

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

Gordon T. Ober<sup>a,\*</sup>, Carol Thornber<sup>a</sup>, Jason Grear<sup>b</sup>, Jason J. Kolbe<sup>a</sup>

<sup>a</sup> Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA

<sup>b</sup> U.S. Environmental Protection Agency, Atlantic Ecology Division, Narragansett, RI 02882, USA

## ARTICLE INFO

### Keywords:

Thermal tolerance  
Thermal sensitivity of performance  
Climate change  
Thermal variation  
Ocean warming

## 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

\* Corresponding author.

E-mail address: [Gordon\\_ober@uri.edu](mailto:Gordon_ober@uri.edu) (G.T. Ober).

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<sup>-1</sup> (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 (Pezzack 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<sub>min</sub>) and critical thermal maximum (CT<sub>max</sub>), 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<sub>max</sub>), 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<sub>max</sub>, 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<sub>max</sub> 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<sub>max</sub>, 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

migrating, the thermal variation experienced within a generation is greater for *N. americana* compared to *H. formosa*. Both species, however, deal with similar and substantial between generation thermal variation due to the seasonality of water temperature within Narragansett Bay. By experiencing more within generation variability, we predict that *N. americana* is a thermal specialist, whereas *H. formosa* is a thermal generalist. This difference between these two sympatric species could have implications in terms of their response to climate change, specifically ocean warming, as thermal specialists are expected to experience a greater impact from warming than thermal generalists (Huey et al., 2012).

Based on the temperatures experienced by both species, we predict the  $CT_{max}$  of *N. americana* to be higher due to exposure to warmer surface waters. As  $CT_{min}$  and  $CT_{max}$  have been shown to be coupled in marine organisms (Pörtner, 2002), we expect this warmer  $CT_{max}$  to result in a warmer  $CT_{min}$  for *N. americana*. Given anticipated differences in within generation temperature variation, we hypothesize that the performance curve of *N. americana* will more closely resemble that of a thermal specialist compared to *H. formosa*, and that differences between the species will reflect a tradeoff between enhanced  $P_{max}$  and performance breadth (Gilchrist, 1995). We interpret our results in the context of physiological performance sensitivity in relation to warming oceans.

## 2. Materials and methods

### 2.1. Specimen collection and laboratory acclimation

*Neomysis americana* and *H. formosa* were collected from the west passage of Narragansett Bay (41°32'5.08"N, 71°24'41.94"W) in June 2014, with water temperatures  $18.6 \pm 0.7$  °C (NarrBay.org). Individuals were collected by scallop dredge fitted with a plankton net and sample jar trawling at a depth of 9–10 m. After capture, individuals were placed in small transport containers with aeration and brought to the US EPA Atlantic Ecology Division (AED) in Narragansett, RI for laboratory acclimation.

All individuals were separated by species and housed in flow-through glass aquaria with 75-L capacity with aerated water kept at a constant 20 °C. Organisms were acclimated to these conditions for two weeks.

### 2.2. Water temperature data extraction

To place thermal tolerances and thermal sensitivity of swimming performance of these mysid species in an appropriate environmental context, we extracted water temperature data using a complete and error-checked version of the monthly 1998–2010 Nu-shuttle surveys from Narrbay.org (West Passage; see Kremer et al. (2010)). We restricted the data to bay segment #11 because it encompassed the area in which all mysids were collected from the field. We averaged towed instrument temperatures measured in the upper two meters (i.e., the part of the water column in which *N. americana* migrates to at night) and lower two meters (i.e., the benthic environment in which *H. formosa* inhabits and where *N. americana* is found during the day) over latitudinal slices of 0.08 decimal degrees. Maximum and minimum temperatures for both surface and bottom waters were determined for each month, and averaged over the 10-year period to provide insight into the temperature variation experienced over the course of one year.

To quantify the amount and frequency of thermal stratification, we divided the data into three month segments (quarters) and calculated the percentage of the slice-by-month combinations within each quarter for which the difference between upper and lower strata was greater than or equal to 4 °C, 3 °C, and 2 °C.

