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7 Ecological differences influence the thermal sensitivity of swimming performance in two co-
8 occurring mysid shrimp species with climate change implications
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1 **Abstract:**

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

23 **Key Words:** thermal tolerance, thermal sensitivity of performance, climate change, thermal
24 variation, ocean warming

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 latitudes that experience less thermal variation have narrower tolerance ranges (Addo-Bediako et al., 2000; Chown et al., 2004;

Janzen, 1967; Pachauri 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

1 stratification occurs in fall and spring seasons. Maximum differences between surface and
2 bottom water in these seasons can be as high as 6-8°C, with warmer waters found at the surface
3 (NarrBay.org). During these months, waters experience a warming rate of 1-2°C hr⁻¹ (National
4 Oceanic and Atmospheric Administration, Station QPTR1-8454049). This variation suggests that
5 species in the bay may have wide thermal tolerances or an ability to migrate or enter dormancy
6 (Sorte et al., 2011; Woolsey et al., 2014). Between 1895 and 1999, water temperatures in
7 Narragansett Bay have warmed 1.2°C (Smith et al., 2010) and are projected to rise another 2-3°C
8 by 2100 (Pachauri et al., 2014).

9 Narragansett Bay is home to several species of mysid shrimp, small marine crustaceans
10 (<1.5cm) in the family Mysidae. Mysids, a close relative of krill, represent a critical link between
11 plankton and fish communities, including commercially valuable species (Jumars et al., 2007).
12 As small ectotherms, the physiology, behavior, and metabolic processes of mysids will likely be
13 impacted by ocean warming (Pörtner and Farrell, 2008). Individual level impacts of warming to
14 key links in marine food webs may ultimately cause major shifts in ecosystem structure and
15 function, as seen in Antarctic krill (Atkinson et al., 2004).

16 *Neomysis americana* and *Heteromysis formosa* are two common mysid shrimp species in
17 Narragansett Bay. Both species have a lifespan of about one year (Allen, 1982; Herman, 1962).
18 These mysid species in Narragansett Bay breed multiple times throughout the year starting in the
19 mid-spring and continuing through summer and fall; they can reach reproductive maturity by
20 four weeks (Pezzack and Corey, 1979; Williams, 1972). *Heteromysis formosa* can breed
21 throughout the year and typically produces one to two broods per year, whereas *N. americana*
22 typically has two to three broods per year (Allen, 1982; Herman, 1962). One critical difference
23 between the two species is that throughout the year *N. americana* vertically migrates at night

1 while remaining benthic during the day (Herman, 1962; Kringel et al., 2003), whereas *H.*
2 *formosa* remains amongst the benthos and tends to seek refuge when not foraging (Allen, 1982).
3 Vertical migration in zooplankton allows for feeding higher in the water column under decreased
4 predation pressure by visual predators (Zaret and Suffern, 1976). Near-shore and coastal
5 environments in Narragansett Bay have been shown to experience stratification in dissolved
6 oxygen (Melrose et al., 2007), an abiotic factor tied to temperature that can influence vertical
7 migrators (Pörtner, 2010; Rosa and Seibel, 2008). However, stratification of dissolved oxygen
8 occurs with greater frequency and severity in the northern parts of Narragansett Bay. In the lower
9 west passage of Narragansett Bay (where the mysids were collected for this study), hypoxic
10 events and significant stratification of dissolved oxygen are rarely recorded (Melrose et al.,
11 2007). Thermal variation within the bay, however, is likely great enough to influence the
12 physiology of vertical migrating organisms. While both species experience seasonal changes in
13 water temperature, as vertical migrators, *N. americana* is exposed to a wider range of
14 temperatures compared to *H. formosa* due to the thermal stratification within Narragansett Bay,
15 particularly in the spring and fall seasons. Living in different thermal environments may impact
16 physiological traits and potential responses to ocean warming between these two species (Huey
17 et al., 2003; Hutchison and Maness, 1979; Kearney et al., 2009; Sunday et al., 2015).

