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Stressor interactions in freshwater habitats: Effects of cold water exposure and food limitation on early-life growth and upper thermal tolerance in white sturgeon, *Acipenser transmontanus*

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Abstract

1. Limited food availability and altered thermal regimes (e.g. cold water releases from dams) are two common stressors threatening the persistence of fishes inhabiting anthropogenically disturbed freshwater systems. Yet, the combined effects of these stressors remain poorly characterised.
2. To remedy this, we examined the isolated and combined effects of low temperature exposure and food restriction on specific growth rate (SGR, % body mass/day) and upper thermal tolerance (critical thermal maxima, CTMax) in larval white sturgeon (*Acipenser transmontanus* [Acipenseridae], 32 days post-hatch, body mass: 0.25 ± 0.03 g, mean \pm standard deviation). A 2×2 factorial design was implemented with fish exposed to one of two ecologically-relevant acclimation temperatures (cold exposure: 11°C or a control temperature: 18°C) and one of two food restriction treatments designed to emulate observed declines in food availability (100% or 40% optimal feed rate) for 6 weeks (N : 3 replicate tanks/treatment, 50 fish/tank).
3. Specific growth rate was affected by both low temperature exposure and food restriction in isolation; low temperature exposure reduced SGR by 56.5% and food restriction reduced SGR by 30.6%. Simultaneous exposure to low temperature and food restriction resulted in a greater but less than additive reduction in SGR (80.6%), indicating that the stressors interacted antagonistically.
4. Critical thermal maxima were *c.* 2°C higher in 18°C-acclimated fish (CTMax = 30.7 ± 0.4 °C, mean \pm standard error) compared to 11°C-acclimated fish (CTMax = 28.6 ± 0.2 °C, mean \pm standard error); however, CTMax was independent of food restriction in both 11°C- and 18°C-acclimated fish.
5. These data highlight the unpredictability of stressor interactions and may guide holistic conservation strategies, which target co-occurring stressors in freshwater habitats.

KEYWORDS

critical thermal maxima, ectotherm, food deprivation, larvae, multiple stressors

1 | INTRODUCTION

Aquatic organisms face an increasing number of concurrent stressors as human demands on freshwater ecosystems intensify (Christensen et al., 2006; Jackson, Loewen, Vinebrooke, & Chimimba, 2016). Critical freshwater habitats have undergone extensive change through the integration of dams and weirs (Liermann, Nilsson, Robertson, & Ng, 2012), addition of thermal and chemical effluent (Webb & Walling, 1993) and the introduction of exotic species (Gido & Brown, 1999; Strayer, 2010). These alterations have created a matrix of stressors for aquatic species to navigate (Fausch, Baxter, & Murakami, 2010; Wepener et al., 2011), but these stressors are often studied in isolation and it is largely unknown how co-occurring stressors combine to impact aquatic organisms (Darling & Côté, 2008; Mothersill, Mosse, & Seymour, 2007; Sala et al., 2000).

Low food availability is a pervasive stressor in developed waterways (Bunn, Thoms, Hamilton, & Capon, 2006; Fausch et al., 2010; Jassby, Cloern, & Cole, 2002). Diminished food resources can stem from exotic species modifying food-web structure (Vander Zanden, Casselman, & Rasmussen, 1999). For instance, a controlled introduction of western mosquitofish, *Gambusia affinis* (Poeciliidae), into a wetland ecosystem in California (U.S.A.) was associated with a 90% decrease in zooplankton abundance and a 50% decline in macroinvertebrate density (Preston et al., 2017). Scarcity of food places energy limits on fish and can decrease stress tolerance through divestment of energy towards protective molecular and cellular responses (Sokolova, 2013). Previous studies have shown food deprived fish to have lower upper thermal tolerance (i.e. critical thermal maxima, CT_{Max}) and an inhibited capacity to overexpress heat shock proteins (Hsps; Deng, Wang, Lee, Bai, & Hung, 2009; Han, Huang, Wang, Deng, & Hung, 2012; Lee, Fangue, Verhille, & Todgham, 2016; Woiwode & Adelman, 1992). However, the most well-documented effect of food restriction is a reduction in energy stores directed towards somatic growth (Jobling, 1994). Growth rates and nutritional status systematically decline with decreasing food availability (Cui, Hung, & Zhu, 1996; Hung, 2017).

In addition to food limitation, fish inhabiting developed waterways are often exposed to *thermal pollution*, which is defined as any human-induced alteration to a habitat's natural thermal regime (Caissie, 2006). To date, research efforts assessing the impacts of altered thermal regimes on fish functional performance have focused on temperature increases simulating climate warming scenarios (Ficke, Myrick, & Hansen, 2007). However, fish inhabiting heavily managed waterways are also exposed to artificial temperature reductions (Caissie, 2006). Hypolimnetic releases from thermally stratified water reservoirs can rapidly lower water temperatures by 10–15°C, with thermal alterations persisting downstream for several hundred kilometres (Lowney, 2000; Preece, 2004). Temperature reductions are most pronounced during spring and summer, a critical period for spawning and larval development in many fishes (Lugg & Copeland, 2014; Todd, Ryan, Nicol, & Bearlin, 2005). Anthropogenic