### 2.3. Minimum and maximum thermal tolerances

Adult male individuals of each species (N=10) were selected and placed into individual mesh cages (250  $\mu$ m) within a water bath. Adult males were selected for this experiment because they were abundant in our field capture; females caught were evenly split between gravid and nongravid. Males of similar sizes for each species were collected, although size (i.e., length) was not recorded for this experiment. Starting at 20 °C, water was slowly cooled 1 °C every 15 min. Individual mysids were observed until they stopped swimming, and this temperature was recorded as their critical thermal minimum ( $CT_{min}$ ). Once each individual ceased swimming, water temperature was increased back to 20 °C in increments of 1 °C every 15 min. Mysids were given two hours to acclimate at 20 °C; all mysids regained normal swimming behavior within this time. The water temperature was then slowly heated 1 °C every 15 min, and the temperature at which each individual mysid ceased swimming was recorded as their critical thermal maximum ( $CT_{max}$ ).

### 2.4. Thermal sensitivity of swimming performance

Determining  $CT_{min}$  and  $CT_{max}$  for each species allowed us to bracket the range of temperatures at which to test swimming performance. Based upon our results, we measured swimming performance at 10, 15, 20, 25, and 30 °C for both species. Adult males of each species (N=20 individuals) were selected from lab-acclimated populations and tested at each temperature. Individuals tested for thermal tolerance were not used for determining swimming performance. Individuals were placed into mesh cages within a water bath at 20 °C. The water bath was either heated or cooled gradually until the desired test temperature was reached; mysids then acclimated for 30 min. After acclimation, individual mysids were removed from their cages and placed into an acrylic swim chamber (10 cm×10 cm×1 cm) with the same temperature water. We backlit the chamber and filmed mysids using Pixelink PLB771G machine-vision camera with a 60 mm Nikon lens, shooting video at 25 frames/second from 1-m distance for 10 s (Grear et al., 2011). During the 10-s video, mysids were gently prodded at their telson using a metal probe to stimulate a burst swimming response. Due to wide variation in unprovoked mysid swimming speeds, burst responses were recorded to determine maximum swimming speed. We measured what was observed to be the fastest burst exhibited over the course of the 10-s video for each individual. Individual mysids were tested at each temperature if possible. Some mortality occurred, in which case new adult individuals were added to the experimental cohort to ensure a sample size of 20 trials per temperature per species. We chose to measure burst speed because of its ecological relevance as a response to a potential predator, thus burst swimming speed should reflect a component of fitness (Angilletta, 2009). If no clear burst movement was exhibited by an individual, then the trial was not included in the analysis.

We used ImageJ ([www.nih.gov](http://www.nih.gov); v.1.49) (Abràmoff et al., 2004) to calculate burst swimming speed as well as to measure mysid size (length in mm). By overlaying the frames of each video, we were able to determine the point at which a mysid exhibited a swimming burst. We defined the burst as the maximum distance between images of the mysid on two consecutive frames divided by the time lapse between frames (0.04 s). Mysid size was measured for each individual by measuring the distance from the tip of the rostrum to the end of the tail.

### 2.5. Statistical analysis

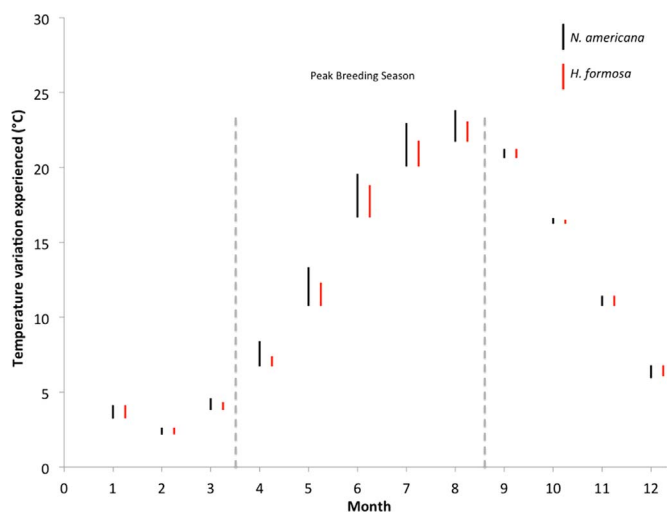
Maximum and minimum temperatures from surface and bottom waters were determined for each month of the Nu-shuttle survey and the mean variation (maximum temperature – minimum temperature) for each month was calculated. Temperature data for the vertically

