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Combined effects of temperature and salinity on the physiology of two geographically-distant eastern oyster populations

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ABSTRACT

Understanding why a species occupies a certain geographic range and predicting how they will be affected by climate change require characterizing physiological traits in geographically-distant populations. The objective of this study was to perform a direct comparison of two eastern oyster (*Crassostrea virginica*) populations that occupy contrasting temperature and salinity habitats, New Brunswick, Canada (47°N – Gulf of St. Lawrence) and Louisiana, USA (29°N – Gulf of Mexico). Specifically, clearance rate, valve opening, and oxygen consumption rate were measured in oysters of both populations following a full factorial design with three temperatures (10, 20, 30 °C) and two salinities (15, 25). New Brunswick oysters had a greater gill area, shell gape angle, and oxygen consumption rate. Temperature was the main driver of clearance rate, valve opening duration and oxygen consumption rate. Clearance rate at 20 °C and 30 °C was significantly higher than at 10 °C, and oysters at 20 °C had their valves opened for a greater percentage of time compared to oysters at 10 °C and 30 °C. Oxygen consumption rate increased gradually from 10 °C to 30 °C and similarly for both populations, with no indications of a thermal breakpoint at 30 °C. Temperature coefficients for the oxygen consumption rate (Q_{10}) were within the normal ecological range for both populations. No physiological differences were observed between salinity treatments in both populations. No latitudinal compensation in the physiological rates was found. Overall, results showed that *C. virginica* is tolerant to a broad range of temperatures and salinities. Such physiological plasticity is consistent with the species' extended geographical range.

1. Introduction

A pattern of intraspecific variation in growth rate along latitudinal gradients has been found in many ectotherm species, with individuals from northern populations growing faster than conspecifics from southern populations when raised under the same conditions (Dehnel, 1955; Conover and Present, 1990; Yamahira and Conover, 2002; Lindgren and Laurila, 2009). Levinton (1983) proposed that those differences evolved in response to adaptation to native temperature regimes such that high-latitude individuals grow faster than low-latitude individuals at low temperatures, but more slowly at high temperatures. Other studies have however demonstrated that high-latitude individuals have higher capacity for growth at both high and low temperatures (Conover and Present, 1990; Yamahira and Conover, 2002) and this latitudinal compensation may be an adaptation to shorter growing seasons. Less is known regarding the underlying molecular, biochemical, and physiological mechanisms and the role that energy allocation (i.e. growth, reproduction) plays in these growth patterns (Angilletta Jr et al., 2004). For example, the metabolic cold adaptation hypothesis states that populations or species from cold environments will have elevated metabolic rates compared to those from warmer waters; however, it has been a topic of debate over many years and some studies have failed to find evidence for latitudinal metabolic compensation (Clarke, 1993; Peck and Conway, 2000; Addo-Bediako et al., 2002).

The eastern oyster *Crassostrea virginica* is an ectotherm and

Abbreviations: CR, Clearance rate; CRi, Individual oyster clearance rate; CRg, Clearance rate standardized by gill area; CRw, Clearance rate standardized by dry meat weight; LA, Louisiana; NB, New Brunswick; OCR, Oxygen consumption rate; OCRi, Individual oxygen consumption rate; OCRw, Oxygen consumption rate standardized by dry meat weight; Q_{10}, Van't Hoff's temperature coefficient

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euryhaline species with a wide latitudinal distribution ranging from the Gulf of St. Lawrence to the Gulf of Mexico and the Caribbean (Galtsoff, 1964; Lazoski et al., 2011). Because of its large geographic extension, oyster populations are exposed to very different thermal and environmental conditions (i.e. food availability, photoperiod, etc.). For example, in the shallow estuaries of the Gulf of St. Lawrence (Canada) water temperature seasonally varies between −1.5 °C and 22 °C, and temperatures above 5 °C, considered to be the lower feeding threshold, occur for about half of the year (Comeau et al., 2012). In contrast, temperature in the northern Gulf of Mexico (USA) varies between 9 °C and 32 °C, a range that is favorable for feeding all year round (Loosanoff, 1958; Casas et al., 2015, 2017; Leonhardt et al., 2017; Lowe et al., 2017). Moreover, genetic differences between Atlantic and Gulf of Mexico *C. virginica* have been repetitively shown (Reeb and Avise, 1990; Murray and Hare, 2006) and there is increasing evidence for the existence of genetic subpopulations (Rose et al., 2006; Varney et al., 2009, 2016). However, there is little information on the comparative physiology of geographically-distant populations. Early studies noted that northern populations begin spawning at a lower temperature than southern populations. For example, oysters from Long Island Sound spawned at temperatures above 16 °C while populations from Galveston Bay required 25 °C (Stauber, 1950; Loosanoff and Nomejko, 1951; Barber et al., 1991). Differences in growth rate between oyster populations across latitudinal clines have also been found, along with higher gill ciliary activity in colder water temperatures in northern populations, supporting the latitudinal compensation hypothesis, since gill ciliary activity is correlated with feeding rate (Dittman, 1997; Dittman et al., 1998).

