


Direct and size-mediated effects of temperature and ration-dependent growth rates on energy reserves in juvenile anadromous alewives (*Alosa pseudoharengus*)

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ABSTRACT

Growth rate and energy reserves are important determinants of fitness and are governed by endogenous and exogenous factors. Thus, examining the influence of individual and multiple stressors on growth and energy reserves can help estimate population health under current and future conditions. In young anadromous fishes, freshwater habitat quality determines physiological state and fitness of juveniles emigrating to marine habitats. In this study, the authors tested how temperature and food availability affect survival, growth and energy reserves in juvenile anadromous alewives (*Alosa pseudoharengus*), a forage fish distributed along the eastern North American continent. Field-collected juvenile anadromous *A. pseudoharengus* were exposed for 21 days to one of two temperatures (21°C and 25°C) and one of two levels of food rations (1% or 2% tank biomass daily) and compared for differences in final size, fat mass-at-length, lean mass-at-length and energy density. Increased temperature and reduced ration both led to lower growth rates, and the effect of reduced ration was greater at higher temperature. Fat mass-at-length decreased with dry mass, and energy density increased with total length, suggesting size-based endogenous influences on energy reserves. Lower ration also directly decreased fat mass-at-length, lean mass-at-length and energy density. Given the fitness implications of size and energy reserves, temperature and food availability should be considered important indicators of nursery habitat quality and incorporated in *A. pseudoharengus* life-history models to improve forecasting of population health under climate change.

KEYWORDS

anadromous juvenile alewife, energy reserves, growth, north-East USA, ration, temperature

1 | INTRODUCTION

Temperature and food availability are important factors affecting survival, growth and energy reserves in young fishes (Houde, 1989; Weatherley *et al.*, 1987). Growth can occur only if assimilated energy exceeds the level required to satisfy routine metabolic needs (Brett & Groves, 1979; Shearer, 1994). The amount of assimilated energy needed for growth changes with endogenous (*e.g.*, size and life stage)

and exogenous (*e.g.*, biotic and abiotic) factors. Habitat factors such as temperature place additional energy demands on growth (Mazeaud & Mazeaud, 1981; Wedemeyer *et al.*, 1984), and the physiological effects of increased energetic demand in suboptimal habitats depend on endogenous and ecological contexts. Temperature and food availability can have complex interacting effects on energetics. For instance, reduced food availability may lower optimal growing temperature (Brandt, 1993; Brett *et al.*, 1969), and fat content is more

strongly affected by food ration at high temperatures compared to low temperatures (Elliott, 1976). Factors which influence energy allocation are critical to survival during early life stages when energy stores are more limited and individuals are accordingly less resilient to environmental stressors (Weatherley, 1990; Weatherley *et al.*, 1987).

Size and energetic condition represent important ecological properties at the individual and population levels. Variation in body size and energy reserves correlates with survival under certain biotic or abiotic conditions, including predation risk and overwintering success (Adams, 1999; Munch *et al.*, 2003; Sogard, 1997). In Atlantic silversides *Menidia menidia* (Linnaeus 1766), smaller fish suffer greater overwinter mortality because of a higher rate of energy reserve depletion (Schultz *et al.*, 1998; Schultz & Conover, 1999). Furthermore, evidence for differential growth and accumulation of energy reserves along a seasonality gradient indicate that environmental factors drive evolution in energy allocation strategies (Schultz *et al.*, 1998; Schultz & Conover, 1997). High lipid prey species are particularly important in food webs, and their inclusion and exclusion from a functional ecosystem role can have system-wide influence (Dias *et al.*, 2019; Österblom *et al.*, 2008). Some species undergo ontogenetic shifts that place additional constraints on growth, perhaps none more so than species that undergo migrations such as diadromous fishes.

The effects of temperature and food on early life stages have not been widely examined in anadromous fishes, except salmonids (Edsall *et al.*, 1999; Elliott, 1976; Zeug *et al.*, 2019). In the anadromous life cycle, freshwater habitat has been identified as the primary driver of physiology and fitness of young fish (Schiemer *et al.*, 2004; Stockner & Macisaac, 1996). Therefore, temperature and food availability in freshwater habitats may determine the timing, condition and abundance of juvenile fish emigrating to estuarine and marine habitats (Benjamin *et al.*, 2013; Zeug *et al.*, 2019). Ongoing rapid environmental changes in climate regimes necessitate that we understand the relative importance of temperature and food availability for the resilience of vulnerable anadromous fish populations (Crozier *et al.*, 2019; Friedman *et al.*, 2019). This includes appropriately interpreting patterns in energy allocation and their influence on survival, growth and body condition.

Alosa pseudoharengus (Wilson 1811), colloquially referred to as alewife or gaspereaux, are an anadromous fish distributed along the Atlantic coast of North America. *A. pseudoharengus* populations have experienced widespread declines because of overfishing and freshwater habitat loss (Hall *et al.*, 2011; Schmidt *et al.*, 2003). Fishing moratoriums, habitat restoration and adult monitoring have been the primary focuses of restoration efforts (Bowden, 2014). Less is known about the role of habitat quality, and specifically temperature and food availability, in driving anadromous juvenile survival and condition, particularly under projected climate change scenarios (Kosa & Mather, 2001; Lynch *et al.*, 2015). Previous studies of habitat quality impacts have focused primarily on landlocked *A. pseudoharengus* populations in the Great Lakes (Rand *et al.*, 1994; Stewart *et al.*, 2010; Stewart & Binkowski, 1986). Depending on the systems of comparison, temperature can influence anadromous juvenile densities and abundance (Devine *et al.*, 2021; Tommasi *et al.*, 2015), or have no effect on

abundance (Kosa & Mather, 2001). In addition, low zooplankton levels reduce juvenile abundance (Kosa & Mather, 2001) and initiate emigration from nursery sites (Yako *et al.*, 2002). Despite their importance, no previous study has examined the joint effects of temperature and food availability on anadromous juvenile growth and condition. As juvenile anadromous *A. pseudoharengus* in the North-eastern USA have a short growing season before emigration to the ocean, sub-optimal conditions that alter growth or energy storage could have significant consequences for predation risk, emigration timing or success, and overwintering survival (Gahagan *et al.*, 2010; Munch *et al.*, 2003; Rowe *et al.*, 1991; Thorpe, 1986). Furthermore, anadromous *A. pseudoharengus* populations are undergoing contraction of their southern range edge, suggesting that temperature may influence their distribution (Nye *et al.*, 2012).

This study focuses on the effects of temperature and food ration on juvenile anadromous *A. pseudoharengus* survival, growth rates and energy reserves (fat mass-at-length, lean mass-at-length and energy density) in relation to the size of individuals. Measuring effects on survival will enable comparison to field studies examining impacts of temperature and/or prey availability on juvenile abundance or densities (Devine *et al.*, 2021; Kosa & Mather, 2001; Tommasi *et al.*, 2015). Examining growth rates and energy reserves elucidates whether nursery habitat quality influences size at emigration and trends in size-based mortality (Kosa & Mather, 2001; Sogard, 1997; Turner & Limburg, 2016). The authors exposed juveniles to one of four treatments for 21 days: 21°C and 1% food ration, 21°C and 2% food ration, 25°C and 1% food ration and 25°C and 2% food ration. These two temperatures are common during the spring and summer months in the juvenile collection site, Upper Mystic Lake in Massachusetts (Supporting Information Table S1, Chase *et al.*, 2010). The highest average temperature during freshwater residence (in July and August) is c. 25°C, whereas 21°C is an optimal hatching temperature for anadromous *A. pseudoharengus* and is most commonly observed in June and September (Kellogg, 1982). Daily rations were chosen to create a limiting (1% tank biomass) and plentiful (2% tank biomass) dry feed ration, based on rations used in other physiological studies with juvenile *A. pseudoharengus* (DiMaggio *et al.*, 2015).

