Impacts of Increasing Temperature on the Metabolism of Confined and Freely Moving American Lobsters (*Homarus americanus*)

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Abstract

*Gulf of Maine waters are warming rapidly, prompting a reevaluation of how commercially important marine species will respond. The goal of this study was to determine the respiratory, cardiac, and locomotory responses of American lobsters (*Homarus americanus*) to increasing water temperatures and to compare these to similar published studies. First, we measured the heart rate and ventilation rate of 10 lobsters that were confined in a temperature-controlled chamber while exposing them to gradually warming temperatures from 16 to 30 °C over 7 h. Both heart rate and ventilation rate increased along with the temperature up to a break point, with the mean heart rate peaking at 26.5 ± 1.6 °C, while the ventilation rate peaked at 27.4 ± 0.8 °C. In a subset of these trials (*n = 5*), oxygen consumption was also monitored and peaked at similar temperatures. In a second experiment, both the heart rate and activity of five lobsters were monitored with custom-built dataloggers while they moved freely in a large tank, while the temperature was increased from 18 to 29 °C over 24 h. The heart rate of these lobsters also increased with temperature, but their initial heart rates were lower than we recorded from confined lobsters. Finally, we confirmed that the low heart rates of the freely moving lobsters were due to the methods used by comparing heart rate data from eight lobsters collected using both methods with each individual animal. Thus, while our overall results are consistent with data from previous studies, they also show that the methods used in studies of physiological and behavioral responses to warming temperatures can impact the results obtained.*

Introduction

Marine ecosystems are undergoing significant alterations as a result of climate change, including unprecedented long-term increases in water temperatures and shorter-term marine heat waves (Pinsky *et al.*, 2019, 2020; Szuwalski, *et al.*, 2023; Friedland *et al.*, 2024). Over the past few decades, the Gulf of Maine (GOM) has warmed faster than 99% of the world's oceans, and this trend is projected to continue (Mills *et al.*, 2013; Kleisner *et al.*, 2017; Behan *et al.*, 2022; Lotze *et al.*, 2022). Consequences of this rapid warming include fisheries declines (Pershing *et al.*, 2015, 2021), shifting stock distributions (Nye *et al.*, 2010; Boudreau *et al.*, 2015; Mazur *et al.*, 2020; Friedland *et al.*, 2021, 2023, 2024), phenological alterations to ecological communities (Mills *et al.*, 2013; Staudinger *et al.*, 2019), changes to trophic dynamics and food webs (Morse *et al.*, 2017; Dijkstra *et al.*, 2019; Friedland *et al.*, 2020), impaired recruitment (Carloni *et al.*, 2018), and altered water chemistry (Klymasz-Swartz *et al.*, 2019). The American lobster, *Homarus americanus*, is the target of the most valuable single-species fishery in North America (NMFS, 2019; ASMFC, 2020), and thus climate-induced changes in the GOM could have severe economic and social consequences. One of our major goals is to better understand the effects of warming temperatures

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Abbreviations: ABT, Arrhenius break temperature; C-HAT, Crustacean Heart and Activity Tracker; CL, carapace length; GOM, Gulf of Maine; HR, heart rate; MI, movement index; OC, oxygen consumption; VR, ventilation rate.

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on the American lobster and, in doing so, help modelers, managers, and fishers predict how this fishery may be impacted by climate change (LeBris *et al.*, 2018; Goode *et al.*, 2019; Tanaka *et al.*, 2020).

American lobsters can sense very small changes in water temperature (Jury and Watson, 2000), and they use this ability to help them behaviorally thermoregulate (Reynolds and Casterlin, 1979; Crossin *et al.*, 1998; Jury and Watson, 2013; Nielsen and McGaw, 2016). When placed in thermal gradient tanks in the laboratory, adult lobsters have been shown to prefer areas that are at temperatures of 14–16 °C, and they generally avoid water that is >20–23 °C (McLeese and Wilder, 1958; Crossin *et al.*, 1998). Based on acoustic telemetry and tag recapture studies, their responses to thermal gradients appear to have a strong influence on their seasonal movements and habitat choices (Lawton and Lavalli, 1995; Watson *et al.*, 1999; Jury and Watson, 2013; Goldstein and Watson, 2015b). Lobsters have been shown to move inshore toward warmer water in the spring and then offshore in the fall, as inshore waters cool more rapidly than deeper, offshore areas. Furthermore, in some areas, when the water gets "too warm" in the summer, such as in shallow inshore bays in southern New England (ASMFC, 2015, 2020) or in the upper reaches of estuaries, they have been reported to move from these warmer waters to deeper, cooler water (Lawton and Lavalli, 1995; Howell *et al.*, 1999; Watson *et al.*, 1999; Glenn *et al.*, 2011; Casey *et al.*, 2023). Adult female lobsters prefer cooler water than their male counterparts, and their differential movements in natural thermal gradients can lead to skewed sex ratios in some areas (Jury and Watson, 2013; Jury *et al.*, 2019). For example, in warmer areas like Buzzards Bay, Massachusetts, and the Great Bay estuary, New Hampshire, sex ratios are skewed toward males (Munro and Therriault, 1983; Howell *et al.*, 1999; Glenn *et al.*, 2011; Jury *et al.*, 2019; Casey *et al.*, 2023), while females are more abundant than males in adjacent cooler, deeper habitats (Goldstein and Watson, 2015a, b; Carloni and Watson, 2018; Jury *et al.*, 2019; Pugh *et al.*, 2023).

While lobsters are clearly capable of behavioral thermoregulation, the underlying neurobiological and physiological mechanisms responsible for their responses to different water temperatures are poorly understood. One possibility is that they might avoid warm water when it reaches an upper critical threshold temperature, at which point their metabolic rate approaches a maximum (Frederich and Lancaster, 2024), and they can no longer maintain aerobic respiration (Pörtner *et al.*, 2017; Pauly *et al.*, 2022). It is possible that some of the biochemical changes associated with this state might be what triggers lobster avoidance responses. If this hypothesis is correct, then their upper critical threshold temperature should match the temperature at which they begin to avoid warm water.

Several previous studies have involved monitoring lobster heart rates (HRs) while increasing the water temperature over various lengths of time and rates of change (Table 1). As expected for an ectotherm, in all cases, HRs increased concomitantly with increases in water temperatures (Camacho *et al.*, 2006; Worden *et al.*, 2006; Qadri *et al.*, 2007; Lyons *et al.*, 2013). However, HR is not the only factor controlling cardiac output, oxygen delivery to the tissues, and metabolic rate, and thus it can be considered only a proxy for metabolic rate, particularly at higher temperatures near their critical threshold temperatures. For example, Worden *et al.* (2006) demonstrated that when lobsters were acclimated to 5 °C, cardiac stroke volume decreased with increasing temperatures and, as a result, cardiac output peaked around

Table 1

Summary of the experimental conditions during this study and previous studies concerning the impact of increasing temperature on lobster heart rates

Study	Size (mm CL)	Acclimation (°C)	Temperature range tested (ramp; °C)	Time (min) in chamber before ramp	Rate of change (°C min^{-1})
Harrington and Hamlin, 2019	50–65[a]	12.3	12–28	25	0.17
Harrington *et al.*, 2020a	50–60[a]	16	16–30	15	0.20
Qadri *et al.*, 2007	Unknown	4–5 (cold), 20–21 (warm)	2–30	Unknown	0.75
Worden *et al.*, 2006	Unknown	5	2–22	30	0.9
Mercaldo-Allen and Thurberg, 1987	61.4–91.2	Each °C for >2 wk over 1 yr	2–18	Seasonal	Seasonal
Camacho *et al.*, 2006	Unknown	4–5 (cold), 20–22 (warm)	2–36	30	0.75
Jost *et al.*, 2012	89 ± 0.2	12	14–34	720	0.1
Current study					
Confined	79.1 ± 5.8[a]	16	16–30	720	0.1 (during step change)
Freely moving	88.8 ± 4.9[a]	17–18	18–29	1440	0.01

Data were obtained from literature sources and compared to the data from the current study that involved both confined and freely moving lobsters. All heart rates were recorded from intact juvenile or adult lobsters, using chronically implanted electrodes with impedance pneumography, except for the study by Jost *et al.* (2012) and the freely moving lobsters in the current study, which both used infrared sensors and photoplethysmography. CL, carapace length.

[a] Female only.

10 °C, even though HR peaked at 18 °C. Furthermore, when considering the impact of warmer seawater on oxygen uptake and circulation, one must also consider that warmer water holds less oxygen, hemocyanin's affinity for oxygen decreases with increasing water temperatures, and oxygen uptake is dependent on the rate at which the scaphognathites (gill bailers) oscillate (Decker *et al.*, 2007; Pörtner *et al.*, 2017; Pauly *et al.*, 2022). Therefore, it is not surprising that it becomes more challenging for lobsters to meet the demands of their higher metabolism when water temperatures approach an upper thermal limit (Stillman, 2019; Frederich and Lancaster, 2024). While lobsters might initially try to avoid warm water, if avoidance is not possible, they could face impaired physiological processes up to the point of mortality, depending on the duration of exposure and prior acclimation, as demonstrated by McLeese (1956).

