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REGULAR ARTICLE

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The effect of early life thermal environment on morphology and growth of yellow perch (*Perca flavescens*)

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Abstract

Early life development in fishes is a period of high phenotypic plasticity. Water temperatures during embryogenesis can lead to alterations in growth and metabolic and morphological phenotypic variations. This study aimed to characterize the effects of temperature on the growth and morphology of yellow perch throughout early development, a species of significant ecological and economic importance in North America. Yellow perch (*Perca flavescens*) embryos were incubated at either constant temperature (12, 15, or 18°C) or under an ambient seasonal regime, where temperature increased throughout embryogenesis until it reached 18°C. All groups were gradually warmed at hatch until they reached 18°C, and morphology was assessed. Inverse relationships between temperature, length and yolk-sac volume were found at the end of the embryonic period. Optimal embryonic growth was associated with the ambient seasonal regime. Fish reared at 15 or 18°C were larger and had higher growth rates when compared to those at 12°C following hatch. However, fish reared in cooler temperatures may possess more advantageous body shapes. Surprisingly, the ambient seasonal incubation had the lowest growth rate post-hatch, even though this most closely mimicked natural incubation for this species. Because suitable larval morphology is related to survival and successful recruitment, these data suggest that yellow perch may be vulnerable to climate change and thermal pollution, although further work is needed to better predict the ecological implications of the phenotypes.

KEYWORDS
body composition, climate change, fish, PCA, thermal pollution

1 | INTRODUCTION

Temperature is a fundamental factor that can directly affect the physiology and the ecology of fishes because they are obligate poikilothermic ectotherms (Beitinger & Fitzpatrick, 1979; Kordas et al., 2011). Water temperature can significantly affect physiology, morphology, performance and fitness by altering development, metabolism and growth rates, aerobic scope, activity, reproduction, sex determination and survival (Angilletta et al., 2004; Dahlke et al., 2020; Godwin et al., 2002; Kingsolver & Huey, 2008; Pankhurst & Munday, 2011). The basis of the physiological significance of temperature lies in the thermodynamic scaling of rates of most enzyme-catalysed biochemical reactions (Beitinger & Fitzpatrick, 1979; Brown et al., 2004; Kordas et al., 2011). Stenothermal fish species with a narrow range of thermal tolerance and high thermal responsiveness are more sensitive compared to eurythermal species, with embryos and spawning adults being highly sensitive life stages (Dahlke et al., 2020).

Embryonic and larval stages are highly sensitive to environmental temperatures due to periods of rapid morphological and physiological transformations (Dahlke et al., 2020; Kestemont et al., 2015). Thermal sensitivity is due to interactions between immature physiology and the intricate relationship between rates of development, growth and metabolism and environmental temperature (Burggren & Dubansky, 2018), with developmental rate being most sensitive to thermal changes (Forster et al., 2011; Kamler, 2007; Verberk et al., 2021). Embryonic and larval periods are characterized by rapid cellular differentiation for the development of integral morphological and anatomical structures and functions, along with somatic growth to increase body size (Jobling, 2002; Pankhurst & Munday, 2011). Thermal changes during these early life stages can alter development rate and hatch timing (Mitz et al., 2019; Ojanguren & Braña, 2003; Réalis-Doyelle et al., 2016, 2018); yolk utilization rate (Eme et al., 2018; Lee et al., 2016; Mueller et al., 2017); size at hatch (Kamler, 2007); the time of onset of exogenous feeding (Ivanova & Svirskaya, 2009; Réalis-Doyelle et al., 2018); malformation rate (Brown et al., 2010; Johnston, 2006; Pittman et al., 1990); myogenesis and skeletogenesis (Brown et al., 2010; Johnston, 2006), and ultimately survival and recruitment success. A recent meta-analysis found that developmental temperatures above or below optimal can alter the phenotypic structures of fish populations and therefore fitness and survival (O'Dea et al., 2019).

The yellow perch (*Perca flavescens*) is a cool-water member of Percidae that is widespread in temperate regions of North America. The yellow perch has cultural and ecological significance, and a large economic value as a commercial and sport fish, particularly in the Great Lakes region. This species is highly important for commercial aquaculture for food, for restocking and release into natural waters as a sport fish (Clay & Bruner, 2021), and is one of the high-priority species for management in the United States (Mailson, 2003; Teletchea & Teletchea, 2020). Yellow perch (*Perca fluviatilis*) spawn in the spring when the water temperature is between 6 and 12°C. They produce ribbons of fertilized eggs that are often associated with underwater structures such as macrophytes (Clay & Bruner, 2021). Existing publications do not provide a clear consensus on optimal temperature ranges for perch embryogenesis. The optimal range for survival at hatch has been reported for Eurasian and yellow perch at 8–12°C (Guma'a, 1978), 12–20°C [Eurasian perch (Wang & Eckmann, 1994)], and 10.1–18.2°C [both species (Hokanson & Kleiner, 1974)]. The optimal temperatures at swim-up and larval phases were 16–20°C (Wang & Eckmann, 1994) and 20–25°C [both species (Kestemont et al., 2015)], respectively. Some of these differences in optimal temperature may reflect differences in species (Eurasian vs. yellow perch) and different source populations of individual species. However, the differences in reported optimal temperature strongly suggest that more thorough characterizations of growth patterning are needed.

Increasingly warmer water may change phenotypic traits in yellow perch, and early life stages are likely the most vulnerable based on their entry to a rapid developmental window (O'Dea et al., 2019). Correspondingly, temperature was shown to be the most important factor affecting the recruitment of perch larvae (Kaemingk et al., 2014). Here we examined the effect of temperature on growth and morphology of yellow perch. The temperatures used in this study represent typical temperatures in early development (12°C), late development (15°C) and warmer than typical (18°C) for the embryonic period; these temperatures are within the range of optimal temperatures previously reported for this species (Hokanson & Kleiner, 1974). We tested four thermal regimes: constant 12, 15 and 18°C and an ambient seasonal incubation, with gradual warming starting from fertilization. The ambient seasonal incubation had a mean incubation of 15°C and was representative of a more natural incubation. All of the treatment groups were moved to a common 18°C following hatch, to assess whether incubation temperature would influence post-hatch growth and morphology.

2 | MATERIALS AND METHODS

2.1 | Fish source and spawning

Sexually mature adult wild yellow perch were caught from Mitchell's Bay, Ontario, Canada, located on the east shore of Lake St. Clair, in spawning season. Fish were held in rectangular outdoor tanks in water from adjacent freshwater ponds (Leadley Environmental Corp, Essex, Ontario) at natural spring temperature, daylight cycle, and provided live minnow feed (*Pimephales promelas*) until spawning. Water pH, conductivity and dissolved oxygen were 8.46, 349 µS and 9.97 mg/L, respectively. A total of 6 males [mean total length (TL) = 172.9 ± 8.0 mm, mean wet weight = 57.1 ± 16.7 g] and 12 females (mean TL = 211.7 ± 20 mm, mean wet weight = 100.8 ± 34.2 g) were used for natural spawning through tank breeding. Fertilized ribbons of eggs were collected with fish nets. Four ribbons containing embryos were transported to McMaster University, Hamilton, Ontario, Canada, within 20 h post spawning. Three small segments of each ribbon were weighed (<2 g wet weight), and the number of embryos was counted in each segment using an Axio Zoom V16 microscope (Carl Zeiss, Toronto Canada); the average embryos per gram were used to

estimate the number of embryos/grams of ribbon based on the total ribbon weight. Ribbons were estimated to have 6051, 5484, 14,343 or 13,988 embryos, respectively. The care and use of experimental animals complied with the Canadian Council for Animal Care animal welfare laws, guidelines and policies as approved by McMaster University's Animal Ethics Research Board (Animal Use Protocol: #20-06-23).

2.2 | Embryo incubation

Embryos were reared in E2 media (15 mM NaCl, 0.5 mM KCl, 1 mM $CaCl_2$, 1 mM $MgSO_4$, 150 μM $KH2PO_4$, 50 μM Na_2HPO_4 and 0.7 mM $NaHCO_3$) and incubated in one of three constant temperature regimes (12, 15 or 18°C) or an ambient seasonal (AS) thermal regime that involved a rolling rise of temperature (1°C rise/3 days) from the start of incubation through the temperature reached 18°C (Table S1). Custom-built temperature-controlled incubators were used as previously described (Mitz et al., 2014), with water temperatures monitored by HOBO TidbiT® data loggers inside the incubators. Starting from hatch onwards, the gradual warming of larvae from the 12 and 15°C incubations was at rates of 1.5°C/2 days and 1°C/3 days, respectively, to move to the common garden temperature of 18°C for larval fish. This ensured that perch were reared at a temperature optimal for the yolk-sac larvae and could be feed trained before the critical period of complete yolk exhaustion (Wang & Eckmann, 1994). Common garden conditions for larvae also ensured that any potential differences between groups would be reflective of embryonic incubation. We provide both the days (from fertilization) and growing degree days to key developmental stages, to contrast the four temperature treatments in Table S2. A developmental staging guide for this species and detailed information on the impact of these temperature regimes on developmental progression, survival and developmental abnormalities are provided elsewhere (Fraz et al., 2024).