18 In this study, we investigated the thermal tolerances and thermal sensitivity of swimming
19 speed in *H. formosa* and *N. americana*. Thermal tolerance, as estimated by critical thermal
20 minimum (CT_{min}) and critical thermal maximum (CT_{max}), along with performance curves (based
21 on traits such as swimming speed, growth, and reproduction rates) help characterize differences
22 between species and can be used to predict how species will respond to ocean warming
23 (Caldwell et al., 2015; Logan et al., 2013; Sunday et al., 2015). For mysid shrimp, swimming

1 performance is critical for feeding and escape from predators (Lindén et al., 2003). Behavioral
2 differences in sympatric species may lead to divergent responses to climate change because
3 swimming sensitivity may be influenced by the daily range of temperatures experienced. We
4 examined ten years of temperature data from Narragansett Bay (both bottom and surface waters)
5 in order to quantify the variation experienced over the course of a year as well as quantify the
6 difference in temperature variation experienced by *N. americana* and *H. formosa*.

7 With the differences in thermal variation experienced, we use the framework of Gilchrist
8 (1995) to interpret thermal sensitivity of performance of two mysid species. In this framework,
9 species experiencing greater temperature variation within a generation will have a narrower
10 thermal tolerance range with a predicted tradeoff for enhanced performance maximum ($P_{\max}$),
11 these species are considered thermal specialists (Angilletta, 2009; Gilchrist, 1995; Levins, 1968;
12 Levins and MacArthur, 1966). Alternatively, species experiencing greater temperature variation
13 between generations will have greater breadth of performance with a tradeoff for decreased $P_{\max}$,
14 these species are considered thermal generalists (Angilletta 2009; Gilchrist 1995). This has been
15 shown in developmental physiology of insects, where high temperature variation between
16 generations results in decreased sensitivity and a generalist performance curve (e.g., Foray et al.,
17 2011).

18 This generalist-specialist constraint on different aspects of performance is predicted to
19 produce a tradeoff between $P_{\max}$ and performance breadth, while the area under the performance
20 curve remains constant (Gilchrist, 1995; Levins, 1968; Levins and MacArthur, 1966; Slatkin and
21 Lande, 1976). However, while this tradeoff is predicted to occur, data supporting this tradeoff in
22 natural systems is often ambiguous (Futuyma and Moreno, 1988; Kingsolver and Huey, 2003),
23 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 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 specialists 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°C +/- 0.7°C (NarrBay.org). Individuals were collected by scallop dredge fitted with a plankton net and sample jar trawling at a depth of 9-10m. 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 microns) 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 minutes. 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 minutes. 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 minutes, 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 minutes. After acclimation, individual mysids were removed from their cages and placed into an acrylic swim chamber (10cm X 10cm X 1cm) with the same temperature water. We backlit the chamber and filmed mysids using Pixelink PLB771G machine-vision camera with a 60mm Nikon lens, shooting video at 25 frames/second from 1-m distance for 10 seconds (Gear et al., 2011). During the 10-second 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-second 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; 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_{opt}) for each species. Peaks of performance curves were used to estimate $P_{\max}$ and T_{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. 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 ($2.11 - 2.91^{\circ}\text{C}$). Similarly, thermal variation experienced for *H. formosa* peaks in these months, but is of a lower magnitude ($1.35 - 2^{\circ}\text{C}$). 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 ± 25.4 mm/sec observed at 25°C, approximately 45% faster than the slowest mean burst swimming (254 ± 23.3 mm/sec 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 ± 20.6 mm/sec was observed at 20°C; only 17% faster than the slowest mean burst swimming (191 ± 16.1 mm/sec 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_{opt};

analysis of the selected models indicate that the T_{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 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 in 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 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).

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

1 impact physiological performance, particularly as temperature affects the amount of oxygen
2 available in the water column (Pörtner, 2010; Rosa and Seibel, 2008). Despite evidence of
3 dissolved oxygen stratification in Narragansett Bay (Melrose et al., 2007), our experimental
4 individuals were collected from an area where oxygen stratification is minimal and hypoxic
5 events are rarely observed. Therefore, we determine temperature stratification and temperatures
6 experienced by mysids to be the primary force in driving thermal tolerance in natural settings.