While laboratory techniques are preferred, and often required, to measure metabolic rates in crustaceans, the choice of experimental method and design is crucially important in interpreting the results (McGaw and Nancollas, 2018). For example, when lobsters are confined within a small chamber, it is possible to simultaneously record HR, ventilation rate (VR), and oxygen consumption (OC) over a range of temperatures. However, the data obtained may not fully represent what occurs in their natural habitat, where they are free to move about. Furthermore, the acclimation temperatures and rate of temperature change may have a significant influence on the ultimate results (Table 1). Previous studies aimed at determining how various conditions impact the metabolism of crustaceans demonstrated that their HRs can be influenced by a range of experimental conditions including lighting, vibrations, acclimation times and temperatures, and type of recording and holding apparatus utilized (McGaw and Nancollas, 2018, 2021; Powell *et al.*, 2023). For example, McGaw and Nancollas (2018) showed that green crabs (*Carcinus maenas*) that were confined had higher and more consistent HRs when exposed to changes in temperature than unconfined crabs (McGaw and Nancollas, 2018, 2021). Furthermore, unconfined crabs had lower initial HRs, and the rate of increase was higher when tested over a range of 15–39 °C. Freely moving *H. americanus* have also been shown to respond to hypoxia differently from confined lobsters (McMahon and Wilkens 1975; McGaw and Nancollas, 2018). Therefore, in this study, we utilized a microcomputer-based datalogger backpack (Gutzler and Watson, 2022) to measure the HRs of freely moving, unconfined lobsters so we could compare their responses to lobsters that were confined in an experimental chamber.

The overall goal of this study was to assess the impacts of increasing water temperatures on lobster metabolism by using multiple methods. To achieve this goal, we monitored lobster HRs, VRs (the frequency of gill bailer movements that serve to circulate water through their branchial chambers), and, in a subset of lobsters, their rates of OC, while slowly raising the water temperature to levels that they might encounter if the GOM continues to warm as expected or if lobsters experienced a marine heat wave. In a complementary experiment, we recorded the HR and locomotory activity of lobsters freely moving in a large tank while exposing them to a similar increase in temperature but at a slower rate. Finally, we conducted a third experiment in which we recorded the HRs of the same lobsters under both experimental conditions to ascertain the effects of measurement methods on lobster cardiac responses. Data from this final study helped us determine how the methods used can impact the physiological data obtained, which facilitated comparison of our results to similar published studies that used a variety of methods to determine how temperature influences lobster metabolism.

Materials and Methods

Animals

Adult female intermolt lobsters (*Homarus americanus* H. Milne Edwards, 1837) were captured along the New Hampshire seacoast from July to September in 2022 by New Hampshire Fish and Game personnel during their routine ventless trap surveys. After capture, all lobsters were held in communal tanks supplied with flow-through natural seawater at the University of New Hampshire Coastal Marine Laboratory in New Castle. The average water temperature was 16.4 ± 2.3 °C (mean ± SD; range: 11.0–20.6), and the salinity was 31.1 ± 0.3 psu (range: 30.0–31.6). Trials on a separate group of five lobsters were carried out at Southern Maine Community College's (SMCC) Marine Science Center in Portland in parallel with the studies at the University of New Hampshire Jackson Estuarine Laboratory (JEL), as described below. Lobsters were transported to both laboratories and acclimated in recirculating natural seawater aquaria at 16 °C for at least 1 week prior to being used for experiments. During this week, lobsters were not fed to avoid the potential influence of nutritional reserves on their response to temperature (Hardison *et al.*, 2021). Data were also recorded from eight additional lobsters (85.6 ± 4.5 mm carapace length [CL]) at each location to determine whether the method used to measure HR had an impact on the results obtained.

Experiment I: confined lobster trials—measurements of heart rate, ventilation rate, and oxygen consumption

The experimental chamber used to hold individual lobsters during each trial consisted of a 2.5-L plastic container with a mesh window on the top that could be closed with a cap. This container was placed horizontally in a larger 47-L insulated holding tank so water flowing into the holding tank could also enter the open end of the recording chamber and out the hole in the top. Water was recirculated through the holding tank from a larger reservoir containing temperature-controlled, aerated, and filtered natural seawater (30–32 psu). A chiller (or submersible heaters with digital controllers) was used to maintain the temperature in the reservoir between 16 and 30 °C during each trial. A stainless steel temperature probe and an optical dissolved oxygen probe (Vernier, Beaverton, OR) were inserted into the recording chamber to continuously monitor temperature and oxygen levels throughout each trial. These were connected to a Vernier LabQuest interface, the output of which was recorded using Vernier Logger Pro software. In a subset of these trials, the openings in the front of the chamber and the top were closed during periods of time when OC was being measured, and because the chamber was housed inside a larger chamber, the temperature remained constant during these ~30-min periods. Further details regarding the OC trials are presented below. Heart and scaphognathite (*i.e.*, the gill bailer that circulates water over the gills) movements were detected and amplified with a UFI impedance converter (model 2991; Morro Bay, CA) (Jury *et al.*, 2000; Dufort *et al.*, 2001; Weineck *et al.*, 2018; Harrington *et al.*, 2020b) and recorded using a PowerLab analog-digital convertor and LabChart version 8.1.24 (ADInstruments, Colorado Springs, CO). The impedance electrodes were made of ~45-cm-long pieces of vinyl-coated steel electrical wire that had ~0.3 mm of the insulation removed from the tip. For heart recordings, two small holes (the same diameter as the coated wire) were made on either side of the heart with a sharp dental tool of the same size. Wires were then inserted into the holes ~0.5 mm so the uninsulated wire was inside the shell and the insulation around the wire plugged the hole, preventing hemolymph loss. Both wires were then secured to the lobster's carapace by using cyanoacrylate glue and a piece of duct tape. The same procedure was used for the scaphognathite electrodes, which were placed on the lateroventral portion of the shell covering one of the branchial chambers.

Lobsters ($n = 10$; 79.5 ± 5.8 mm CL) were prepared as described above for recording HR and VR on day 1 and then placed in the recording chamber and allowed to acclimate overnight at 16 °C prior to exposing them to gradually increasing water temperatures on day 2. On day 2, after collecting data at 16 °C for 1 h, the water temperature was increased in 2 °C increments from 16 to 30 °C from about 9:00 a.m. to 4:00 p.m. (~7 h). Typically, it took 20 min to increase the temperature by 2 °C (0.1 °C min^{-1} rate of change during step change; 2 °C h^{-1} overall rate of change), then lobsters were held at the new temperature for another 30–40 min (Fig. 1). During the OC experiments, after a lobster was at a given temperature for 20 min, the two openings in the respirometer chamber were closed and the decrease in oxygen in the chamber was recorded for 20–30 min prior to opening it and moving up to the next temperature (Fig. 1B). Sometimes at the higher temperatures if the HRs or VRs became very erratic, the chamber was opened after a shorter period of time.

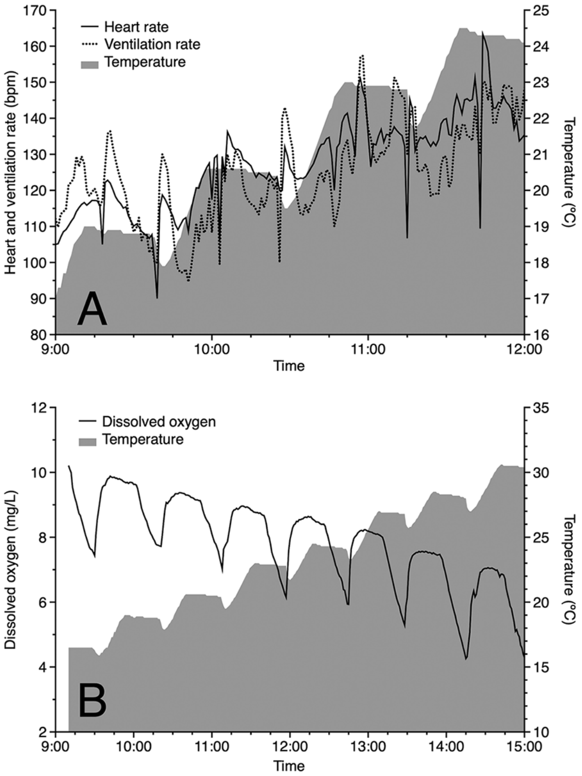

Figure 1. Representative data from two individual confined lobsters exposed to increasing water temperature. (A) Changes in a lobster's heart rate (HR) and ventilation rate (VR) in response to gradually increasing the water temperature from 16 to 24 °C, over 3 h. Water temperature was increased in 2 °C steps, then held at a given temperature for about 20 min until the HR and VR stabilized, before increasing the temperature by another 2 °C. This procedure continued from 16 to 30 °C. (B) Changes in the oxygen concentration in the respiration chamber over 6 h as the water temperature was increased in 2 °C steps, from 16 to 30 °C. During each temperature step the respirometry chamber was closed, and as the lobster consumed oxygen, the oxygen levels dropped. Note how the ambient oxygen levels also decreased as the temperature increased.

