



Ecological differences influence the thermal sensitivity of swimming performance in two co-occurring mysid shrimp species with climate change implications

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ABSTRACT

Temperature strongly affects performance in ectotherms. As ocean warming continues, performance of marine species will be impacted. Many studies have focused on how warming will impact physiology, life history, and behavior, but few studies have investigated how ecological and behavioral traits of organisms will affect their response to changing thermal environments. Here, we assessed the thermal tolerances and thermal sensitivity of swimming performance of two sympatric mysid shrimp species of the Northwest Atlantic. *Neomysis americana* and *Heteromysis formosa* overlap in habitat and many aspects of their ecological niche, but only *N. americana* exhibits vertical migration. In temperate coastal ecosystems, temperature stratification of the water column exposes vertical migrators to a wider range of temperatures on a daily basis. We found that *N. americana* had a significantly lower critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}). However, both mysid species had a buffer of at least 4 °C between their CT_{max} and the 100-year projection for mean summer water temperatures of 28 °C. Swimming performance of the vertically migrating species was more sensitive to temperature variation, and this species exhibited faster burst swimming speeds. The generalist performance curve of *H. formosa* and specialist curve of *N. americana* are consistent with predictions based on the exposure of each species to temperature variation such that higher within-generation variability promotes specialization. However, these species violate the assumption of the specialist-generalist tradeoff in that the area under their performance curves is not constant. Our results highlight the importance of incorporating species-specific responses to temperature based on the ecology and behavior of organisms into climate change prediction models.

1. Introduction

Marine ecosystems are changing rapidly, with climate change altering species distributions (Loarie et al., 2009) and disrupting ecosystem functions (Fabry et al., 2008). These effects are associated with an increase in mean global sea surface temperature of 0.67 °C over the past century, yet ocean temperatures are predicted to increase between 1.0 and 3.3 °C over the next century (Pachauri et al., 2014). Projections for ocean warming vary by location, with mid to high latitudes warming at a faster rate. Along with range shifts for mobile species (Nye et al., 2009; Parmesan and Yohe, 2003), warming also increases the risk of local extinction (Hoegh-Guldberg et al., 2005), causes phenological changes (Walther et al., 2002), and enhances species invasion rates (Stachowicz et al., 2002). These studies highlight how changes in temperature can alter ecological processes by affecting

organismal physiology, in which responses are exhibited at both individual and population-levels. More studies are needed investigating whether thermal responses of related species differ based on ecological and behavioral traits and how that corresponds to their physiological traits.

Ocean warming initially prompts physiological or behavioral responses (Caldwell et al., 2015), which are likely to be species-specific (Lord and Whitlatch, 2015; Sunday et al., 2015). For ectothermic marine organisms, warming waters may increase metabolic activity and locomotor performance (O'Connor et al., 2009), and populations may respond positively to temperature change if they still operate within their thermal tolerance range. Alternatively, temperature can impair physiological processes (Pörtner, 2002; Pörtner and Farrell, 2008). Thermal variation is typically high at mid and high latitudes and results in broader thermal tolerances for species; conversely, species at lower

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latitudes that experience less thermal variation have narrower tolerance ranges (Addo-Bediako et al., 2000; Chown et al., 2004; Janzen, 1967; Pachaouri et al., 2014; Parmesan, 2007). In understanding species' response to ocean warming, it is necessary to consider both the rate of environmental temperature change and species vulnerability, such as the proximity of maximum performance to thermal maxima (Deutsch et al., 2008; Huey et al., 2009). We can predict responses to warming by evaluating both temperatures that organisms will be exposed to and their physiological traits, such as thermal tolerance range and performance (Hofmann and Todgham, 2010; Huey et al., 2009). Even sympatric species, inhabiting the same latitudes, may have different responses to changing temperatures (Fromentin and Planque, 1996), and locally adapted populations across a species' range may respond differently to environmental change (Sanford and Kelly, 2011). Will differences in behavioral, ecological, or life history traits that expose organisms to different temperature extremes or variation in temperatures lead to different responses to climate change (Parmesan and Yohe, 2003; Van Damme et al., 1989)? Here, we investigate how differences in ecological and behavioral traits between sympatric species at the same trophic level will influence their response to warming oceans.

Narragansett Bay, Rhode Island has a well-documented history of warming and other anthropogenic influences on marine ecosystems (Desbonnet and Costa-Pierce, 2008). The bay is shallow and well mixed near its ocean boundary and is seasonally stratified near the more urbanized northern end. Narragansett Bay also experiences large seasonal variation in water temperatures ranging from 0 °C in the winter to 26 °C in the summer (Desbonnet and Costa-Pierce, 2008). Within summer and winter seasons, thermal stratification between surface and bottom waters exists but is typically small; summer temperatures average around 24 °C at the surface and 22 °C at the bottom and winter temperatures average around 2 °C at the surface and 3 °C at the bottom. While thermal stratification within the bay can occur year-round, the greatest stratification occurs in fall and spring seasons. Maximum differences between surface and bottom water in these seasons can be as high as 6–8 °C, with warmer waters found at the surface (NarrBay.org). During these months, waters experience a warming rate of 1–2 °C h⁻¹ (National Oceanic and Atmospheric Administration, Station QPTR1-8454049). This variation suggests that species in the bay may have wide thermal tolerances or an ability to migrate or enter dormancy (Sorte et al., 2011; Woolsey et al., 2014). Between 1895 and 1999, water temperatures in Narragansett Bay have warmed 1.2 °C (Smith et al., 2010) and are projected to rise another 2–3 °C by 2100 (Pachaouri et al., 2014).