shifts in environmental temperature are particularly threatening to ectotherms (almost all fish, reptiles, and amphibians) where body temperature is closely tied to the thermal environment (Fry, 1967). The functional capacity of ectotherms is optimised within a limited range of body temperatures resulting from the thermal sensitivity of molecular, cellular and metabolic processes (Hochachka, 1967; Hochachka & Somero, 1968). Fish exposed to rapid decreases in temperature outside this range typically exhibit metabolic depression (Ibarz et al., 2007), lowered swimming performance (Fangue, Mandic, Richards, & Schulte, 2007; Rodgers et al., 2014), reduced CT_{Max} (Healy & Schulte, 2012; Schulte, Healy, & Fangue, 2011), and immunosuppression (Bly & Clem, 1992; Le Morvan, Troutaud, & Deschaux, 1998). Low temperatures also have pronounced, depressive effects on fish growth rates (Burel et al., 1996). For example, cold water releases from dams significantly curbed larvae growth of four teleost species in the Colorado River, U.S.A. (Robinson & Childs, 2001).

The combined effects of food restriction and cold water exposure on growth rates and stress tolerance remains largely uncharacterised in fishes. The combined effect of co-occurring stressors can be complex, and simply summing the separate effect of each isolated stressor can result in erroneous predictions (Crain, Kroeker, & Halpern, 2008; McBryan, Anttila, Healy, & Schulte, 2013; Todgham & Stillman, 2013). Combined effects are typically categorised as either additive (interaction is equal to the sum of the individual effects of each stressor in isolation), antagonistic (interactive effect of the two stressors is weaker than the sum of each stressor in isolation), or synergistic (the interactive effect of the two stressors is stronger than the sum of each stressor in isolation) (Piggott, Townsend, & Matthaei, 2015).

The present study aimed to assess the isolated and combined effects of food restriction and low temperature exposure on growth rates and stress tolerance (measured as CT_{Max}) in larval white sturgeon, *Acipenser transmontanus* (Acipenseridae). White sturgeon are highly valued, from ecological, economic, and recreational standpoints (Moyle, 2002), but several populations are listed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2012) and as S2 status (contracting geographic range and low abundance) in the California Natural Diversity Database (2009). White sturgeon are native to the Pacific coast of North America and inhabit three major river systems: Fraser, Columbia, and Sacramento–San Joaquin (S–SJ) rivers (Moyle, 2002). As a semi-anadromous species, adults primarily reside in estuaries and migrate to freshwater habitats to spawn (Moyle, 2002).

Recruitment failure (i.e. larvae/juveniles not surviving to be added to a population) is cited as the primary driver of population declines in *A. transmontanus* and probably stems from early life-history stages being restricted to heavily degraded freshwater habitats prior to the development of osmoregulatory capacities (COSEWIC, 2012). The S–SJ catchment is a critical spawning and nursery ground for *A. transmontanus* but this habitat has been extensively modified since the mid-1800s when hydraulic gold mining operations were pervasive and dense human settlement followed

(Dasmann, 1999). The ecosystem has been further altered by channelisation, inputs of effluent and contaminants, the installation of water reservoirs/diversions and the introduction of invasive species (Cloern & Jassby, 2012). White sturgeon probably experience unseasonably cold temperatures and prey scarcity in tandem as embryos and larvae—the most vulnerable life-history stages (Dettlaff, Ginsburg, & Schmalhausen, 1993). Water reservoir operations can result in unseasonably low temperatures of 10–11°C in spring—the peak spawning period for *A. transmontanus* (Moyle, 2002; Pike et al., 2013; Van Eenennaam, Linares-Casenave, Deng, & Doroshov, 2005). Larval *A. transmontanus* feed on zooplankton (predominantly gammarid amphipods, [*Corophium* spp.] and copepods [Cyclopoida]; Muir, McCabe, Parsley, & Hinton, 2000), but record declines in zooplankton biomass have been observed in the S-SJ catchment over the past four decades (Carlton, Thompson, Schemel, & Nichols, 1990; Cloern et al., 1983; Cloern, Foster, & Kleckner, 2014; Winder & Jassby, 2011). On average, major genera of zooplankton declined in biomass by 61% between 1972 and 2008 (Winder & Jassby, 2011).

Depressed early-life growth rates have important consequences because smaller body sizes often confer decreased competitiveness over resources (Johnsson, Nobbelin, & Bohlin, 1999) and lowered survival rates (Carlson, Olsen, & Vøllestad, 2008). The impact of food restriction on growth and stress tolerance may be exacerbated at low temperatures because feed conversion efficiency and the upregulation of protective mechanisms typically decrease with temperature (Jobling, 1994; Somero, 1995). Conversely, metabolic demands are reduced at low temperatures, potentially leaving more energy available to be directed towards growth and stress responses, so that the interaction between food restriction and low temperatures may be antagonistic. We therefore predicted that the two stressors would interact either synergistically or antagonistically to affect growth and CT_{Max}. Fish were exposed to one of two food restriction levels designed to emulate observed declines in zooplankton biomass in the S-SJ catchment (i.e. unrestricted—100% optimal feed rate, OFR; restricted—60% decline), and one of two temperatures, with the low temperature reflecting a hypolimnetic water release during spring (i.e. control, 18°C; low temperature, 11°C). The isolated and combined effects of the two stressors were assessed to provide an ecologically-relevant index of how they interact.