HR and VR values for subsequent analyses were calculated from the data obtained during the last 10 min that a lobster was at a given temperature. From these 10-min time periods, we selected as many sections of data as possible, at each temperature, that were at least 3 min long and during which both rates were relatively constant and there were no respiratory pauses or movement artifacts. The HRs and VRs during these segments were calculated using LabChart. To determine the upper critical threshold temperatures, piecewise regressions on individual HRs and VRs were plotted to determine Arrhenius break temperatures (ABTs), as described in Stenseng *et al.* (2005), Camacho *et al.* (2006), and Harrington *et al.* (2020a). The ABT is the temperature when there is a clear decrease in HR or VR when a certain critical temperature is reached. It is determined as the intercept of linear regressions fitted to the slopes of the increase and decrease of HR or VR. Only eight of the 10 lobsters in experiment 1 showed a break temperature for HR and VR. The ABTs were not calculated for freely moving lobster HRs (see experiment II, below) because only two of these five lobsters showed a clear break over the range of temperatures tested.

The OC rates at each temperature were measured based on the slope of a regression line fitted to the last 10 min of oxygen data. Mass-specific metabolic rate (MR) was calculated as follows: MR = OC (mg L^{-1} h^{-1}) × volume (L) × 1 mL 1 mg^{-1} × 1/mass (g). We also conducted linear regressions to test the correlations between HR, VR, and OC across the temperatures tested. The Q_{10}, which is the factor by which a given rate changes when the temperature is increased by 10 °C, was calculated using the following formula: $Q_{10} = (R_2/R_1)^{(10/T_2-T_1)}$, where R_1 is the rate at T_1 and R_2 is the rate at T_2.

Experiment II—freely moving lobsters: measurements of heart rate and locomotor activity

Crustacean Heart and Activity Trackers (C-HATs) are custom-made dataloggers that allow for the continuous monitoring of the HR and movements of freely moving lobsters (see details in Gutzler and Watson, 2022). Briefly, this system contains an accelerometer and an infrared heart rate sensor connected to an Arduino microcontroller that records data at 5 Hz. The system is housed in a watertight enclosure (75 mm × 65 mm × 40 mm, 180 g) that is neutrally buoyant and can be affixed to the dorsal carapace of a lobster over the heart, allowing for monitoring of HR *via* photoplethysmography. In these experiments a C-HAT was attached to a lobster ($n = 5$; 88.8 ± 4.9 mm CL), and then the lobster was placed into a trough filled with seawater (3 m × 0.6 m × 25 cm) that was located inside a larger temperature-controlled bath (3.1 m × 1.2 m × 25 cm) made of 1.9 cm AZEK PVC (AZEK Exteriors, Chicago, IL). Temperatures were maintained in the inner trough over each 48-h trial by heating or chilling the outer bath by using two Hydrofarm AACH25 recirculating chillers (Shoemakersville, PA) and four 100-W immersion heaters attached to a temperature controller (Aqua Logic NEMA 4X, Monroe, NC). The tank was covered with 25 mm of foam insulation to help maintain the temperature, but ambient light was allowed to enter on the edges to provide seasonal light/dark cues. Lobsters were allowed to acclimate overnight for 12–14 h, and then the next morning heaters were turned on (and chillers turned off) to cause the temperature to slowly increase to 29 °C, over about 24 h (target rate of change: 0.01 °C min^{-1}, 0.6 °C h^{-1}). There was some variability in starting and ending temperatures between trials due to daily fluctuations in room temperature that influenced the rate of heating or chilling of the tank.

For each trial, HR, temperature, and relative activity were averaged every 30 min in LabChart. Relative activity was assessed *via* accelerometry to produce a movement index (MI), as described in Gutzler and Watson (2022). Briefly, the MI is constructed by differentiating each of the three axes of acceleration, squaring the differentiated values, summing these values, and taking the square root of the sum. The MI represents overall movement activity rather than locomotion in a particular direction. Lobsters were considered active when the mean MI was greater than 0.4 for a given 30-min period. This 0.4 value was based on comparing time-lapse videos of lobsters moving around in a tank with the MI calculations obtained during the same time. When lobsters were not moving, the MI was always <0.4.

We compared HRs at 18 and 26 °C (chosen as consistent endpoints for each method) between these freely moving lobsters and confined lobsters (experiment I, above), using a two-factor ANOVA in R version 4.2.1 (R Core Team, 2022) and R Studio version 2023.06.0 + 421 (Posit Software, Boston, MA). Test assumptions were verified *via* inspection of residuals.

Experiment III—comparisons of heart rate recording methods

Based on preliminary data from both confined and freely moving lobsters, it appeared that confined lobsters had higher resting HRs than freely moving lobsters and required longer to settle down after they were placed in their recording chamber. To determine whether this difference was due to the methods used, or from differences in the lobsters used in each experiment, we recorded HRs from the same eight female lobsters (not used in any prior tests), using both methods. Data were initially obtained from half of the lobsters at JEL, and then they were transported to SMCC for a subsequent trial. The other half of the lobsters were initially tested at SMCC and then tested again at JEL. We recorded the HRs of the same eight lobsters, at each location, for 48 h at 16 °C, using both methods. We averaged 1 h of data from the first day (day 1) after the lobsters had been in their apparatus for 2 h, and we also averaged another 1 h of data obtained 24 h later, near the beginning of the second day (day 2). The HRs were then compared between days, and method and location, using a two-factor ANOVA with time (day 1 *vs.* day 2) and measurement conditions (confined *vs.* freely moving) as the factors, with test assumptions checked by inspection of residuals.

Results

Confined lobsters: heart, ventilation, and oxygen consumption rates

As the temperature in the recording chamber was raised incrementally, lobster HRs and VRs typically increased and then leveled off before the next 2 °C increase in temperature (Fig. 1). The average initial HR at 16 °C before beginning the temperature ramp on day 2 was 77.5 ± 14.6 bpm (range: 58–107 bpm), while the baseline VR was 117.8 ± 34.4 bpm (range: 58–165) (Fig. 2). The HRs and VRs both increased with rising water temperatures (Figs. 1A, 2), and there was a strong correlation between

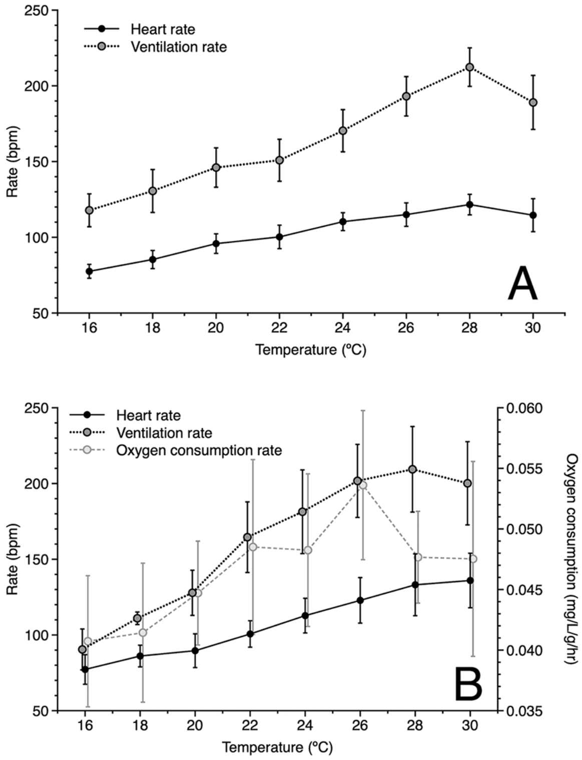

Figure 2. Relationship between water temperature and lobster heart and ventilation rates. (A) Average (±SEM) heart and ventilation rates for 10 female lobsters exposed to water temperatures between 16 and 30 °C. These lobsters were acclimated at 16 °C for at least a week in communal tanks and then confined at 16 °C in the experimental chamber overnight before commencing the temperature ramp. Note how the heart rate (HR) and ventilation rate (VR) both reach a maximum at 28 °C, consistent with prior studies. (B) Heart, ventilation, and oxygen consumption rates (mean ± SEM) for a subset ($n = 5$) of the lobsters depicted in (A).

mean HR and mean VR between 16 and 26 °C (linear regression, $F_{1,4} = 460.7$, $P < 0.001$, $R^2 = 0.991$). While both HR and VR increased as the seawater was warmed in the experimental chamber, eventually they reached a maximum rate that varied somewhat between individuals, and then they either declined or leveled off (Fig. 2). Based on an ABT analysis, the warm critical temperature threshold for HR was 26.5 ± 1.6 °C ($n = 8$), while the warm critical temperature threshold for VR was 27.4 ± 0.8 °C ($n = 8$). Between 16 and 26 °C the Q_{10} for HR was 1.5, and for VR it was 1.7. The mean (±SD) maximum HR was 121.6 ± 21.5 bpm, while for VR it was 212.3 ± 12.7 bpm. These values correspond to a 55% increase in the HR from the initial baseline value at 16 °C and an 81% increase in VR. It should also be noted that at the warmest temperatures (28–30 °C), heart and ventilation rhythms often became somewhat erratic, with frequent HR and VR pauses, as has been seen in other crustacean studies (Powell *et al.*, 2023).