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

21 Our results for burst swimming performance highlighted significant differences in
22 sensitivity to temperature between species. The performance curve *N. americana* fit the typical,
23 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 out perform 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

1 maximum temperatures reaching 30°C. This increase in temperature will not result in mean
2 summer temperatures that exceed the CT_{max} of either *H. formosa* or *N. americana*, measured at
3 32.7 and 31.4°C, respectively. Thus, the expected temperature increase is unlikely to result in
4 direct mortality for either species. However, surface waters in Narragansett Bay already reach
5 temperatures above 25°C, which is greater than the T_{opt} for *N. americana*. While end-of-century
6 temperatures are not expected to reach the CT_{max} of *N. americana*, temperatures above T_{opt} will
7 occur with greater frequency and duration, resulting in decreased swimming performance. This
8 might influence their ability to escape predators during vertical migrations. Huey et al. (2012)
9 highlights the greater influence that warming will have on temperature specialists as opposed to
10 generalists, indicating that *N. americana* will likely experience greater impacts from expected
11 warming.

12 It is important to note that our study was on the adult stage of mysids; early life stages of
13 invertebrates can be more susceptible to thermal stress and climate change (Nozawa and
14 Harrison, 2007). Early stages of kelp crab larvae increased oxygen consumption with increased
15 temperature, whereas later stages decreased oxygen consumption in temperatures higher than
16 summer maxima (Storch et al., 2011). In addition, while the direct effects of increased
17 temperature on swimming performance may not immediately impact mysid shrimp, indirect
18 effects of warming may be detrimental. Mysid shrimp are influenced by the timing, magnitude,
19 and duration of phytoplankton blooms, as phytoplankton form the base of their food web. The
20 presence of phytoplankton supports microzooplankton populations; mysids can directly consume
21 both phytoplankton and microzooplankton (Jerling and Wooldridge, 1995). With changes in
22 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.

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References:

- Abràmoff, M.D., Magalhães, P.J., Ram, S.J., 2004. Image processing with ImageJ. *Biophotonics international* 11, 36–42.
- Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2002. Metabolic cold adaptation in insects: a large-scale perspective. *Functional Ecology* 16, 332–338. doi:10.1046/j.1365-2435.2002.00634.x
- Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2000. Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society of London B: Biological Sciences* 267, 739–745.
- Allen, D.M., 1982. Autecology of the cryptic mysid crustacean, *Heteromysis formosa* SI Smith 1873, in a temperate estuary. *Hydrobiologia* 93, 1–7.
- Angilletta Jr., M.J., Niewiarowski, P.H., Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27, 249–268. doi:10.1016/S0306-4565(01)00094-8
- Angilletta Jr, M.J., Wilson, R.S., Navas, C.A., James, R.S., 2003. Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology & Evolution* 18, 234–240. doi:10.1016/S0169-5347(03)00087-9
- Angilletta, M.J., 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press.
- Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103. doi:10.1038/nature02996
- Brett, J.R., 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *J. Fish. Res. Bd. Can.* 24, 1731–1741. doi:10.1139/f67-142