Rearing of embryos was carried out in rectangular food-grade clear plastic containers (capacity: 4 L, material: HDPE, dimensions: 31 × 18 × 9.3 cm). Each container had a small strand cut from the whole ribbon that was affixed to a white grid aquarium divider (polycarbonate plastic, dimensions: 22.7 × 10.2 cm) using cable ties held in approximately 2.5 L of E2 medium, with continuous air supply. Aquarium rocks were used to keep the grid submerged under water. Three replicate containers from each of the four ribbons were prepared for each incubation regime. To prevent fungal growth, ribbons were treated with formalin (Sigma Aldrich, Oakville, Canada) disinfection at 200 mg/L for 15 min (Abd El-Gawad et al., 2015), from 48 hpf to the eyed stage along with 100% media renewal every other day.

After hatch, larvae were reared in square food-grade plastic containers (capacity: 3.3 L, dimensions: 22 × 22 × 10 cm, material: HDPE) that were covered in grey duct tape on the outer walls and the bottom (Tamazouzt et al., 2000). Larvae were reared at a density of ~50/L under natural spring daylight cycle conditions in Hamilton, Ontario, Canada. Larvae were initially fed 4 times a day with 1st instar artemia alone (twice a day). At 4 weeks post-hatch, they were fed 3 times a day with artemia alone or supplemented with Gemma® micro150 (twice a day, Skretting, Salt Lake City, USA). The excess food was removed at the end of the day with 80%–85% daily water renewal.

During embryonic incubation and larval rearing, water temperatures were monitored with HOBO TidbiT® data loggers (Onset, Bourne USA). Water temperatures for the constant temperature incubation regimes of 12, 15 and 18°C were recorded as 11.71 ± 0.71, 15.10 ± 0.44 and 18.50 ± 0.35°C, respectively. The recorded temperature for the ambient seasonal experiment changed across developmental periods as expected; temperature variation was similar to the constant temperature regimes (Table S1). Full records of water temperature can be accessed from the data repository (see Supplemental Information). Water quality parameters were monitored weekly in the static culture for pH (7.45–7.51), dissolved oxygen (>80%), conductivity (1038.3–1064.2 μS/cm), general hardness (60 mg/L), carbonate hardness (40 mg/L), ammonia (0–0.25 ppm), nitrate (0 ppm) and nitrites (0 ppm). The pH, dissolved oxygen and conductivity were measured using a handheld meter (YSI®, model 556 MPS, YSI Incorporated, Yellow Springs, USA). An API 34 Freshwater Master Test Kit (Mars Fishcare, Chalfont, USA) was used to monitor general hardness, carbonate hardness, ammonia, nitrate and nitrites.

2.3 | Sample collection, imaging and morphometrics

Embryos or larvae were sampled at nine developmental timepoints (Table S3) to assess the impacts of temperature throughout early development. The details of developmental staging, terminology and definitions are described previously (Fraz et al., 2024). Sampling spanned five developmental time points in the embryonic period (T1–T5; $n = 78–84$), at hatching (T6; $n = 82–84$), and three time points in the larval period between swim-up and exogenous feeding (T7–T9; $n = 80–85$) phases when larvae reached yolk exhaustion and shift to food by mouth. Briefly, embryos were sampled during organogenesis 1 (T1; formation of the body axis and neural keel) and 2 (T2; formation of the brain, and detachment of the tail from the yolk) and at the beginning (T3; spontaneous muscle contractions), middle (T4; heartbeat) and end (T5; complete eye pigmentation and visible circulation on yolk) of organogenesis 3. T6 is at hatch which occurred in organogenesis 4. The three time points in the larval period corresponding to organogenesis 5 were swim-up (T7), mixed feeding (T8) and exogenous feeding (T9) phases. These developmental phases were based on markers easily observable under light microscopy, and are described previously in detail (Fraz et al., 2024) and briefly introduced in Table S3. Embryos or larvae were euthanized with an overdose of 250 mg/L MS222 with 500 mg/L sodium bicarbonate (Sigma Aldrich, Oakville, Canada), fixed in 10% neutral buffered formalin (Sigma Aldrich) for 48 h. at 4°C, rinsed with PBS, preserved in 70% ethanol and stored at 4°C.

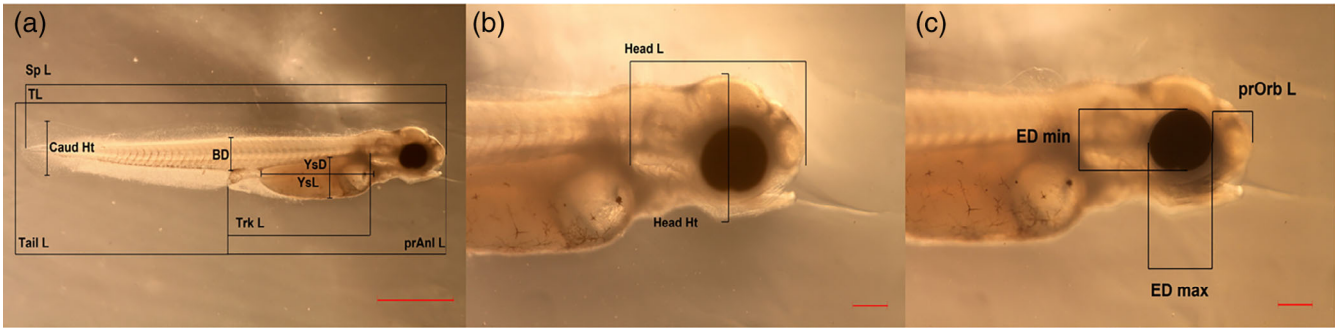

FIGURE 1 Representative images of the morphometric parameters studied in the larval period. Total length (TL), spinal cord length (Sp L), caudal-fin height (Caud Ht), tail length (Tail L), body depth (BD), pre-anal length (prAnl L), trunk length (Trk L), head length (HL), head height (H Ht), yolk-sac length (YsL), yolk-sac depth (YsD), minimum eye diameter (EDmin), max eye diameter (EDmax), and pre-orbital length (prOrb L) were measured at T6 (hatching), T7 (swim-up) and T8 (mixed feeding) stages. All parameters were measured at T9 (exogenous feeding) except for YsL and YsD because the yolk was largely resorbed. Full body lateral images (panel a, scale bar = 1000 μm) were used to measure TL, Sp L, Caud Ht, Tail L, BD and prAnl L, Trk L, YsL and YsD, whereas lateral images (panels b, c, scale bar = 200 μm) were required for measurements of HL, H Ht and EDmin, EDmax and preOrb L, respectively.

Preserved samples were imaged with an Axio Zoom V16 microscope (Carl Zeiss, Toronto Canada) coupled to a Canon EOS Rebel T1i camera using Zeiss AxioVision (Rel. 4.8) digital image processing software. Preserved, unhatched embryos at time points (T1–T5) were first dissected using fine forceps to remove them from chorions before imaging (Figure S1). To image samples at time points (T6–T9), a minimum of two images from a lateral view were taken of the full and anterior body at 10–50× magnification (Figure 1). Additional images were taken at higher magnification (100×) to provide clear demarcation of eye and head margins and achieve greater focus on the operculum and gill cover (Figure 1b,c).

A suite of 14 morphometric measurements (Table S4) were made, close to the nearest hundredth of 1 μm, using the Zeiss AxioVision (Rel. 4.8) digital image processing software. An image of larval fish with labels of all morphometric measurements is shown in Figure 1. For body length, we measured total and spinal cord length. Tail morphology was captured by tail length and caudal-fin height. The morphology of the anterior body was determined by trunk length, pre-anal length, body depth, head length and height, eye diameter (minimum and maximum) and pre-orbital length. Because the yolk is not spherical, both length and depth were measured. The absence of anatomical structures at certain developmental time points made it unfeasible to determine all 14 morphometric measurements at each time point. Decisions on which structures could be reliably measured at a given time point were guided by developmental milestones (Table S3) and careful judgement of the image library. For instance, eye diameter was not measured in the earliest four embryonic developmental time points (T1–T4) because eyes were not pigmented, and the margins of the eye could not be reliably demarcated. Yolk measurements were not taken at the exogenous feeding phase (T9), because the yolk was nearly exhausted. This agrees with the observations in Norden (1961) that the yolk sac of yellow perch larvae can no longer be reliably measured once the larvae attain a TL of approximately 6.8 mm. Yolk-sac volumes were calculated from measured yolk-sac lengths and depths using the formula for the volume of a prolate spheroid (Watanabe et al., 1999):

$$V = (\pi/6) l \times h^2,$$

where V is the yolk-sac volume (YsV, mm^3), l is the yolk-sac length (YsL, mm) and h is the yolk-sac depth (YsD, mm).