The rate of OC, as well as HR and VR, was recorded from a subset of five lobsters over the full temperature range (16–30 °C). As expected, OC also increased as the lobsters were exposed to warmer water (Fig. 2B). Over the 16 to 26 °C range, there were good correlations between mean VRs and OC rates (linear regression, $F_{1,4} = 100.3$, $P < 0.001$, $R^2 = 0.962$) and mean HRs and OC rates (linear regression, $F_{1,4} = 51.96$, $P = 0.002$, $R^2 = 0.929$).

Freely moving lobsters: heart rates and activity

Freely moving lobsters had consistently lower HRs than confined lobsters, but their HRs also increased with temperature, at a similar rate, up to ~29 °C (Figs. 3, 4). When temperature endpoints were compared between the two methods, there was a significant difference in lobster HRs both between 18 and 26 °C and between freely moving and confined lobsters (two-factor ANOVA, Table 2). Furthermore, there was no significant interactive effect between method and temperature on HR (Table 2), suggesting that the HR responded similarly to temperature with both methods and the slope of the change was unaffected by measurement methodology. The average HR for confined lobsters at 18 °C was 86.1 ± 16.0 bpm ($n = 10$), while for freely moving lobsters it was only 38.2 ± 5.4 bpm ($n = 5$). When the temperature was increased to 26 °C, the HR of confined lobsters increased by 38.7% to 117.4 bpm, while the HR of freely moving lobsters increased by 73.9% to 67.5 bpm. The HR Q_{10} of freely moving lobsters between 18 and 28 °C was 1.7, while for confined lobsters it was 1.4. However, while the HRs of confined lobsters plateaued, or reached a break point, at temperatures of 26–27 °C, this did not happen with most of the freely moving lobsters. The HRs of four of five of the freely moving lobsters continued to increase right up to the final temperature of 29 °C (Fig. 4). Given that the lobsters used were of the same size and sex, obtained from the same source, and acclimated to the same temperatures, our conclusion is that this difference is due to their low initial HRs and perhaps the slower rate of temperature increase.

The freely moving lobsters showed variable levels of activity, within and between individuals, before we started to increase the temperature in the tank. Some lobsters expressed more bouts of activity shortly after the temperature increased (Fig. 4). However, once the temperature reached >25 °C, they tended to become less active. This might have occurred because these test lobsters were near their upper thermal limit.

Comparison of heart rates of confined versus *freely moving lobsters*

A two-factor ANOVA found significant effects of both time (day 1 *vs.* day 2) and method (confined *vs.* freely moving) but, like the previous analysis testing the effects of temperature and method on HRs, found no interactive effect between factors (Table 3; Fig. 5). Freely moving lobsters had significantly lower HRs than did confined lobsters on both day 1 and day 2, and HRs were significantly lower on the second day than the first day. These data indicate

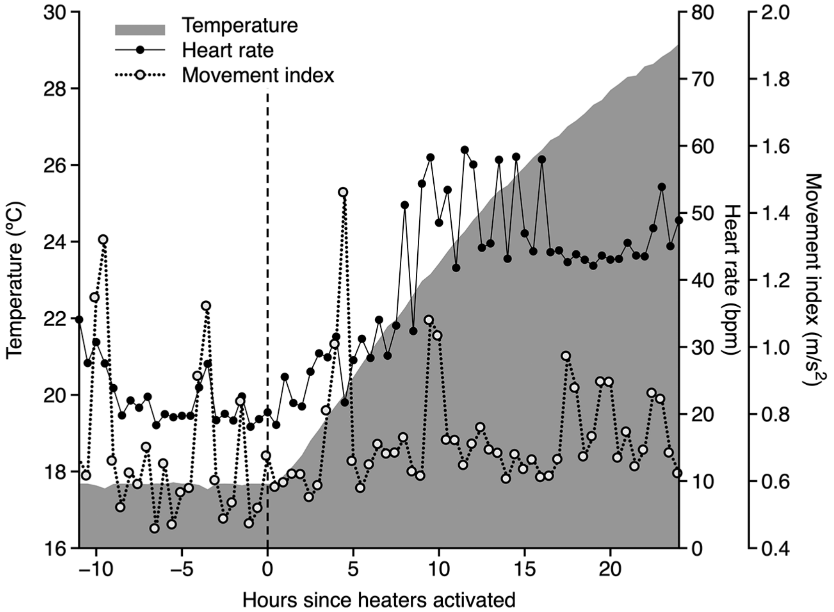

Figure 3. Heart rate (HR) and activity (movement index [MI]) for one freely moving female lobster before, and during, a gradual increase in water temperature (*i.e.*, ramp) from 17 to 29 °C. Values are 30-min means. The *x*-axis reflects hours since the heaters were turned on to begin the temperature ramp (indicated by the dashed vertical line). The HR and MI were recorded with a custom datalogger, which allowed the lobster to move freely in a 3 × 0.6 × 0.25-m-deep rectangular tank. Overall, the HRs in freely moving lobsters were lower than in the confined lobsters, as well as those reported in the literature.

that (1) it is important to allow lobsters sufficient time to recover from being handled before initiating a trial of this type and (2) data obtained from freely moving lobsters might yield results that are more indicative of lobsters that are in the wild because they are closer to a natural state than confined lobsters.

Discussion

The impact of temperature on lobster metabolism

Given the areas that American lobsters typically inhabit, previous studies of lobster metabolism have historically focused on temperatures <20 °C. Furthermore, in 2005

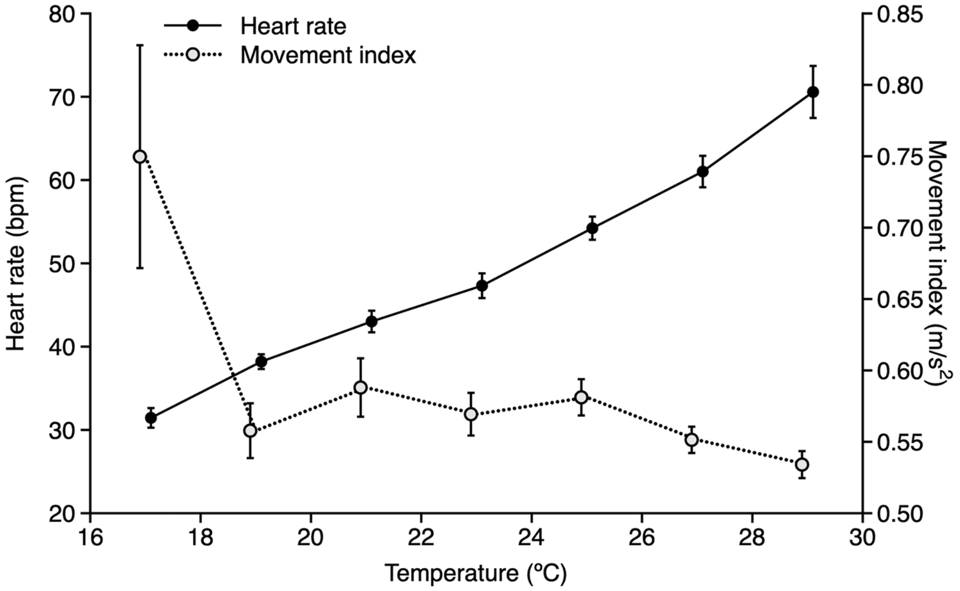

Figure 4. Relationship between temperature, heart rate (HR), and relative activity (movement index [MI]) (mean ± SEM) for five freely moving lobsters. The water temperature was gradually increased from 17 to 29 °C over 24 h, leading to cardiac responses that were similar to those observed in confined lobsters. However, the HR of freely moving lobsters did not show a break point at the higher temperatures, like the confined lobsters. Relative activity was variable between individuals but generally increased when the temperature ramp commenced, then decreased when the water temperature reached 26–27 °C. Note that the increased activity seen at 17 °C is largely reflective of one lobster moving throughout the tank before the heaters were activated.