- 1 Caldwell, A.J., While, G.M., Beeton, N.J., Wapstra, E., 2015. Potential for thermal tolerance to
2 mediate climate change effects on three members of a cool temperate lizard genus,
3 *Niveoscincus*. Journal of Thermal Biology 52, 14–23.
4 doi:10.1016/j.jtherbio.2015.05.002
- 5 Carvalho, G.R., Crisp, D.J., 1987. The clonal ecology of *Daphnia magna* (Crustacea:
6 Cladocera): I. Temporal changes in the clonal structure of a natural population. The
7 Journal of Animal Ecology 453–468.
- 8 Chown, S.L., Gaston, K.J., Robinson, D., 2004. Macrophysiology: large-scale patterns in
9 physiological traits and their ecological implications. Functional Ecology 18, 159–
10 167.
- 11 Crisp, D.J., Ritz, D.A., 1967. Changes in temperature tolerance of *Balanus balanoides* during
12 its life-cycle. Helgoländer wissenschaftliche Meeresuntersuchungen 15, 98.
13 doi:10.1007/BF01618612
- 14 Cuculescu, M., Hyde, D., Bowler, K., 1998. Thermal tolerance of two species of marine crab,
15 *Cancer pagurus* and *Carcinus maenas*. Journal of Thermal Biology 23, 107–110.
16 doi:10.1016/S0306-4565(98)00008-4
- 17 Desbonnet, A., Costa-Pierce, B.A., 2008. Science of ecosystem-based management:
18 Narragansett Bay in the 21st Century. Springer Science & Business Media.
- 19 Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin,
20 P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude.
21 Proceedings of the National Academy of Sciences 105, 6668–6672.
- 22 Fabry, V.J., Seibel, B.A., Feely, R.A., Orr, J.C., 2008. Impacts of ocean acidification on marine
23 fauna and ecosystem processes. ICES Journal of Marine Science: Journal du Conseil
24 65, 414–432.
- 25 Feder, M.E., 1983. The relation of air breathing and locomotion to predation on tadpoles,
26 *Rana berlandieri*, by turtles. Physiological Zoology 522–531.
- 27 Foray, V., Gibert, P., Desouhant, E., 2011. Differential thermal performance curves in
28 response to different habitats in the parasitoid *Venturia canescens*.
29 Naturwissenschaften 98, 683–691.
- 30 Fromentin, J.M., Planque, B., 1996. *Calanus* and environment in the eastern North Atlantic.
31 2. Role of the North Atlantic Oscillation on *Calanus finmarchicus* and *C.*
32 *helgolandicus*. Marine Ecology Progress Series 134, 11–118.
- 33 Fuiman, L.A., 1986. Burst-swimming performance of larval *Zebra danios* and the effects of
34 diel temperature fluctuations. Transactions of the American Fisheries Society 115,
35 143–148. doi:10.1577/1548-8659(1986)115<143:BPOLZD>2.0.CO;2
- 36 Futuyma, D.J., Moreno, G., 1988. The Evolution of Ecological Specialization. Annual Review
37 of Ecology and Systematics 19, 207–233.
- 38 Gilchrist, G.W., 1996. A quantitative genetic analysis of thermal sensitivity in the locomotor
39 performance curve of *Aphidius ervi*. Evolution 1560–1572.
- 40 Gilchrist, G.W., 1995. Specialists and generalists in changing environments. I. Fitness
41 landscapes of thermal sensitivity. American Naturalist 252–270.
- 42 Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size and
43 temperature on metabolic rate. Science 293, 2248–2251.
44 doi:10.1126/science.1061967