The authors hypothesized that an increase in temperature from 21 to 25°C would increase juvenile routine metabolic rates, thus limiting energy available for growth and maintaining energy reserves. As ration levels determine how much energy is available for metabolism and growth, juveniles in the 1% ration should have less energy available for somatic growth and energy reserves. The authors predict that juveniles at 25°C or at the 1% ration would have lower growth rates and energy reserves, demonstrated by smaller final sizes, lower fat mass-at-length and lower energy density. Temperature and ration should act additively, such that juveniles at the 21°C, 2% ration would have the greatest size and energy reserves, and 25°C, 1% ration juveniles would have the smallest size and energy reserves. This research provides physiological data on the impact of current temperatures on growth rates and energy storage that can inform restoration efforts and life-history models for a data-poor anadromous species (Nelson *et al.*, 2020).

2 | METHODS

2.1 | Ethical statement

The care and use of experimental animals complied with United States animal welfare laws, guidelines and policies as approved by University of Massachusetts Amherst Institutional Animal Care and Use Committee (research facility #14-R-0036, permit #135). All fish were euthanized at the end of the experiment for tissue sampling.

2.2 | Collection and housing

The methods for collecting wild *A. pseudoharengus* are described in detail in Devine *et al.* (2018). Briefly, juvenile *A. pseudoharengus* were collected via two purse-seine hauls after sunset (21.00–23.00 hours) from Upper Mystic Lake, Massachusetts (42.432915, –71.149517) on 20 July 2017. Surface water temperature during collection was 28.5°C, which was above average for this system in July (Supporting Information Table S1). To reduce transport stress, API® Ammo Lock and Instant Ocean Sea Salt (salinity: 5) were added to water from Upper Mystic Lake in each of two 190 l trash bins. Juveniles were transported to Cronin Aquatic Resource Centre (United States Fish and Wildlife Service) in Sunderland, Massachusetts. Fish were transferred to a 227 l stock tank with flow-through Sunderland well water and were trained to feed on commercial fish feed (50%–50% mix of Otohime B2 and C1, 360–840 µm, 51% crude protein, 11% crude fat). The stock tank was maintained at 21.0 ± 0.7 °C (mean ± s.d.), and fish were fed *ad libitum*.

2.3 | Experimental design

Seven days before the experiment, fish were randomly transferred to eight 64 l experimental tanks. Each tank was randomly assigned one of four treatments: 21°C and 1% ration, 21°C and 2% ration, 25°C and 1% ration, and 25°C and 2% ration. Two tanks were used per treatment ($n = 18$ –23 fish per tank, density = 0.28–0.36 fish per litre). During this acclimation period, fish were maintained in flow-through well water at 20–21°C (Supporting Information Table S2), and fish were fed *ad libitum*. Header well water was aerated through bio-filter balls and recirculation, and supplemental aeration was provided for all tanks to maintain oxygen levels between 90% and 100% saturation. Tank temperature was maintained using a temperature control system (similar to Bayse *et al.*, 2020; Chadwick & McCormick, 2017). Briefly, heated well water (32.2°C) was added as needed to achieve the desired temperature. Heated water flow was controlled by a proportional–integral–derivative (PID) controller (model SYL-23X2P-24, Auber Instruments, Alpharetta, GA, USA) connected to a solenoid valve (model 8210G002, Automatic Transfer Switch Company, Florham Park, NJ, USA). Tank temperature was monitored by a miniature RTD sensor probe (model Pt100MN, Auber Instruments, Alpharetta, GA, USA) connected to the PID

controller. Tanks were supplemented with well water (10–13°C) at a rate of 200–240 ml min⁻¹ for 21°C tanks and 80–120 ml min⁻¹ for 25°C tanks to offset differences in incoming heated water between temperature treatments. Combined cool and heated well water flows ranged from 260 to 300 ml min⁻¹, resulting in greater than five turnovers in tank volume daily and no detectable levels of ammonia, nitrite or nitrate.

Daily rations were dependent on estimates of the total mass (M) of fish in a tank. To calculate the starting daily ration, fish were weighed before the experiment (day –3). Before handling, incoming water was turned off and ProLine Aqua-Coat and Instant Ocean Sea Salt were added to bring the tank to isosmotic salinity (10) to reduce stress. The authors used a rapid method to individually weigh juveniles without anaesthesia, as *A. pseudoharengus* are extremely sensitive to MS-222 anaesthesia. Each fish was individually netted and placed in a synthetic chamois-lined 120 ml specimen cup. Total mass was recorded using a balance (Model: AMF203 AM Fisher Science Education™ Hanover Park, Illinois, USA), and the fish was released. The cup was then reweighed to record the mass of water that was added with the live fish. After 30 min, all the fish were weighed, and incoming water was turned on so that the salt and aqua-coat would wash out at a steady rate. All masses of fish within a tank were summed to calculate a total tank biomass.

The day before the start of the experiment (day –1), temperatures were increased 0.5°C h⁻¹ to the experimental temperature (Supporting Information Table S2). The experiment began on 10 August 2017, when temperatures attained treatment levels and rations began. Throughout the experiment, daily mortalities were recorded and their total length and mass were measured. Masses of dead fish were subtracted from the tank biomass to adjust daily food ration. Fish feed was weighed based on the previous day's total tank biomass. To present the same density of food for each feeding, fish in 2% treatments were fed 0.5% of the tank biomass four times per day, whereas fish in the 1% treatments were fed 0.5% of the tank biomass two times per day. On day 8, all fish were weighed as previously described to adjust daily ration and for initial values to estimate growth rate.

On day 21, fish were euthanized using 200 mg l⁻¹ buffered MS-222. Fish were measured (total length and total mass) and dissected. A transverse cut was made at the posterior edge of the operculum to sever the head. The trunk was reweighed to obtain wet mass before freezing. All samples were stored at –20°C for age and energy reserve analysis.

2.4 | Analysis of growth rate, survival, age and energy reserves

Juvenile *A. pseudoharengus* are relatively intolerant of handling, and so the authors did not tag or mark the individuals. Thus, all direct measurements of growth rate could be calculated only at the tank level. Specific growth rates (% mass day⁻¹) were calculated for each tank from days 8 to 21 using the equation:

$$\text{Specific growth rate} = \frac{\ln(M_{\text{final}}) - \ln(M_{\text{initial}})}{\text{Days}} \times 100.$$

Survival was also measured at the tank level using the equation:

$$\text{Survival} = \frac{\text{Final number of fish}}{\text{Initial number of fish}} \times 100.$$

Daily age was measured for all fish using otoliths (Sismour, 1994). Otoliths were extracted from the otic vesicles under a dissecting microscope and cleaned with water. After air-drying for at least 24 h, otoliths were mounted sulcus side down in Crystalbond 509[®] adhesive. Otoliths from fish larger than c. 35 mm generally required sanding to prepare for imaging. 1500 sandpaper was manually applied (wet and dry) for 10–15 s (dependent on otolith size), followed by 5 s of 3 μm polishing paper (3 M, USA). A drop of immersion oil was placed on the otolith before imaging. Using ImagePro Insight (Media Cybernetics, Rockville, Maryland, USA) and an Infinity 2 Lumenera camera (Ottawa, Ontario, Canada) mounted on a Micro Optical Solutions compound microscope, otoliths were imaged under reflected light at $20 \times 1.5 \mu\text{m}$ magnification. Otoliths were aged by counting the number of dark rings along the major posterior axis (opposite of rostrum). All otoliths were blind double-aged by at least two or three separate readers, and otoliths aged with a >10% difference in CV were aged again by at least two readers. After the second round, nine fish were still aged with a >10% difference in CV and were excluded from analyses.

