2014-047 and 2017-039).

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There was no external funding for this study.

CONFLICTS OF INTEREST

There are no conflicts of interest to declare.

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