- 1 Gösta Rudstam, L., Lee Hetherington, A., Martonius Mohammadian, A., 1999. Effect of
2 Temperature on Feeding and Survival of *Mysis relicta*. Journal of Great Lakes
3 Research 25, 363–371. doi:10.1016/S0380-1330(99)70745-8
- 4 Graham, J.B., Dewar, H., Lai, N.C., Lowell, W.R., Arce, S.M., 1990. Aspects of shark swimming
5 performance determined using a large water tunnel. Journal of Experimental
6 Biology 151, 175–192.
- 7 Grear, J.S., Horowitz, D.B., Gutjahr-Gobell, R., 2011. Mysid population responses to resource
8 limitation differ from those predicted by cohort studies. Marine Ecology Progress
9 Series 432, 115–123.
- 10 Gunderson, A.R., Stillman, J.H., 2015. Plasticity in thermal tolerance has limited potential to
11 buffer ectotherms from global warming. Proc. R. Soc. B 282, 20150401.
12 doi:10.1098/rspb.2015.0401
- 13 Herman, S.S., 1962. Spectral sensitivity and phototaxis in the opossum shrimp, *Neomysis*
14 *americana* Smith. The Biological Bulletin 123, 562–570.
- 15 Hoegh-Guldberg, O., Fine, M., Skirving, W., Johnstone, R., Dove, S., Strong, A., 2005. Coral
16 bleaching following wintry weather. Limnol. Oceanogr. 50, 265–271.
17 doi:10.4319/lo.2005.50.1.0265
- 18 Hoffmann, A.A., Chown, S.L., Clusella-Trullas, S., 2013. Upper thermal limits in terrestrial
19 ectotherms: how constrained are they? Funct Ecol 27, 934–949. doi:10.1111/j.1365-
20 2435.2012.02036.x
- 21 Hofmann, G.E., Todgham, A.E., 2010. Living in the Now: Physiological Mechanisms to
22 Tolerate a Rapidly Changing Environment. Annu. Rev. Physiol. 72, 127–145.
23 doi:10.1146/annurev-physiol-021909-135900
- 24 Hopkin, R.S., Qari, S., Bowler, K., Hyde, D., Cuculescu, M., 2006. Seasonal thermal tolerance
25 in marine Crustacea. Journal of Experimental Marine Biology and Ecology 331, 74–
26 81. doi:10.1016/j.jembe.2005.10.007
- 27 Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles, in: Biology of the
28 Reptilia. Citeseer.
- 29 Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Pérez, H.J.Á., Garland, T., 2009.
30 Why tropical forest lizards are vulnerable to climate warming. Proceedings of the
31 Royal Society of London B: Biological Sciences rspb–2008.
- 32 Huey, R.B., Hertz, P.E., 1984. Is a jack-of-all-temperatures a master of none? Evolution 441–
33 444.
- 34 Huey, R.B., Hertz, P.E., Sinervo, B., 2003. Behavioral drive versus behavioral inertia in
35 evolution: a null model approach. The American Naturalist 161, 357–366.
- 36 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M., Williams, S.E., 2012.
37 Predicting organismal vulnerability to climate warming: roles of behaviour,
38 physiology and adaptation. Phil. Trans. R. Soc. B 367, 1665–1679.
39 doi:10.1098/rstb.2012.0005
- 40 Huey, R.B., Kingsolver, J.G., 1993. Evolution of resistance to high temperature in
41 ectotherms. American Naturalist S21–S46.
- 42 Hutchison, V.H., Maness, J.D., 1979. The role of behavior in temperature acclimation and
43 tolerance in ectotherms. American zoologist 19, 367–384.
- 44 Janzen, D.H., 1967. Why mountain passes are higher in the tropics. American Naturalist
45 233–249.