To measure energy reserves, gravimetric methods as described in Schultz and Conover (1997) were used on whole trunk samples. Briefly, thawed trunk samples were transferred to medium-porosity Alundum[®] extraction thimbles and weighed. Thimbles loaded with samples were dried for at least 24 h in a drying oven (60°C) to achieve a constant dry weight. Samples were cooled for 15 min in a desiccator and then weighed to obtain a trunk dry mass. Thimbles were placed in a custom-made, high throughput Soxhlet apparatus (Schultz & Conover, 1997). Petroleum ether was used as a solvent to extract metabolically accessible lipids from tissues. The Soxhlet was constructed to soak samples in clean solvent for c. 15 min, flush and repeat. All samples were extracted for 3.5 h and then returned to the drying oven (60°C) for at least 24 h. Samples were then cooled and weighed (as previously described); this mass was considered the lean mass. Three juvenile alewife, which had previously been lipid-extracted and dried using the same protocol, were simultaneously processed with fresh samples to serve as lean controls. Next, three dried ash controls (previously ashed) were also weighed and, with the samples, placed in a muffle furnace for 4 h at 550°C. The samples were cooled and weighed directly from the oven (60°C); this ash mass represents non-metabolizable parts of the fish (e.g., bones). Fat content (mg) was calculated as the total dried mass – lean mass. Protein content (mg) was calculated as the lean mass – ash mass. Ash is assumed to have no energetic value to the fish. Using methods described in Peig and Green (2009), fat and lean mass were scaled by length to account for differences in length between and among treatments on day 21.

To determine the total caloric content (kCal) and energy densities (kCal g⁻¹) of collected trunk samples, literature values were used (Brett & Groves, 1979):

$$\text{Energy content} = \left(M_{\text{fat}} \times 39.5 \frac{\text{kJ}}{\text{g}} \right) + \left(M_{\text{lean}} \times 20.1 \frac{\text{kJ}}{\text{g}} \right),$$

$$\text{Energy density} = \frac{\text{Energy content}}{M_{\text{dry}}}.$$

2.5 | Statistical methods

Analyses were conducted in R version 3.5.3 (RStudio Team 2019) using packages *EnvStats* (Millard, 2013), *smatr* (Warton *et al.*, 2012) and *emmeans* (Lenth *et al.*, 2017). Prior to analyses, assumptions for statistical tests were checked to ensure normality of residuals and homogenous variances. ANOVA tests (type II) were used to test for tank differences in pre-experimental mass and age. Two-way ANOVAs (type III) were used to test the fixed effects of ration, temperature and their interaction on survival, specific growth rate, final mass, fat mass-at-length, lean mass-at-length and energy density. Analyses for tank level measures (*i.e.*, survival and specific growth rate) should be interpreted with caution because of low sample sizes ($n = 2$). Permutation ANOVAs were used to confirm that ANOVA results for tank level measures were robust. Trunk dry mass was included as a covariate in models of fat mass-at-length and lean mass-at-length to determine whether there are intrinsic differences in energy reserves based on mass. Total length was used instead of dry mass as the only covariate in the model for energy density, as energy density was calculated using dry trunk mass. Two-factor models for individual measures were initially run as linear mixed effect models with tank as a random effect. Nonetheless, tank had little effect on model results and in some cases drove overfitting in the model; thus, it was removed and all models were run with only fixed effects and covariates when appropriate. Orthogonal contrasts were specified for all categorical variables.

3 | RESULTS

Prior to the experiment, there were no statistical differences in mass among tanks (one-way ANOVA, $F_{7,159} = 1.851$, $P = 0.081$; Figure 1a; Supporting Information Table S3). One 21°C, 2% tank contained fish that were 30% heavier than the pre-experimental average mass of all tanks (1084 mg), and as a result 21°C, 2% replicates had the highest pre-experimental standard deviation in mass (± 683 mg compared to 394–512 in other treatments). Age at the end of the experiment also did not vary among the tanks (one-way ANOVA, $F_{7,136} = 0.772$, $P = 0.612$; Supporting Information Tables S4 and S5).

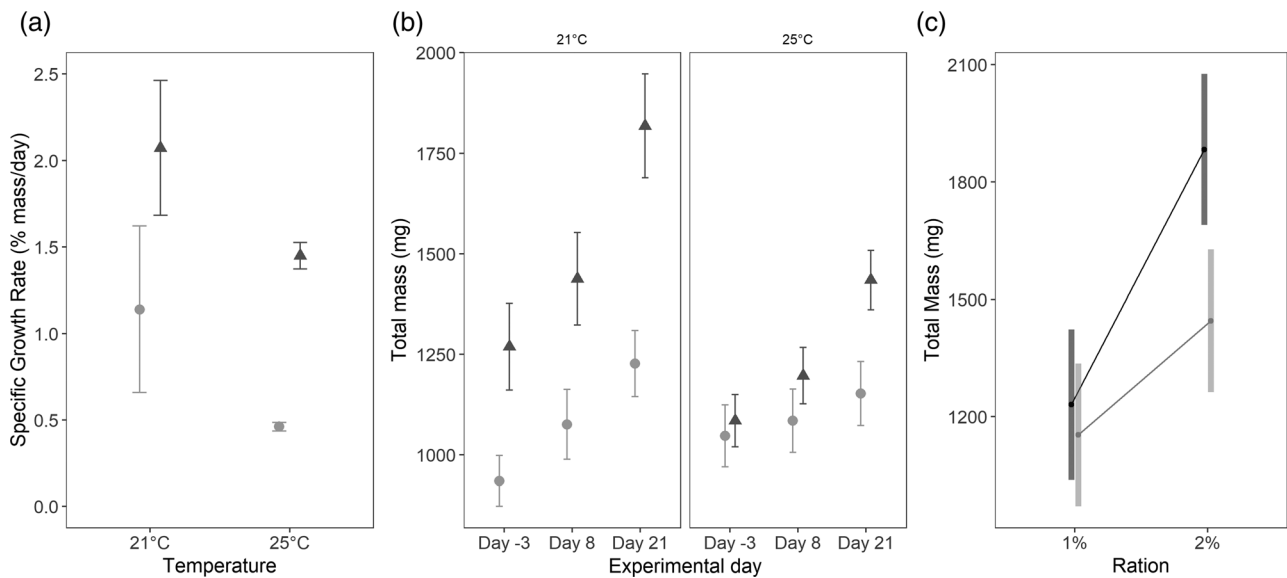


FIGURE 1 Effect of temperature and ration on mass of juvenile *Alosa pseudoharengus*. (a) Tank-level specific growth rate (% mass day⁻¹) of *A. pseudoharengus* from day 8 to day 20 measured at 21°C and 25°C, at 1% (light grey) and 2% (dark grey) ($n = 2$) (●) 1% (▲) 2%. (b) Total mass (mean + s.e.) before the experiment on day -3 ($n = 39-44$), mid-experiment on day 8 ($n = 37-43$) and at the end of the experiment on day 21 ($n = 36-42$) at each temperature and ration (●) 1% (▲) 2%. (c) Interaction effect plot of ration and temperature treatments on total mass on day 21 (95% C.L.; Supporting Information Table S7) (⊕) 21°C (⊖) 25°C

	Treatments			
	21°C, 1%	21°C, 2%	25°C, 1%	25°C, 2%
Survival (%)	94.8 ± 0.6	92.5 ± 3.5	86.0 ± 13.8	95.5 ± 0.4
Final total length (mm)	56 ± 8	63 ± 8	54 ± 8	58 ± 7

TABLE 1 Effect of temperature and ration on survival and growth of juvenile *Alosa pseudoharengus*. Average (±s.d.) tank survival ($n = 2$) and final total length ($n = 36-42$) by treatment

3.1 | Survival

All treatments had survival rates greater than 90% except the 25°C, 1% ration treatment which had a survival rate of 86% (Table 1). Neither ration, temperature or their interaction affected survival (two-way ANOVA; ration: $F_{1,4} = 0.511$, $P = 0.514$; temperature: $F_{1,4} = 0.343$, $P = 0.590$; ration × temperature: $F_{1,4} = 1.371$, $P = 0.307$; Supporting Information Table S6).