Table 2

Results of ANOVA comparing the effects of temperatures and measurement conditions on lobster heart rates

	df	MS	*F*	*P*
Temperature	1	4400.3	11.375	0.002
Measurement condition	1	17,116.4	44.246	<0.001
Temperature × measurement condition	1	101.2	0.262	0.614
Error	25	386.9		

Both temperature (18 *vs.* 26 °C) and condition (confined *vs.* freely moving) significantly impacted heart rates, but there was no interactive effect present.

Dove *et al.* published a study showing that temperatures >20 °C were thermally stressful. They held lobsters at either 16 or 23 °C for 31 days and monitored their blood chemistry for indicators of physiological stress. Based on their results, and those of two similar previous studies (Paterson and Stewart, 1974; Steenbergen *et al.*, 1978), it was concluded that temperatures >20 °C were stressful because they reduced a lobster's ability to fight off pathogens. However, due to the impacts of climate change on water temperatures in the GOM, temperatures are trending higher (*e.g.*, Stillman, 2019; Tanaka *et al.*, 2020; Pershing *et al.*, 2021), and scientists are actively running models to predict changes in the distribution of lobsters based on their tolerance for these higher temperatures (Mills *et al.*, 2013; Kleisner *et al.*, 2017; LeBris *et al.*, 2018; Mazur *et al.*, 2020; Tanaka *et al.*, 2020; Pershing *et al.*, 2021; Behan *et al.*, 2022; Lotze *et al.*, 2022). Therefore, a primary goal of the current study was to extend the temperature range of the previous studies up to, and beyond, the temperatures that lobsters have been shown to avoid (>23 °C; Crossin *et al.*, 1998). We also used slower rates of change than many of the previous studies, so that lobster HRs and VRs could reach an equilibrium at each temperature before it was raised further (see Fig. 6; Table 1). Overall, our findings demonstrate that in lobsters both confined in a small experimental chamber and freely moving, HR (as well as VR and OC) increased as the temperature went up and generally peaked at temperatures >26 °C.

Previous studies of crustacean metabolism generally support the hypothesis that temperature-dependent performance curves are shaped, at least in part, by their capacity for delivering oxygen to tissues in need, relative to their oxygen demand (Lagerspetz and Vaino, 2006; Twiname *et al.*, 2020; see review by Verberk *et al.*, 2016). For example, when Camacho *et al.* (2006) increased the water temperature from 2 to 36 °C over ~60 min using *Homarus americanus* acclimated to 20 °C, their HRs increased linearly and peaked at 25 °C, when the HR was ~90 bpm (Fig. 6). Qadri *et al.* (2007) and Camacho *et al.* (2006) also demonstrated that American lobsters acclimated to 20 °C reached their maximum HRs at warmer temperatures than those acclimated to 2 or 4 °C (Fig. 1). Lobster HRs have been shown to be closely correlated with their VRs (Wilkens *et al.*, 1974; O'Grady *et al.*, 2001; Chabot and Webb, 2008; Fig. 2), and thus, as expected, temperature has been shown to have a similar impact on the rhythmic movements of lobster scaphognathites (Qadri *et al.*, 2007). Furthermore, in this study, we demonstrated that there is a very good correlation between HRs and OC, as well as between VRs and OC. Therefore, as water temperature is increased, a lobster's metabolic rate increases, leading to the activation of the appropriate physiological processes to increase the delivery of oxygen to the tissues. However, it is likely that, for a variety of reasons that are context dependent, such as acclimation history, nutritional reserves, neurohormonal status, and so on, for any given lobster there is a maximum rate at which their heart and scaphognathites can beat, and when this is reached, they can no longer keep up with the oxygen demands associated with being exposed to warm water (see review by Frederich and Lancaster, 2024). While we did not hold our lobsters long enough for them to die at the warmest temperatures to which we exposed them, in 1956 McLeese showed that, depending on their acclimation history, a temperature of ~28 °C is the upper thermal lethal limit for American lobsters. The similarity between this value and the temperatures when HRs and VRs reached a maximum in this study, and previous studies, suggests that death at temperatures ≥28 °C may be linked to an inability to maintain aerobic metabolism.

Table 3

Results of ANOVA comparing the effects of time since experiment start and measurement method on lobster heart rates

	df	MS	*F*	*P*
Time	1	2158.0	12.138	0.001
Measurement method	1	1653.8	9.302	0.004
Temperature × measurement condition	1	224.7	1.264	0.268
Error	36	177.8		

Both time (day 1 *vs.* day 2) and method (confined *vs.* freely moving) significantly impacted heart rates, but there was no interactive effect present.

The rate of change of water temperature is also an important variable in laboratory studies, and by necessity it is typically faster than lobsters would experience under natural conditions in most of their habitats. In our studies, for the confined lobster trials, we gradually increased the temperature in 2 °C steps from 16 to 30 °C over ~7 h. We also gave them time to adjust to each temperature change before obtaining physiological data for each temperature step. This was important because when we initiated a temperature increase, lobsters responded with a brief period of tachycardia (increased HR, Fig. 1). In the experiments with freely moving lobsters, we covered approximately this same temperature range over 24 h. Both of these experimental designs led to rates of temperature increase that were generally slower than in previous studies (Fig. 6; Table 1). In our experiments with confined lobsters, and in previously published studies, HRs tended to peak

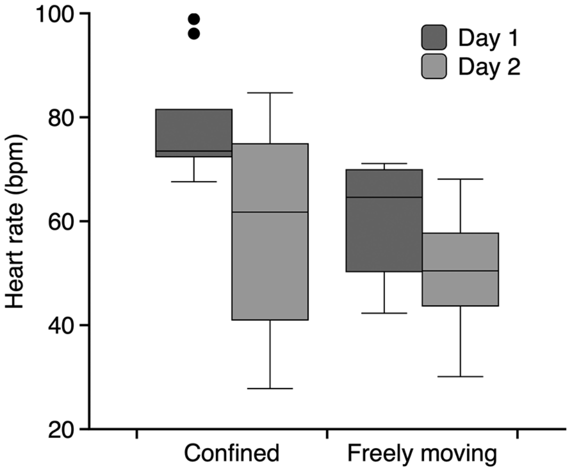

Figure 5. Boxplot comparing heart rates (HRs) of the same lobsters ($n = 8$) at 16 °C, using two different recording methods (confined *vs.* freely moving). The horizontal line within each box indicates the median; whiskers are the extent of data within 1.5 × the interquartile range, and dots are outliers. Confined lobsters were held in a recording chamber, and their HRs were measured using implanted electrodes, while freely moving lobsters were fitted with a custom datalogger that used infrared sensors to obtain HR data while they could move freely in a tank. There were significant differences in HRs between methods and days but no interactive effect.

before the maximum temperatures were obtained (Fig. 6), suggesting that a critical temperature threshold had been reached. However, when lobsters were not confined and the water was warmed at a much slower rate, the HR of four of five of the lobsters never plateaued. This is likely because the freely moving lobsters had much lower HRs when the experiment commenced, and thus, even though their HR increased as the water warmed at the same rate as the confined lobsters, by the time they reached 26 °C, their HR was only 61.0 ± 14.4 bpm, while the HR for the confined lobsters at this temperature was 122.8 ± 33.6 bpm (Fig. 6).

The impact of temperature on the HR of intact lobsters is also more complex than with assays on isolated hearts. For example, Worden *et al.* (2006) found that while the HR of intact lobsters peaked at 111 bpm at 22 °C, isolated hearts reached a maximum of 99 bpm at 20 °C. Therefore, the HR of an intact lobster is not simply a response of the heart to temperature; it is also responding to the release of hormones or neuromodulators that serve to both increase the HR and influence the stroke volume (Worden *et al.*, 2006; Powell *et al.*, 2023). Worden *et al.* (2006) also noted that isolated hearts, like the hearts of intact lobsters, would often start to beat erratically at the warmest temperatures, indicating that lobster hearts probably have maximal sustainable HRs that are somewhat temperature dependent. In our experiments with confined lobsters, we also noticed that the HRs and VRs of many of the lobsters became erratic at the higher temperatures. For a given lobster, based on its size, sex, nutritional state, and so on, there might be a theoretical maximum HR. Thus, if lobsters started at a lower baseline value, their respective HRs (and VRs) may increase as their metabolism increases more than if they started with a higher baseline, because they are influenced from handling, confinement, duration of acclimation, and so on, as we found in the current study. These results should be considered when interpreting metabolism data obtained using different methods (Fig. 6).

Comparison of methods used to measure lobster heart rates

A direct comparison of the confined *versus* freely moving approaches to measuring HR provided several insights. First, the HR of confined lobsters was significantly lower after being given sufficient time (*e.g.*, overnight) to recover from being handled and time to adjust to the recording chamber (Table 3; Fig. 5). Based on these data and similar previous studies (see Fig. 6; Table 1; McMahon, 1999; McGaw and Nancollas, 2018), sufficient time should be provided for them to recover from being restrained or handled before commencing studies to determine the impact of changing environmental conditions on their behavior and/or physiology. We noticed this during our preliminary studies, so all the confined lobster data presented in this paper were obtained from lobsters that were allowed to acclimate overnight prior to exposure to the temperature ramp. Second, freely moving lobsters fitted with C-HATs had consistently lower basal HRs than the confined lobsters, as well as HRs recorded from lobsters in their natural habitat (~60 bpm at ~14 °C; Gutzler and Watson, 2022). This difference between the HRs of the freely moving lobsters in our study compared with those in the field might be due to the fact that lobsters in their natural habitat are often searching for prey and avoiding predators, while the lobsters in our study were isolated in a large, relatively dark tank.

