



Effects of feed restriction on the upper temperature tolerance and heat shock response in juvenile green and white sturgeon



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ABSTRACT

The objective of the current study was to investigate the effects of feed restriction on whole-organism upper thermal tolerance and the heat shock response of green and white sturgeon to determine how changes in food amount might influence physiological performance of each species when faced with temperature stress. Two parallel feed restriction trials were carried out for juvenile green (202 g; 222-day post hatch: dph) and white sturgeon (205 g; 197-dph) to manipulate nutritional status at 12.5%, 25%, 50%, or 100% of optimum feeding rate (100% OFR were 1.6% and 1.8% body weight/day, respectively) for four weeks. Following the trials, the critical thermal maximum (CTMax, 0.3 °C/min) of sturgeon ($N = 12$ /treatment/species) was assessed as an indicator of whole-organism upper thermal tolerance. To assess temperature sensitivity, sturgeon ($N = 9$ /treatment/species) were acutely transferred to two temperature treatments (28 °C and 18 °C as a handling control) for 2 h followed by 2 h of recovery at 18 °C before being sacrificed, and gill, brain, and mucus sampled for measurements of 70-kDa heat shock protein levels (Hsc/Hsp70). Feeding rate had species-specific effects on CTMax in green and white sturgeon such that CTMax of green sturgeon decreased as the magnitude of feed restriction increased; whereas, CTMax of white sturgeon did not change with feed restriction. Elevated temperature (28 °C) and feed restriction increased Hsc/Hsp70 levels in the gill tissue of green sturgeon, while heat shock increased Hsc/Hsp70 levels in the mucus of white sturgeon. Our results suggest that green sturgeon may be more susceptible to temperature stress under food-limited conditions.

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1. Introduction

Global climate change (GCC) will profoundly change our aquatic ecosystems with projections forecasting increases in water temperature and sea level along with a multitude of changes in other physical, chemical and biological factors (IPCC, 2014). It has been well documented that increased temperature can shift geographic distributions and result in population collapses and/or local extinctions (Fields et al., 1993; Lubchenco et al., 1993; Hofmann and Todgham, 2010); however, recent studies have revealed that species' distribution and abundance will also be affected by changes in other factors such as ocean chemistry, ocean circulation, and food web dynamics (reviewed by Harley et al., 2006). To more accurately predict the vulnerability of aquatic organisms to

projected changes in local environments and GCC, an understanding of the physiological responses of aquatic organisms to concurrent changes in multiple environmental factors is critical (Todgham and Stillman, 2013).

The San Francisco Bay Delta (SFBD) has been highly modified through anthropogenic activities (e.g., water diversion, urban development, invasive species) driven by dense human settlement following the Gold Rush in California and is expected to experience continued environmental change due to GCC projections (Dasmann, 1999; Cloern and Jassby, 2012). The projected regional effects of GCC in the SFBD not only include increasing water temperature (ca. 0.3 °C per decade for the A2 scenario, Cloern et al., 2011) but also increasing salinity as a result of 1) precipitation shifts from snow to rain which result in a lower spring freshwater runoff from the Sierra Nevada mountains and 2) seawater intrusion into the SFBD associated with sea level rise (Knowles and Cayan, 2002, 2004; Cayan et al., 2008a, 2008b; Cloern et al., 2011). Modifications to local food web dynamics driven by GCC, such as declining phytoplankton production as well as disruption of trophic linkages between phytoplankton and zooplankton (Winder and Schindler, 2004; Auad et al., 2006; Boyce et al., 2010) have become

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important issues with respect to indirect effects of GCC on species' vulnerability to environmental change due to the potential for reduced energy flow among trophic levels. The SFBD is considered an estuary of low productivity in comparison to other estuaries worldwide (Cloern et al., 2014), due in large part to the introduction of the invasive Asian clam (*Corbula amurensis*) in the 1980s (Carlton et al., 1990; Cloern and Jassby, 2012). The high feeding efficiency of the Asian clam exceeds the local production of phytoplankton biomass (Thompson, 2005) and has contributed to substantial declines of fish population in the SFBD (Kimmerer, 2006; Moyle et al., 2012). Importantly, impacts to lower trophic levels and overall food availability on fishes are likely to be exacerbated by the effects of global and local climate change, including low freshwater inflow, salinity intrusion, and amplification of the drought effect by water diversions (Cloern and Jassby, 2012; Glibert et al., 2014). Thus, anticipated food web alterations driven by the anthropogenic activities occurring in the SFBD may add another stressor for aquatic organisms at higher trophic levels that manifests as a reduction in nutritional status.

Green (*Acipenser medirostris*) and white sturgeon (*Acipenser transmontanus*) are native to the SFBD and are of high ecological and economic value (Moyle, 2002). These species of sturgeon have received a lot of attention due to their vulnerability to anthropogenic activities such as overfishing, habitat alterations, and chemical contaminants (Kohlhorst, 1980; Linville et al., 2002; NMFS, 2006). The Southern Distinct Population Segment (DPS) of green sturgeon that inhabit in the SFBD (Adams et al., 2007) are currently listed as threatened under the Endangered Species Act (NMFS, 2006), and white sturgeon are listed as State S2 status (low abundance, restricted range, and potentially endangered species) in the California Natural Diversity Database (2009). Given the anticipated climate change impacts in the SFBD, environmental alterations such as decreasing food availability and increasing salinity have been recently spotlighted due to the implications for green and white sturgeon population resilience (Haller et al., 2015; Klimley et al., 2015; Lee et al., 2015; Vaz et al., 2015). Currently, there is limited information available on integrative physiological performance of green and white sturgeon when faced with increased water temperature and low food availability.