3.2 | Growth rate and final size

Fish in the 21°C, 2% ration had the highest specific growth rate (% mass day⁻¹), with fish in the 25°C, 2%, 21°C, 1% and 25°C, 1% ration treatments growing 33%, 47% and 76% more slowly, respectively (Figure 1a). Lower ration decreased specific growth rate, but there were no detectable effects of temperature or an interaction of ration and temperature on specific growth rate (two-way ANOVA; ration: $F_{1,4} = 9.459$, $P = 0.037$; temperature: $F_{1,4} = 0.008$, $P = 0.105$; ration × temperature: $F_{1,4} = 1.371$, $P = 0.934$; Supporting Information Table S7). Specific growth rate variance between replicates was greater in 21°C treatments compared to 25°C. This may have resulted

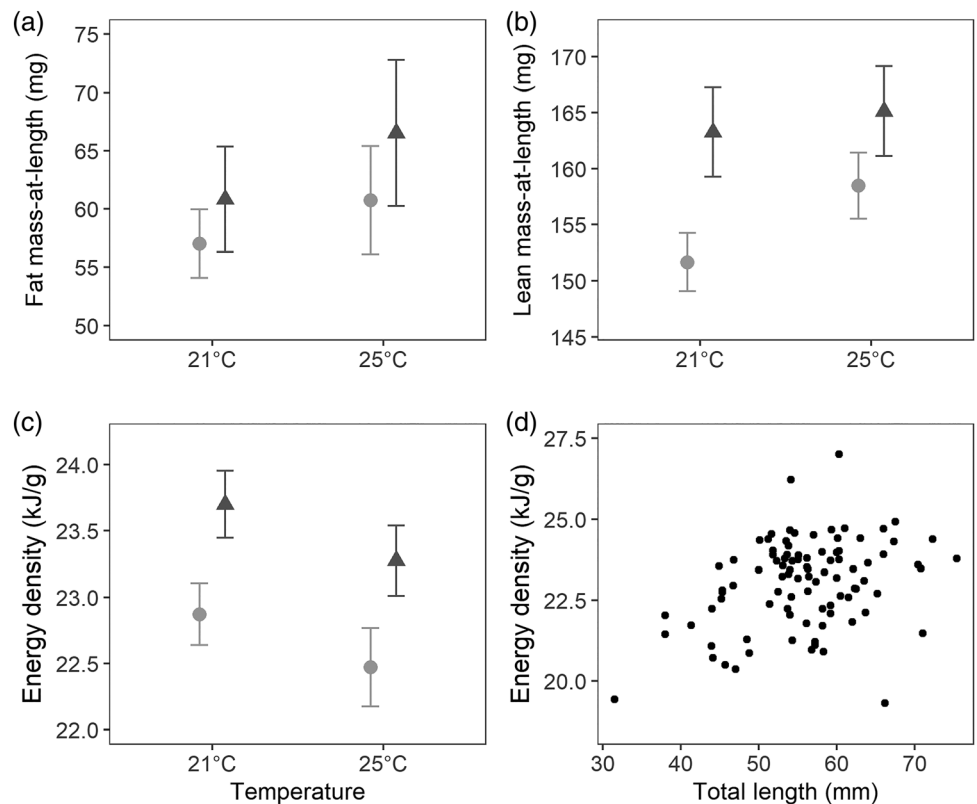
from greater differences in pre-experimental mass between replicates, as there was no evidence for poorer condition based on comparison of mass-length relationships between replicates (Supporting Information Figure S1 and Table S8).

Temperature and ration affected final size (Figure 1b). The largest fish were in the 21°C, 2% ration treatment. Fish in the 25°C, 2% treatment were c. 22% smaller, and both 1% ration treatments had similar sized, c. 33% smaller fish than the 21°C, 2% food ration treatment. Fish were smaller in the 1% rations and at 25°C (two-way ANOVA; ration: $F_{1,140} = 24.769$, $P < 0.001$; temperature: $F_{1,140} = 7.380$, $P = 0.007$; Supporting Information Table S9). There was an interaction between food and temperature (two-way ANOVA, $F_{1,140} = 3.603$, $P = 0.060$) on final mass (Figure 1c).

3.3 | Energy reserves

Size, ration and temperature influenced energy reserves in heterogeneous ways. Reducing ration to 1% decreased fat mass-at-length, whereas temperature had no effect on fat mass-at-length (two-way ANCOVA; ration: $F_{1,89} = 9.038$, $P = 0.003$; temperature: $F_{1,89} = 0.053$, $P = 0.819$; Figure 2a, Supporting Information Table S10). Lean

FIGURE 2 Effect of temperature, ration and size on energy reserves of juvenile *Alosa pseudoharengus*. (a) Fat mass at length (mean \pm S.E.) measured at 21°C and 25°C, at 1% (light grey) and 2% (dark grey) rations on day 21 ($n = 20$ –26). (b) Lean mass at length (mean \pm S.E.) measured at 21°C and 25°C, at 1% (light grey) and 2% (dark grey) rations on day 21 ($n = 22$ –26) (●) 1% (▲) 2%. (c) Energy density (mean \pm S.E.) measured at 21°C and 25°C, at 1% (light grey) and 2% (dark grey) rations on day 21 ($n = 20$ –26). (d) Energy density by total length for all fish ($n = 94$)



mass-at-length (Figure 2b) was also reduced in the 1% food ration but was not affected by temperature (two-way ANCOVA; ration: $F_{1,91} = 7.674$, $P = 0.007$; temperature: $F_{1,91} = 1.031$, $P = 0.313$; Supporting Information Table S11). Larger fish had less fat mass-at-length (two-way ANCOVA; $F_{1,89} = 19.709$, $P < 0.001$) but similar lean mass-at-length as smaller fish (two-way ANCOVA; $F_{1,91} = 0.877$, $P = 0.352$). Energy density decreased with lower ration and increased with juvenile length (two-way ANCOVA; total length: $F_{1,89} = 4.884$, $P = 0.030$; ration: $F_{1,89} = 4.473$, $P = 0.037$; temperature: $F_{1,89} = 1.283$, $P = 0.260$; Figure 2c,d, Supporting Information - Table S12). There was no interaction between temperature and ration on any of these measurements.

4 | DISCUSSION

In the present study, the authors manipulated temperature and ration to determine the sensitivity of juvenile anadromous *A. pseudoharengus* survival, growth and energy reserves to relevant environmental conditions. Ration and temperature affected final mass and energy reserves across the range of experimental conditions, suggesting each factor plays an important role in promoting growth and energy allocation.

4.1 | Temperature and ration effects on size

Of the fixed effects examined, the strongest predictor of final mass was ration, followed by temperature. Many fish species have higher

juvenile growth rates following increased rations because greater assimilated energy allows more scope for growth (Du *et al.*, 2006; Miglavs & Jobling, 1989; Weatherley *et al.*, 1987). Food availability in natural systems is likely a significant driver of growth and thus *A. pseudoharengus* juvenile size. The Mystic Lake system contains high densities of juvenile fish related to its large spawning run (Devine *et al.*, 2021), and prey levels may be limiting. The findings of this study support field studies which have found density-dependent effects on juvenile *A. pseudoharengus* growth when there is intraspecific or interspecific competition for zooplankton resources (Iafate & Oliveira, 2008; Jones & Post, 2013; Kohler, 1980; Nigro & Ney, 1982; O'Gorman *et al.*, 1997). Zooplankton densities and composition change throughout the growing season, triggering juvenile *A. pseudoharengus* diet shifts and emigration (Hondorp *et al.*, 2005; Yako *et al.*, 2002). Thus, a clearer connection between natural prey availability and anadromous juvenile *A. pseudoharengus* growth is needed. Although the maximum specific growth rate observed in this study was similar to juvenile *A. pseudoharengus* (144 days post-hatch) fed a 2%–3% daily ration at multiple salinities (DiMaggio *et al.*, 2015), 1%–2% rations may be limiting and more consistent than natural food availability. Anadromous or landlocked juvenile *A. pseudoharengus* may be able to consume up to 5% of artificial feed per body mass per day (Guo *et al.*, unpublished) or 33.2%–42.7% of wild prey per body mass per day (Stewart & Binkowski, 1986). As differences in food availability affect size distributions of juvenile *A. pseudoharengus*, density and quality of prey items should be further explored as potentially critical predictors of suitable nursery habitat.