Lobster behavioral thermoregulation

While the HR responses of freely moving lobsters in our experiments are probably indicative of how temperature increases might impact the metabolism of lobsters in their natural habitat, lobsters in the field also would have the option to move to avoid high temperatures. Thus, it is likely that mobile adult American lobsters would never experience the temperatures we exposed them to, because they would sense the increasingly unfavorable environmental conditions and move toward areas with temperatures closer to their preferred range. However, it might not always be possible to move far, or fast, enough to avoid large increases in water temperature, and this might lead to potential die-offs or mortality events, as occurred in the Long Island Sound in 1999 (Pearce and Balcom, 2005).

In the current study, freely moving lobsters generally increased their activity when first exposed to increasing water temperatures, but then at higher temperatures they became less active (Fig. 4). This was not expected, in part,

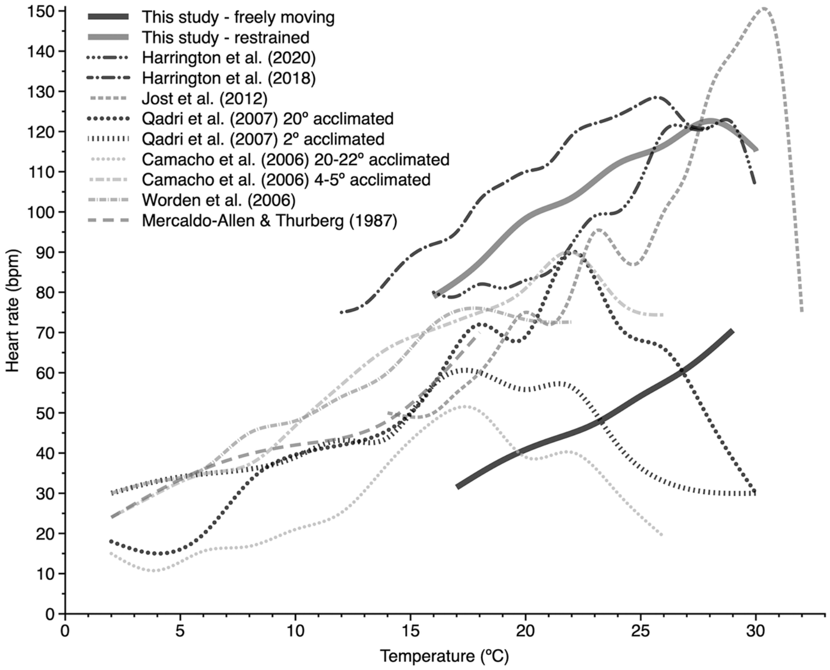

Figure 6. Comparative summary of heart rate (HR) responses to increasing water temperatures. Data from the current study and from reported values from previous studies show both the consistent effect of temperature on lobster HRs and the variability between methods. The rate at which the temperature was increased varied widely between studies, as did the amount of time lobsters were allowed to recover from being prepared for the experiment and the ramp starting temperatures. Note that lobsters that started at a lower temperature reached maximum HRs at cooler temperatures than lobsters that started at warmer temperatures. Nevertheless, the HR responses to increasing temperature were very similar up to 20 °C. After 20 °C, HR responses to temperature were more variable, and at >23 °C they tended to show break points in most studies.

because lobsters are nocturnal (Jury *et al.*, 2005; Golet *et al.*, 2006) and their HR generally increases at night (Chabot and Webb, 2008) and the freely moving lobsters experienced some of the warmest temperatures at night. This result could be because their metabolism was already elevated due to the warmer temperatures and so the metabolic cost of increased locomotion limited their activity. In a previous study, we observed a similar pattern when we exposed lobsters to a slow decrease in salinity while monitoring their activity and HRs (O'Grady, 2001). Initially, as we lowered the salinity, they became hyperactive, as if they were trying to avoid the low-salinity conditions (note that they were restrained on a treadmill in this experiment). However, when the salinity dropped close to lethal levels (10–12 psu), these lobsters stopped moving, presumably because they did not have sufficient energetic reserves to both move and osmoregulate (Jury *et al.*, 1994).

One of the goals of this study was to determine whether the upper critical thermal threshold of lobsters was associated with the temperatures they have been reported to avoid. Previously, we demonstrated that lobsters acclimated to summer water temperatures of 15–16 °C avoided water warmer than 23.5 °C (Crossin *et al.*, 1998). Based on the results from this study, and findings from other comparable published studies (Fig. 6; Table 1), depending upon experimental conditions, a water temperature of 26–27 °C is likely the upper critical temperature threshold for lobsters acclimated to 15–16 °C. Therefore, while certain areas might warm too fast for lobsters to avoid potentially lethal conditions, such as in estuaries or during marine heat waves (Monteiro *et al.*, 2023; Smith *et al.*, 2023), the more likely scenario is that warming oceans will lead to a change in the distribution of lobsters in places such as the GOM. It remains to be seen how such a change in their distribution will impact their overall reproductive output and abundance, but the potential repercussions are certainly important to investigate. Locating lobster thermoreceptors and determining their thresholds should lead to a better understanding of the neural mechanisms underlying lobster responses to warming waters.

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Literature Cited

ASMFC (Atlantic States Marine Fisheries Commission). 2015. *American Lobster Stock Assessment for Peer Review*. Atlantic States Marine Fisheries Commission, Washington, DC.

ASMFC (Atlantic States Marine Fishery Commission). 2020. *American Lobster Benchmark Stock Assessment and Peer Review Report*. Atlantic States Marine Fisheries Commission, Arlingon, VA.

Behan, J. T., C. T. Hodgdon, and Y. Chen. 2022. Scale-dependent assumptions influence habitat suitability estimates for the American lobster (*Homarus americanus*): implications for a changing Gulf of Maine. *Ecol. Model.* **470:** 110030.

Boudreau, S. A., S. C. Anderson, and B. Worm. 2015. Top-down and bottom-up forces interact at thermal range extremes on American lobster. *J. Anim. Ecol.* **84:** 840–850.

Camacho, J. S., A. Qadri, H. Wang, and M. K. Worden. 2006. Temperature acclimation alters cardiac performance in the lobster *Homarus americanus*. *J. Comp. Physiol. A* **192:** 1327–1334.

Carloni, J. T., and W. H. Watson III. 2018. Distribution of ovigerous American lobsters near the Isles of Shoals, New Hampshire. *Bull. Mar. Sci.* **94:** 555–570.

Carloni, J. T., R. A. Wahle, P. Geoghegan, and E. Bjorkstedt. 2018. Bridging the spawner-recruit disconnect: trends in American lobster recruitment linked to the pelagic food web. *Bull. Mar. Sci.* **94:** 719–735.

Casey, F., J. Churchill, G. Cowles, T. L. Pugh, R. A. Wahle, K. Stokesbury, and R. P. Glenn. 2023. The impact of ocean warming on juvenile American lobster recruitment off southeastern Massachusetts. *Fish. Oceanogr.* **32:** 229–244.

Chabot, C. C., and L. K. Webb. 2008. Circadian rhythms of heart rate in freely moving and confined American lobsters, *Homarus americanus*. *Mar. Freshw. Behav. Physiol.* **41:** 29–41.

Crossin, G. T., S. Abdulazziz Al-Ayoub, S. H. Jury, W. H. Howell, and W. H. Watson III. 1998. Behavioral thermoregulation in the American lobster *Homarus americanus*. *J. Exp. Biol.* **201:** 365–374.

Decker, H., N. Hellmann, E. Jaenicke, B. Lieb, U. Meissner, and J. Markl. 2007. Minireview: recent progress in hemocyanin research. *Integr. Comp. Biol.* **47:** 631–644.

Dijkstra, J. A., A. Litterer, K. Mello, B. S. O'Brien, and Y. Rzhanov. 2019. Temperature, phenology, and turf macroalgae drive seascape change: connections to mid-trophic level species. *Ecosphere* **10:** e02923.

Dove, A. D., B. Allam, J. J. Powers, and M. S. Sokolowski. 2005. A prolonged thermal stress experiment on the American lobster, *Homarus americanus*. *J. Shellfish Res.* **24:** 761–765.

Dufort, C. G., S. H. Jury, J. M. Newcomb, D. F. O'Grady, and W. H. Watson III. 2001. Detection of salinity by the lobster, *Homarus americanus*. *Biol. Bull.* **201:** 424–434.