2.4 | Proximate analysis

Total lipid, protein, glucose and glycogen levels in whole larvae were measured at hatching (T6) and all larval phases (T7: swim-up, T8: mixed feeding and T9: exogenous feeding) in each of the four temperature treatments (12, 15 and 18°C and ambient seasonal) using methods previously described (Thompson & Vijayan, 2021). Pools of larvae (2–6) were sampled, euthanized with MS222 (250 mg/L buffered with 500 mg/L sodium bicarbonate), flash frozen and stored at −80°C. For total lipids, samples were sonicated (Sonifier cell disruptor 350; Branson, Danbury USA) in 200 μL of methanol. Lipids were determined by a modified Folch method (Folch et al., 1957; Thompson & Vijayan, 2021), which employed extraction of lipids into a 2:1 v/v mixture of chloroform. Extracted samples were air evaporated to dryness for ~72 h and weighed. For protein, glucose and glycogen assays, separate sets of samples were sonicated on ice in a solution of protease inhibitor and Tris buffer (50 mM, pH 7.5). The homogenate was divided equally into two tubes for the protein and glycogen assay or stored at −80°C for the glucose assay. Total protein was determined by spectrophotometric absorbance in 96-well plates, with the QuantiPro BCA kit (Sigma-Aldrich) and bovine serum albumin (Sigma-Aldrich) as a standard (Thompson & Vijayan, 2021). Glycogen content was determined after enzymatic hydrolysis with amyloglucosidase (Bergmeyer & Bernt, 1974). Glucose was determined by spectrophotometric absorbance in 96-well plates.

2.5 | Statistical analyses

Statistical analyses were conducted using R v4.3.1 on R Studio version 1.3.1073 or Sigma plot version 13.0. Statistical analysis was divided into the following steps: (i) Data visualization through summary statistics, density plots, box plots and correlation analyses to understand the data properties and structure, and relationships between various morphological parameters; (ii) principal components analysis (PCA) of post hatch dataset to reduce the multidimensionality (iii) estimation of larval growth rate by linear regression of the principal components accounting for highest variation of body size with developmental timepoint and temperature; (iv) interaction contrasts of post hatch dataset to look at the interactions between changes in body size and body shape with developmental timepoint and rearing temperatures.

In addition to functions in base R (lm, prcomp), the following libraries were used for custom contrasts from the linear models: emmeans v1.8.8 (Lenth, 2017). Summary statistics were calculated to produce the mean and standard deviation for each morphometric parameter's raw data in the embryonic and larval periods. The shapes of raw morphometric data distributions were visualized using density plots, with most of the data not normally distributed. Boxplots of raw morphometrics data (embryonic and larval periods) were used to visualize the changes in the size of morphological structures across developmental time points (Figures S2–S13) for each of the treatment groups that is, 12, 15, 18°C and AS. Pearson correlation coefficients ($p < 0.0001$) for all morphometric parameters at the last time point of the embryonic period (T5) and four time points of the larval period (T6–T9) were determined for pairs of morphometric parameters because strong correlations were expected between measures of body size during early development (Parichy et al., 2009).

After visualization in density plots and a series of diagnostic plots (normal QQ plots, residuals vs. fitted), the raw data of the larval period (T6–T9) were $\log_{10}$ transformed. PCA (based on a variance–covariance matrix) was used to reduce the multidimensionality of the log-transformed data of the morphological parameters that would describe growth as a change in larval body size or shape. Further analysis was performed to reduce the number of predictor variables and to eliminate the multicollinearity between variables. Positive correlations of the majority of the morphometrics parameters and PC1 were obvious from their loadings on PC1 which included TL, spinal cord length, tail length, trunk length, pre-anal length, head length, head height and eye diameter (minimum and maximum). PC2 has a strong positive loading of pre-orbital length, while negative loadings of body depth and caudal-fin height (Table S5). The importance of the principal components is given in Table S6. A cut-off point of less than 5% variation was applied to select PCs for further analysis. PC1 and PC2 accounted for the largest cumulative proportion of variation approximately ~87%, whereas PC3 and beyond accounted for less than 5% variation. Because PC1 accounted for the highest variance of data, and measures related to overall growth (e.g., TL) were strong loadings (Table S5), PC1 was regressed as the dependent variable in a linear model with developmental timepoint, temperature and their interactions as predictors; and growth rate was estimated from the regression coefficients (based on the assumption that growth of larvae occurs prominently through change in body size). A type II analysis of variance (ANOVA) was used (based on sum-to-zero contrasts) using the car v3.1.2 library (Fox & Weisberg, 2019). To compare across developmental timepoint and rearing temperature, contrasts and confidence intervals of PC1 and PC2 were estimated using emmeans v1.8.0 (Lenth, 2017). We additionally performed contrasts of length and caudal-fin height against body shape to visualize changes driven by temperature on shape.

Analyses were performed on $\log_{10}$-transformed data. Kruskal-Wallis ANOVA (Dunn's post hoc test for pair-wise comparisons, Bonferroni adjusted $p < 0.017$) tests were completed across different temperature regimes within each developmental time point (T1–T9). As we did not perform a PCA on pre-hatch data, we employed a two-way ANOVA to identify interactions between developmental stage and temperature.

Data of proximate composition (protein, lipid, glucose, and glycogen) were analysed by ANOVA with Holm-Sidak post hoc test for multiple comparisons with Bonferroni adjusted $p < 0.017$. All pairwise comparisons within each developmental time point (T6–T9) compared across the four temperature regimes (12, 15, 18°C and AS) were analysed. All data, including the raw and $\log_{10}$-transformed data, density plots, diagnostic plots, PCA, linear model and model coefficients used in the statistical analyses, along with R codes and the image library are deposited in the Federated Research Data Repository of Canada (available at https://doi.org/10.20383/103.0852).

3 | RESULTS

3.1 | Changes in body size in the embryonic (pre-hatch) period

Throughout the embryonic period, TL increased with development progression in all incubation groups (Figure 2). By the end of the eye pigmentation phase (T5), the mean TL was largest for yellow perch in the ambient seasonal incubation regime, followed by those reared at 12°C > 15°C > 18°C constant temperature incubations (Figure 2, Kruskal-Wallis ANOVA, Dunn's post hoc test with Bonferroni adjusted $p < 0.017$). This indicates a negative relationship between constant incubation temperature and mean TL at the end of the embryonic period. We see large reductions in yolk-sac volume between T3, when the embryo starts spontaneous body movements, and T5, when eye pigmentation was complete; this was most obvious in the cultures of constant 12 and 15°C (Figure S2). Embryos reared under the ambient seasonal regime had a large decrease in yolk-sac volume between T4 (the middle of organogenesis 3) and T5, when the incubation temperature was the highest (Figure S2).

At hatching, perch had distinct phenotypes related to their embryonic incubation temperatures. Representative images of the heads and full lateral sides of larvae showing the phenotypic features are provided in supplemental Figure S14. Prominent differences were noticed in craniofacial morphology, digestive tract development and

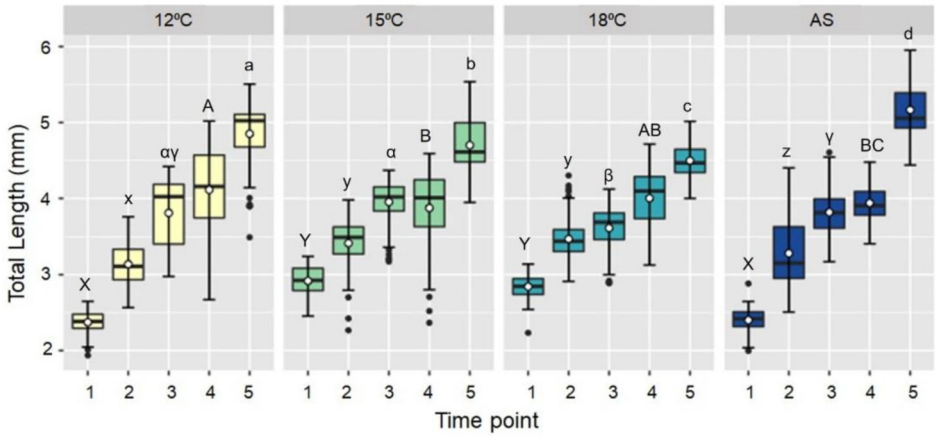

FIGURE 2 Total body length of yellow perch embryos reared in different incubation temperatures (12, 15 and 18°C or an ambient seasonal incubation temperature, see text for details of incubation). Data were collected at five developmental timepoints before hatch: Organogenesis 1 (T1), organogenesis 2 (T2), end of organogenesis 2 and beginning of organogenesis 3 (T3), mid-organogenesis 3 period (T4) and end of organogenesis 3 period (T5); descriptions of these timepoints are provided in the text and in Table S2. The box plots show raw data, where open circles represent the mean, closed circles represent outliers, boxes represent the interquartile range and horizontal lines within boxes represent the median. Statistical analyses were completed across different temperature regimes within each developmental time point (T1–T5). Different letters indicate statistical differences across temperature treatments using a Kruskal Wallis analysis of variance (ANOVA) with Dunn's post hoc; Bonferroni adjusted $p < 0.017$, for each developmental timepoint.

fin development across treatment groups. Fish reared at 12°C had a rounded head with incomplete flexion, smaller head height, head trunk angles and a thick snout compared to fish reared at 15 and 18°C. Perch reared at 15°C had an open mouth in more than 80% of individuals examined, increased head flexion and more developed upper and lower jaws. By hatching, many perch from the 15 and 18°C groups had an anus (observations from lateral images), indicating higher digestive tract development than those reared at 12°C, where an anus was infrequently found by hatching. The dorsal and caudal fins of fish reared at higher incubation temperatures appeared more developed by hatching (observation from lateral images).