In the current study, 21°C was more optimal for growth than 25°C. In non-reproductive life stages, incoming energy resources must first be allocated to routine metabolism and then to growth (Brett & Groves, 1979; Shearer, 1994). An increase in temperature from 21 to 25°C likely increased routine metabolic rate and lowered the energy available for growth. Activity rate may also have increased, leading to less energetic scope for growth. Lowered growth at higher temperatures or low rations is unlikely to be a product of poor fish health, as there was no difference in survival or mass-length relationships among treatments. Future studies should consider measuring metabolic rate and swimming activity to determine the mechanism for lowered growth rates. The temperatures used in this study are typical in Upper Mystic Lake, where July temperatures average 25°C ± 1.75°C and reach as low as 21.8°C and as high as 29.4°C. Thus, Upper Mystic Lake juvenile *A. pseudoharengus* commonly experience temperatures that can alter body size. As temperatures warm and exceed 25°C more often, less growth should be expected during summer months. Juveniles may also use cooler refugia to escape supra-optimal temperatures (Otto *et al.*, 1976; Stewart *et al.*, 2010; Wells, 1968). Nonetheless, cold microhabitats within lakes during summer are often below the thermocline and poorly oxygenated, and appear to limit populations (Devine *et al.*, 2021). The result may be that movement into estuarine habitat and cooler ocean temperatures is an advantageous strategy in certain years (Turner & Limburg, 2016).

Anadromous juveniles in this study demonstrated an optimal temperature for growth (<25°C) below preferred and optimal growth temperatures measured for anadromous larvae and juveniles in previous studies. Larval anadromous *A. pseudoharengus* (Hudson River) grew the fastest at 26.4°C (Kellogg, 1982). Juvenile anadromous *A. pseudoharengus* (Hudson River) demonstrated a behavioural preference for 26.3°C (Kellogg, 1982), whereas landlocked juvenile *A. pseudoharengus* (Lake Michigan) preferred 19.0–25.0°C, depending on acclimation temperature and time of year (Otto *et al.*, 1976). Differences in measurements of optimal performance could be due to size differences (*i.e.*, larger fish have lower thermal optimums) or a lower ration, as the ration used was not reported in these previous studies. Given the significant influence of size and ration on temperature performance curves, physiological studies on juvenile *A. pseudoharengus* should always report these features of experimental design. Alternatively, a lower thermal optimum could be due to population-level differences, wherein southern populations of anadromous *A. pseudoharengus* have evolved a greater tolerance for warmer temperatures compared to northern populations.

Juveniles at both temperatures showed a decrease in final size with lower ration, but the effect of ration was steeper at 21°C compared to 25°C. Numerous studies have examined the joint effects of temperature and ration and found that increased metabolic demands at higher temperatures require increased consumption to maintain growth rates (Boehlert & Yoklavich, 1983; Edsall *et al.*, 1999). Although metabolic rate was not measured directly, the fact that fish size was smallest at 25°C suggests that an increased metabolic rate under static food availability reduced the energetic scope available for growth. Prey production could potentially offset increased metabolic

needs when below the threshold temperature for feeding. Based on the linear relationships of ration, temperature and final mass that were identified, at least a 3.5% ration would be required for juveniles at 25°C to achieve a similar mass as 21°C, 2% ration juveniles. Nonetheless, increasingly greater amounts of prey would be required as food conversion efficiency is inversely related to supraoptimal temperatures (Hofmann & Fischer, 2003). Therefore, the interaction of food availability and temperature may help determine which nursery habitats will yield larger juvenile *A. pseudoharengus*.

Final mass is an important metric of future fitness, because smaller fish can have greater predation risk, lower resilience to starvation and lower physiological tolerance (Sogard, 1997). Therefore, small differences in temperature and food availability in freshwater nursery habitat could cumulatively drive patterns in productivity of juvenile *A. pseudoharengus* (*sensu* Houde, 1987). Environmental factors that suppress growth rates could significantly impact the final size attained by young-of-year *A. pseudoharengus*. Juvenile emigration size has been loosely correlated with environmental temperatures, wherein cooler temperature led to smaller fish at emigration (Stokesbury & Dadswell, 1989). Because juvenile *A. pseudoharengus* emigrate at a wide range of sizes and in multiple pulses (Gahagan *et al.*, 2010; lafrate & Oliveira, 2008; Turner & Limburg, 2016), it is valuable to understand how nursery conditions influence emigration size and subsequent survival.

4.2 | Energy reserves

Larger juvenile *A. pseudoharengus* have greater energy density, as was found previously for this and numerous other fish species (Flath & Diana, 1985; Hondorp *et al.*, 2005). If suboptimal conditions stunt growth, smaller *A. pseudoharengus* will have lower energy density and thus could experience lowered survival and fitness, reducing population resilience even with slight shifts in environmental conditions. Small size and/or lowered condition could delay emigration to the ocean, as emigrating juvenile anadromous *A. pseudoharengus* are larger, faster growing and in greater condition compared to non-migrant fish (Gahagan *et al.*, 2010). Stunted juveniles may stopover in river and estuarine habitats to increase growth or condition before entering saltwater, at the risk of increased predation (Turner & Limburg, 2016). In addition, smaller fish have been shown to deplete energy reserves more rapidly than larger fish, exposing them to greater overwintering mortality (Schultz & Conover, 1999). There are additional implications for the food webs in which *A. pseudoharengus* are critical prey items. If suboptimal conditions lead to smaller, less energy-dense individuals, less energy will be available for upper trophic levels, leading to lowered condition and productivity in predator species (Rand *et al.*, 1994). At landscape scales, these impacts could alter food web energy flow in coastal ecosystems (Dias *et al.*, 2019).

Ration and temperature affect trunk energy reserves *via* different pathways, each with singular as well as additive effects on juvenile body condition and thus long-term fitness. One mechanism by which ration and temperature had indirect effects on fat mass-at-length was

by driving size differences among treatments. Heavier juveniles had lower fat mass-at-length, but similar lean mass-at-length as small individuals. The negative relationship of dry mass with fat mass-at-length holds within each combination of temperature and ration. This relationship contrasts with other studies where fat content increases with size (Schultz & Conover, 1997) and may result from limited ration, space or activity intrinsic to laboratory studies. The opposing relationships of fat mass-at-length with dry mass and energy density with length may result from differences in how each metric was adjusted for size (see Methods). Size-dependent changes in fat mass-at-length are consistent with the findings of previous studies that energy reserves may change significantly with size (Love, 1970; Shearer, 1994), thus scaling fat and lean mass by length and including size as a covariate in models is important. Changes in energy allocation with size suggest the effects of exogenous factors on body condition and long-term impacts depend on the timing of suboptimal conditions in nursery habitats.

Reduced ration also led to decreases in fat mass-at-length, lean mass-at-length and energy density that were not attributed to differences in size. In other species, lipid stores change with ration, whereas protein content remains relatively stable (Brett *et al.*, 1969; Reinitz, 1983). Protein content tends to be size-dependent and is typically conserved as a relative proportion of total body composition, compared to lipid content that is more dynamic under changing exogenous factors (*e.g.*, food ration and environmental stressors) (Shearer, 1994). Across species, fish have demonstrated primary use of glycogen and lipid stores for energy, with protein stores only being utilized after significant decreases in lipids (Love, 1970). Juveniles in the 1% ration may have expended lipid and begun utilizing protein stores to maintain metabolism and growth; alternatively, juveniles may have changed energy allocation strategies to prioritize growth over increasing lipid and protein stores. Depletion of lipid stores significantly influences individual survival and fitness by reducing resilience to overwintering in temperate ecosystems, flexibility in energy allocation and physiological tolerance (Adams, 1999). The abundance and composition of prey items in nursery habitats are important determinants of lipid and protein stores in juvenile *A. pseudoharengus*, thereby affecting individual fitness and overall recruitment success. Lower energy density in low ration treatments suggest that juvenile *A. pseudoharengus* transfer less energy to predators when zooplankton abundance is low. Differences in zooplankton density or composition have also been linked to differences in the energy density of larger *A. pseudoharengus* (>100 mm) (Hondorp *et al.*, 2005). Further investigation of the influence of natural food items on energy reserves and energy density of early life stages will further elucidate characteristics of productive freshwater nursery habitats for anadromous *A. pseudoharengus*.

