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Running head: R.J. CHAPINA *ET AL*: METABOLIC RATES OF MYSIDS AT THREE DIFFERENT CONDITIONS

Metabolic rates of *Neomysis americana* (Smith, 1873) (Mysida: Mysidae) from a temperate estuary vary in response to summer temperature and salinity conditions

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ABSTRACT

The mysid *Neomysis americana* (Smith, 1873) is native to shallow shelf waters and estuaries of the western Atlantic coast of North America. Despite the important role mysids such as *N. americana* play in estuarine ecosystems as both consumers and as prey for higher trophic levels, there is limited information on how metabolism influences their spatial ecology and habitat requirements. In tributaries of Chesapeake Bay, MD, USA, previous research has shown that summer water temperatures can approach the lethal upper tolerance limit for *N. americana*. We measured the per capita metabolic rate ($\mu gO_2\ min^{-1}$) of *N. americana* from the upper Patuxent River near Benedict, MD, a tributary of Chesapeake Bay in the laboratory to evaluate the metabolic response to salinity and temperature conditions that mysids experience in natural habitats. Sex-specific and diel patterns in metabolic rate were quantified. Metabolic rates did not differ between night and day and there was no significant difference in metabolic rate between males and females, exclusive of gravid females. Metabolic rates were lowest in salinity treatments of 2 and 8 at 29 °C, and highest in the salinity 2 treatment at 22 °C. Only temperature had a statistically significant, albeit unexpected, effect. This study shows that the metabolic response of *N. americana* to temperature and salinity conditions is complex and plastic, and that metabolic rates can vary 3–4 fold within realistic summer temperature and salinity conditions. As environmental conditions continue to change, understanding metabolic response of mysids to realistic salinity and temperature conditions is necessary for understanding their distributions in temperate estuaries.

Key Words: bioenergetics, Chesapeake Bay, crustaceans, estuaries, metabolism, mysids, plankton

INTRODUCTION

Mysids (Mysida) are malacostracan crustaceans that link multiple trophic pathways as omnivorous consumers, as prey for a wide range of vertebrate and invertebrate predators, and by transferring energy and materials across ecological boundaries through their vertical and horizontal migrations (Zargursky & Feller, 1985; Fockedey & Mees, 1999; Jumars, 2007; Winkler *et al*., 2007; Latour *et al*., 2008). Mysids undergo diel vertical migration, where the population remains near the bottom during daytime then disperses into the water column at night (Jumars, 2007). Their daily vertical migrations provide a route for energy and nutrient transfer between pelagic and benthic food webs (e.g., Pitt *et al*., 2008; Woodland & Secor, 2013; Kiljunen *et al*., 2020). Mysids, like all animals, disperse the energy they assimilate among respiratory needs (e.g., costs of maintenance of homeostasis and activity reflected in metabolic rates) and residual investments in growth and reproduction. There is a priority allocation of energy to respiration/metabolism, which can potentially lead to reductions in growth or reproduction when resources are limiting (e.g. Rudstam, 1989; Verslycke & Janssen, 2002). Understanding how the respiratory needs of mysids change in response to local environmental conditions can provide insights into which habitats or conditions are conducive to population growth, via relationships between maintenance metabolic expenditures and their population vital rates (e.g., survival, growth, reproduction).

Abiotic factors in estuaries such as temperature and salinity can change drastically over space and time, and can have strong effects on animal bioenergetics, including mysids (Newell & Branch, 1980; Roast *et al*., 1999) and possibly population and community structure (Dunson & Travis, 1991; Rowe, 2002). Estuarine mysids are often eurythermal and euryhaline (Mauchline, 1980; Jumars, 2007). For example, evidence suggests that *Neomysis americana* (Smith, 1873), one of the most abundant coastal mysid taxa along the US Atlantic coast (Jumars, 2007), is