3.2 | Changes in body size and shape in the larval (post hatch) period

In the larval period, mean TL (Figure 3a) increased with developmental progression in all incubation groups and TL was highly correlated with PC1 (Figure 3b). At hatch (T6), the mean TL was smallest for yellow perch reared at 12°C; the fish with the largest length were those reared at 15°C. However, by exogenous feeding (T9), mean TL was the largest (and more variable) in yellow perch reared at 18 and 15°C (Kruskal-Wallis ANOVA, Dunn's post hoc; $p < 0.017$). Surprisingly, fish reared in the ambient seasonal incubation regime were smaller than at all other groups, both at hatching (T6) and at exogenous feeding (T9).

There were positive and significant correlations between all measured morphological structures of exogenous feeding larvae (Figure 4, Pearson correlation coefficients, $p < 0.0001$), except for correlations with yolk-sac volume which were negative, as expected. Correlation plots between pairs of body structures (Figure S15–S18) for all treatment groups and larval phases indicate rearing temperature influenced the strength of these relationships in yellow perch. More highly correlated morphometric measurements were typically seen in the 15 and 18°C incubation groups; correlations were weakest in fish reared at 12°C. The developmental phase also influenced these relationships; correlations were weakest at the mixed feeding phase for the constant incubation groups.

Pre-orbital length, body depth and caudal-fin height were considered measures of larval shape. Like other morphometrics, body depth (Figure S4), pre-orbital length (Figure 5a) and caudal-fin height (Figure S5) increased across larval phases. These latter measurements reflect changes in the shape of the tail and the anterior head, respectively. The linear positive relationship between PC2 and pre-orbital length (loading of 0.85; Figure 5b) and negative relationships between PC2 and body depth and caudal-fin height were found for larval stages (T6–T9; loadings of BD: −0.39 and Caud Ht: −0.33). Patterns across treatment groups were highly similar to those in TL at hatch (T6) and exogenous feeding (T9; Figures 5a and S4).

Due to the high (but expected) correlation between linear morphometric measurements, we performed a PCA analysis of the measurements in the larval period. It was evident from the biplot of PC1 and PC2 (Figure 6a) that the vectors of TL, spinal cord length, trunk length, tail length, pre-anal length, eye diameters, head length and head height all extended along PC1, and the close angles of these vectors with one another agreed with the positive correlation between these parameters. PC2 explained the variation in the remaining morphometric parameters, that is, body depth, caudal-fin height and pre-orbital length (Figures 3b and 4b). Therefore, it was evident that PC1 captured size variation in size or overall growth of larvae, whereas PC2 captured body shape variation in the larval stages. The total data variation showed by the first two principal components was 87.68%; PC1, PC2 and PC3 explained 82.15%, 5.53% and 4.27% of the variation, respectively.

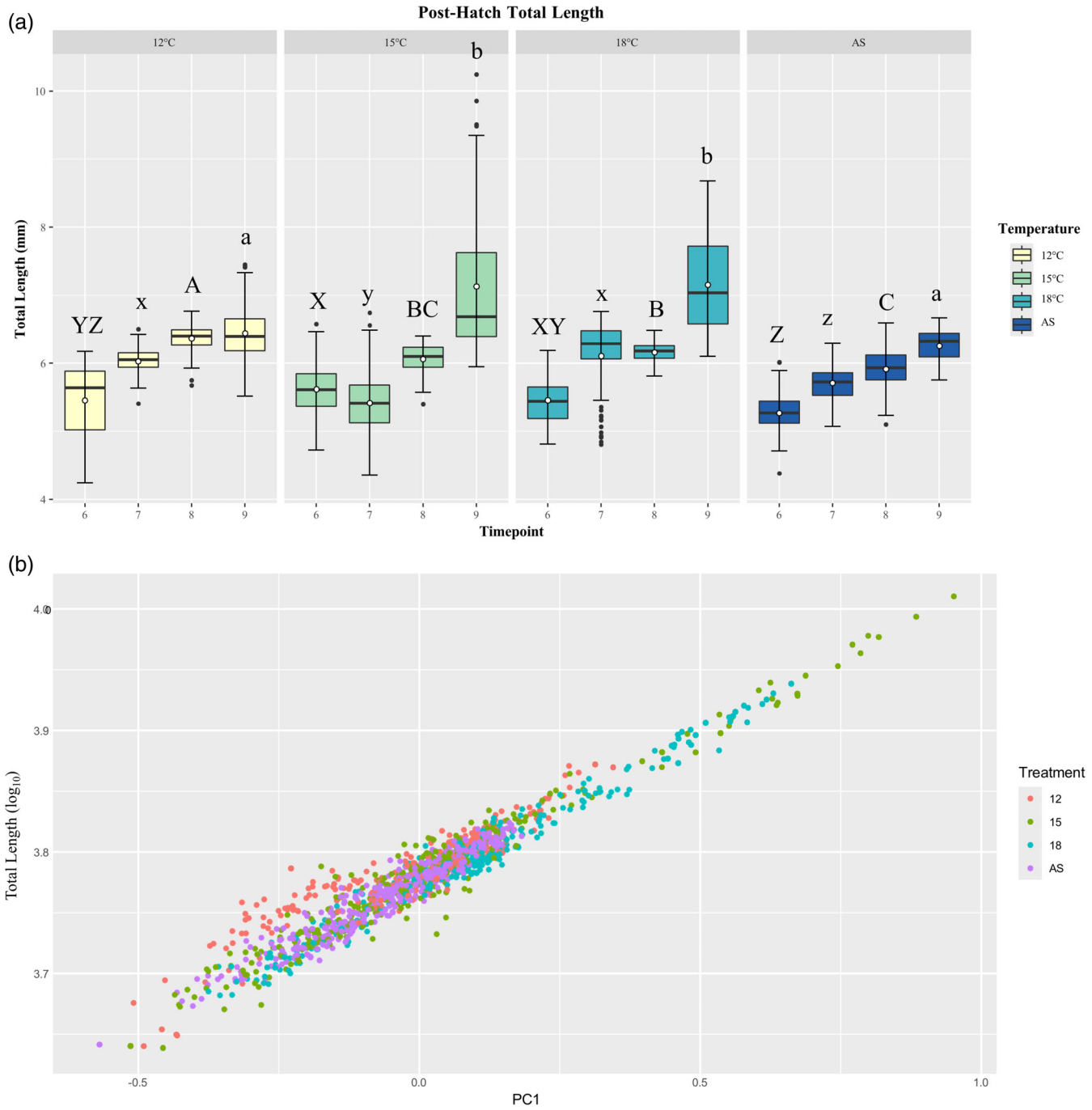

FIGURE 3 Total body length of yellow perch larvae reared in different incubation temperatures. (a) Total length at hatch (T6), swim-up (T7), mixed feeding (T8) and exogenous feeding phases (T9) for larvae reared at constant 12, 15 and 18°C or an ambient seasonal (AS) incubation temperature (see text for details of incubation). The box plots show raw data, where open circles represent the mean, closed circles represent outliers, boxes represent the interquartile range and horizontal lines within boxes represent the median for each group. Statistical analyses were completed across different temperature regimes within each developmental time point (T6–T9). Different letters indicate statistical significance; Kruskal Wallis analysis of variance (ANOVA), Dunn's post hoc; Bonferroni adjusted $p < 0.017$ for each developmental timepoint. (b) Scatter plot of PC1 versus total length (TL) of larval yellow perch using log-transformed data from all stages in the post hatch period (T6–T9). Closed circles of different colours indicate different temperature treatments.