Frederich, M., and E. R. Lancaster. 2024. Temperature thresholds of crustaceans in the age of climate change. Pp. 175–228 in *Frontiers in Invertebrate Physiology: A Collection of Reviews*, Vol. 2, *Crustacea*, S. Saleuddin, S. P. Leys, R. D. Roer, and I. C. Wilkie, eds. Apple Academic, New York.

Friedland, K. D., J. A. Langan, S. I. Large, R. L. Selden, J. S. Link, R. A. Watson, and J. S. Collie. 2020. Changes in higher trophic level productivity, diversity and niche space in a rapidly warming continental shelf ecosystem. *Sci. Total Environ.* **704:** 135270.

Friedland, K. D., S. Smoliński, and K. R. Tanaka. 2021. Contrasting patterns in the occurrence and biomass centers of gravity among fish and macroinvertebrates in a continental shelf ecosystem. *Ecol. Evol.* **11:** 2050–2063.

Friedland, K. D., K. R. Tanaka, S. Smoliński, Y. Wang, C. Hodgdon, M. Mazur, J. Wiedenmann, C. Goetsch, and D. E. Pendleton. 2023. Trends in area of occurrence and biomass of fish and macroinvertebrates on the Northeast U.S. Shelf ecosystem. *Mar. Coast. Fish.* **15:** e10235.

Friedland, K. D., H. du Pontavice, J. Palter, D. W. Townsend, P. Fratatoni, A. Silver, and A. Gangopadhyay. 2024. Regime change in northwest Atlantic sea surface temperatures revealed using a quantile approach. *Reg. Stud. Mar. Sci.* **71:** 103398.

Glenn, R. P., K. Whitmore, T. L. Pugh, J. Manning, M. Gibson, R. Wahle, L. Dellinger, A. DeCosta, T. Angell, and S. Wilcox. 2011. *Examining Settlement Dynamics of Postlarval American Lobster (*Homarus americanus*) in Lobster Management Area 2: Final Report to the Southern New England Collaborative Research Initiative*. NOAA, Washington, DC.

Goldstein, J. S., and W. H. Watson III. 2015a. The influence of natural inshore and offshore thermal regimes on egg development and time of hatch in the American lobster, *Homarus americanus*. *Biol. Bull.* **228:** 1–12.

Goldstein, J. S., and W. H. Watson III. 2015b. Seasonal movements of American lobsters in New Hampshire coastal waters: patterns, environmental triggers and implications for larval hatch. *Mar. Ecol. Prog. Ser.* **524:** 197–211.

Golet, W. J., D. A. Scopel, A. B. Cooper, and W. H. Watson III. 2006. Daily patterns of locomotion expressed by American lobsters (*Homarus americanus*) in their natural habitat. *J. Crustac. Biol.* **26:** 610–620.

Goode, A. G., D. C. Brady, R. S. Steneck, and R. A. Wahle. 2019. The brighter side of climate change: how local oceanography amplified a lobster boom in the Gulf of Maine. *Glob. Change Biol.* **25:** 3906–3917.

Gutzler, B. C., and W. H. Watson III. 2022. Measurements of American lobster heart rate and movements in the wild using a low-cost open source datalogger. *Mar. Biol.* **169:** 52.

Hardison, E. A., K. Karaskura, J. Van Wert, T. Nguyen, and E. J. Eliason. 2021. Diet mediates thermal performance traits: implications for marine ectotherms. *J. Exp. Biol.* **224:** 1–13.

Harrington, A. M. H., and H. J. Hamlin. 2019. Ocean acidification alters thermal cardiac performance, hemocyte abundance, and hemolymph chemistry in subadult American lobsters *Homarus americanus* H. Milne Edwards, 1837 (Decapoda: Malcostraca: Nephropidae). *J. Crustac. Biol.* **39:** 468–476.

Harrington, A. M., R. J. Harrington, D. A. Bouchard, and H. J. Hamlin 2020a. The synergistic effects of elevated temperature and CO_2-induced ocean acidification reduce cardiac performance and increase disease susceptibility in subadult, female American lobsters *Homarus americanus* H. Milne Edwards, 1837 (Decpoda: Astacidea: Nephropidae) from the Gulf of Maine. *J. Crustac. Biol.* **40:** 634–646.

Harrington, A. M., H. Haverkamp, and H. J. Hamlin. 2020b. Impedance pneumography for minimally invasive measurement of heart rate in late-stage invertebrates. *J. Vis. Exp.* **158:** e61096.

Howell, W. H., W. H. Watson III, and S. H. Jury. 1999. Skewed sex ratio in an estuarine lobster (*Homarus americanus*) population. *J. Shellfish Res.* **18:** 193–201.

Jost, J. A., S. M. Podolski, and M. Frederich. 2012. Enhancing thermal tolerance by eliminating the pejus range: a comparative study with three decapod crustaceans. *Mar. Ecol. Prog. Ser.* **444:** 263–274.

Jury, S. H., and W. H. Watson III. 2000. Thermosensitivity of the American lobster, *Homarus americanus* as determined by cardiac assay. *Biol. Bull.* **199:** 257–264.

Jury, S. H., and W. H. Watson III. 2013. Seasonal and sexual differences in the thermal preferences and movements of American lobsters. *Can. J. Fish. Aquat. Sci.* **70:** 1650–1657.

Jury, S. H., M. T. Kinnison, W. H. Howell, and W. H. Watson III. 1994. Metabolic responses of lobsters exposed to reduced salinity. *J. Exp. Mar. Biol. Ecol.* **176:** 167–185.

Jury, S. H., C. C. Chabot, and W. H. Watson III. 2005. Daily and circadian rhythms of locomotor activity in the American lobster, *Homarus americanus*. *J. Exp. Mar. Biol. Ecol.* **47:** 606–612.

Jury, S. H., T. L. Pugh, H. Henninger, J. T. Carloni, and W. H. Watson III. 2019. Patterns and possible causes of skewed sex ratios in American lobster (*Homarus americanus*) populations. *Invertebr. Reprod. Dev.* **63:** 189–199.

Kleisner, K. M., M. J. Fogarty, S. McGee, J. A. Hare, S. Moret, C. T. Perretti, and V. S. Saba. 2017. Marine species distribution shifts on the U.S. northeast continental shelf under continued ocean warming. *Prog. Oceanogr.* **153:** 24–36.

Klymasz-Swartz, A. K., G. J. P. Allen, J. R. Treberg, G. R. Yoon, A. Tripp, A. R. Quijada-Rodriguez, and D. Wihrauch D. 2019. Impact of climate change on the American lobster (*Homarus americanus*): physiological responses to combined exposure of elevated temperature and pCO_2. *Comp. Biochem. Physiol.* **235:** 202–210.

Lagerspetz, K. Y. H., and L. A. Vainio. 2006. Thermal behaviour of crustaceans. *Biol. Rev.* **81:** 237–258.

Lawton, P., and K. Lavalli. 1995. Postlarval, juvenile, adolescent, and adult ecology. Pp. 47–88 in *Biology of the Lobster* Homarus americanus, J. R. Factor, ed. Academic Press, San Diego, CA.

LeBris, A., K. E. Mills, R. A. Wahle, Y. Chen, M. A. Alexander, A. J. Allyn, J. G. Schuetz, J. D. Scott, and A. J. Pershing. 2018. Climate vulnerability and resilience in the most valuable North American fishery. *Proc. Natl. Acad. Sci. U.S.A.* **115:** 1831–1836.

Lotze, H. K., S. Mellon, J. Coyne, M. Betts, M. Burchell, K. Fennel, M. A. Dusseault, S. D. Fuller, E. Galbraith, L. Garcia Suarez *et al.* 2022. Long-term ocean and resource dynamics in a hotspot of climate change. *FACETS* **7:** 1142–1184.

Lyons, G. N., L. G. Halsey, E. C. Pope, J. D. Eddington, and J. D. R. Houghton. 2013. Energy expenditure during activity in the American lobster *Homarus americanus*: correlations with body acceleration. *Comp. Biochem. Physiol. A* **166:** 278–284.

Mazur, M. D., K. D. Friedland, M. C. McManus, and A. G. Goode. 2020. Dynamic changes in American lobster suitable habitat distribution on the Northeast U.S. Shelf linked to oceanographic conditions. *Fish. Oceanogr.* **29:** 349–365.

McGaw, I. J., and S. J. Nancollas. 2018. Experimental setup influences the cardiovascular responses of decapod crustaceans to environmental change. *Can. J. Zool.* **96:** 1043–1052.

McGaw, I. J., and S. J. Nancollas. 2021. Patterns of heart rate and cardiac pausing in unconfined resting decapod crustaceans. *J. Exp. Zool. A* **2021:** 1–13.

McLeese, D. 1956. Effects of temperature, salinity and oxygen on the survival of the American lobster. *J. Fish. Res. Board Can.* **13:** 247–272.

McLeese, D., and D. Wilder. 1958. The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. *J. Fish. Board Can.* **15:** 1345–1354.