commonly observed in shallow, estuarine habitats near the salt-front where summertime water temperatures and salinity conditions are dynamic (Schiariti *et al*., 2006; Bouchard & Winkler, 2018). In tributaries of Chesapeake Bay, US Atlantic coast, where summer water temperatures often approach 30 °C, *N. americana* is an abundant component of surface nighttime zooplankton communities (Fig. 1.). Individuals are vulnerable to incremental changes in ambient temperature above 30 °C, whereas increases of 1–2 °C above this threshold yield > 50% mortality (Mihursky & Kennedy, 1972). While *N. americana* is euryhaline, often inhabiting waters with salinities ranging from ≥ 2 to 35 (salinity is reported on the unitless practical salinity scale; UNESCO, 1985), it is unable to survive in fresh water (Paul & Calliari, 2017). Despite their intolerance of freshwater conditions, individuals are often present at high densities in oligo- to mesohaline salinities (Hulburt 1957; Schiariti *et al*., 2006; Bouchard & Winkler, 2018), suggesting these animals are physiologically adapted to rapid changes in ambient salinity near the boundary of their salinity threshold. Given that *N. americana* can be found near their temperature and salinity tolerance thresholds in temperate estuaries during the summer, measuring indicators of standard metabolism, such as metabolic rates (MR) by resting, unfed animals under different environmental conditions provides a means to evaluate the potential effects of environmental conditions on individuals that may influence their populations (Maltby *et al*., 2001). Such analyses can also provide evidence of ecological tradeoffs in which animals select metabolically sub-optimal habitats in exchange for alternative ecological benefits (e.g., better feeding opportunities; Rahel & Nutzman, 1994).

The objective of this study was to determine the MR by measuring oxygen consumption (e.g. Elliott & Davison, 1975) of *N. americana* at three realistic summer temperatures and salinity conditions, and to compare daytime *versus* nighttime MR of individuals. Our research

represents the first published information on MR of *N. americana* under a range of estuarine temperature and salinity conditions, helping us understand how spatial and temporal changes in local conditions might influence the metabolism of the species. Based on previous research (Roast *et al*., 1999) on a congener (*Neomysis integer* (Leach, 1814)) we hypothesized that MR would rise as temperature increased and as salinity decreased. Because mysids are highly active in natural settings at night, we hypothesized that MR would be higher in the water column during the night as a result of influences of activity. Understanding the metabolic response of *N. americana* under multiple temperature and salinity conditions is vital for understanding their distribution in nature and the environmental conditions that influence their growth and reproduction (Roast *et al*., 1999; Bouchard & Winkler, 2018).

METHODS

Sampling

Neomysis americana were collected at night (2100–0300 EDT) from the upper Patuxent River near Benedict, MD, USA (38.5106° N, 76.6798° W). Approximately 150–200 mysids were collected with a 0.5 m diameter plankton net with 180 µm mesh deployed for approximately 3–5 min just below the surface. Mean temperature and salinity measured with a Manta2 multiprobe (Eureka Water Probes, Austin, TX, USA) in the field at the time of capture were 23 °C and 7, respectively. Mysids were kept in large, aerated containers under ambient conditions in the field and then transferred to 5 l aquaria at the University of Maryland Center for Environmental Science Chesapeake Biological Laboratory, Solomons, MD, USA.

Experimental setup

Approximately 15–20 mysids were placed in each of nine aerated aquaria, and held in each aquarium for 21 d. Groups of three aquaria were randomly assigned to one of nine combinations of temperature (22, 26, 29 °C) and salinity (2, 8, 16). Temperatures and salinity levels were selected to mimic typical summer water conditions observed in the Patuxent River (Fig. 1). Aquaria assigned to the 26 and 29 °C temperature treatments were maintained in constant-temperature incubators (Thermo Fisher Scientific, Waltham, MA, USA), whereas the 22 °C treatments were held in an isolated experimental area under ambient laboratory temperatures. Mysids were acclimated more than 8 d to experimental conditions by adjusting water temperatures by 1 °C day^{-1} and salinities by 2 day^{-1} until the desired temperature and salinity had been achieved. A day:night light cycle of 16:8 hr was maintained using full spectrum growth lights in order to mimic natural light regimes. In the aquaria, groups of mysids were fed < 24 hr old *Artemia* naupilii at concentrations yielding approximately 75–80 nauplii $mysid^{-1}$ in the morning and at night for a total feeding rate of 150 naupilii $mysid^{-1}$ day^{-1}. *Artemia* naupilii were cultured in the laboratory at 22 °C and salinities of 15–16 under constant aeration.