2 | METHODS

2.1 | Study animals

White sturgeon larvae were obtained from Sterling Caviar hatchery (Elverta, CA, U.S.A.; 38.735565, -121.491178). Broodstock were vernalised during winter at 10–12°C and transported to the hatchery in spring where spawning was artificially induced at 15°C. Eggs were incubated at 15 ± 1°C and resulting larvae (1-day post-hatch, dph) were transported to the Center for Aquatic Biology and Aquaculture (University of California, Davis, CA, U.S.A.) on

26 May 2017. Larvae were housed in an 815 L circular, fibreglass flow-through tank continuously supplied with non-chlorinated, degassed well water. Water temperatures were held at 18 ± 1°C and fish were exposed to a natural photoperiod. Exogenous feeding was initiated at 7 dph and fish were continuously supplied with commercial soft-moist, starter feed (Rangen Inc, Idaho, U.S.A.) using a belt-feeder (Zeigler Brothers Inc., Gardners, PA, U.S.A.). Proximate composition (%) of the feed was reported as ≥45% crude protein, ≥18% crude fat, ≤3% crude fibre, ≤12% ash and ≤2% added mineral ingredients. Feed size was increased at 32 dph for all fish to a mixture consisting of 50% starter (size < 0.6 mm) and 50% soft moist feed (size = 0.8 mm). A continuous supply of food was required to ensure optimal growth because *A. transmontanus* are nibble feeders (Cui, Hung, Dong-Fang, & Yunxia, 1997). Excess food and solid wastes were siphoned from the tank twice daily. Experimental and animal care procedures were approved by the University of California Davis Institutional Animal Care and Use Committee (protocols #18767; #19928) and complied with the US National Research Council's Guide for the Care and Use of Laboratory Animals, the US Public Health Service's Policy on Humane Care and Use of Laboratory Animals, and Guide for the Care and Use of Laboratory Animals.

2.2 | Experimental design

At 25 dph, 600 fish were distributed between 12 circular, flow-through tanks (194.3 L volume, 94 cm inner diameter, 42 cm height, filled to 28 cm, flow rate: 5 L/min) held at 18 ± 0.5°C (N: 50/fish tank). Fish were allowed a 5-day adjustment period, after which tanks were randomly assigned to one of two acclimation temperatures (11 ± 0.5°C or 18 ± 0.5°C) using a random number generator. Water temperature in the cold treatment (i.e. 11°C) tanks was reduced at a rate of 2°C/day. Once the target water temperature was reached, tanks were randomly assigned to one of two food restriction treatments (i.e. 100% optimal feed rate, OFR or 40% OFR), resulting in three replicate tanks for each acclimation temperature × food restriction combination. Empirically validated OFR models were used to inform feeding rates, where OFR was defined as the feeding rate at which additional food provides no growth gains (Cui & Hung, 1995; Lee et al., 2014). Optimal feed rates are expressed as % body mass (BM)/day and calculated using Lee et al. (2014)'s model (Equation 1) calibrated for 0.05–764 g *A. transmontanus* maintained between 17.9 and 23.1°C.

$$100\% \text{ OFR}(18^\circ\text{C}) = 0.00344e^{-5.684 \ln(\sqrt{\text{BM}})} + 8.695e^{-0.549 \ln(\sqrt{\text{BM}})} \quad (1)$$

Optimal feed rates were reduced by 60% to calculate the 40% OFR (Equation 2):

$$40\% \text{ OFR}(18^\circ\text{C}) = 100\% \text{ OFR}(18^\circ\text{C}) \times 0.4 \quad (2)$$

Optimal feed rates decrease with a reduction in water/body temperature in *A. transmontanus* (Cui & Hung, 1995). For example, OFR decreased

by c.71% between 18°C and 11°C (Cui & Hung, 1995). Therefore, OFRs were temperature adjusted using the following equations:

$$100\% \text{ OFR}(11^\circ\text{C}) = 100\% \text{ OFR}(18^\circ\text{C}) \times 0.29 \quad (3)$$

$$40\% \text{ OFR}(11^\circ\text{C}) = 40\% \text{ OFR}(18^\circ\text{C}) \times 0.29 \quad (4)$$

The experimental trial began at 32 dph and ran for 6 weeks. A subset of fish (30/tank) were weighed every 2 weeks and OFRs were updated accordingly.

2.3 | Growth assessment

Wet BM (g) and total length (TL, cm) were measured in a subset of fish (BM N: 30/tank; 90/treatment; TL N: 10/tank, 30/treatment) at four time-points (time 0, week 2, week 4, and week 6). Fish were batch-weighed (10/batch) using an electronic balance (A-200DS, Denver Instrument Company, NY, U.S.A.) and immediately returned to a recovery tank. Specific growth rates (SGR, %BM/day) were calculated for the entire trial (i.e. 42 days) in terms of percentage increase in BM (Equation 5) per day for each tank (Hopkins, 1992):

$$\text{SGR}_{\text{BM}} = 100 (\ln(\text{BM}_f) - \ln(\text{BM}_i)) / t \quad (5)$$

where BM_f and BM_i are mean final and initial BM (g) per fish, respectively and t is the growth period (days). Fish were fasted for 24 hr prior to all measurements.