McMahon, B. R. 1999. Intrinsic and extrinsic influences on cardiac rhythms in crustaceans. *Comp. Biochem. Physiol. A* **124:** 539–547.

McMahon, B. R., and J. L. Wilkens. 1975. Respiratory and circulatory responses to hypoxia in the lobster *Homarus americanus*. *J. Exp. Biol.* **562:** 637–652.

Mercaldo-Allen, R., and F. Thurberg. 1987. Heart and gill ventilatory activity in the lobster, *Homarus americanus*, at various temperatures. *Fish. Bull.* **85:** 643–644.

Mills, K. E., A. J. Pershing, C. J. Brown, Y. Chen, F.-S. Chiang, D. S. Holland, S. Lehuta, J. A. Nye, J. C. Sun, A. C. Thomas, and R. A. Wahle. 2013. Fisheries management in a changing climate: lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* **26:** 191–195.

Monteiro, M., S. L. P. de Castro, S. C. Marques, R. Freitas, and U. M. Azeiteiro. 2023. An emergent treat: marine heatwaves. Implications for marine decapod species: an overview. *Environ. Res.* **229:** 116004.

Morse, R. E., K. D. Friedland, D. Tommasi, C. Stock, and J. Nye. 2017. Distinct zooplankton regime shift patterns across ecoregions of the U.S. Northeast continental shelf Large Marine Ecosystem. *J. Mar. Syst.* **165:** 77–91.

Munro, J., and J. C. Therriault. 1983. Migrations saisonnieres du homard (*Homarus americanus*) entre la cote et les lagunes des Ilesde-la-Madeleine. *Can. J. Fish. Aquat. Sci.* **40:** 905–918.

Nielsen, T. V., and I. J. McGaw. 2016. Behavioral thermoregulation and trade-offs in juvenile lobster *Homarus americanus*. *Biol. Bull.* **230:** 35–50.

NMFS (National Marine Fisheries Service). 2019. U.S. commercial landings. [Online]. Available: www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings-with-group-subtotals/index [2021, January 5].

Nye, J. 2010. *State of the Gulf of Maine Report: Climate Change and Its Effects on Ecosystems, Habitats and Biota*. NOAA and the Gulf of Maine Council on the Marine Environment, Woods Hole, MA.

O'Grady, D. F. 2001. Changes in heart and ventilation rates during locomotion in the American lobster. MS thesis, University of New Hampshire, Durham.

O'Grady, D. F., S. H. Jury, and W. H. Watson III. 2001. Use of a treadmill to study the relationship between walking, ventilation and heart rate in the lobster *Homarus americanus*. *Mar. Freshw. Res.* **52:** 1387–1394.

Paterson, W. D., and J. E. Stewart. 1974. *In vitro* phagocytosis by hemocytes of the American lobster (*Homarus americanus*). *J. Fish. Res. Board Can.* **31:** 1051–1056.

Pauly, D., S. A. Upali, E. Chu, K. Meirelles F. Freire, E. Vázquez, and M. J. Butler IV. 2022. The growth, respiration, and reproduction of crustaceans: a synthesis through the gill-oxygen limitation theory (GOLT). *J. Crustac. Biol.* **42:** 1–13.

Pearce, J., and N. Balcom. 2005. The 1999 Long Island Sound lobster mortality event: findings of the comprehensive research initiative. *J. Shellfish Res.* **24:** 691–697.

Pershing, A. J., M. A. Alexander, C. M. Hernandez, L. A. Kerr, A. Le Bris, K. E. Mills, J. A. Nye, N. R. Record, H. A. Scannell, J. D. Scott *et al.* 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* **350:** 809–812.

Pershing, A. J., M. A. Alexander, D. C. Brady, D. Brickman, E. N. Curchitser, A. W. Diamond, L. McClenachan, K. E. Mills, O. C. Nichols, D. E. Pendleton *et al.* 2021. Climate impacts on the Gulf of Maine ecosystem: a review of observed and expected changes in 2050 from rising temperatures. *Elementa* **9:** 1.

Pinsky, M. L., A. M. Eikeset, D. J. McCauley, J. L. Payne, and J. M. Sunday. 2019. Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* **569:** 108–111.

Pinsky, M. L., R. L. Selden, and Z. J. Kitchel. 2020. Climate-driven shifts in marine species ranges: scaling from organisms to communities. *Annu. Rev. Mar. Sci.* **12:** 153–179.

Pörtner, H.-O., C. Bock, and F. C. Mark. 2017. Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. *J. Exp. Biol.* **220:** 2685–2696.

Powell, D. J., E. Owens, M. M. Bergsund, M. Cooper, P. Newstein, E. Berner, R. Janmohamed, and P. S. Dickinson. 2023. The role of feedback and modulation in determining temperature resiliency in the lobster cardiac nervous system. *Front. Neurosci.* **17:** 1113843.

Pugh, T. L., R. Glenn, and W. H. Watson III. 2023. Spatial differences in female lobster mating success and population characteristics in southern Massachusetts. *Mar. Ecol. Prog. Ser.* **718:** 69–84.

Qadri, S. A., J. Camacho, H. Wang, J. R. Taylor, M. Grosell, and M. K. Worden. 2007. Temperature and acid-base balance in the American lobster *Homarus americanus*. *J. Exp. Biol.* **210:** 1245–1254.

R Core Team. 2022. R: a language and environment for statistical computing. [Online]. R Foundation for Statistical Computing, Vienna. Available: https://www.R-project.org.

Reynolds, W. W., and M. E. Casterlin. 1979. Behavioral thermoregulation and activity in *Homarus americanus*. *Comp. Biochem. Physiol. A* **64:** 25–28.

Smith, K. E., M. T. Burrows, A. J. Hobday, N. G. King, P. J. Moore, A. S. Gupta, M. S. Thomsen, T. Wernberg, and D. A. Smale. 2023. Biological impacts of marine heatwaves. *Annu. Rev. Mar. Sci.* **15:** 119–145.

Staudinger, M. D., K. E. Mills, K. Stamieszkin, N. R. Record, C. A. Hudak, A. Allyn, A. Diamond, K. D. Friedland, W. Golet, M. E. Henderson *et al.* 2019. It's about time: a synthesis of changing phenology in the Gulf of Maine ecosystem. *Fish. Oceanogr.* **28:** 532–566.

Steenbergen, J. F., S. M. Steenbergen, and H. C. Shapiro. 1978. Effects of temperature on phagocytosis in *Homarus americanus*. *Aquaculture* **14:** 23–30.

Stenseng, E., C. E. Braby, and G. N. Somero. 2005. Evolutionary and acclimation-induced variation in the thermal limits of heart function in congeneric marine snails (genus *Tegula*): implications of vertical zonation. *Biol. Bull.* **208:** 138–144.

Stillman, J. H. 2019. Heat waves, the new normal: summertime temperature extremes will impact animals, ecosystems, and human communities. *Physiology* **34:** 86–100.

Szuwalski, C. S., K. Ayadin, E. J. Fedewa, B. Garber-Yonts, and M. A. Litzow. 2023. The collapse of eastern Bering Sea snow crab. *Science* **382:** 306–310.

Tanaka, K. R., M. P. Torre, V. S. Saba, C. A. Stock, and Y. Chen. 2020. An ensemble high-resolution projection of changes in the future habitat of American lobster and sea scallop in the Northeast US continental shelf. *Divers. Distrib.* **26:** 987–1001.

Twiname, S., Q. P. Fitzgibbon, A. J. Hobday, C. G. Carter, M. Oellermann, and G. T. Pecl. 2020. Mismatch of thermal optima between performance measures, life stages and species of spiny lobster. *Sci. Rep.* **10:** 21235.

Verberk, W. C. E. P., J. Overgaard, R. Ern, M. Bayley, T. Wang, L. Boardman, and J. S. Terblanche. 2016. Does oxygen limit thermal tolerance in arthropods? a critical review of current evidence. *Comp. Biochem. Physiol. A* **192:** 64–78.

Watson, W. H., III, A. Vetrovs, and W. H. Howell. 1999. Lobster movements in an estuary. *Mar. Biol.* **134:** 65–75.

Weineck, K. I., A. J. Ray, L. J. Fleckenstein, M. Medley, N. Dzubuk, E. Piana, and R. L. Cooper. 2018. Physiological changes as a measure of crustacean welfare under different standardized stunning techniques: cooling and electroshock. *Animals* **8:** 158.

Wilkens, J. L., L. A. Wilkens, and B. R. McMahon. 1974. Central control of cardiac and scaphognathite pacemakers in the crab, *Carcinus maenas*. *J. Comp. Physiol.* **90:** 89–104.

Worden, M. K., C. M. Clark, M. Conaway, and S. A. Qadri. 2006. Temperature dependence of cardiac performance in the lobster *Homarus americanus*. *J. Exp. Biol.* **209:** 1024–1034.