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RESEARCH ARTICLE

Effects of high temperatures on threatened estuarine fishes during periods of extreme drought

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ABSTRACT

Climate change and associated increases in water temperatures may impact physiological performance in ectotherms and exacerbate endangered species declines. We used an integrative approach to assess the impact of elevated water temperature on two fishes of immediate conservation concern in a large estuary system, the threatened longfin smelt (*Spirinchus thaleichthys*) and endangered delta smelt (*Hypomesus transpacificus*). Abundances have reached record lows in California, USA, and these populations are at imminent risk of extirpation. California is currently impacted by a severe drought, resulting in high water temperatures, conditions that will become more common as a result of climate change. We exposed fish to environmentally relevant temperatures (14°C and 20°C) and used RNA sequencing to examine the transcriptome-wide responses to elevated water temperature in both species. Consistent with having a lower temperature tolerance, longfin smelt exhibited a pronounced cellular stress response, with an upregulation of heat shock proteins, after exposure to 20°C that was not observed in delta smelt. We detected an increase in metabolic rate in delta smelt at 20°C and increased expression of genes involved in metabolic processes and protein synthesis, patterns not observed in longfin smelt. Through examination of responses across multiple levels of biological organization, and by linking these responses to habitat distributions in the wild, we demonstrate that longfin smelt may be more susceptible than delta smelt to increases in temperatures, and they have little room to tolerate future warming in California. Understanding the species-specific physiological responses of sensitive species to environmental stressors is crucial for conservation efforts and managing aquatic systems globally.

KEY WORDS: Longfin smelt, *Spirinchus thaleichthys*, Delta smelt, *Hypomesus transpacificus*, Transcriptomics, Endangered fishes

INTRODUCTION

Increases in water temperatures as a result of climate change have already impacted fish populations (Perry et al., 2005; Graham and Harrod, 2009). Future climate change may substantially affect migratory fish species as direct and indirect effects of changing environmental conditions are integrated across their different life stages (Dudgeon et al., 2006; Reist et al., 2006; Crozier et al., 2008; Robinson et al., 2009). For example, increases in water temperature during development may alter the timing of seaward migration in anadromous species, causing individuals to miss optimal feeding conditions in the marine environment (Taylor, 2008). While the majority of knowledge on the effects of climate change on migratory fishes is from studying economically important anadromous species, such as Pacific salmon and Atlantic salmon (e.g. Jonsson and Jonsson, 2009; Martins et al., 2012), much less is known about the effects on anadromous and semi-anadromous species that are less important economically, yet contribute greatly to aquatic biodiversity. For anadromous and semi-anadromous fishes, estuaries provide critical rearing grounds and migratory corridors that connect the marine environment with freshwater watersheds (Levy and Northcote, 1982; Ray, 2005). Given the importance of estuaries worldwide for resident and migratory fishes, it is crucial to understand the effects of water temperature on these systems.

Estuaries can be influenced by various global and local environmental factors, in addition to anthropogenic activities and natural processes throughout the upstream watershed (Dudgeon et al., 2006; Cloern et al., 2011). Therefore, fishes reared in estuaries may be impacted by multiple environmental stressors that include habitat loss, nutrient and contaminant inputs, and colonization of invasive species (Kemp et al., 2005; Brooks et al., 2012; Cloern and Jassby, 2012). These stressors can interact with increases in water temperature, making it difficult to predict the consequences of climate change on estuarine fishes. The San Francisco Estuary/Sacramento–San Joaquin Rivers Delta system, California, USA, hereafter called the 'Delta', is a heavily altered estuary that has been impacted by the aforementioned stressors, in addition to substantial water diversions from the system for human use (Sommer et al., 2007). At the crossroads of human demands for water and conservation of the Delta are several high-profile native pelagic fishes (Sommer et al., 2007). These include two estuary-dependent Osmeridae fishes, the threatened anadromous longfin smelt (*Spirinchus thaleichthys*), the southernmost population of the species that ranges from California to Alaska, and the endangered delta smelt (*Hypomesus transpacificus*), a semi-anadromous species with a distribution confined to the Delta (Moyle, 2002; Sommer and Mejia, 2013). Abundances have reached record lows in California, and conservation efforts to protect these species by regulating water withdrawals from the system are particularly contentious as this affects the water supply for >25 million people and a multibillion dollar agriculture industry (Brown et al., 2013). California is in the midst of a historic drought [2012–2016 (ongoing)] that has further reduced freshwater availability (Diffenbaugh et al., 2015). California normally experiences intense wet or dry periods; however, 2014–2015 was exceptionally dry, with the drought

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