Maintenance of good nutritional status is critical because food-limited fish are more susceptible to predation (Metcalf et al., 1998; Metcalf and Steele, 2001), disease (Oliva-Teles, 2012), and other environmental factors (e.g., salinity; Haller et al., 2015; Lee et al., 2015). Energy allocation to different molecular and cellular pathways essential to the stress response can be limited in fish with reduced nutritional status (i.e., physiological trade-offs), resulting in decreased stress tolerance (Sokolova, 2013). Previous studies investigating the effects of feed restriction on salinity tolerance in green and white sturgeon revealed that osmoregulatory capacities in sturgeon are energy-dependent (Haller et al., 2015; Lee et al., 2015). Feed-restricted sturgeon that exhibited negative growth following a four-week feeding trial demonstrated a slower recovery from osmotic stress than non-feed-restricted sturgeon (Haller et al., 2015; Lee et al., 2015). Under conditions of low food availability and increasing water temperature, energy balance may be significantly shifted, potentially lowering upper thermal tolerance limits in green and white sturgeon (Verhille et al., 2015).

Since green and white sturgeon are closely related and white sturgeon have relatively large populations compared to the threatened green sturgeon, white sturgeon have been considered a surrogate model for green sturgeon for predicting possible biological responses of green sturgeon to environmental alterations. Comparative studies of white and green sturgeon from our group have shown that these species differ significantly in their sensitivity to chemical contaminants such as mercury and selenium (Lee et al., 2011, 2012; De Riu et al., 2014), to salinity challenges (Haller et al., 2015; Lee et al., 2015) and show behavioral differences to variable water velocities around water diversions (e.g., Poletto et al., 2014). Taken together, results from these studies demonstrate that green sturgeon in general are more

sensitive to environmental change than white sturgeon and therefore white sturgeon serve as a poor surrogate species for green sturgeon when it comes to understanding stress tolerance, effects of food limitation, and overall vulnerability to GCC.

The current study was conducted to test the following predictions: 1) food limitation would decrease the temperature tolerance of juvenile green and white sturgeon, and 2) food limitation would result in greater temperature sensitivity of green sturgeon. Two parallel feed restriction trials were carried out for four weeks to manipulate nutritional status of green and white sturgeon. Following the trials, feed-restricted and non-feed-restricted groups were subjected to temperature stress in order to measure critical thermal maximum (CTMax) as an indicator of whole-organism upper thermal tolerance and to measure relative 70-kDa heat shock protein levels (Hsc/Hsp70) in different tissues as an indicator of temperature sensitivity. Findings from the current study will enhance our predictive capacity on the impacts of the projected increases in water temperature and decreases in food availability derived from the global and local climate change impacts in the SFBD on performance of green and white sturgeon.

2. Materials and methods

2.1. Animal source and husbandry

Green sturgeon larvae were F2 offspring from captive F1 broodstock originating from wild-caught Klamath River Northern DPS sturgeon (Van Eenennaam et al., 2008, 2012). The captive F1 broodstock were maintained at an annual mean temperature of 18.5 ± 1.3 °C (mean \pm SD) and artificially spawned at 15 ± 0.5 °C at the Center for Aquatic Biology and Aquaculture (CABA) at the University of California, Davis, CA, USA. Fertilized eggs were incubated at 15 ± 0.5 °C until hatch and then green sturgeon larvae were transferred to stocking tanks (ca. 152 cm diameter, 45 cm height, 750 L water volume) supplied with 18.5 ± 0.5 °C flow-through degassed well water. White sturgeon larvae were acquired from domesticated broodstock at a local fish farm (Lazy Q Fish Ranch LLC, Dixon, CA, USA). White sturgeon broodstock were reared at a fish farm located near UC Davis (<25 km) at similar temperatures (ca. 18 °C) to the green sturgeon broodstock. When white sturgeon broodstock were matured, they were maintained and spawned at 13 – 15.5 °C. Fertilized eggs were incubated at 15.5 ± 0.5 °C on a recirculating hatchery system. After hatch, white sturgeon larvae were switched to a flow-through tank system with water at 18 – 19 °C for three days. Then, white sturgeon larvae (3 days post hatch; dph) were transported to CABA for rearing and experimentation.

Both green and white sturgeon larvae were reared under similar conditions until reaching a target size as juvenile fish (~170 g, approximately 6.5 to 7 months). Details of rearing practices for green and white sturgeon can be found in Haller et al. (2015) and Lee et al. (2015), respectively. All handling, care, and experimental procedures were approved by the UC Davis Institutional Animal Care and Use Committee (Protocol #16541).

2.2. Feed restriction trial

Two parallel feed restriction trials were carried out for juvenile green and white sturgeon. Juvenile green ($N = 840$, 174 ± 0.4 g (mean \pm SEM), 214-dph) and white ($N = 840$, 173.2 ± 0.6 g, 189-dph) sturgeon were randomly distributed into fiberglass tanks (ca. 750 L), resulting in 70 fish per tank and 12 tanks per species. During the acclimation period (8 days), fish were fed at an optimum feeding rate (OFR) estimated by an OFR prediction model. The OFR is defined as the rate (% body weight per day) at which growth is maximal. A prototype model developed for white sturgeon (Cui and Hung, 1995) was used to estimate an OFR for green sturgeon, since no feeding model exists for green sturgeon, and a modified prediction model (Lee et al., 2014) was applied to estimate OFR for white sturgeon. Although different models were used, the

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