3.3 | Changes in other morphological structures in the larval (post-hatch) period

There was an overall increase in the size of body structures measured across the larval period (mean head length, head height, eye diameter, tail length, trunk length, pre-anal length and spinal cord length; Figures S6–S13). In all structures, the mean lengths at the exogenous feeding phase (T9) were always larger in the 15 and 18°C treatments compared to the 12°C or ambient seasonal treatments despite the attainment of common

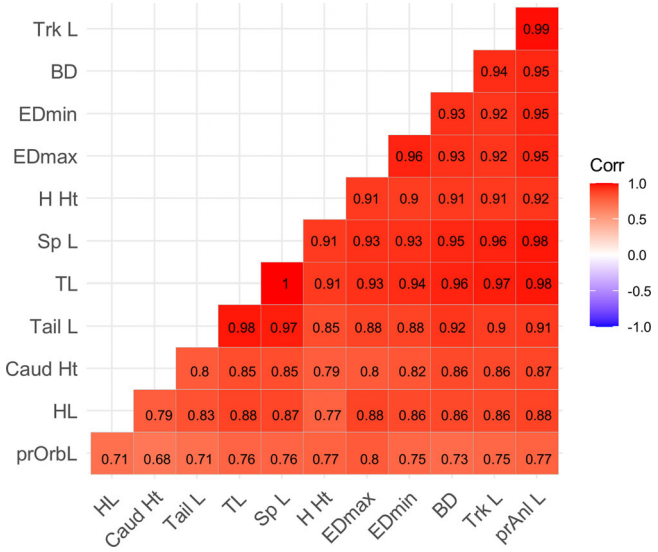

FIGURE 4 Pearson correlation coefficients for morphometric parameters of exogenous feeding yellow perch larvae reared at a constant temperature of 18°C. Only significant correlations ($p < 0.0001$) have been shown on the plot, with red and blue indicating positive and negative relationships, respectively. The darker the colour, the more closely the Pearson correlation coefficient is to (±)1; the coefficient is given inside the box. BD, body depth; Caud Ht, caudal-fin height; EDmax, maximum eye diameter; EDmin, minimum eye diameter; H Ht, head height; HL, head length; prAnl L, pre-anal length; prOrb L, pre-orbital length; Sp L, spinal cord length; Tail L, tail length; TL, total length; Trk L, trunk length.

garden conditions for all treatments by the mixed feeding phase (T8).

Mean yolk-sac volumes could not be calculated at the exogenous feeding phase (T9) because the yolk was largely resorbed. Between hatch (T6) and mixed feeding (T8), yolk-sac volume had remarkable decreases in fish from all constant incubation temperatures (Figure S3). There was a marked decrease in yolk-sac volume in the larval period observed in the constant 12°C incubation regime from the hatch phase (T6) to the swim-up phase (T7). The constant 15 and 18°C incubation regimes had little difference in mean yolk-sac volume from the hatch phase (T6) to the swim-up phase (T7), followed by a marked reduction at the exogenous feeding phase (T8, Figure S3). Only the fish from the ambient seasonal incubation regime had gradual reductions in yolk volume across the larval phases. At hatch (T6), larvae incubated at 12°C had the largest, whereas those from the ambient seasonal regime had the smallest yolk-sac volume (Figure S3), but this was reversed at mixed feeding (T8).

3.4 | Growth rate in the larval stages

The inclusion of PC1 as a dependent variable in a general linear model with two predictors (incubation temperature and developmental stage) yielded model coefficients that enabled approximation of growth rates across treatment groups from model coefficients. The result of the model is presented as a scatter plot where the *x*-axis represents the regression model coefficients, and the zero line is the null hypothesis line of 'no effect' (Figure 6b). In this model, treatment (12, 15, 18°C and AS) was categorical, and the timepoint (T6–T9) was numeric. Growth rate (GR) is the slope per developmental time point that estimates the expected size increase from one-time point to the next. Yellow perch reared at 18°C had the highest estimated growth rate between consecutive time points (14.5%), though this was not significantly different from those in the 15°C treatment (14.0%) based on a high degree of overlap in their 95% confidence intervals in the coefficient plot (Figure 6b). Fish reared at 12°C had an estimated growth rate of 10.8%, and those in the ambient seasonal thermal regime had the smallest growth rate of 9.15%.

3.5 | Interaction contrasts

As the larvae developed, clear trends were observed in PC1 or growth (Figure 7a). Fish reared at 15°C were smaller than other temperatures between T6 and T7, with smaller differences seen in groups compared between T7 and T8. Instead, between T8 and T9, similarities in size were seen between 15 and 18°C, with these temperatures larger than 12°C and AS treatments. Regarding body shape, earlier stages post-hatch appeared to be variable (Figure 7b). The transition between T6 and T7 produced preferential larger changes in the shape of all treatments relative to 12°C fish. Between T7 and T8, instead, 12°C fish appear to exhibit greater responses in shape between the developmental stages.

When comparing TL to body depth (Figure 8a), shorter fish relative to their body size were seen at 12°C between T6 and T7, with 15°C fish exhibiting a slightly larger length to body size between T8 and T9. More expansive changes were seen in body shape between T8 and T9 (Figure 8b), where relative to 18°C fish, colder-reared yellow perch exhibit a greater caudal-fin height by body depth.

3.6 | Proximate analysis

Proximate analysis was completed for fish at hatch (T6) and throughout the larval phases (T7–T9; Table 1, one-way ANOVA or Kruskal-Wallis ANOVA, Bonferroni adjusted $p < 0.017$). In general, the treatment groups that were significantly different in lipid, protein, glucose or glycogen were either in the 18°C or ambient seasonal incubation groups. At hatching (T6), larvae had significantly lower glucose and lipids when reared at 18°C; fish from ambient seasonal had lower glucose levels (Table 1). Glucose levels were higher at the exogenous feeding phase (T9) in fish from the ambient seasonal regime. At the mixed feeding phase (T8), lipids were lower and protein higher in fish reared at 18°C, compared to all other groups. Glycogen was largely unimpacted by incubation temperature.

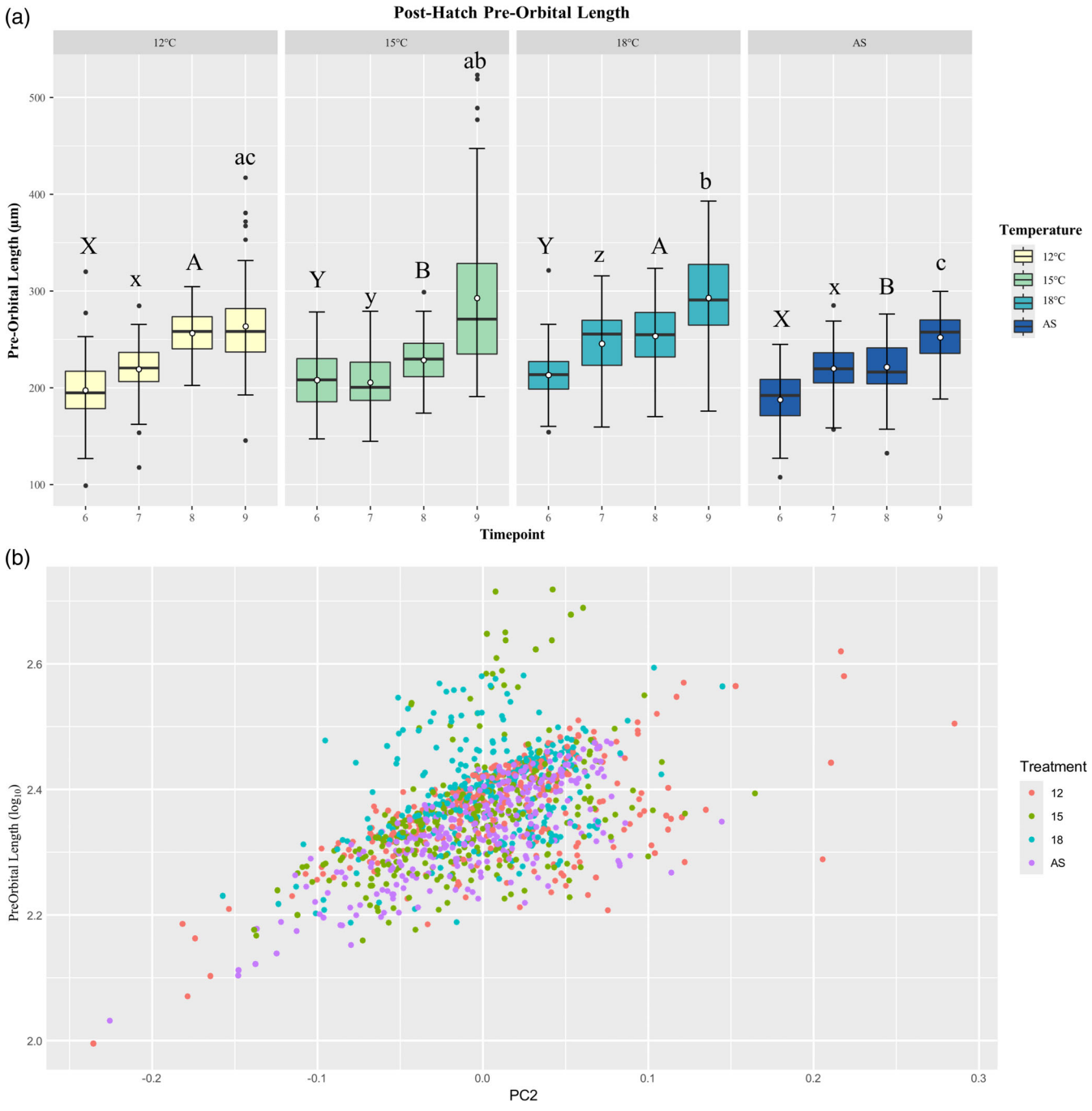

FIGURE 5 Pre-orbital length of yellow perch larvae reared in different incubation temperatures. (a) Pre-orbital length at hatch (T6), swim-up (T7), mixed feeding (T8) and exogenous feeding phases (T9) for larvae reared at constant 12, 15, and 18°C or an ambient seasonal incubation temperature (see test for details of incubation). The box plots show raw data, where open circles represent the mean, closed circles represent outliers, boxes represent the interquartile range and horizontal lines within boxes represent the median for each group. Statistical analyses were completed across different temperature regimes within each developmental time point (T6–T9). Different letters indicate statistical significance; Kruskal Wallis analysis of variance (ANOVA), Dunn's post hoc; Bonferroni adjusted $p < 0.017$ for each developmental stage. (b) Scatter plot of PC2 versus pre-orbital length (prOrb L) of larvae using log-transformed data from all time points in the post hatch period (T6–T9). Closed circles of different colours indicate different temperature treatments.