2.4 | Critical thermal maxima

Critical thermal maxima were assessed in fish from all four treatment groups at the end of the food restriction trial (N: 9–11/treatment; 77–80 dph). The CTMax test chamber was an insulated, glass aquarium (L: 50.5 cm, W: 26.0 cm, H: 30.0 cm, filled with 14 L), where water temperature was manipulated using a YSI 74 Proportional Temperature Controller (YSI, Yellow Springs, OH, U.S.A.). Water mixing was maintained using a submersible 5.3 W pump (Rio Plus, model: Rio⁺ 50, TAAM, Camarillo, CA, U.S.A.). Following a 24-hr fasting period, fish were individually placed within one of five cylindrical, glass chambers (inner D: 4.5 cm, H: 11.0 cm), filled with 100 ml of water matching thermal acclimation temperature. Water within chambers was constantly aerated by running airlines attached to pipette tips (10 μl , Thermo Fisher Scientific, Waltham, U.S.A.) into each chamber. Fish were allowed a 1-hr adjustment period before water temperature was increased at a rate of 0.3°C/min (Fangue, Hofmeister, & Schulte, 2006; Sardella, Sanmarti, & Kültz, 2008; Verhille, Todgham, Hung, & Fangue, 2015). Chamber water temperatures were monitored and recorded using an alcohol thermometer calibrated against a certified standard mercury thermometer (Thermo Fisher Scientific), and a calibrated optic shuttle temperature logger (Onset Computer Corporation, Bourne, MA, U.S.A.) also recorded temperature every 15 s. Fish were observed throughout the trials and loss of

equilibrium (LOE), defined as an inability to maintain an upright position in the water column for 10 s, was used as an endpoint (Lee et al., 2016). Following LOE, fish were immediately placed in an aerated recovery tank matching acclimation temperature. Fish were kept in individual, flow-through chambers to track post-trial survival for 24 hr, after which fish were euthanised with an overdose of MS-222 and TL and BM measurements were recorded. Post CTMax trial survival was 100% for all treatments.

2.5 | Data analyses

Data analyses were performed using R Studio (version 3.4.3; <http://www.R-project.org/>) and response variables were \log_{10} -transformed where necessary. A linear mixed effects (lme) model was run to determine the effect of acclimation temperature (two-level, fixed factor) and food restriction (two-level, fixed factor), and the interaction between these factors on SGR, using the nlme package (Linear and Non-linear Mixed Effects Models; <https://CRAN.R-project.org/package=nlme>). Tank ID was included as a random effect in all mixed effects models. A generalised linear mixed-effects model (glmm) with a quasipoisson error term was run to examine the effect of acclimation temperature and food restriction, and the interaction between these factors on CTMax using the MASS package (Modern Applied Statistics with S; <https://cran.r-project.org/web/packages/MASS/MASS.pdf>), and BM was included as a covariate. A follow-up analysis adjusted CTMax values for BM using analysis of covariance (ANCOVA), and corrected means were compared using the general linear hypotheses *post hoc* test (glht). A separate lme model was run to compare mass and length changes between treatments at trial time-points (i.e. week 0–6). An autoregressive correlation structure (corAR1) was specified to account for temporal autocorrelation inherent to all timepoint comparisons. Tukey's *post hoc* tests were run to discern statistical differences among treatment groups and time-points using the lsmeans (least-squares means; <https://cran.r-project.org/web/packages/lsmeans/index.html>) and multcomp (simultaneous inference in general parametric models; <https://cran.rproject.org/web/packages/multcomp/index.html>) packages. Statistical significance was accepted at $p \leq .05$.

3 | RESULTS

3.1 | Specific growth rate

Time-point analyses showed the effect of low temperature exposure on BM was evident from week 2 onwards ($p < .001$, lme; Figure 1a). The effect of food restriction on body mass emerged at week 4 and persisted to the end of the trial ($p < .01$, lme, Figure 1a). Changes in TL were slower to emerge; the effect of acclimation temperature was evident from week 4 onwards ($p < .001$, lme) and the effect of food restriction was apparent at week 6 ($p < .05$, lme, Figure 1b).

Specific growth rate was affected by both low temperature exposure ($F_{1,8} = 295.6$, $p < .001$, lme) and food restriction