The authors found no effect of temperature on fat mass-at-length, lean mass-at-length or energy density in this study. Previous studies show that temperature can affect lipid levels, but not protein stores in fed fish (Brett *et al.*, 1969; Stickney & Andrews, 1971). The experimental temperatures of this study were perhaps not high enough to cause increased energy expenditure leading to loss in

weight (Wedemeyer *et al.*, 1984), as would be expected because temperatures were typical of early and mid-summer in the native tributary. If future studies with higher temperatures consistently show no direct effect of temperature on body condition, then temperature may only affect energy stores by affecting juvenile size. In contrast, ration did affect juvenile size and fat mass-at-length. Thus, juvenile *A. pseudoharengus* may exhibit a more sensitive or plastic response to decreases in food availability than increases in temperature over the ranges tested in this study. Future studies should examine whether temperatures closer to juvenile *A. pseudoharengus* upper thermal limits cause changes in body composition that are not accounted for by size. Quantifying the relative contributions of direct and size-mediated effects on growth and body composition will help better predict landscape and ecosystem changes in a warming climate.

4.3 | Broader implications

This is the first study examining the combined effects of temperature and ration on growth rates and energy reserves in juvenile anadromous *A. pseudoharengus*. The authors demonstrate that differences in ration and temperature can significantly affect juvenile size and energy reserves. Because slight differences in size and lipid stores can confer cumulative advantages for survival and fitness (Adams, 1999; Houde, 1987), both temperature and food availability are significant drivers of productivity for young-of-year *A. pseudoharengus*. *A. pseudoharengus* are a keystone species, driving increased productivity by providing energy and nutrients to freshwater and marine environments (Dias *et al.*, 2019; Durbin *et al.*, 1979; Hanson & Curry, 2005; Mattocks *et al.*, 2017; Walters *et al.*, 2009). Their designation as a Species of Concern and candidacy for an Endangered Species listing has driven habitat restoration efforts to target fish passage and dam removals. There needs to be a better accounting for temperature, prey availability and growth rates across habitat types to improve restoration prioritization and habitat management priorities. Although temperature is already incorporated in current *A. pseudoharengus* population models (Nelson *et al.*, 2020), future improvements should incorporate food availability and reflect changes in growth and associated biological processes (*e.g.*, mortality). Further investigation of the impacts of food availability and temperature on juvenile *A. pseudoharengus* physiology could contribute to understanding recruitment variability, optimizing habitat prioritization and better predicting ongoing climate-related range shifts.

Food availability and thermal regimes are more dynamic in natural systems than in laboratory conditions, making it difficult to know how patterns in natural growth rates and therefore productivity may differ. Additional environmental stressors could impose further restrictions on growth rate by increasing energy expenditure, thereby reducing energy stores available for growth (Mazeaud & Mazeaud, 1981; Wedemeyer *et al.*, 1984). Nonetheless, juvenile *A. pseudoharengus* may move between microhabitats to take advantage of different or shifting environmental conditions (Otto *et al.*, 1976; Stewart *et al.*, 2010; Wells, 1968), including more abundant or variable food

sources (Ali & Wootton, 1998). Although it has not yet been observed in juvenile *A. pseudoharengus*, many fishes have demonstrated a significant capacity for compensatory growth (Broekhuizen *et al.*, 1994; Jobling *et al.*, 1993). Even if suboptimal temperatures and food conditions occur, if they are short in duration and followed by improved conditions, juveniles may be able to increase their growth rates and regain lost sizes (Huang *et al.*, 2008; Jobling *et al.*, 1993). Nonetheless, longer periods of depressed growth require longer periods for recovery (Abdel-Tawwab *et al.*, 2006; Heide *et al.*, 2006), and such rapid growth can require trade-offs which affect long-term fitness in other ways, including reduced reproduction, decreased energy storage and increased predation risk (Auer *et al.*, 2010; Hurst *et al.*, 2005; Metcalfe & Monaghan, 2001). Further research is needed to evaluate juvenile growth rates within natural environmental conditions, to determine which conditions contribute significantly to patterns in age-0 size distributions and the long-term impacts of temperature-related growth differences.

5 | CONCLUDING REMARKS

Many anadromous fishes are vulnerable as they require bidirectional access to quality freshwater habitat (Haeseker *et al.*, 2012; Nehlsen *et al.*, 1991). Freshwater systems will likely change (e.g., temperature, flow rate and nutrient loads) at a faster rate than marine systems because of climate change and shifting land-use, suggesting climate effects may operate on anadromous populations first by affecting population recruitment (Moore *et al.*, 1997). Furthermore, high latitude populations are likely to experience faster rates of warming and thus are at higher risk (Hare *et al.*, 2016; Hoegh-Guldberg *et al.*, 2014). As energy allocation changes rapidly during early ontogeny, larval and juvenile fish energy stores and growth rates are more susceptible to suboptimal conditions (Shearer, 1994). Even small changes in food availability or temperature can have significant effects on growth and energy reserves through both indirect (size-based) and direct (metabolic) mechanisms. Food and temperature have complex effects on juvenile physiology which will determine how climate change affects fitness or timing of life-history events. Conditions which maintain high growth and body condition should be considered characteristics of quality habitat or climate refugia for anadromous species and inform assessments of vulnerability.

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AUTHOR CONTRIBUTIONS

L. G. contributed to experimental design, funding, data generation, data analysis and manuscript preparation. S. D. M. contributed to experimental design, data analysis and manuscript preparation. E. T. S. contributed to data generation, data analysis and manuscript preparation. A. J. contributed to experimental design, funding, data analysis and manuscript preparation.

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REFERENCES

- Abdel-Tawwab, M., Yassir, E., Ahmad, M., & Shalaby, A. (2006). Compensatory growth, feed utilization, whole-body composition, and hematological changes in starved juvenile Nile Tilapia, *Oreochromis niloticus* (L.). *Journal of Applied Aquaculture*, 18, 17–36.
- Adams, S. M. (1999). Ecological role of lipids in the health and success of fish populations. In M. T. Arts & B. C. Wainman (Eds.), *Lipids in freshwater ecosystems* (pp. 132–160). New York, NY: Springer.
- Ali, M., & Wootton, R. J. (1998). Do random fluctuations in the intervals between feeding affect growth rate in juvenile three-spined sticklebacks? *Journal of Fish Biology*, 53, 1006–1014.
- Auer, S. K., Arendt, J. D., Chandramouli, R., & Reznick, D. N. (2010). Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (*Poecilia reticulata*). *Ecology Letters*, 13, 998–1007.
- Bayse, S. M., Shaughnessy, C. A., Regish, A. M., & McCormick, S. D. (2020). Upper thermal tolerance and heat shock protein response of juvenile American Shad (*Alosa sapidissima*). *Estuaries and Coasts*, 43, 182–188.
- Benjamin, J. R., Connolly, P. J., Romine, J. G., & Perry, R. W. (2013). Potential effects of changes in temperature and food resources on life history trajectories of juvenile *Oncorhynchus mykiss*. *Transactions of the American Fisheries Society*, 142, 208–220.
- Boehlert, G. W., & Yoklavich, M. M. (1983). Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. *Environmental Biology of Fishes*, 8, 17–28.
- Bowden, A. A. (2014). Towards a comprehensive strategy to recover river herring on the Atlantic seaboard: lessons from Pacific salmon. *ICES Journal of Marine Science*, 71, 666–671.
- Brandt, S. B. (1993). The effect of thermal fronts on fish growth: a bioenergetics evaluation of food and temperature. *Estuaries*, 16, 142–159.
- Brett, J., & Groves, T. (1979). Physiological energetics. In W. S. Hoar & D. J. Randall (Eds.), *Fish physiology* (pp. 280–352). New York: Academic Press Inc.
- Brett, J., Shelbourn, J., & Shoop, C. (1969). Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Board of Canada*, 26, 2363–2394.
- Broekhuizen, N., Gurney, W. S. C., Jones, A., & Bryant, A. D. (1994). Modelling compensatory growth. *Functional Ecology*, 8, 770–782.
- Chadwick, J. G., & McCormick, S. D. (2017). Upper thermal limits of growth in brook trout and their relationship to stress physiology. *The Journal of Experimental Biology*, 220, 3976–3987.