4 | DISCUSSION

The current study is among the first to examine the developmental effects of temperature on the growth and morphological phenotypes of yellow perch. We focused on temperatures within the optima suggested by previous studies on Eurasian (*P. fluviatilis*) and yellow perch (Guma'a, 1978; Hokanson & Kleiner, 1974; Wang & Eckmann, 1994). Our analysis revealed that yellow perch that experienced increases in

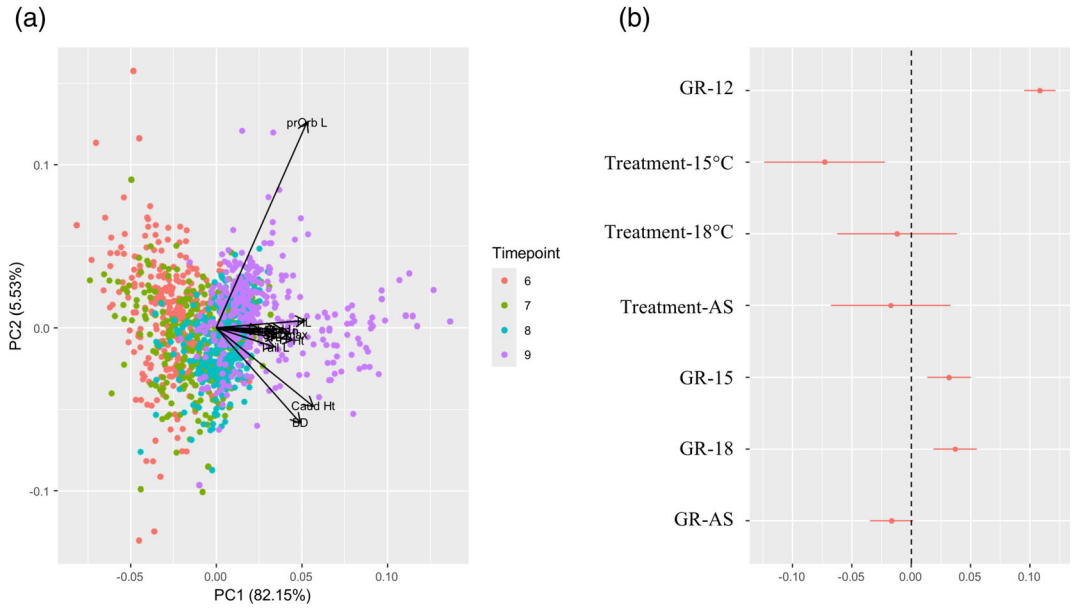

FIGURE 6 Principal component analysis (PCA) of morphometric data and estimated growth rates of yellow perch larvae. (a) is a biplot of PC1 and PC2 obtained from the PCA. Collectively, PC1 and PC2 explain 87.7% of the variation in the data. Yolk-sac length and depth (YsL and YsD) were excluded from the analysis due to the absence of measurements at T9. Different colours represent larvae from different treatment groups. Arrows show specific morphometric measures as a function of PC1 and PC 2; measures highly correlated to total length primarily align with PC1, and pre-orbital length (pOrbL), body depth (BD) and caudal-fin height (CaudHt) align with PC2. A linear model of PC1 with treatment and developmental stage as predictor variables was used to estimate growth rates (GR); (b) is the plot of the coefficient estimates and 95% confidence intervals from the linear model. The *x*-axis represents model coefficients, where the zero line is the null hypothesis line of 'no effect between groups'. In this model, treatment (12, 15, 18°C and AS) was categorical, and timepoint (T6–T9) was numeric. GR is the slope per developmental time point that estimates the expected increase in the growth rate estimate from one timepoint to the next. Approximate growth rates between consecutive post-hatch timepoints were 10.8% at 12°C (GR-12; comparison point), 14.0% at 15°C (GR-15; relative change to GR-12), 14.5% at 18°C (GR-18; relative change to GR-12) and 9.15% at AS (GR-AS; relative change to GR-12).

rearing temperature exhibited an elevated growth rate in the larval period; thus, the effect of temperature persisted beyond the embryonic incubation period. On the contrary, the ambient seasonal condition, or the rolling temperature implemented to increase the temperature throughout embryogenesis and simulate spring conditions, exhibited the slowest growth rate of all groups tested. The results from the present study suggest that deviations in the rearing temperature of yellow perch may lead to unique life-history alterations in energy utilization and periods of advanced growth leading to larger larvae in fish previously reared in warmer environments. However, our results may also suggest that yellow perch reared in colder temperatures may be better positioned to survive in ecological settings.

Although the overall growth of yellow perch appeared to increase with increasing rearing temperature in this study, differential patterns were observed within the embryonic and larval periods. The temperature experienced during rearing imposes a distinctive allocation of internal nutrients throughout development (Zera & Harshman, 2001), creating life-history trade-offs for yellow perch at hatch. For example, it has been well established that colder temperatures slow the rate of development, prolonging the absolute time of embryogenesis and producing a larger animal size-at-hatch [lake whitefish (Mitz et al., 2019); brown trout (Ojanguren & Braña, 2003; Réalis-Doyelle et al., 2016; Réalis-Doyelle et al., 2018); Atlantic cod (Jordaan et al., 2006); rainbow trout (Melendez & Mueller, 2021)]. In this study, yellow perch reared at 12°C exhibited a greater TL at several stages during embryogenesis (T3–T5, Figure 2) and at hatch (T6, Figure 3), supported by the previous observation that colder rearing temperatures delay hatching in this species (Fraz et al., 2024). Increased growth during embryogenesis in colder-reared fish appears to be linked to yolk-sac consumption, as the depletion of which appears to mirror growth. The yolk-sac comprises most of the body size of a freshly fertilized fish egg, providing key protein and fat to serve as an energy source for the developing organism (Kamler, 2007). Larval fish reared at 15 and 18°C grew rapidly, fuelled primarily by expedited consumption of their yolk sac, and had the longest TL by exogenous feeding (T9, Figures 3 and 7a). However, these compromises in traits may lead to limitations in ecological settings. For instance, fish with reduced length at hatch, as seen with yellow perch reared in warmer temperatures, may be limited in swimming performance, as smaller larvae possess reduced locomotion (Fisher et al., 2000), and diminished feeding success (Pepin, 2022). Further, larger yolk sacs in larvae reared at warmer temperatures observed in this study, while possessing a rich reservoir of nutrients for growth, may impose limitations in movement, as yolk-sac size exhibits a negative relationship with swimming performance in fish (Deslauriers et al., 2018). The longer length and smaller yolk sac,