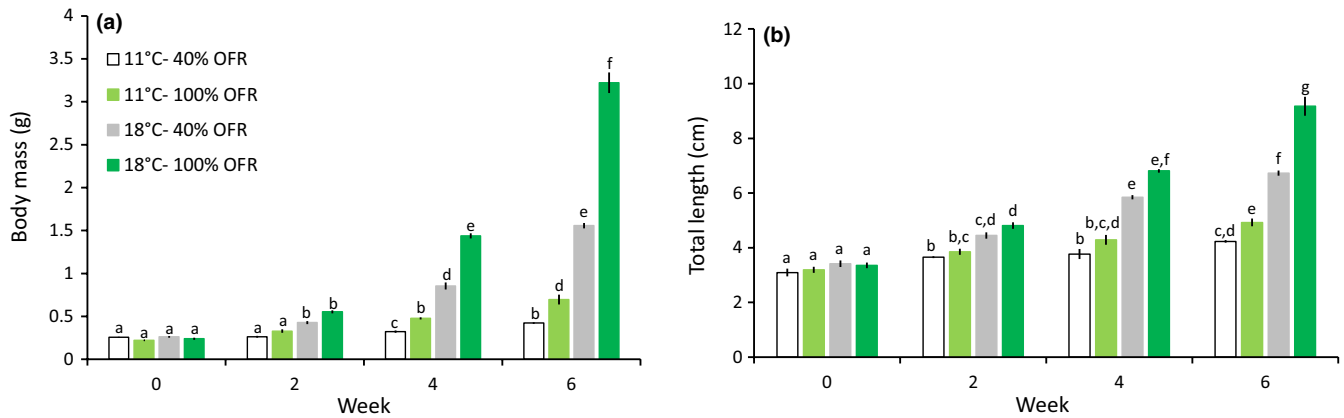


FIGURE 1 Time-point assessment of the effects of food restriction and low temperature exposure on (a) wet body mass (BM, g) and (b) total length (TL, cm) of larval white sturgeon, *Acipenser transmontanus* (Acipenseridae). Fish were exposed to one of two acclimation temperatures (cold exposure: 11°C or a control temperature: 18°C) and one of two food restriction treatments (100% optimal feed rate, OFR or 40% OFR) for 6 weeks. Measurements were recorded every 2 weeks (time 0, week 2, week 4, and week 6) in a subset of fish from each treatment (BM N: 30/tank; 90/treatment; TL N: 10/tank, 30/treatment). Mean BM and TL differed between all treatments by week 6, but changes in TL were slower to emerge. Values are shown as mean \pm standard error and different lowercase letters indicate statistical differences ($p \leq .05$) [Colour figure can be viewed at wileyonlinelibrary.com]

($F_{1,8} = 122.7, p < .001, \text{lme}$) in isolation (Figure 2). The main effect of low temperature exposure was greater than the main effect of food restriction (Figure 3); cold temperature exposure reduced SGR by 56.5% and food restriction reduced SGR by 30.6%. Simultaneous exposure to low temperature and food restriction resulted in a greater reduction in SGR (80.6%) than exposure to a single stressor (Figure 3). Low temperature exposure and food restriction interacted antagonistically and the observed reduction in SGR was 6.5% less than would be predicted from the sum of the isolated effects of each stressor ($F_{1,8} = 18.3, p < .05, \text{lme}$; Figure 3).

3.2 | Critical thermal maxima

Marked differences were observed in CTMax between thermal acclimation treatments ($p < .0001, F_{1,8} = 42.71, \text{glmm}$); CTMax was c.2°C higher in 18°C-acclimated fish (CTMax = $30.7 \pm 0.4^\circ\text{C}$; mean \pm standard error) compared to 11°C-acclimated fish (CTMax = $28.6 \pm 0.2^\circ\text{C}$; mean \pm standard error) at 100% OFR. In contrast, CTMax was independent of food restriction treatment ($p = .42, F_{1,8} = 0.001, \text{glmm}$) in both 11°C- and 18°C-acclimated fish (Table 1). Chamber number had no effect on CTMax ($F_{1,23} = 0.0006, p = .30, \text{glmm}$) and was excluded from the final model. Mass-adjusted CTMax means were higher than raw means in 18°C-acclimated fish (+0.1 to 1.32°C) and lower than raw means in the 11°C-acclimated fish (-0.55 to 0.84°C) (ANCOVA, Table 1). *Post hoc* analyses on adjusted means showed that results did not change following mass corrections, as CTMax was affected by acclimation temperature ($p < .0001, \text{glht}$) but not food restriction ($p = .42, \text{glht}$).

4 | DISCUSSION

The ecological relevance of multi-stressor studies is becoming increasingly recognised (Todgham & Stillman, 2013) but understanding

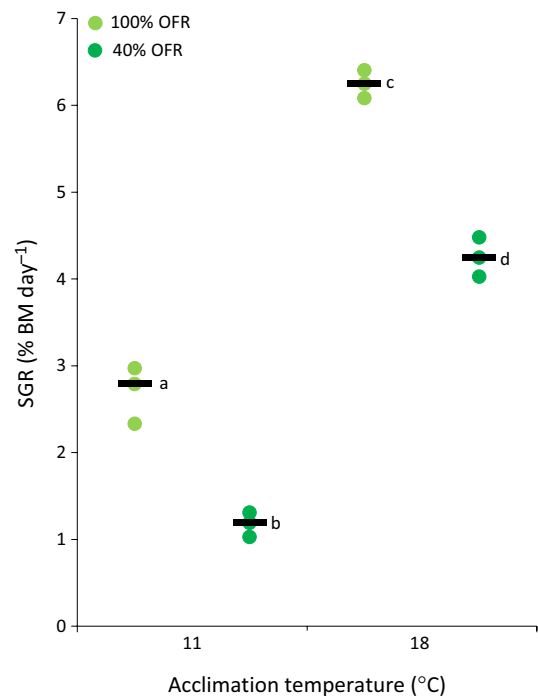


FIGURE 2 Effect of food restriction and low temperature exposure on specific growth rate (SGR, % body mass/day; N: 3 tanks/treatment) in larval white sturgeon, *Acipenser transmontanus* (Acipenseridae). Fish were exposed to one of two acclimation temperatures (cold exposure: 11°C or a control temperature: 18°C) and one of two food restriction treatments (100% optimal feed rate, OFR or 40% OFR) for 6 weeks. Values are shown as raw data points and black lines mark treatment means. Different letters indicate statistical differences ($p \leq .05$) [Colour figure can be viewed at wileyonlinelibrary.com]