- Chase, B., Callaghan, T., Dechant, M. B., & Patel, P. (2010). *River herring spawning and nursery habitat assessment: Upper Mystic Lake, 2007–2008*. Technical Report 44. Massachusetts Division of Marine Fisheries.
- Crozier, L. G., McClure, M. M., Beechie, T., Bograd, S. J., Boughton, D. A., Carr, M., ... Willis-Norton, E. (2019). Climate vulnerability assessment for Pacific salmon and steelhead in the California current large marine ecosystem. *PLoS One*, *14*, e0217711.
- Devine, M. T., Roy, A. H., Whiteley, A. R., Gahagan, B. I., Armstrong, M. P., & Jordaan, A. (2018). Precision and relative effectiveness of a purse seine for sampling Age-0 river herring in lakes. *North American Journal of Fisheries Management*, *38*, 650–662.
- Devine, M. T., Rosset, J., Roy, A. H., Gahagan, B. I., Armstrong, M. P., Whiteley, A. R., & Jordaan, A. (2021). Feeling the squeeze: adult run size and habitat availability limit juvenile river herring densities in lakes. *Transactions of the American Fisheries Society*, *150*, 207–221.
- Dias, B. S., Frisk, M. G., & Jordaan, A. (2019). Opening the tap: increased riverine connectivity strengthens marine food web pathways. *PLoS One*, *14*, e0217008.
- DiMaggio, M., Pine, H., Kenter, L., & Berlinsky, D. (2015). Spawning, Larviculture, and salinity tolerance of alewives and blueback herring in captivity. *North American Journal of Aquaculture*, *77*, 302–311.
- Du, Z.-Y., Liu, Y.-J., Tian, L.-X., He, J.-G., Cao, J.-M., & Liang, G.-Y. (2006). The influence of feeding rate on growth, feed efficiency and body composition of juvenile grass carp (*Ctenopharyngodon idella*). *Aquaculture International*, *14*, 247–257.
- Durbin, A. G., Nixon, S. W., & Oviatt, C. A. (1979). Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. *Ecology*, *60*, 8–17.
- Edsall, T. A., Frank, A. M., Rottiers, D. V., & Adams, J. V. (1999). The effect of temperature and ration size on the growth, body composition, and energy content of juvenile Coho Salmon. *Journal of Great Lakes Research*, *25*, 355–362.
- Elliott, J. M. (1976). Body composition of Brown trout (*Salmo trutta* L.) in relation to temperature and ration size. *Journal of Animal Ecology*, *45*, 273–289.
- Flath, L. E., & Diana, J. S. (1985). Seasonal energy dynamics of the alewife in southeastern Lake Michigan. *Transactions of the American Fisheries Society*, *114*, 324–337.
- Friedman, W. R., Martin, B. T., Wells, B. K., Warzybok, P., Michel, C. J., Danner, E. M., & Lindley, S. T. (2019). Modeling composite effects of marine and freshwater processes on migratory species. *Ecosphere*, *10*, e02743.
- Gahagan, B. I., Gherard, K. E., & Schultz, E. T. (2010). Environmental and endogenous factors influencing emigration in juvenile anadromous alewives. *Transactions of the American Fisheries Society*, *139*, 1069–1082.
- Haeseker, S. L., McCann, J. A., Tuomikoski, J., & Chockley, B. (2012). Assessing freshwater and marine environmental influences on life-stage-specific survival rates of Snake River spring-summer Chinook Salmon and Steelhead. *Transactions of the American Fisheries Society*, *141*, 121–138.
- Hall, C. J., Jordaan, A., & Frisk, M. G. (2011). The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. *Landscape Ecology*, *26*, 95–107.
- Hanson, S. D., & Curry, R. A. (2005). Effects of size structure on trophic interactions between Age-0 smallmouth bass and juvenile anadromous alewives. *Transactions of the American Fisheries Society*, *134*, 356–368.
- Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., ... Griswold, C. A. (2016). A vulnerability assessment of fish and invertebrates to climate change on the northeast U.S. continental shelf. *PLOS ONE*, *11*, e0146756.
- Heide, A., Foss, A., Stefansson, S. O., Mayer, I., Norberg, B., Roth, B., ... Imsland, A. K. (2006). Compensatory growth and fillet crude composition in juvenile Atlantic halibut: effects of short term starvation periods and subsequent feeding. *Aquaculture*, *261*, 109–117.
- Hoegh-Guldberg, O., Cai, R., Poloczanska, E., Brewer, P., Sundby, S., Hilmi, K., ... Jung, S. (2014). *The Ocean*. Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. pp. 1655–1731.
- Hofmann, N., & Fischer, P. (2003). Impact of temperature on food intake and growth in juvenile burbot. *Journal of Fish Biology*, *63*, 1295–1305.
- Hondorp, D. W., Pothoven, S. A., & Brandt, S. B. (2005). Influence of Diporeia density on diet composition, relative abundance, and energy density of Planktivorous fishes in Southeast Lake Michigan. *Transactions of the American Fisheries Society*, *134*, 588–601.
- Houde, E. (1987). Fish early life dynamics and recruitment variability. *Transactions of the American Fisheries Society* (pp. 17–29).
- Houde, E. D. (1989). Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fisheries Bulletin*, *87*, 471–495.
- Huang, G., Wei, L., Zhang, X., & Gao, T. (2008). Compensatory growth of juvenile brown flounder *Paralichthys olivaceus* (Temminck & Schlegel) following thermal manipulation. *Journal of Fish Biology*, *72*, 2534–2542.
- Hurst, T., Spencer, M., Sogard, S., & Stoner, A. (2005). Compensatory growth, energy storage and behavior of juvenile Pacific halibut *Hippoglossus stenolepis* following thermally induced growth reduction. *Marine Ecology Progress Series*, *293*, 233–240.
- Iafate, J., & Oliveira, K. (2008). Factors affecting migration patterns of juvenile river herring in a coastal Massachusetts stream. *Environmental Biology of Fishes*, *81*, 101–110.
- Jobling, M., Jørgensen, E. H., & Siikavuopio, S. I. (1993). The influence of previous feeding regime on the compensatory growth response of maturing and immature Arctic charr, *Salvelinus alpinus*. *Journal of Fish Biology*, *43*, 409–419.
- Jones, A. W., & Post, D. M. (2013). Consumer interaction strength may limit the diversifying effect of intraspecific competition: a test in alewife (*Alosa pseudoharengus*). *The American Naturalist*, *181*, 815–826.
- Kellogg, R. L. (1982). Temperature requirements for the survival and early development of the anadromous alewife. *The Progressive Fish Culturist*, *44*, 63–73.
- Kohler, C. C. (1980). Trophic ecology of an introduced, land-locked alewife (*Alosa pseudoharengus*) population. Virginia Polytechnic Institute and State University.
- Kosa, J. T., & Mather, M. E. (2001). Processes contributing to variability in regional patterns of Juvenile River herring abundance across small coastal systems. *Transactions of the American Fisheries Society*, *130*, 600–619.
- Lenth, R., Buerkner, P., Herve, M., Love, J., Riebl, H., & Singmann, H. (2017). Emmeans: estimated marginal means, aka least-squares means.
- Love, R. M. (1970). *The chemical biology of fishes. With a key to the chemical literature*. New York: Academic Press Inc.
- Lynch, P. D., Nye, J. A., Hare, J. A., Stock, C. A., Alexander, M. A., Scott, J. D., ... Drew, K. (2015). Projected ocean warming creates a conservation challenge for river herring populations. *ICES Journal of Marine Science*, *72*, 374–387.
- Mattocks, S., Hall, C. J., & Jordaan, A. (2017). Damming, lost connectivity, and the historical role of anadromous fish in freshwater ecosystem dynamics. *Bioscience*, *67*, 713–728.
- Mazeaud, M. M., & Mazeaud, F. (1981). Adrenergic responses to stress in fish. *Stress and Fish*, 49–75.
- Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution*, *16*, 254–260.
- Miglavs, I., & Jobling, M. (1989). The effects of feeding regime on proximate body composition and patterns of energy deposition in juvenile Arctic charr, *Salvelinus alpinus*. *Journal of Fish Biology*, *35*, 1–11.
- Millard, S. (2013). *EnvStats: An R package for environmental statistics*. New York: Springer.