migrating *N. americana* included both surface and bottom water, whereas only bottom water temperature data were used for the non-migrating *H. formosa*. Mean total (annual) variation experienced by mysids was calculated based on the monthly mean variation described above and was compared between species using a one-way analysis of variance (ANOVA). Values for  $CT_{\min}$  and  $CT_{\max}$  were independent and fit the assumptions of normality and homogeneity of variance. Mean values were compared between species using a one-way analysis of variance (ANOVA) (JMP v11). Burst speeds were compared among temperatures using a one-way mixed-model ANOVA to determine whether swimming performance of each species was temperature sensitive. Here, we designated individual as a random effect to account for individual variation, as the same individuals were used in all temperature treatments when possible. Tukey's HSD tests were run post-hoc to determine which temperatures resulted in significantly different burst swimming speeds. Burst swimming values were used to create thermal performance curves. We input mean burst swimming data into TableCurve 2.0 (SysStat Software Inc, San Jose, CA) and fit 20 "asymmetrical peak functions" (Logan et al., 2013). These functions were selected based on their ecological relevance and to meet the assumptions of asymmetrical performance curves (Krenek et al., 2011). Model functions for both species were selected based on  $r^2$  values. Selected models were then compared between species to evaluate species differences. As only a subset of temperatures were tested, we relied on modeled performance curves to determine the maximum performance ( $P_{\max}$ ) and the optimal temperature for performance ( $T_{\text{opt}}$ ) for each species. Peaks of performance curves were used to estimate  $P_{\max}$  and  $T_{\text{opt}}$  (Huey, 1982).

In order to compare the two mysid species and highlight potential differences in performance, burst swimming speed was analyzed in a mixed-model three-way ANOVA (JMP v.11) with temperature, species, and size as fixed factors, and individual as a random effect.

### 3. Results

*Neomysis americana* experiences significantly greater thermal variation over the course of a year (based on the mean of monthly variation, that is, maximum temperature – minimum temperature experienced per month) than *H. formosa* ( $F_{1,220} = 6.16$ ,  $p = 0.014$ ; Fig. 1). Over the course of one year, *N. americana* is exposed to a mean of 1.38 °C temperature variation compared to 0.97 °C for *H.*



**Fig. 1.** Monthly temperature variation (max °C – min °C) experienced by *N. americana* (black, surface and bottom water temperatures) and *H. formosa* (red, bottom water temperature). Temperature variation averaged from 1998 to 2010 Nu-shuttle surveys of segment #11 in Narragansett Bay. Peak breeding season occurs within dashed gray lines. Both mysid species are assumed to produce a new generation approximately every four weeks.

*formosa*. The greatest temperature variation experienced (months where there is the greatest difference between maximum temperatures and minimum temperatures) occurs during the breeding season (early spring through August), where temperature variation experienced by *N. americana* is relatively large (2.11–2.91 °C). Similarly, thermal variation experienced for *H. formosa* peaks in these months, but is of a lower magnitude (1.35–2 °C). The largest and most frequent thermal stratification in Narragansett Bay (section #11; see Kremer et al. (2010)) occurs between April and July, when surface water temperatures were at least 2 °C higher than bottom water temperatures on 19.8% of days and stratification was at least 4 °C for 5.4% of days (Table 1). Minimal stratification occurs between October and January, when differences between surface and bottom water temperatures were never greater than 2 °C (Table 1). The maximum temperature observed over the 12 years of recording was 25.7 °C and the minimum was –0.4 °C (Table 1).

*Neomysis americana* had a mean  $CT_{\min}$  of 3.0 °C, which was significantly lower than *H. formosa* at 4.2 °C ( $F_{1,19} = 9.53$ ,  $p = 0.006$ ; Fig. 2a). Mean  $CT_{\max}$  for *N. americana* (31.4 °C) was significantly lower than *H. formosa* (32.7 °C) ( $F_{1,19} = 7.15$ ,  $p = 0.014$ ; Fig. 2b). The thermal tolerance range was nearly identical for the two species (28.4 °C for *N. americana*, and 28.5 °C for *H. formosa*).