the combined effects of stressors is still regarded as one of the largest knowledge deficiencies in ecological conservation (Darling & Côté, 2008; Mothersill et al., 2007; Sala et al., 2000). To this end, we assessed

the interactive effects of food restriction and low temperature exposure on SGR and CTMax in larval *A. transmontanus*. The two stressors interacted antagonistically to affect SGR, but CTMax was only affected by acclimation temperature. These data highlight the unpredictability of stressor interactions and may guide conservation efforts.

4.1 | Isolated and combined effects of stressors on SGR

The thermal sensitivity of growth rates in fishes and other ectotherms is well understood (Angilletta, Steury, & Sears, 2004; Ojanguren,

Reyes-Gavilán, & Florentino, 2001). Growth rates of *A. transmontanus* are optimised between 18 and 23°C, and declines are observed at temperatures above and below this range (Hung, Lutes, Shqueir, & Conte, 1993; Cui & Hung, 1995). In the present study, 11°C-acclimated fish grew at approximately half the rate of 18°C-acclimated fish. Similar observations of depressed growth rates at cold temperatures have been made for other sturgeon species. In juvenile shovelnose sturgeon, *Scaphirhynchus platyrhynchus* (Acipenseridae), feed efficiency was reduced at temperatures below 18°C and growth ceased at temperatures below 10°C (Kappenman, Fraser, Toner, Dean, & Webb, 2009). Similarly, growth rates in both lake sturgeon, *A. fulvescens* (Acipenseridae), and green sturgeon, *A. medirostris* (Acipenseridae), decreased precipitously with declining temperatures (Fortin, Dumont, & Guenette, 1996; Mayfield & Cech, 2004).

Food deprivation typically results in low long-term and short-term energy substrates, and less energy devoted towards somatic growth (Verhille et al., 2015). In isolation, food restriction resulted in a 30.6% reduction in SGR at 18°C. This finding aligns with previously observed trends in food restriction trials, where growth rates decreased with declining feed rations (Deng et al., 2009). In the present study, an antagonistic interaction between low temperature exposure and food restriction was observed in fish simultaneously exposed to both stressors. Simple addition of the isolated effect of each stressor predicts an 87.1% reduction in SGR would be observed when stressors are combined; however, SGR only declined by 80.6% in fish simultaneously exposed to both stressors. Fish often employ similar mechanisms to respond to low temperature exposure and food deprivation. Behavioural and physiological changes that reduce energy turnover are at the forefront of adaptive responses to low food availability (Wang, Hung, & Randall, 2006). Food-restricted fish typically downregulate activity levels as an energy saving strategy, with some species reducing daily activity by 50% (Van Dijk, Staaks, & Hardewig, 2002). Similarly, activity levels also decrease at low temperatures in ectotherms (Fukuhara, 1990). Energetic demands can also be lowered by changes in standard metabolic rate whereby maintenance costs are reduced. Ectotherm metabolic demands lower with declines in body/environmental temperature (Q_{10} effect), and energy required to cover metabolism at 11°C would be much less than at 18°C. Indeed, the thermal sensitivity of SGR ($Q_{10} = 3.3$) aligned with typical Q_{10} values for fishes (2–3), suggesting that passive physico-chemical effects of low temperatures on metabolism were responsible (Speers-Roesch, Norin, & Driedzic, 2018).