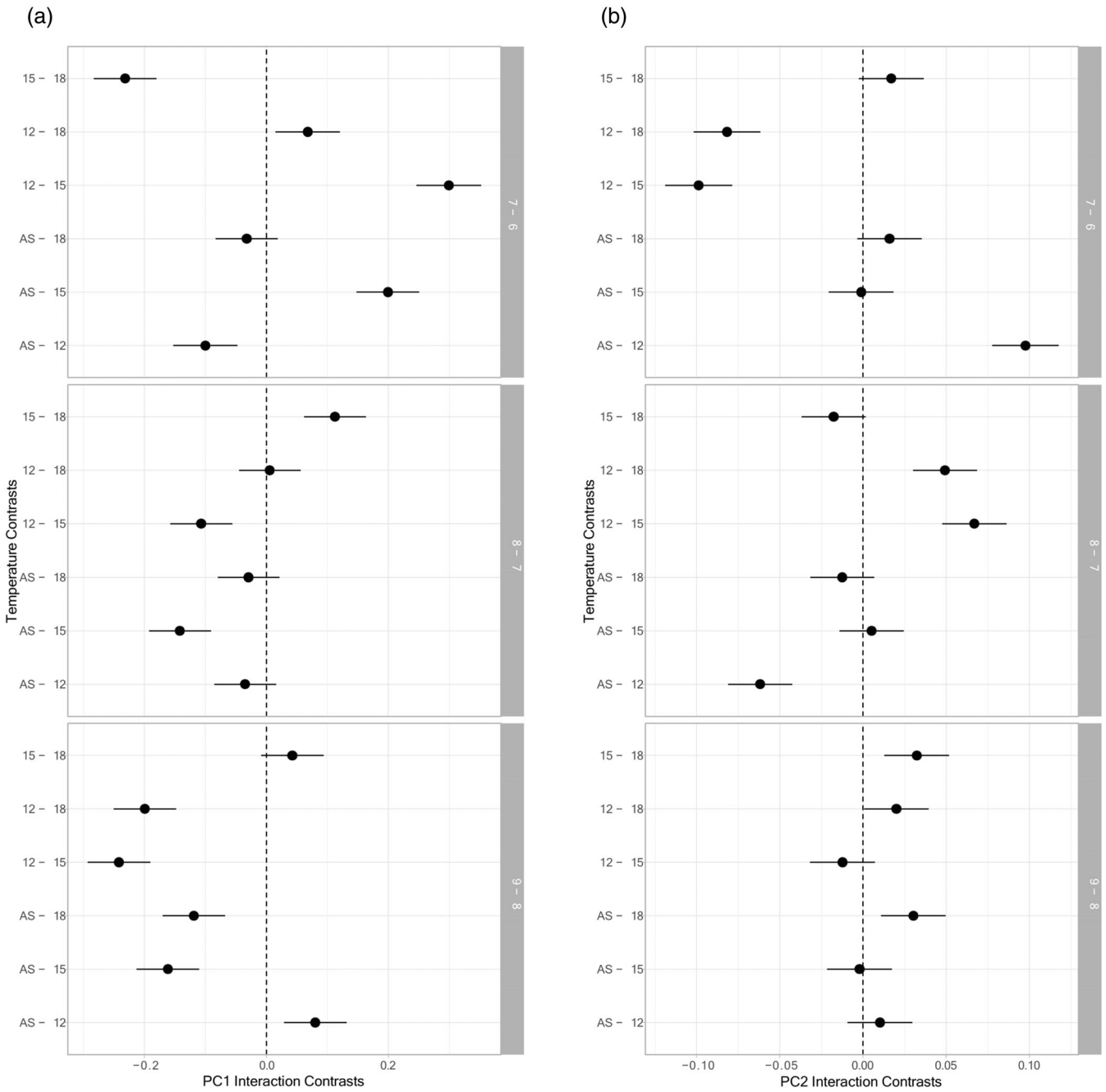

FIGURE 7 Plots of contrasts comparing individual temperatures within developmental stages. (a) Compares morphological traits comprising PC1, with (b) representing morphological traits within PC2. Log_{10}-transformed data were used to generate plots, allowing the visualization of patterns within the data. Error bars represent 95% confidence intervals of contrasts.

combined with increased body reserves of lipid and glucose with cooler incubation observed at hatch in the present study, may leave fish reared at 12°C better equipped to deal with novel environments during the transition to food by mouth (Hunter, 1981). However, more expansive characterizations of behavioural performance during the hatching window may be prudent to further support such a contention.

Using a PCA and linear model of PCQ, growth rates were estimated in the larval period and were higher for the warmer temperature incubations. Links between growth rate and temperature in fish have been well established, with increased temperature typically leading to rapid growth in fish, if the temperature increase remains within the preferred range of the species (Jobling, 1997). In the present study, we used a previously annotated developmental staging of the yellow perch (Fraz et al., 2024), to determine whether temperature during embryogenesis can alter the developmental programming in this species. By the time fish were at the exogenous feeding phase, fish reared at 18°C exhibited the largest body size and

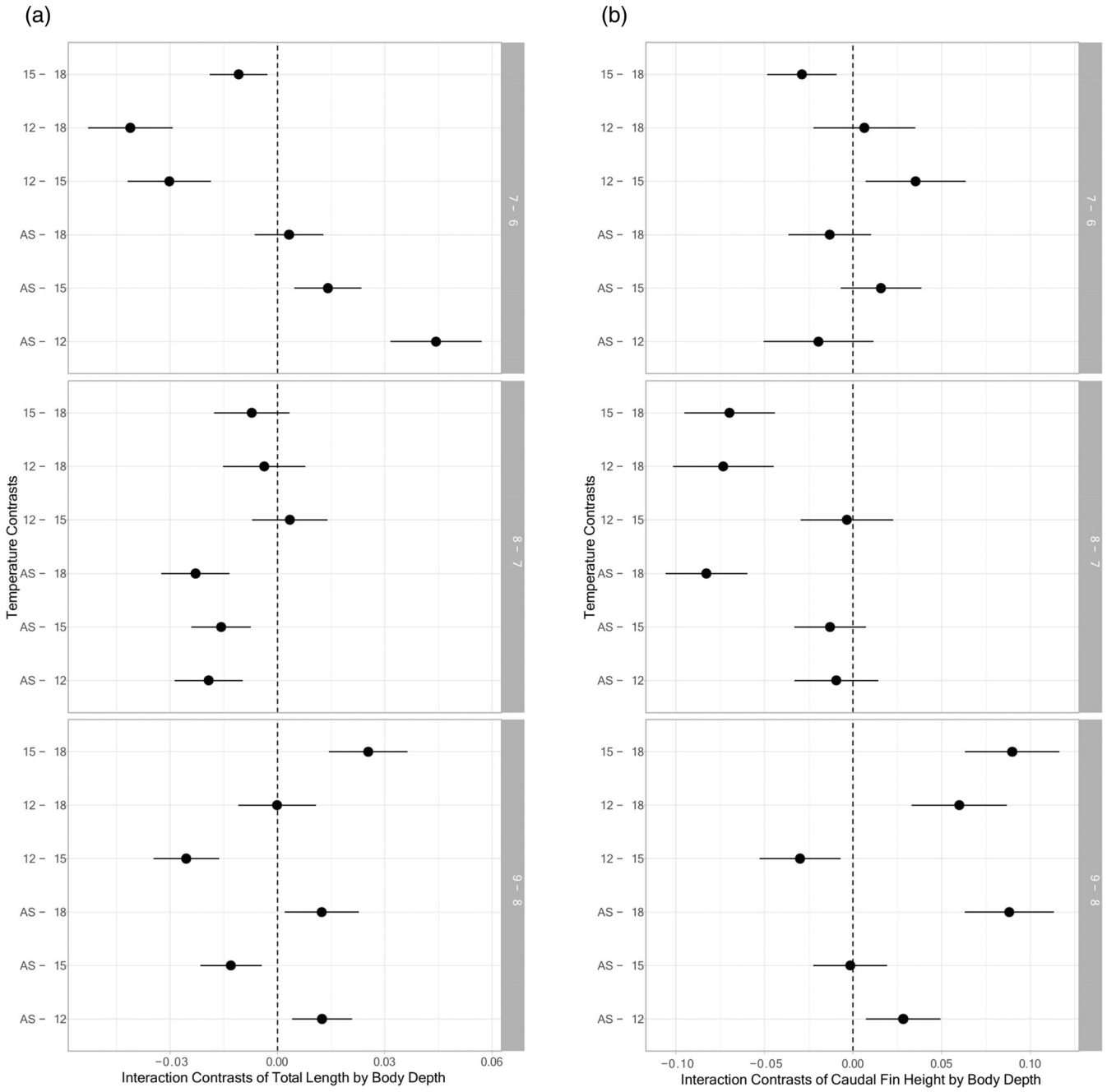

FIGURE 8 Interaction contrasts representing the total length by body depth (a), and caudal-fin height against body depth (b). Data were $\log_{10}$ transformed, and comparisons were performed against individual temperature treatments grouped by the developmental stage. Error bars represent 95% confidence intervals of contrasts.

TL, with 15°C also significantly larger than 12°C fish (Figure 3). This is a departure from the observations of the embryonic period and earlier in the larval periods in this study, suggesting that a major shift in growth rate occurs following hatch. Moreover, it appears that this increase in rearing temperature changes the development plan of the body apart from general length, including eye and cranial size. This finding agrees with results seen in Atlantic salmon [*Salmo salar* (Burgerhout et al., 2017; Finstad & Jonsson, 2012)], where increases in temperature during rearing can produce larger individuals through development. The capacity to grow bigger, and faster, has been proposed to maximize survival against predators (Miller et al., 1988). Specifically, in the larval period of marine fish, longer fish have been shown to exhibit higher levels of swimming performance, increasing total swimming speed and endurance (Baptista et al., 2019; Downie et al., 2020). However, other implications of shape have been raised, as a suboptimal body shape can increase drag and raise the energetic cost of movement (Wardle et al., 1995). To this end, we performed contrasts utilizing the TL and caudal-fin height against body depth

TABLE 1 Body composition of yellow perch larvae reared in different temperatures (see text for details of incubation).