Temperature had a significant effect on the burst swimming ability of *N. americana* ( $F_{4,79} = 5.45$ ,  $p = 0.0006$ ; Fig. 3a).  $P_{\max}$  for *N. americana* was  $370 \pm 25.4$  mm/s observed at 25 °C, approximately 45% faster than the slowest mean burst swimming ( $254 \pm 23.3$  mm/s observed at 10 °C). Temperature did not significantly affect the burst swimming speed of *H. formosa* ( $F_{4,53} = 0.81$ ,  $p = 0.52$ ; Fig. 2b) where a  $P_{\max}$  of  $223 \pm 20.6$  mm/s was observed at 20 °C; only 17% faster than the slowest mean burst swimming ( $191 \pm 16.1$  mm/s observed at 10 °C).

Performance curves for both species were plotted using the mean burst swimming speed at each temperature and were bounded by  $CT_{\min}$  and  $CT_{\max}$  for each species (Fig. 4). The best-fit model for *N. americana* was a half Gaussian modified Gaussian model (GMG), whereas the best-fit model for *H. formosa* was an asymmetric double sigmoidal curve (ADS) (Fig. 4). Curves for both species were variants of Gaussian distributions. Best-fit models for each species were applied to the other for comparison. *Neomysis americana* burst swimming could not be fit with the ADS model, whereas a lower  $r^2$  value of 0.76 was observed for *H. formosa* burst swimming fit to the GMG model. We modeled burst swimming performance in order to estimate  $T_{\text{opt}}$ ; analysis of the selected models indicate that the  $T_{\text{opt}}$  is 24.8 °C for *N. americana* and 28.7 °C for *H. formosa*.

Overall, *N. americana* had a faster burst swimming speed than *H. formosa* (Table 2). Size alone was not a significant factor in determining swimming speed, however, we observed a significant three-way interaction between size, species, and temperature. Due to the inclusion of size (a continuous variable), post-hoc analysis was not performed for this interaction. Inspection of the data indicate that larger *N. americana* individuals had faster burst swimming speeds than smaller individuals at 20 and 25 °C. Regardless of size, *N. americana* individuals had similar burst ability at 10, 15, and 30 °C. *Heteromysis formosa* size did not appear to influence burst swimming ability.

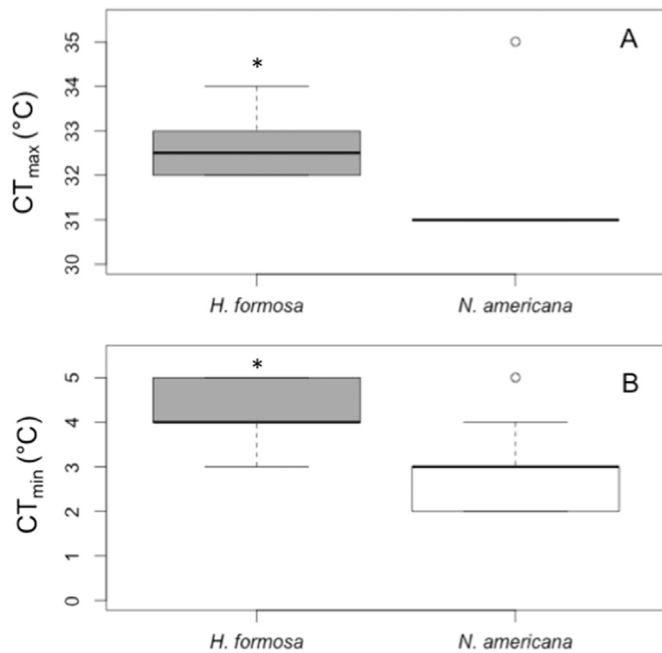
### 4. Discussion

As small ectotherms, we assume that mysid shrimp body temperatures equal water temperatures and differences in ecological and behavioral traits of *N. americana* and *H. formosa* inform the type of temperature variation experienced by both species. Our investigation of surface and bottom water temperatures in Narragansett Bay indicate that during mysid breeding seasons thermal stratification can be quite high (upwards of 7–8 °C). As such, vertical migration exposes *N. americana* to higher daily temperature variation, particularly during

**Table 1**

Water temperature data from the 1998–2010 Nu-shuttle surveys of segment #11 in Narragansett Bay, showing the percentage of sampled days within each quarter where surface waters are  $\geq 4$  °C,  $\geq 3$  °C, and  $\geq 2$  °C warmer than bottom waters. Minimum and maximum temperatures are reported for each quarter.