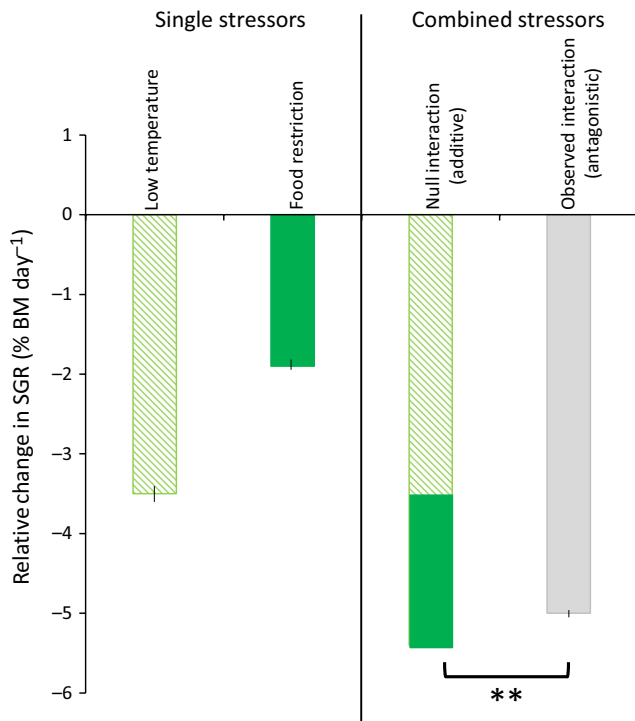


FIGURE 3 Isolated and combined effects of low temperature exposure and food restriction on specific growth rate (SGR, % body mass [BM]/day) in larval white sturgeon, *Acipenser transmontanus* (Acipenseridae). Fish were exposed to one of two acclimation temperatures (cold exposure: 11°C or a control temperature: 18°C) and one of two food restriction treatments (100% optimal feed rate, OFR or 40% OFR) for 6 weeks. Values are shown as relative changes (mean \pm standard error) compared to control conditions (18°C 100% OFR). Low temperature exposure and food restriction interacted antagonistically. Asterisks indicate statistical differences (** $p < .01$) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Critical thermal maxima (CTMax) means (\bar{x}) for each treatment group, sample size (N), wet body mass and mass-adjusted CTMax means

Treatment group	Measured CTMax (°C)		Wet mass $\bar{x} \pm SD$ (g)	CTMax (°C) corrected for wet mass
	N	$\bar{x} \pm SE$		
18°C 100% OFR	10	30.69 \pm 0.44	2.43 \pm 0.83	32.01
18°C 40% OFR	10	31.74 \pm 0.26	1.33 \pm 0.44	31.84
11°C 100% OFR	9	28.60 \pm 0.16	0.74 \pm 0.10	28.05
11°C 40% OFR	11	28.51 \pm 0.31	0.48 \pm 0.22	27.67

SD, standard deviation; SE, standard error; OFR, optimal feed rate.

Since food restriction and low temperature exposure can be countered by the same compensatory mechanisms, it can be speculated that compensatory responses induced by one stressor may have been associated with heightened tolerance to the other stressor. Instances where protective mechanisms against one stressor heightens resilience to another stressor are termed *cross-tolerance* (Kampinga, Brunsting, Stege, Burgman, & Konings, 1995). Several cases of cross-tolerance have been documented in aquatic ectotherms. Exposure to heat shock (+12°C) in tidepool sculpins, *Oligocottus maculosus* (Cottidae), increased survival when exposed to subsequent osmotic and hypoxic stressors (Todgham, Schulte, & Iwama, 2005). The induction of Hsps from the priming stressor (stressor experienced first) is thought to be a key mechanism underlying cross-tolerance, because Hsps play a critical role in aiding recovery from cellular stress (reviewed in Basu et al., 2002). Both cold shock and food deprivation can induce significant overexpression of Hsp70 levels in multiple tissues of *A. transmontanus* (Wang, Deng, De Riu, Moniello, & Hung, 2013), although some studies show food restriction to inhibit Hsp induction in response to thermal stress (25–30 dph; Deng et al., 2009; Han et al., 2012). Cross-tolerance between low temperature exposure and food restriction may underlie the antagonistic interaction observed here, but further experimental work is required, where the order of stressor exposure is manipulated, to confirm this. Cross-tolerance is generally observed between stressors which co-occur in natural habitats (Sinclair, Ferguson, Salehipour-Shirazi, & MacMillan, 2013). Seasonal declines in food availability are common in freshwater habitats and cross-tolerance between low temperatures and low food availability is likely to allow organisms to survive natural fluctuations in food supply. Indeed, food restricted fish typically demonstrate a behavioural preference for cooler temperatures, termed behavioural hypothermia (Sogard & Olla, 1996; Van Dijk et al., 2002) and examinations of how temperature preference changes with food ration in larval *A. transmontanus* would provide valuable insight.

Comparative data on the interactive effects of low temperature exposure and food restriction are scant in ectothermic vertebrates. However, the combined effects of high temperature exposure and food restriction have been examined in juvenile *A. transmontanus*. Hung et al. (1993) found growth rate and feed efficiency to decrease with food restriction and high temperature exposure (i.e. 26°C), but the two stressors did not interact (i.e. additive effect). Combined with our results, these findings suggest that coupling food restriction with elevated temperatures (i.e. $> T_{\text{opt-growth}}$) is more detrimental to *A. transmontanus* growth compared to coupling with low temperatures (i.e. $< T_{\text{opt-growth}}$). It can be speculated that this difference may stem from a lack of cross-tolerance between elevated temperatures and food restriction, as ectotherm metabolic demands and activity levels rise exponentially with rising temperature, potentially surpassing sustainable limits.

4.2 | Isolated and combined effects of stressors on CTMax

Food restriction can disrupt energy homeostasis and decrease stress tolerance due to less energy being available for protective responses

(Sokolova, 2013; Sokolova, Frederich, Bagwe, Lannig, & Sukhotin, 2012). Countering our prediction, food restriction had no effect on CTMax in *A. transmontanus*, suggesting that energy was preferentially directed towards maintaining heat tolerance. Food limited organisms may divest energy from all physiological processes equally, or preferentially direct energy towards some processes at the cost of less energy directed towards others. For example, food-restricted Dungeness crabs (*Metacarcinus magister* [Cancridae]) maintained CTMax at the cost of depressed growth rates (McLean & Todgham, 2015). Trade-offs in energy allocation between growth and stress tolerance may explain our observed results, but further experimental work is required to determine how energy in food restricted *A. transmontanus* was distributed between basal maintenance (e.g. ion regulation and circulation), aerobic scope functions (e.g. growth and activity), and protective stress responses (e.g. Hsp induction and antioxidant defence mechanisms).