Stage	Temp. (°C)	Lipids (mg/g dry wt.)	Protein (mg/g wet wt.)	Glucose (μM/g wet wt.)	Glycogen (μM/g wet wt.)
T6	12	1.86 ± 0.08^{a}	17.45 ± 3.87^{a}	0.71 ± 0.16^{a}	14.05 ± 3.80^{a}
	15	2.10 ± 0.24^{a}	10.95 ± 1.82^{a}	0.63 ± 0.12^{ab}	8.59 ± 2.40^{a}
	18	**0.57 ± 0.10^{b}**	8.55 ± 1.25^{a}	**0.21 ± 0.04^{b}**	3.37 ± 0.90^{a}
	AS	1.56 ± 0.13^{a}	6.19 ± 1.73^{a}	0.20 ± 0.09^{ab}	2.53 ± 0.69^{a}
T7	12	2.31 ± 0.59^{a}	21.79 ± 3.03^{a}	0.51 ± 0.05^{a}	11.10 ± 2.08^{a}
	15	2.28 ± 0.49^{a}	20.37 ± 3.90^{a}	0.91 ± 0.17^{a}	9.98 ± 2.82^{a}
	18	3.28 ± 0.73^{a}	12.92 ± 2.07^{a}	0.53 ± 0.08^{a}	7.65 ± 1.75^{a}
	AS	1.45 ± 0.3^{a}	20.07 ± 1.67^{a}	0.72 ± 0.07^{a}	18.54 ± 3.25^{a}
T8	12	9.04 ± 1.26^{a}	5.98 ± 0.75^{a}	0.26 ± 0.05^{a}	14.62 ± 2.81^{a}
	15	7.89 ± 1.43^{a}	5.02 ± 0.93^{a}	0.31 ± 0.07^{a}	10.53 ± 4.12^{a}
	18	**2.40 ± 0.53^{b}**	**10.18 ± 0.5^{b}**	0.45 ± 0.06^{a}	27.87 ± 6.96^{a}
	AS	11.53 ± 2.22^{a}	5.25 ± 0.67^{a}	0.33 ± 0.04^{a}	11.43 ± 4.18^{a}
T9	12	0.84 ± 0.3^{a}	6.60 ± 0.98^{a}	0.71 ± 0.14^{ac}	26.11 ± 4.90^{a}
	15	0.26 ± 0.06^{a}	4.46 ± 1.02^{a}	0.56 ± 0.13^{a}	11.71 ± 2.47^{a}
	18	0.49 ± 0.12^{a}	7.11 ± 1.62^{a}	**9.22 ± 1.01^{bc}**	9.80 ± 1.22^{a}
	AS	0.26 ± 0.02^{a}	6.91 ± 2.12^{a}	**22.75 ± 3.66 ^{b}**	34.35 ± 14.06^{a}

Note: Fish were sampled at hatching (T6), swim-up (T7), mixed feeding (T8), and exogenous feeding (T9) phases. Data are provided as mean ± standard error mean (SEM). All data were analysed with a one-way analysis of variance (ANOVA), and Holm-Sidak post hoc test for multiple comparisons with Bonferroni adjusted $p < 0.017$. However, T9-glucose and T6-glycogen data were analysed by Kruskal Wallis ANOVA and Dunn's post hoc test for multiple comparisons with Bonferroni adjusted $p < 0.017$. Different letters indicate statistical differences across temperature treatments ($n = 3–6$ for lipids, 4–8 for proteins, 4–10 for glucose and 4–10 for glycogen per treatment group) within each developmental time point. Those marked in bold are different from at least one other incubation temperature.

(Figure 8), representative measures of fineness and peduncle depth factor, respectively. These measures positively correlate with swimming capabilities of freshwater and coral reef fish (Rubio-Gracia et al., 2020; Walker et al., 2013). The trends in body shape, particularly regarding caudal-fin height (Figure 8b), point to diminishments of fish reared at warmer temperatures as the animal grows. It is possible, however, that increased size may offset deficiencies in body shape. For example, adult Atlantic salmon exhibit improved myonuclear density and fibre diameter following elevations in rearing temperature (Macqueen et al., 2008). Explicit testing of yellow perch behavioural and kinematics profiles throughout development may be necessary to understand the implications of changing body shape and trade-offs between overall size and body shape on swimming performance in this species.

Fish reared in warmer water (15 and 18°C) exhibited a rapid increase in growth, particularly after the mixed feeding phase. Although this, in part, may still be driven by consumption of the yolk sac, at this stage yolk volume is relatively similar. Instead, we noted reductions in lipid levels in both 15 and 18°C fish at the later larval phases investigated (Table 1; mixed and exogenous feeding). Further, in 18°C fish specifically, we noted a significant accumulation of protein at the mixed feeding phase. The positive accretion of protein is the primary driver of weight gain in fish (Sadoul & Vijayan, 2016), and given that this increase is noted around the onset of feeding, it may imply that 18°C fish adapted to successful feeding by mouth faster than their conspecifics. Observations at the hatch lend credence to this idea, as higher proportions of both 15 and 18°C fish possessed open mouths, advanced development of the jaw and anuses. There is a linear relationship between mouth size and the particle consumption of fish larvae (Dabrowski & Bardega, 1984), which may suggest that yellow perch reared in warmer water may benefit from an expanded breadth of prey size at early larval phases. Additionally, temperature has been shown to influence gut microbiota communities in fish (Huyben et al., 2018), possibly influencing digestive performance at these early larval phases. Together with the clear increase in total protein in 18°C fish, this may suggest that warmer temperatures position yellow perch, and indeed, warmer fish to reach the exogenous feeding phase faster (Fraz et al., 2024).

An interesting discovery of this study was the relatively slow growth of our ambient group. We originally imposed the ambient seasonal condition to reflect environmental conditions, with a rolling temperature throughout development to match the temperature change typically seen in lake environments (based on the seasonal surface water temperature of Lake Erie, Lake Ontario and Lake Huron between 2015 and 2019; data not shown). To our surprise, the ambient seasonal group experienced the largest size prior to hatch and was the smallest size at the exogenous feeding phase. This may be a combination of the increased developmental time in the embryonic period (Fraz et al., 2024) and reduced post-hatch yolk consumption. In terms of comparisons, the ambient seasonal group appeared to be most like our 12°C constant group, being in the range of this treatment for most of our collected indices, despite experiencing a 1°C

increase in temperature every third day. Within this study, incubation groups that were exposed to higher constant temperatures displayed increases in growth metrics, a result that was not reflected in our ambient seasonal condition. This may imply the importance of the earliest window in development in the programming of growth rate post-hatch in yellow perch. Indeed, in lake whitefish (*Coregonus clupeaformis*), rearing embryos during gastrulation at colder temperatures led to instances of improvement in the cost of development (the amount of oxygen required to build a unit of mass), yolk conversion efficiency and survival (Mueller et al., 2015). The ambient seasonal result may be indicative of a preference for colder waters for optimal growth in this species, particularly in early development.

5 | CONCLUSIONS

With climate change predictions for Great Lakes regional temperatures forecasting elevations between $+3 \pm 1°C$ and $+5 \pm 1.2°C$ by 2040–2069 (Hayhoe et al., 2010), understanding the implications of shifts in thermal environments for possibly susceptible species is paramount. Early windows of development are of great importance for successful recruitment of larval fish (Bergenius et al., 2002), and larval size has been directly correlated with survival (Miller et al., 1988). Here, we demonstrate that constant exposure to warm temperatures during embryogenesis leads to smaller yellow perch larvae near hatch, but larger animals at the onset of feeding. It is unclear whether this will be an advantage or a disadvantage for larvae. Combined with the observations of altered energetic stores, these phenotypes may indicate that temperature alters energy mobilization and utilization in the long term, supported by the changes in body plan seen here. The ambient seasonal condition, implemented to reflect natural conditions, best reflects colder conditions, which may indicate a preference for colder temperatures during embryogenesis in the yellow perch. Early gastrulation has been identified as a critical thermal window in other fish species (Bloomer et al., 2022; Mueller et al., 2015), and the ambient seasonal condition, which experienced the coldest temperatures in early development windows, supports this. Given that yellow perch are vulnerable to climate change–led reduction in larvae recruitment (Collingsworth et al., 2017) further research into the performance of these animals following these temperature conditions is necessary to understand ecological impacts.

AUTHOR CONTRIBUTIONS

The study was conceptualized by J.Y.W., R.M., C.M.S. and S.F. The study was conducted with funds granted to J.Y.W., R.M. and C.M.S. Investigation was done by S.F., M.S.G., M.A., W.A.T., M.E., P.H. and LL. Data visualization and formal analyses were done by I.D., M.E., M.G., S.F. and W.A.T. All authors contributed to manuscript preparation and editing.

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