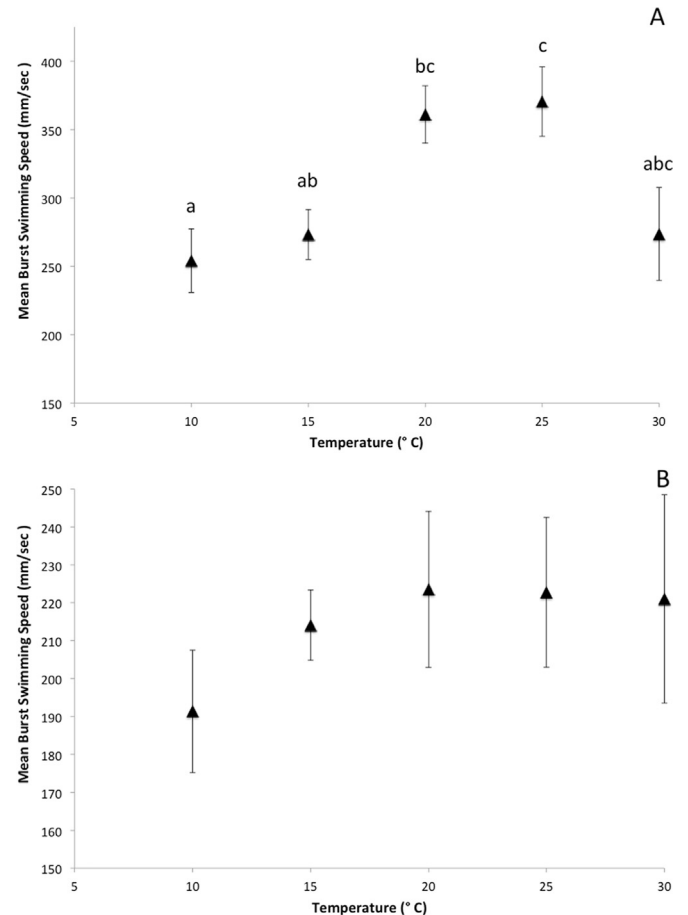
Time Span	$\geq 4$ °C	$\geq 3$ °C	$\geq 2$ °C	Minimum Surface Temperature (°C)	Maximum Surface Temperature (°C)	Minimum Bottom Temperature (°C)	Maximum Bottom Temperature (°C)	Largest Observed Difference (Surface – Bottom)
Jan–Apr	0.0	0.0	1.1	−0.4	8.3	−0.4	8.4	2.1
Apr–Jul	5.4	11.3	19.8	4.0	22.2	3.6	21.5	7.8
Jul–Oct	2.6	6.4	12.2	19.4	25.7	16.7	24.8	7.3
Oct–Jan	0.0	0.0	0.0	3.3	19.0	3.7	19.1	−1.1



**Fig. 2.** Boxplots for A)  $CT_{max}$  and B)  $CT_{min}$  for *H. formosa* and *N. americana*. Lines represent mean values, box boundaries and whiskers represent quartiles. All *N. americana* individuals tested had a  $CT_{max}$  of 31 °C (dark line) with the exception of one outlier (open circle). Asterisk denotes a significant difference between species ( $p < 0.05$ ).

peak breeding season. Conversely, *H. formosa* is only exposed to temperature variation on seasonal times scales. The temperature experienced by an organism should influence the evolution of performance ability (Huey and Kingsolver, 1993). While Huey and Kingsolver (1993) highlighted thermal variation as a driver behind wider performance breadth, Gilchrist (1995) separated individual thermal variation into within- and between-generation components. Thermal specialists and generalists will arise from high within-generation temperature variability and between-generation variability, respectively.