Previous studies have reported lower CTMax values in food restricted fish (Lee et al., 2016; Woiwode & Adelman, 1992). Although statistically significant, these CTMax declines in food deprived fish were very small (0.35–0.38°C) and the biological relevance of the declines is arguable. The magnitude of food restriction used in studies is also likely to mediate the observed effect on CTMax. Woiwode and Adelman (1992), for example, starved treatment fish for 5–7 weeks prior to measuring CTMax. When fish are food restricted but not starved, energy may still be directed towards maintaining thermal tolerance, and our findings suggest that maintaining thermal tolerance is an energetic priority in larval *A. transmontanus*. Similar findings have been observed in juvenile *A. transmontanus* (Lee et al., 2016), where CTMax was independent of food availability, even when food rations were very low (12.5% OFR). The effect of starvation on CTMax in *A. transmontanus*, however, remains untested.

Upper and lower thermal tolerance limits typically increase with rising acclimation temperature (Beitinger & Bennett, 2000), and as such CTMax of 11°C-acclimated fish was c.2°C lower than 18°C-acclimated fish. Higher CTMax values (1°C higher) have been reported in *A. transmontanus* despite the use of identical acclimation temperature (18°C), heating rate (0.3°C/min) and end point (LOE) (Lee et al., 2016). However, fish in the previous study were older and larger (205 g; 197 dph) and differences in CTMax probably reflect ontogenetic or size dependent changes in thermal tolerance (Komoroske et al., 2014). Together, our findings suggest that food restricted *A. transmontanus* are resilient to acute thermal extremes, but unseasonably cold temperatures may increase their susceptibility to heat waves within the S-SJ, which are predicted to increase in frequency over the next century (Cloern et al., 2011).

4.3 | Ecological implications

Nutritional deficits during critical developmental stages can be profound and permanently affect life-history trajectories (Metcalf & Monaghan, 2001). Despite this, feed restriction-growth assessments in *A. transmontanus* have focused on juvenile life-stages and less is known about larvae (Cui & Hung, 1995; Cui et al., 1997; Lee

et al., 2016). For example, Hung et al. (1993) used 30 g juveniles to examine the effect of food restriction and thermal stress on growth rates, whereas 0.2 g larvae (25 dph) were used in the present study, representing a 150-fold size difference. Larvae are likely to be more vulnerable to the threat of starvation than juveniles, due to their comparatively small endogenous energy reserves (Rainuzzo, Reitan, & Olsen, 1997). Moreover, the digestive tract of sturgeon develops during the larval stage and is sensitive to changes in food availability (Gisbert & Doroshov, 2003). Food deprivation in green sturgeon larvae results in deterioration of the digestive system, including tissue degeneration and shrinkage of digestive epithelia (Gisbert & Doroshov, 2003).

Although an antagonistic interaction was observed between food restriction and low temperature, the presence of two stressors was more detrimental to growth rates than the presence of a single stressor. Conservation efforts should therefore aim to minimise the presence of both stressors. Mitigating hypolimnetic water releases within the S-SJ catchment during peak reproductive periods (i.e. Spring) for *A. transmontanus* may buffer larval growth rates from the depressive effects of cold temperatures. Water reservoirs can be retrofitted to ensure that water releases have minimal impacts on downstream thermal regimes (Olden & Naiman, 2010). Retrofit options include installing multi-level intake devices to allow for selective withdrawals from the water column or thermal destratification by increasing water mixing using aeration systems, surface pumps, or draft tubes (Sherman, 2000; Olden & Naiman, 2010). Several water reservoirs within the S-SJ catchment have already been retrofitted with temperature control devices (e.g. Shasta Dam); however, hypolimnetic water releases still occur frequently (Pike et al., 2013). Dam operations within the S-SJ catchment are currently geared toward conserving endangered Chinook salmon, *Oncorhynchus tshawytscha* (Salmonidae), without considering the thermal requirements of other fishes in the system (National Marine Fisheries Service, 2009). Compliance points govern water operations so that downstream water temperatures are maintained below 13.3°C during late spring – late fall (National Marine Fisheries Service, 2009). Maintaining temperatures below this threshold is likely to depress growth rates in larval *A. transmontanus*, as demonstrated here, and may lead to lower recruitment rates. Our findings call for a re-evaluation of this temperature compliance point and suggest that revisions consider the thermal requirements of *A. transmontanus* larvae and other fishes in the system. Temperature guidelines may benefit from greater flexibility so that natural thermal regimes can be mimicked throughout the year and correspond with peak spawning periods of various fishes.

Restoration of natural food-web dynamics may also alleviate the threat of food scarcity during early-life stages. Reversing disrupted food-web linkages in the S-SJ may be achieved by restoring natural water flow regimes and controlling invasive primary consumers, which disrupt the food-web from its base (Cloern et al., 1983; Strayer, 2010), but controlling invasive species is an ongoing challenge for biologists and managers (Strayer, 2010). Nonetheless, our findings

show low temperature exposure and food restriction interact in a nonadditive manner to affect growth rate. The interactive effect of the stressors on growth rates highlights the need for holistic conservation strategies, which target multiple environmental stressors.

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

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