Recently, macro-physiology studies examining how widely-distributed organisms are affected by the high variability of environmental conditions have arisen to understand and predict how species and ecosystems will respond to climate change (Osovitz and Hofmann, 2007). The need for studies to assess organismal condition and physiological performance across entire species' ranges has therefore increased. Such research, however, is not very common due to the logistical challenges of working at large spatial scales. Jansen et al. (2007) measured the oxygen consumption rates of 16 populations of mussel species (*Mytilus* spp.) distributed along the European coast. Measurements were done at five temperatures (3–31 °C) and at different times of the year. Temperature sensitivity of the oxygen consumption rate was characterized by calculating Q_{10} or van't Hoff's temperature coefficient; Q_{10} values ~ 2 occur when the rate is measured within the ecological temperature range of the species, and Q_{10} values < 1 mean that a breakpoint temperature is reached and respiration rate decreases with increasing temperature (Jansen et al., 2007; Pörtner, 2001; Bayne, 2017). Mean oxygen consumption rates in *Mytilus* spp. increased from 3 °C to 24 °C and then decreased after reaching a breakpoint temperature between 24 °C and 31 °C (Jansen et al., 2007) with Q_{10} < 1 occurring at lower temperatures in northern than southern populations. Interestingly, a breakpoint temperature was reached in summer at one of the southern population location, and was associated with mussel mortalities. Recent studies have documented climate-related mortality events, changes in population abundances, and shifts in the geographical distribution of ectothermic animals (Helmuth et al., 2005; Perry et al., 2005). In species with a wide latitudinal range, climate change will probably have the most deleterious consequences in the southern populations because they are currently living closer to their breakpoint temperature (Pörtner, 2001; Jansen et al., 2007). Regarding *C. virginica* populations, it is largely unknown how climate change will affect their abundance and geographical distribution, and the thermal sensitivity of the oxygen consumption rate of geographically-distant populations has not been compared.

Salinity also affects *C. virginica* physiology and distribution and differences in performance between populations growing under the same conditions has been documented (Powell et al., 1992; Shumway, 1996; Lavaud et al., 2017; Leonhardt et al., 2017). There is surprisingly little information available for the combined effect of temperature and salinity on the physiological rates of geographically-distant oyster populations when temperature and salinity control every aspect of their biology (Shumway, 1996; Bayne, 2017). The objective in this study was to compare the physiological performance of a northern (47°N – Gulf of St. Lawrence) and a southern (29°N – Gulf of Mexico) *C. virginica* populations. Specifically, clearance rate, valve opening, and oxygen consumption were measured in oysters of both populations following a full factorial design in the laboratory with three temperatures (10, 20, 30 °C) and two salinities (15, 25). We tested the hypothesis that physiological performance of distant oyster populations adapted to contrasting thermal and saline environments may differ when tested under a range of temperature and salinity laboratory conditions. This experiment was designed to test latitudinal compensation in the physiological rates of two geographically-distant populations and to provide one of the first insights into performance, physiological plasticity, and thermal tolerance of *C. virginica* populations.

2. Materials and methods

2.1. Oysters

Wild oysters were collected from Baie Saint-Simon-Sud (47.7173°N; 64.7822°W), New Brunswick (NB), Canada and southeast Louisiana (LA), (Bay Gardene [29.5910°N; 89.6425°W] and Sister Lake [29.2341°N; 90.9172°W]), USA. Baie Saint-Simon-Sud is characterized by water salinity ranging from 18 to 31, and temperatures from −1.5 °C to 22 °C (Comeau et al., 2012, 2017), whereas southeast Louisiana is characterized by water salinity ranging from 1 to 28, and temperatures from 9 °C to 32 °C (Casas et al., 2015; Leonhardt et al., 2017; Lowe et al., 2017). Oysters from Canada (Fig. 1) were approximately six years old with a shell height of 71.1 ± 4.9 mm, *N* = 50 (mean ± standard deviation). Oysters collected from southeast Louisiana were maintained at the Louisiana Sea Grant Oyster Research Hatchery and Demonstration Farm (Grand Isle, LA, USA) prior to experimentation and were estimated to be about one and a half years old and 70.3 ± 7.2 mm in shell height, *N* = 50 (Fig. 1). The study was timed at the end of the fall to wait for both populations to finish with their reproduction and be in resting gonadal stage, and to collect the New Brunswick oysters before freezing of the seawater.

2.2. Experimental design

In October 2015, 350 oysters from each population were collected and transported to Louisiana State University. At the time of collection, water temperature and salinity in Baie Saint-Simon-Sud and Grand Isle were 8 °C and 26, and 21 °C and 12, respectively. In the laboratory, oysters of each population were scrubbed and divided into six groups. Each group was placed in a 200–500 L tank filled with artificial seawater (Crystal Sea, Marinemix Marine Enterprises International, Baltimore, Maryland, USA) adjusted to the salinity of the place of collection and 16 °C. Salinity was gradually modified, at a rate of 3 units per day, every other day, until the experimental salinities of 15 and 25 were reached. Next, water temperature in the tanks was gradually

Fig. 1. Photograph illustrating the differences in shape between New Brunswick and Louisiana oysters.