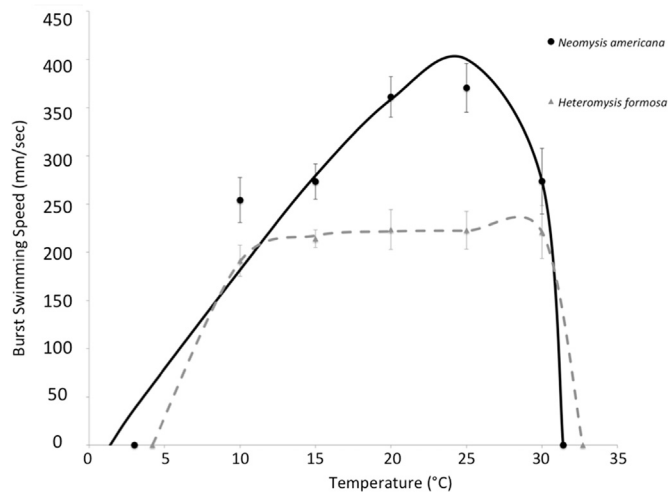
*Neomysis americana* experiences greater within-generation temperature variation than *H. formosa*, but the seasonality of water temperature within Narragansett Bay also yields high between-generation variation for both species. Our data on mysid burst swimming performance indicates that *H. formosa* fits a generalist curve, whereas *N. americana* fits a specialist curve, as defined by a distinct  $P_{max}$  for *N. americana* and consistent performance across temperatures for *H. formosa* (Fig. 4) (Angilletta, 2009; Gilchrist, 1995). However, while the shapes of these performance curves appear to support this categorization of swimming performance, the area under the performance curve for these species differs. Both species have similar performance breadths (Fig. 4), but *N. americana* has a higher  $P_{max}$ , resulting it a larger area under its curve. Therefore, these species do not conform to this prediction of the specialist-generalist tradeoff (Gilchrist, 1995; Huey and Hertz, 1984). However, evolutionary tradeoffs may not constrain locomotion, and enhanced physiological performance at



**Fig. 3.** Burst swimming speeds across treatment temperatures for A) *N. americana* and B) *H. formosa*. Values plotted are mean  $\pm$  SE. Letters indicate significant differences among temperatures for *N. americana* ( $p < 0.05$ ) as determined by Tukey's HSD tests.

one temperature may not imply that performance is sacrificed at other temperatures (Angilletta et al., 2002; Malloy and Targett, 1994; Navas, 1996). Alternatively, performance tradeoffs are not bound to generalist-specialist, and other tradeoffs in resource allocation and acquisition may ultimately contribute to performance differences in mysid shrimp (Angilletta et al., 2003).

The distinct  $P_{max}$  observed in *N. americana* may help in avoiding predation. While vertical migration decreases exposure to visual predators, *N. americana* is still exposed to predation pressure when traveling to surface waters at night. In Narragansett Bay, surface waters are typically warmer than bottom waters for much of the year. As such, an increased burst swimming ability in warmer temperatures will enhance escape from predation (Feder, 1983; Watkins, 1996). Lower bottom water temperatures result in decreased performance for *N. americana*, but predation pressure is released when mysids are in the benthos (Loose and Dawidowicz, 1994; Stich and Lampert, 1981; Zaret and Suffern, 1976).



**Fig. 4.** Burst swimming performance curves for mysid species. Plotted values are mean  $\pm$  SE of burst swimming speed for *N. americana* (black circles) and *H. formosa* (gray triangles). Performance curves were fit using the mean swimming speeds across treatment temperatures bounded by  $CT_{min}$  and  $CT_{max}$  for each species using TableCurve 2D. The best-fit model for *N. americana* (solid black line) was a half Gaussian modified Gaussian (GMG) with  $r^2=0.96$  and for *H. formosa* (dashed gray line) was an asymmetric double sigmoidal (ADS) with  $r^2=0.99$ .

**Table 2**

Summary of the fixed factors from a three-way mixed-model ANOVA evaluating the effects of species, temperature, size, and their interactions on the burst swimming speed of mysid shrimp.

Model source	df	F	P
Species	1, 42	6.83	0.012*
Temperature	4, 126	0.33	0.85
Size	1, 44	1.62	0.13
Species X Temperature	4, 126	1.81	0.21
Species X Size	1, 44	0.40	0.53
Temperature X Size	4, 127	0.32	0.87
Species X Temperature X Size	4, 127	2.46	0.048*

Listed values are degrees of freedom (df), F-ratio (F), and P-values (P). Asterisks indicate P-values that are significant ( $P \leq 0.05$ ). Mysid ID (a random effect) contributed 12.1% of the total variation.