After acclimation, MR assays were conducted on mysids from each treatment. Prior to each assay, mysids were fasted for a period of 24 hr to minimize influences of feeding and digestion on MR (see McCue, 2006). Individual mysids were then transferred to 20 ml vials completely filled with 0.2 μm filtered water that was taken from buckets with acclimated water placed in each treatment, and changes in dissolved oxygen (DO) concentration were measured at 15 sec intervals over a 5 hr period using a FirestingO2 optical oxygen sensor (Pyroscience, Aachen, Germany). Assays were conducted twice for each individual mysid, in the morning starting at 0800 hr and at night starting at 2100 hr. Assays were conducted on the same day, the morning assay was always conducted first for consistency; at the end of the first assay mysids

were individually placed in mason jars. Mysids remained active upon placing them in vials, but seemed to settle down shortly after. Each of three Firesting units provided four data channels, allowing up to three mysids per unit and one reference blank serving as a control to be measured simultaneously. The blank showed constant O_2 throughout experiments. Temperature was monitored using a temperature sensor included in the blank respiratory vial, which also provided temperature compensation for the calculated O_2 consumption rate. Temperature variation was negligible within a trial (e.g., for a 29 °C assay, temperatures ranged from 28.4 to 29.6). Assays were all conducted within a week and all treatments were run at the same time for every assay.

At the end of the experiment, individual mysids were blotted and weighed to obtain wet weight (mg), then dried at 60 °C for ≥ 2 d and reweighed to obtain dry weight. A total of 128 individuals were used in these experiments. The sex of each mysid was determined based on primary sexual characteristics, males identified by an elongation of the fourth pleopod, females by the presence of an empty marsupium (brood sac), and gravid females were identified by the presence of embryos in the marsupium (Mauchline, 1980; Bouchard & Winkler, 2018). Subadults were not distinguished from sexually mature adults, with the exception of gravid females.

Statistical analyses

Data collected within the first two hours of the metabolic assays were excluded due to nonlinearities in MR as mysids acclimated to the experimental chambers. Metabolic rate was calculated as the slope of the dissolved oxygen concentration ($\mu gO_2\ ml^{-1}$) regressed against time (min) and corrected for the volume of the sample vial (0.024 l), yielding a final respiration index (MR) = $\mu gO_2\ min^{-1}$. Initial testing of ln-transformed MR as a function of sex and body size (ln-transformed dry weight) indicated gravid females had higher MR at a given body size compared

to non-gravid females and males (ANCOVA, $F_{2,132} = 3.90$, $P = 0.02$; least-squares means estimates of ln-transformed MR: gravid females = 0.12 ± 0.01 [SE], non-gravid females = 0.09 ± 0.01, males = 0.09 ± 0.01) and were skewing results. After excluding gravid females from the analysis there was no statistical significance in respiration rates between sex groups; therefore, gravid females ($N = 17$) were excluded from all further statistical analysis. Additionally, gravid females were removed from the statistical analyses due to their small sample size.

A mixed-effects general linear model (GLM) was used to test for main effects of temperature, salinity, and diel group. Individual mysids were treated as a random effect to account for autocorrelation of repeated measures from the same individual and ln-transformed dry weight was included as a continuous covariate. Homogeneity of variance among treatment groups was verified and MR were ln-transformed to satisfy the parametric assumption of normally distributed residuals for the mixed-effects GLM. The interaction between salinity and temperature was excluded from the mixed-effects GLM given that it was not significant ($P > 0.05$).