Narragansett Bay is home to several species of mysid shrimp, small marine crustaceans (< 1.5 cm) in the family Mysidae. Mysids, a close relative of krill, represent a critical link between plankton and fish communities, including commercially valuable species (Jumars et al., 2007). As small ectotherms, the physiology, behavior, and metabolic processes of mysids will likely be impacted by ocean warming (Pörtner and Farrell, 2008). Individual level impacts of warming to key links in marine food webs may ultimately cause major shifts in ecosystem structure and function, as seen in Antarctic krill (Atkinson et al., 2004).

Neomysis americana and *Heteromysis formosa* are two common mysid shrimp species in Narragansett Bay. Both species have a lifespan of about one year (Allen, 1982; Herman, 1962). These mysid species in Narragansett Bay breed multiple times throughout the year starting in the mid-spring and continuing through summer and fall; they can reach reproductive maturity by four weeks (Pezack and Corey, 1979; Williams, 1972). *Heteromysis formosa* can breed throughout the year and typically produces one to two broods per year, whereas *N. americana* typically has two to three broods per year (Allen, 1982; Herman, 1962). One critical difference between the two species is that throughout the year *N. americana* vertically migrates at night while remaining benthic during the day (Herman, 1962; Kringel et al., 2003), whereas *H. formosa* remains amongst the benthos and tends to seek

refuge when not foraging (Allen, 1982). Vertical migration in zooplankton allows for feeding higher in the water column under decreased predation pressure by visual predators (Zaret and Suffern, 1976). Near-shore and coastal environments in Narragansett Bay have been shown to experience stratification in dissolved oxygen (Melrose et al., 2007), an abiotic factor tied to temperature that can influence vertical migrators (Pörtner, 2010; Rosa and Seibel, 2008). However, stratification of dissolved oxygen occurs with greater frequency and severity in the northern parts of Narragansett Bay. In the lower west passage of Narragansett Bay (where the mysids were collected for this study), hypoxic events and significant stratification of dissolved oxygen are rarely recorded (Melrose et al., 2007). Thermal variation within the bay, however, is likely great enough to influence the physiology of vertical migrating organisms. While both species experience seasonal changes in water temperature, as vertical migrators, *N. americana* is exposed to a wider range of temperatures compared to *H. formosa* due to the thermal stratification within Narragansett Bay, particularly in the spring and fall seasons. Living in different thermal environments may impact physiological traits and potential responses to ocean warming between these two species (Huey et al., 2003; Hutchison and Maness, 1979; Kearney et al., 2009; Sunday et al., 2015).

In this study, we investigated the thermal tolerances and thermal sensitivity of swimming speed in *H. formosa* and *N. americana*. Thermal tolerance, as estimated by critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}), along with performance curves (based on traits such as swimming speed, growth, and reproduction rates) help characterize differences between species and can be used to predict how species will respond to ocean warming (Caldwell et al., 2015; Logan et al., 2013; Sunday et al., 2015). For mysid shrimp, swimming performance is critical for feeding and escape from predators (Lindén et al., 2003). Behavioral differences in sympatric species may lead to divergent responses to climate change because swimming sensitivity may be influenced by the daily range of temperatures experienced. We examined ten years of temperature data from Narragansett Bay (both bottom and surface waters) in order to quantify the variation experienced over the course of a year as well as quantify the difference in temperature variation experienced by *N. americana* and *H. formosa*.

With the differences in thermal variation experienced, we use the framework of Gilchrist (1995) to interpret thermal sensitivity of performance of two mysid species. In this framework, species experiencing greater temperature variation within a generation will have a narrower thermal tolerance range with a predicted tradeoff for enhanced performance maximum (P_{max}), these species are considered thermal specialists (Angilletta, 2009; Gilchrist, 1995; Levins, 1968; Levins and MacArthur, 1966). Alternatively, species experiencing greater temperature variation between generations will have greater breadth of performance with a tradeoff for decreased P_{max}, these species are considered thermal generalists (Angilletta, 2009; Gilchrist, 1995). This has been shown in developmental physiology of insects, where high temperature variation between generations results in decreased sensitivity and a generalist performance curve (e.g., Foray et al., 2011).

This generalist-specialist constraint on different aspects of performance is predicted to produce a tradeoff between P_{max} and performance breadth, while the area under the performance curve remains constant (Gilchrist, 1995; Levins, 1968; Levins and MacArthur, 1966; Slatkin and Lande, 1976). However, while this tradeoff is predicted to occur, data supporting this tradeoff in natural systems is often ambiguous (Futuyma and Moreno, 1988; Kingsolver and Huey, 2003), and few studies have investigated the generalist-specialist tradeoff (Angilletta et al., 2002), but (Gilchrist, 1996) observed a negative correlation between breadth of performance and P_{max}, highlighting a potential tradeoff. Here, the life histories of our mysid species lend to testing the Gilchrist (1995) framework. Both species have a generation time of about four weeks (or about one month). By vertically

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