We found that *N. americana* and *H. formosa* had similar thermal tolerance ranges, with respect to  $CT_{min}$  and  $CT_{max}$ , despite differences in behavioral and ecological traits. In Narragansett Bay, large thermoclines (upwards of 8 °C) can exist in the spring, but smaller thermoclines exist year round. In some cases, surface water temperatures in winter months can be colder than bottom water and the increased ability of *N. americana* to withstand colder temperatures may allow this species to function in near freezing waters. In winter months, bottom water can be 1.5–2 °C warmer than surface waters; by remaining at the benthos, *H. formosa* avoids its  $CT_{min}$ . Studies of thermal limits in terrestrial invertebrates indicate that upper limits appear to be more fixed than lower limits, with lower limits showing more variation (Addo-Bediako et al., 2002; Gunderson and Stillman, 2015; Hoffmann et al., 2013). This could explain some of the difference we found between *H. formosa* and *N. americana*, where we expected a warmer  $CT_{min}$  for *N. americana*.

We also found that both species were able to tolerate temperatures above 31 °C, exceeding by 5 °C the maximum daily water temperature in Narragansett Bay, which was observed to be almost 26 °C. This suggests that cold temperatures may exert greater influence on cellular mechanisms and adaptive responses for these species than warm temperatures. The buffer found between summer maximum water temperatures and the  $CT_{max}$  of both species appears to be greater than that found in freshwater mysids. Gösta Rudstam et al. (1999) observed

a buffer of about 2–3 °C between maximum water temperatures and  $CT_{max}$  for the vertically migrating *Mysis relicta*. Other abiotic factors, such as dissolved oxygen, have the ability to impact physiological performance, particularly as temperature affects the amount of oxygen available in the water column (Pörtner, 2010; Rosa and Seibel, 2008). Despite evidence of dissolved oxygen stratification in Narragansett Bay (Melrose et al., 2007), our experimental individuals were collected from an area where oxygen stratification is minimal and hypoxic events are rarely observed. Therefore, we determine temperature stratification and temperatures experienced by mysids to be the primary force in driving thermal tolerance in natural settings.

We tested thermal tolerance in mysids that were caught during the summer, but evidence of seasonal acclimation and influence of seasonality on thermal limits in crustaceans has been well documented (Carvalho and Crisp, 1987; Crisp and Ritz, 1967; Cuculescu et al., 1998; Kinne, 1964). For example, winter-caught marine crustacea (order Decapoda) had significantly lower  $CT_{max}$  than summer-caught organisms (Hopkin et al., 2006). In order to better understand thermal limits within these mysid species, it will be necessary to capture potential seasonal differences. Additionally, we used ramping methods of testing thermal tolerance in mysids, which in some cases may underestimate tolerance (Terblanche et al., 2011). It is necessary to note that thermal tolerance and thermal stress are not just driven by temperature, but include additional parameters such as time and food availability (Terblanche et al., 2011). We tested the response of mysids to acute thermal stress, but new evidence highlights a potential tradeoff between tolerating short durations of extreme temperatures with poor performance during chronic thermal stress (Rezende et al., 2014). Therefore, while our documentation of thermal tolerance for both mysid species provides context, it may be an incomplete picture.

Our results for burst swimming performance highlighted significant differences in sensitivity to temperature between species. The performance curve *N. americana* fit the typical, asymmetrical pattern for ectotherm performance across temperatures (Angilletta, 2009; Lynch and Gabriel, 1987), where performance increases as temperature increases until  $P_{max}$  (the greatest observed burst speed within the thermal range of a species) and then sharply declines (Huey and Kingsolver, 1993). *Neomysis americana* had greater burst swimming ability than *H. formosa*, but was more sensitive to temperature, as indicated by significant differences in swimming speeds across temperature. Our significant three-way interaction highlighted that mysid size was important at warmer temperatures for *N. americana* only. Body size and temperature have both been shown to affect metabolism and performance (Gillooly et al., 2001). With respect to ectotherm performance, our results support previous findings where larger individuals tend to outperform smaller individuals (Fuiman, 1986; Graham et al., 1990; Taylor and McPhail, 1985), and extreme high temperatures are met with decreased performance (Brett, 1967; Deutsch et al., 2008). However, our results take the relationship between size and temperature a step further. Here, large *N. americana* individuals do outperform smaller individuals at all temperatures. At temperatures near their  $T_{opt}$ , large *N. americana* exhibit significantly faster burst swimming, but at extreme high and low temperatures, mysid performance is unaffected by size. This data provides evidence that, for certain species, the effects of size on performance are dependent on temperature. By contrast, burst swimming speed for *H. formosa* did not fit the typical asymmetrical curve, as swimming performance for this species was relatively insensitive to temperatures between 10–30 °C.