- 1 Jerling, H.L., Wooldridge, T.H., 1995. Feeding of two mysid species on plankton in a
2 temperate South African estuary. *Journal of Experimental Marine Biology and*
3 *Ecology* 188, 243–259. doi:10.1016/0022-0981(95)00007-E
- 4 Jumars, P.A., Dorgan, K.M., Mayer, L.M., Boudreau, B.P., Johnson, B.D., 2007. Material
5 constraints on infaunal lifestyles: May the persistent and strong forces be with you.
6 *Trace fossils: concepts, problems, prospects*. Elsevier, Amsterdam 441–456.
- 7 Kearney, M., Porter, W.P., 2004. Mapping the fundamental niche: physiology, climate, and
8 the distribution of a nocturnal lizard. *Ecology* 85, 3119–3131.
- 9 Kearney, M., Shine, R., Porter, W.P., 2009. The potential for behavioral thermoregulation to
10 buffer “cold-blooded” animals against climate warming. *Proceedings of the National*
11 *Academy of Sciences* 106, 3835–3840.
- 12 Kingsolver, J.G., Huey, R.B., 2003. Introduction: The evolution of morphology, performance,
13 and fitness. *Integr. Comp. Biol.* 43, 361–366. doi:10.1093/icb/43.3.361
- 14 Kingsolver, J.G., Woods, H.A., 1997. Thermal sensitivity of growth and feeding in *Manduca*
15 *sexta* caterpillars. *Physiological and Biochemical Zoology* 70, 631–638.
- 16 Kinne, O., 1964. Non-genetic adaptation to temperature and salinity. *Helgoländer*
17 *wissenschaftliche Meeresuntersuchungen* 9, 433.
- 18 Kremer, J.N., Vaudrey, J.M., Ullman, D.S., Bergondo, D.L., LaSota, N., Kincaid, C., Codiga, D.L.,
19 Brush, M.J., 2010. Simulating property exchange in estuarine ecosystem models at
20 ecologically appropriate scales. *Ecological Modeling* 221, 1080–1088.
- 21 Krensek, S., Berendonk, T.U., Petzoldt, T., 2011. Thermal performance curves of *Paramecium*
22 *caudatum*: a model selection approach. *European journal of protistology* 47, 124–
23 137.
- 24 Kringel, K., Jumars, P.A., Holliday, D.V., 2003. A shallow scattering layer: High-resolution
25 acoustic analysis of nocturnal vertical migration from the seabed. *Limnology and*
26 *Oceanography* 48, 1223–1234.
- 27 Levins, R., 1968. *Evolution in changing environments: some theoretical explorations*.
28 Princeton University Press.
- 29 Levins, R., MacArthur, R., 1966. The maintenance of genetic polymorphism in a spatially
30 heterogeneous environment: variations on a theme by Howard Levene. *American*
31 *Naturalist* 585–589.
- 32 Lindén, E., Lehtiniemi, M., Viitasalo, M., 2003. Predator avoidance behaviour of Baltic
33 littoral mysids *Neomysis integer* and *Praunus flexuosus*. *Marine Biology* 143, 845–
34 850.
- 35 Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity
36 of climate change. *Nature* 462, 1052–1055. doi:10.1038/nature08649
- 37 Logan, M.L., Huynh, R.K., Precious, R.A., Calsbeek, R.G., 2013. The impact of climate change
38 measured at relevant spatial scales: new hope for tropical lizards. *Global change*
39 *biology* 19, 3093–3102.
- 40 Loose, C.J., Dawidowicz, P., 1994. Trade-offs in diel vertical migration by zooplankton: the
41 costs of predator avoidance. *Ecology* 2255–2263.
- 42 Lord, J., Whitlatch, R., 2015. Predicting competitive shifts and responses to climate change
43 based on latitudinal distributions of species assemblages. *Ecology* 96, 1264–1274.
- 44 Lynch, M., Gabriel, W., 1987. Environmental tolerance. *American Naturalist* 283–303.