RESULTS AND DISCUSSION

Mean body weight of experimental *N. americana* ranged from 0.017to 4.952 mg wet weight and from 0.010 to 1.176 mg dry weight. These weights correspond to estimated body lengths of 1.8 to 9.8 mm based on a rostrum-telson body length (L in mm) to dry weight (W in mg) conversion derived from the same population of *N. americana* as part of an unrelated study ($L = 9.24 \times W^{0.366}$, $N = 133$, $R^2 = 0.97$; RW, unpublished data). There were slightly more males than females in the experiment (69 males, 59 females) but both sexes were represented in each of the experimental treatments. MR ranged from 0.002 to 0.244 $\mu gO_2\ min^{-1}$. Analysis showed a linear effect of ln-transformed body size (dry weight) on MR (linear regression: $N = 128$, $F = 147.28$, P

< 0.0001, $R^2 = 0.51$). There was no interaction between MR at ln-transformed body size and either temperature (ANCOVA, interaction: temperature × ln-transformed body size, F = 0.306, *P* = 0.581) or salinity (ANCOVA, interaction: salinity × ln-transformed body size, F = 0.431, *P* = 0.512).

Mass-specific respiration rates ranged from 0.004 to 0.082 $\mu gO_2\ min^{-1}\ mg^{-1}$ dry wt. Respiration values were similar to the values obtained in Smith & Hargraeves (1984). Modlin & Froelich (1997) found that MR increased with body size, which agree with our observations. Our finding that mass-specific MR did not differ between non-gravid females and males is contrary to what was found by Weisse & Rudstam (1989) and Roast *et al*. (1999) for *N. integer* and by Smith & Hargreaves (1984) for *N. americana*. Our initial observation that MR in gravid females were higher than in non-gravid females and males could reflect a bioenergetic cost of parental care or respiration by the developing brood (Fig. 2). Gravid females were larger and could potentially consume more oxygen per unit mass due to increased metabolic demands associated with swimming in the presence of a full marsupium, active oxygenation of the marsupium by the female, or through the direct uptake of oxygen by the progeny in the marsupium. Increased metabolic demands in egg-bearing females has been observed in other crustaceans such as intertidal crabs *Heterozius rotundifrons* A. Milne-Edwards, 1867 and *Cyclograpsus lavauxi* (H. Milne Edwards, 1853) (Taylor & Leelapiyanart, 2001).

Across temperature and salinity treatments, the lowest MR were observed in the highest temperature treatment at salinities of 2 and 8 during the day (0.028 $\mu gO_2\ min^{-1}$) and at night (0.026 $\mu gO_2\ min^{-1}$). At 16 salinity, MR increased in the high temperature treatment to an average of 0.069 $\mu gO_2\ min^{-1}$ during the day. With the exception of the 2-salinity treatment at 26 °C, the 16 salinity treatment at 22 °C and 8 salinity treatment at 29 °C, mass-specific MR were not

elevated during the night as hypothesized, but the daytime rates were more variable among treatments than nighttime rates. We did not observe a cyclic diel pattern; however, Smith & Hargreaves (1984) did observe a cyclic diel pattern in MR, such that the highest respiration rates were found late afternoon/early evening.

In their natural environment, *N. americana* form dense aggregations that actively swim during the day, albeit in deep or near-bottom waters, thus our experimental observation that MR did not differ between diel periods may reflect realistic conditions in the estuarine environment during the day even if findings were not as expected. The only previous study to have examined (and identified) diel differences in MR of *N. americana* was conducted over a finer temporal scale (Smith & Hargreaves, 1984) and it is possible that our study design failed to capture the specific timing of diel respiration cycles.

In the mixed-effects GLM, we hypothesized that MR would increase at higher temperatures, similar to the relationships previously identified for *N. americana* (Raymont & Conover, 1961) and *N. integer* (Roast *et al*., 1999). MR were significantly affected by temperature ($F_{2,52} = 3.21$, $P = 0.048$) and increased with body size ($F_{1,52} = 9.85$, $P = 0.003$; Table 1; Fig. 3); however, MR were highest at 22 °C (0.104 ± 0.006 $\mu gO_2\ min^{-1}$; Fig. 2) and lowest at 29 °C (0.081 ± 0.006 $\mu gO_2\ min^{-1}$), contrary to expectations (e.g. Raymont & Conover 1961; Roast *et al*., 1999). There was an average decrease in MR from the 22 °C treatment to the 29 °C treatment of 0.023 ± 0.009 $\mu gO_2\ min^{-1}$, a 22% decline from the 22 °C treatment. A previous study by Raymont & Conover (1961) showed a positive effect of temperature on *N. americana* MR but the temperatures used in that study (4 °C and 10 °C) were substantially lower than even the lowest temperature treatment used in our study. In light of Raymont & Conover's (1961) observations of increased MR at 10 °C relative to 4 °C, it was unexpected that, within a higher