- Moore, M. V., Pace, M. L., Mather, J. R., Murdoch, P. S., Howarth, R. W., Folt, C. L., ... Driscoll, C. T. (1997). Potential effects of climate change on freshwater ecosystems of the New England/mid-Atlantic region. *Hydrological Processes*, 11, 925–947.
- Munch, S. B., Mangel, M., & Conover, D. O. (2003). Quantifying natural selection on body size from field data: winter mortality in *Menidia menidia*. *Ecology*, 84, 2168–2177.
- Nehlsen, W., Williams, J. E., & Lichatowich, J. A. (1991). Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. 16, 18.
- Nelson, G. A., Gahagan, B. I., Armstrong, M. P., Jordaan, A., & Bowden, A. (2020). A life cycle simulation model for exploring causes of population change in alewife (*Alosa pseudoharengus*). *Ecological Modelling*, 422, 109004.
- Nigro, A. A., & Ney, J. J. (1982). Reproduction and early-life accommodations of landlocked alewives to a southern range extension. *Transactions of the American Fisheries Society*, 111, 559–569.
- Nye, J., Lynch, P., Alexander, M., Stock, C., & Hare, J. (2012). *Results of preliminary analyses of the effect of climate change on river herring*. Annual Report.
- O’Gorman, R., Johannsson, O. E., & Schneider, C. P. (1997). Age and growth of alewives in the changing Pelagia of Lake Ontario, 1978–1992. *Transactions of the American Fisheries Society*, 126, 112–126.
- Österblom, H., Olsson, O., Blenckner, T., & Furness, R. W. (2008). Junk food in marine ecosystems. *Oikos*, 117, 967–977.
- Otto, R. G., Kitchel, M. A., & Rice, J. O. (1976). Lethal and preferred temperatures of the alewife (*Alosa pseudoharengus*) in Lake Michigan. *Transactions of the American Fisheries Society*, 105, 96–106.
- Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos*, 118, 1883–1891.
- Rand, P., Lantry, B., O’Gorman, R., Owens, R., & Stewart, D. (1994). Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for Salmonine energetics. *Transactions of the American Fisheries Society*, 123, 519–534.
- RStudio Team (2019). *RStudio: Integrated Development for R*. RStudio, Inc., Boston, MA. <http://www.rstudio.com/>.
- Reinitz, G. (1983). Relative effect of age, diet, and feeding rate on the body composition of young rainbow trout (*Salmo gairdneri*). *Aquaculture*, 35, 19–27.
- Rowe, D., Thorpe, J., & Shanks, A. (1991). Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 405–413.
- Schiemer, F., Keckeis, H., Nemeschkal, H., Schludermann, E., Winkler, G., & Zweimüller, I. (2004). Ontogenetic patterns in thermal adaptation of fish vs. long-term temperature trends in large rivers. *International Congress Series*, 1275, 209–217.
- Schmidt, R., Jessop, B., & Hightower, J. (2003). Status of river herring stocks in large Rivers. *American Fisheries Society Symposium*, 35, 171–182.
- Schultz, E. T., & Conover, D. (1997). Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). *Oecologia*, 109, 516–529.
- Schultz, E. T., & Conover, D. (1999). The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. *Oecologia*, 119, 474–483.
- Schultz, E. T., Conover, D. O., & Ehtisham, A. (1998). The dead of winter: size-dependent variation and genetic differences in seasonal mortality among Atlantic silverside (Atherinidae: *Menidia menidia*) from different latitudes. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 1149–1157.
- Shearer, K. D. (1994). Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. *Aquaculture*, 119, 63–88.
- Sismour, E. (1994). Contributions to the early life histories of alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*): rearing, identification, ageing, and ecology.
- Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review, 60, 1129–1157.
- Stewart, D. J., & Binkowski, F. P. (1986). Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. *Transactions of the American Fisheries Society*, 115, 643–661.
- Stewart, T. J., O’Gorman, R., Sprules, W. G., & Lantry, B. F. (2010). The bio-energetic consequences of invasive-induced food web disruption to Lake Ontario alewives. *North American Journal of Fisheries Management*, 30, 1485–1504.
- Stickney, R. R., & Andrews, J. W. (1971). Combined effects of dietary lipids and environmental temperature on growth, metabolism and body composition of channel catfish (*Ictalurus punctatus*). *The Journal of Nutrition*, 101, 1703–1710.
- Stockner, J. G., & Macisaac, E. A. (1996). British Columbia lake enrichment programme: two decades of habitat enhancement for sockeye salmon. *Regulated Rivers-Research & Management*, 12, 547–561.
- Stokesbury, K., & Dadswell, M. (1989). Seaward migration of juveniles of three herring species, *Alosa*, from an estuary in the Annapolis River, Nova Scotia. *Canadian Field-Naturalist*, 103, 388–393.
- Thorpe, J. (1986). Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 89, 7–14.
- Tommasi, D., Nye, J., Stock, C., Hare, J. A., Alexander, M., & Drew, K. (2015). Effect of environmental conditions on juvenile recruitment of alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) in fresh water: a coastwide perspective. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 1037–1047.
- Turner, S. M., & Limburg, K. (2016). Juvenile river herring habitat use and marine emigration trends: comparing populations. *Oecologia*, 180, 77–89.
- Walters, A., Titus Barnes, R., & Post, D. (2009). Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 439–448.
- Warton, D., Duursma, R., Falster, D., & Taskinen, S. (2012). Smatr 3 - an R package for estimation and inference about allometric lines.
- Weatherley, A. (1990). Approaches to understanding fish growth. *Transactions of the American Fisheries Society*, 119, 662672.
- Weatherley, A. H., Gill, H. S., & Casselman, J. M. (1987). *Biology of fish growth*. New York: Academic Press.
- Wedemeyer, G., McLeay, D., & Goodyear, C. P. (1984). Assessing the tolerance of fish and fish populations to environmental stress: the problems and methods of monitoring (pp. 164–195).
- Wells, L. (1968). Seasonal distribution depth of fish in southeastern Lake Michigan. *Fishery Bulletin*, 67, 1–15.
- Yako, L. A., Mather, M. E., & Juanes, F. (2002). Mechanisms for migration of anadromous herring: an ecological basis for effective conservation. *Ecological Applications*, 12, 521–534.
- Zeug, S. C., Wiesenfeld, J., Sellheim, K., Brodsky, A., & Merz, J. E. (2019). Assessment of juvenile Chinook Salmon rearing habitat potential prior to species reintroduction. *North American Journal of Fisheries Management*, 39, 762–777.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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