- 1 Malloy, K.D., Targett, T.E., 1994. Effects of ration limitation and low temperature on growth,
2 biochemical condition, and survival of juvenile summer flounder from two Atlantic
3 coast nurseries. *Transactions of the American Fisheries Society* 123, 182–193.
- 4 Melrose, D.C., Oviatt, C.A., Berman, M.S., 2007. Hypoxic events in Narragansett Bay, Rhode
5 Island, during the summer of 2001. *Estuaries and Coasts* 30, 47–53.
- 6 Navas, C.A., 1996. Metabolic physiology, locomotor performance, and thermal niche
7 breadth in neotropical anurans. *Physiological Zoology* 1481–1501.
- 8 Navas, C.A., Bevier, C.R., 2001. Thermal dependency of calling performance in the
9 eurythermic frog *Colostethus subpunctatus*. *Herpetologica* 384–395.
- 10 Nozawa, Y., Harrison, P.L., 2007. Effects of elevated temperature on larval settlement and
11 post-settlement survival in scleractinian corals, *Acropora solitaryensis* and *Favites*
12 *chinensis*. *Mar Biol* 152, 1181–1185. doi:10.1007/s00227-007-0765-2
- 13 Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution of fish
14 stocks in relation to climate and population size on the Northeast United States
15 continental shelf. *Mar Ecol Prog Ser* 393, 111–129. doi:10.3354/meps08220
- 16 Orsi, J.J., Mecum, W.L., 1996. Food limitation as the probable cause of a long-term decline in
17 the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento-San
18 Joaquin estuary. *San Francisco Bay: the ecosystem*. American Association for the
19 Advancement of Science, San Francisco 375–401.
- 20 Oviatt, C., Keller, A., Reed, L., 2002. Annual primary production in Narragansett Bay with no
21 bay-wide winter–spring phytoplankton bloom. *Estuarine, Coastal and Shelf Science*
22 54, 1013–1026.
- 23 Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke,
24 L., Dahe, Q., Dasgupta, P., Dubash, N.K., Edenhofer, O., Elgizouli, I., Field, C.B., Forster,
25 P., Friedlingstein, P., Fuglestvedt, J., Gomez-Echeverri, L., Hallegatte, S., Hegerl, G.,
26 Howden, M., Jiang, K., Jimenez Cisneroz, B., Kattsov, V., Lee, H., Mach, K.J., Marotzke,
27 J., Mastrandrea, M.D., Meyer, L., Minx, J., Mulugetta, Y., O'Brien, K., Oppenheimer, M.,
28 Pereira, J.J., Pichs-Madruga, R., Plattner, G.-K., Pörtner, H.-O., Power, S.B., Preston, B.,
29 Ravindranath, N.H., Reisinger, A., Riahi, K., Rusticucci, M., Scholes, R., Seyboth, K.,
30 Sokona, Y., Stavins, R., Stocker, T.F., Tschakert, P., van Vuuren, D., van Ypserle, J.-P.,
31 2014. *Climate Change 2014: Synthesis Report*. Contribution of Working Groups I, II
32 and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate
33 Change. IPCC, Geneva, Switzerland.
- 34 Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E., Butchart, S.H., Kovacs, K.M., Scheffers, B.R.,
35 Hole, D.G., Martin, T.G., Akçakaya, H.R., others, 2015. Assessing species vulnerability
36 to climate change. *Nature Climate Change* 5, 215–224.
- 37 Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of
38 phenological response to global warming. *Global Change Biology* 13, 1860–1872.
- 39 Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annual*
40 *Review of Ecology, Evolution, and Systematics* 637–669.
- 41 Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts
42 across natural systems. *Nature* 421, 37–42. doi:10.1038/nature01286
- 43 Pezzack, D.S., Corey, S., 1979. The life history and distribution of *Neomysis americana*
44 (Smith)(Crustacea, Mysidacea) in Passamaquoddy Bay. *Canadian Journal of Zoology*
45 57, 785–793.

- 1 Pörtner, H.-O., 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for
2 integrating climate-related stressor effects in marine ecosystems. *Journal of*
3 *Experimental Biology* 213, 881–893. doi:10.1242/jeb.037523
- 4 Pörtner, H.-O., 2002. Climate variations and the physiological basis of temperature
5 dependent biogeography: systemic to molecular hierarchy of thermal tolerance in
6 animals. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative*
7 *Physiology* 132, 739–761.
- 8 Pörtner, H.-O., Farrell, A.P., 2008. Physiology and climate change. *Science* 322, 690–692.
- 9 Régnière, J., Bentz, B.J., Powell, J.A., St-Amant, R., 2015. Individual-based modeling:
10 mountain pine beetle seasonal biology in response to climate, in: Perera, A.H.,
11 Sturtevant, B.R., Buse, L.J. (Eds.), *Simulation Modeling of Forest Landscape*
12 *Disturbances*. Springer International Publishing, pp. 135–164.
- 13 Rezende, E.L., Castañeda, L.E., Santos, M., 2014. Tolerance landscapes in thermal ecology.
14 *Funct Ecol* 28, 799–809. doi:10.1111/1365-2435.12268
- 15 Rosa, R., Seibel, B.A., 2008. Synergistic effects of climate-related variables suggest future
16 physiological impairment in a top oceanic predator. *PNAS* 105, 20776–20780.
17 doi:10.1073/pnas.0806886105
- 18 Sanford, E., Kelly, M.W., 2011. Local adaptation in marine invertebrates. *Annual Review of*
19 *Marine Science* 3, 509–535. doi:10.1146/annurev-marine-120709-142756
- 20 Slatkin, M., Lande, R., 1976. Niche width in a fluctuating environment-density independent
21 model. *The American Naturalist* 110, 31–55.
- 22 Smayda, T.J., 1998. Patterns of variability characterizing marine phytoplankton, with
23 examples from Narragansett Bay. *ICES J. Mar. Sci.* 55, 562–573.
24 doi:10.1006/jmsc.1998.0385
- 25 Smith, L.M., Whitehouse, S., Oviatt, C.A., 2010. Impacts of Climate Change on Narragansett
26 Bay. *Northeastern Naturalist* 17, 77–90. doi:10.1656/045.017.0106
- 27 Somero, G.N., 2010. The physiology of climate change: how potentials for acclimatization
28 and genetic adaptation will determine “winners” and “losers.” *The Journal of*
29 *experimental biology* 213, 912–920.
- 30 Sorte, C.J., Jones, S.J., Miller, L.P., 2011. Geographic variation in temperature tolerance as an
31 indicator of potential population responses to climate change. *Journal of*
32 *Experimental Marine Biology and Ecology* 400, 209–217.
- 33 Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., Osman, R.W., 2002. Nonlinear partial
34 differential equations and applications: Linking climate change and biological
35 invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings*
36 *of the National Academy of Sciences* 99, 15497–15500.
37 doi:10.1073/pnas.242437499
- 38 Stich, H.-B., Lampert, W., 1981. Predator evasion as an explanation of diurnal vertical
39 migration by zooplankton. *Nature* 293, 396–398.
- 40 Storch, D., Fernández, M., Navarrete, S.A., Pörtner, H.-O., 2011. Thermal tolerance of larval
41 stages of the Chilean kelp crab *Taliepus dentatus*. *Marine Ecology Progress Series*
42 429, 157–167.
- 43 Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., Edgar, G.J., Stuart-
44 Smith, R., Barrett, N., Wernberg, T., others, 2015. Species traits and climate velocity
45 explain geographic range shifts in an ocean-warming hotspot. *Ecology letters* 18,
46 944–953.