temperature range (22–29°C), we would observe thermal independence. Very high variability in MR results at 29 °C could suggest metabolic disruption and/or perhaps anaerobic metabolic subsides. Mihursky & Kennedy (1972) reported elevated mortality at 30 °C, but in our study the 29 °C treatment did not cause mortality of any mysids.

As expected, MR increased with body size (Fig. 3). Despite the exclusion of gravid females, there was some evidence of positively skewed residuals among the very largest mysids included in the model. We did not observe differences in MR across salinities ($F_{2,52} = 1.86$, $P = 0.165$) or between diel periods in the mixed-effects linear model ($F_{1,52} = 0.22$, $P = 0.64$). The absence of a consistent salinity effect is consistent with results from some studies of other mysid species that found no effect or variable effects of salinity on metabolism within salinity tolerance ranges (e.g., Modlin & Froelich 1997; Marshall *et al*. 2003). Modlin & Froelich (1997) observed no effects of salinity (18, 22, 26) on MR of *Americamysis bahia* (Molenock, 1969), another mysid common to estuaries and coastal waters of the western Atlantic Ocean. Conversely, the metabolism of the congener *N. integer* was found to increase with decreasing salinity at three different temperatures (Roast *et al*. 1999). While not directly comparable, it is also noteworthy to note that our experimental findings suggest *N. americana* populations in Chesapeake Bay are more tolerant of higher temperatures at low salinities than an invasive population in the Laguna de Rocha estuary, Uruguay (Paul & Calliari, 2017). Survival of sub-adult *N. americana* was poor in salinities < 10 at 72 hr but increased at mesohaline salinities of 15 (Paul & Calliari, 2017). The same study found that survival among sub-adult *N. americana* was lowest at combinations of low or high salinity and low or high temperature, survival rates were highest at intermediate salinities (15) and temperatures (20 °C). Sub-adult *N. americana* are routinely sampled in salinities < 5 and at water temperatures exceeding 25 °C in Chesapeake Bay (Fig. 1). Our

findings provide insight into the physiological mechanisms and metabolic plasticity that could explain the persistence of *N. americana* in estuarine habitats near their thermal and osmotic tolerance thresholds. Our results also lay the groundwork for future studies on the metabolic costs associated with local water quality and how (or if) spatial patterns in the distribution of *N. americana* in Chesapeake Bay or elsewhere in its range correlate with energetically optimal conditions during the summer.

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Figure captions

Figure 1. Average monthly temperature (top) and salinity (middle) conditions from 2011–2015 in the Patuxent River, Maryland, USA at five long-term monitoring stations spanning the full oligo- to mesohaline reach of the saline portion of the estuary (Chesapeake Bay Program Water Quality Monitoring Program stations: 1, LE1.1; 2, TF1.7; 3, TF1.6; 4, TF1.5) where *Neomysis americana* has been consistently observed (bottom; *N. americana* average monthly concentrations from co-located Chesapeake Bay Program Zooplankton Monitoring Program stations, 1984–2002).

Figure 2. Least-squares means estimates (+ 1 SE) for *Neomysis americana* ln-transformed metabolic rates (MR, $\mu gO_2\ min^{-1}$) from two separate analyses: a comparison of gravid female (GF), non-gravid female (NGF), and male (M) MR using ANCOVA (solid bars, left), and a comparison of MR at three experimental temperatures using a mixed-effects general linear model (open bars, right). Shared letters next to bars in each group indicate no significant difference at $\alpha = 0.05$.

Figure 3. Partial residual plot of ln-transformed metabolic rates ($\mu gO_2\ min^{-1}$) of *Neomysis americana* in relation to ln-transformed dry weight (mg).