How can our understanding of mysid thermal tolerance and sensitivity of performance be used in predicting responses to future climate change? Many marine species live close to their thermal maximum; these species are likely the most vulnerable to climate change (Somero, 2010; Tewksbury et al., 2008). By the year 2100, we expect water temperatures in Narragansett Bay to increase by 2–4 °C (Pachauri et al., 2014), resulting in a summer average of 26–28 °C with

maximum temperatures reaching 30 °C. This increase in temperature will not result in mean summer temperatures that exceed the  $CT_{max}$  of either *H. formosa* or *N. americana*, measured at 32.7 and 31.4 °C, respectively. Thus, the expected temperature increase is unlikely to result in direct mortality for either species. However, surface waters in Narragansett Bay already reach temperatures above 25 °C, which is greater than the  $T_{opt}$  for *N. americana*. While end-of-century temperatures are not expected to reach the  $CT_{max}$  of *N. americana*, temperatures above  $T_{opt}$  will occur with greater frequency and duration, resulting in decreased swimming performance. This might influence their ability to escape predators during vertical migrations. Huey et al. (2012) highlights the greater influence that warming will have on temperature specialists as opposed to generalists, indicating that *N. americana* will likely experience greater impacts from expected warming.

It is important to note that our study was on the adult stage of mysids; early life stages of invertebrates can be more susceptible to thermal stress and climate change (Nozawa and Harrison, 2007). Early stages of kelp larvae increased oxygen consumption with increased temperature, whereas later stages decreased oxygen consumption in temperatures higher than summer maxima (Storch et al., 2011). In addition, while the direct effects of increased temperature on swimming performance may not immediately impact mysid shrimp, indirect effects of warming may be detrimental. Mysid shrimp are influenced by the timing, magnitude, and duration of phytoplankton blooms, as phytoplankton form the base of their food web. The presence of phytoplankton supports microzooplankton populations; mysids can directly consume both phytoplankton and microzooplankton (Jerling and Wooldridge, 1995). With changes in global ocean temperatures and weather events, blooms are becoming more unpredictable (Smayda, 1998) and in some years blooms are not occurring (Oviatt et al., 2002), resulting in bottom-up effects on the food web including decline in mysid density (Orsi and Mecum, 1996).

Investigations of thermal tolerance and performance have highlighted the influence that temperature and thermal physiology can have on ecology and behavior (Huey, 1982; Kingsolver and Woods, 1997; Navas and Bevier, 2001). Alternatively, our results indicate the influence of ecology and behavior on thermal sensitivity. Species-specific responses, such as those we have identified here, along with associated behavioral and ecological dynamics, support the use of mechanistic niche models (Kearney et al., 2009; Pacifici et al., 2015) and should be incorporated into models of climate change response. Modeling efforts are critical in establishing trends in species movement and focusing conservation priorities. These models often integrate geographic information systems (GIS) and physiological data, describing a fundamental niche for a focal species to determine potential effects of future climate (Kearney and Porter, 2004; Régnière et al., 2015). Here, we show the need for models to account for interspecific performance variation based on ecological differences between species. This difference in sensitivity of swimming performance in mysids thus supports our hypothesis that the behavior and ecology of these two species influences their physiological performance and response to temperature. Although *N. americana* and *H. formosa* are sympatric and overlap in their ecological niches they may respond differently to climate change (Parmesan, 2006; Parmesan and Yohe, 2003), as the difference in their behavior related to their feeding strategies exposes them to different daily temperature variation, which may influence the thermal sensitivity of their swimming performance.

## Acknowledgments

We thank Nathan Andrews, Kelli Butler, Andrew Fiorenzano, Fiona MacKechnie, and Ushuaia Milstead for their work in the field capturing mysid shrimp and their work recording and analyzing mysid videos. This research has been supported by a grant from the U.S. Environmental Protection Agency's Science to Achieve Results

(STAR) program fellowship number FP917627. This material is based upon work supported in part by the National Science Foundation EPSCoR Cooperative Agreement #EPS-1004057. This work was funded by a Rhode Island Science and Technology Advisory Council grant to J. Kolbe and C. Thornber. Although the research described in this article was funded in part by EPA, it has not been subjected to agency review and does not necessarily reflect the views of the agency. We thank two anonymous reviewers for their feedback and insights that have significantly improved this study.

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