- 1 Taylor, E.B., McPhail, J.D., 1985. Burst swimming and size-related predation of newly
2 emerged coho salmon *Oncorhynchus kisutch*. Transactions of the American Fisheries
3 Society 114, 546–551. doi:10.1577/1548-8659(1985)114<546:BSASPO>2.0.CO;2
- 4 Terblanche, J.S., Hoffmann, A.A., Mitchell, K.A., Rako, L., le Roux, P.C., Chown, S.L., 2011.
5 Ecologically relevant measures of tolerance to potentially lethal temperatures.
6 Journal of Experimental Biology 214, 3713–3725. doi:10.1242/jeb.061283
- 7 Tewksbury, J.J., Huey, R.B., Deutsch, C.A., others, 2008. Putting the heat on tropical animals.
8 Science-New York then Washington- 320, 1296.
- 9 Van Damme, R., Bauwens, D., Castilla, A.M., Verheyen, R.F., 1989. Altitudinal variation of the
10 thermal biology and running performance in the lizard *Podarcis tiliguerta*. Oecologia
11 80, 516–524.
- 12 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M.,
13 Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate
14 change. Nature 416, 389–395. doi:10.1038/416389a
- 15 Watkins, T.B., 1996. Predator-mediated selection on burst swimming performance in
16 tadpoles of the Pacific tree frog, *Pseudacris regilla*. Physiological Zoology 154–167.
- 17 Williams, A.B., 1972. A ten-year study of meroplankton in North Carolina estuaries: Mysid
18 shrimps. Chesapeake Science 13, 254–262.
- 19 Woolsey, E.S., Keith, S.A., Byrne, M., Schmidt-Roach, S., Baird, A.H., 2014. Latitudinal
20 variation in thermal tolerance thresholds of early life stages of corals. Coral Reefs
21 34, 471–478. doi:10.1007/s00338-014-1253-z
- 22 Zaret, T.M., Suffern, J.S., 1976. Vertical migration in zooplankton as a predator avoidance
23 mechanism1. Limnology and oceanography 21, 804–813.
- 24

Figure 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 1998-2010 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.

Figure 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 ($p < 0.05$).

Figure 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.

Figure 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 $r^2=0.99$.