

Thermal Preference and Tolerance of Alvinellids

Peter R. Girguis^{1*} and Raymond W. Lee^{2*}

The thermal tolerance of marine animals has been debated for some time (1, 2). At deep-sea hydrothermal vents, temperatures can exceed 350°C, although nearly all vent animals live at temperatures below 30°C. However, the polychaete worms *Alvinella pompejana* and *Paralvinella sulfincola* (family Alvinellidae) live directly on high-temperature vents in the Eastern and Northeastern Pacific, respectively, where temperatures up to 81° and 90°C have been measured around *A. pompejana* and *P. sulfincola* tube openings (1, 3, 4). Although it has been suggested that alvinellids thrive at these temperatures (1), earlier studies have found that the rapid mixing of hot vent fluids and cold seawater produces a dynamic thermal regime that is difficult to characterize (3, 5). As such, it is impractical to ascertain alvinellid thermotolerance via in situ measurements. To determine directly *P. sulfincola* thermal tolerance and preference, we developed a high-pressure aquarium that mimics the thermal gradients found in situ, allows the worms to occupy their preferred thermal regime, and permits viewing of the worms' distribution within the aquarium (fig. S1). Our results show that *P. sulfincola* are thermotaxic and extremely thermotolerant, preferring temperatures between 40° and 50°C, with individuals surviving 7 hours of chronic exposure to 50°C and 15 min of acute exposure to 55°C (Fig. 1, B and C).

During all trials, *P. sulfincola* were placed at random into the aquarium, and then the aquarium was repressurized to in situ pressures. The aquarium was flushed with seawater resembling vent effluent (6) and maintained at room temperature (26°C) for 1 hour. Soon after, worms began moving within the chamber, although their distributions remained haphazard. When the heating and cooling units were activated to establish a stable thermal gradient of 20° to 61°C, *P. sulfincola* rapidly migrated toward warmer regions, and by 45 min, all worms were in regions above 40°C (Fig. 1, A to C). During the second trial, four worms migrated into the 50°C region and remained there for the duration of the experiment (2.25 hours), exhibiting typical behaviors such as gill irrigation (Fig. 1B). One worm migrated into 55°C for 15 min before returning to cooler regions (Fig. 1B). During the third trial, two worms remained at 50°C for 7

hours (the duration of the experiment), once again irrigating their gills (Fig. 1C). At the end of all three trials, temperature was returned to a uniform 26°C and worms migrated to the formerly hotter regions of the aquarium. All worms survived the thermal gradient trials, exhibiting typical behaviors for at least 24 hours. However, when the aquarium was uniformly heated to 55°C for two hours, all worms ($N = 4$) showed signs of physiological dysfunction such as severe contortion, and were not visibly active when temperature was returned to 26°C. When the aquarium was uniformly heated to 60°C, all worms ($N = 5$) died within minutes. In a separate trial, *Paralvinella palmiformis*, a congener that inhabits diffuse vents with cooler temperatures, was subjected to a 20° to 55°C thermal gradient, and the worms consistently avoided temperatures above 35°C (Fig. 1D).

In light of its ability to tolerate high temperatures, *P. sulfincola* is among the most

thermotolerant of animals. By comparison, the aquatic ostracod *Potamocypris* sp. exhibited 50% mortality when exposed to 50°C for 1 hour (7), and the ant *Cataglyphis bicolor* exhibited systemic dysfunction when exposed to 55°C for 1 min (8). The fungi *Chaetomium thermophile* grows at temperatures up to 55°C, making it the most thermotolerant eukaryote known (9).

To our knowledge, *P. sulfincola* is the only animal that prefers chronic exposure to such high temperatures. Although the behaviors and mechanisms underlying this thermo-preference and tolerance remain unknown, this capacity may enable *P. sulfincola* to exploit resources inaccessible to other organisms such as the microbial mats that grow at higher temperatures.

The results presented here are the first direct measure of alvinellid thermotolerance and preference, and they emphasize the difference between acute and chronic tolerance. These results also illustrate the utility of conducting thermal gradient experiments that can provide a more accurate depiction of an organism's thermal biology. Similar experiments may be applied to other species, including *Alvinella pompejana* (10). Regardless, all metazoans may be constrained to living in environs below 55°C, the temperature at which mitochondria appear to dysfunction (11). Further investigations into alvinellids and other animals that live in thermally challenging environments will help better our understanding of the thermal constraints on metazoan life.

References and Notes

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Supporting Online Material

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Materials and Methods

Fig. S1

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¹Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA. ²School of Biological Sciences, Washington State University, Pullman, WA 99164, USA.

*To whom correspondence should be addressed. E-mail: rlee@mail.wsu.edu (R.W.L.); pgirguis@oeb.harvard.edu (P.R.G.)

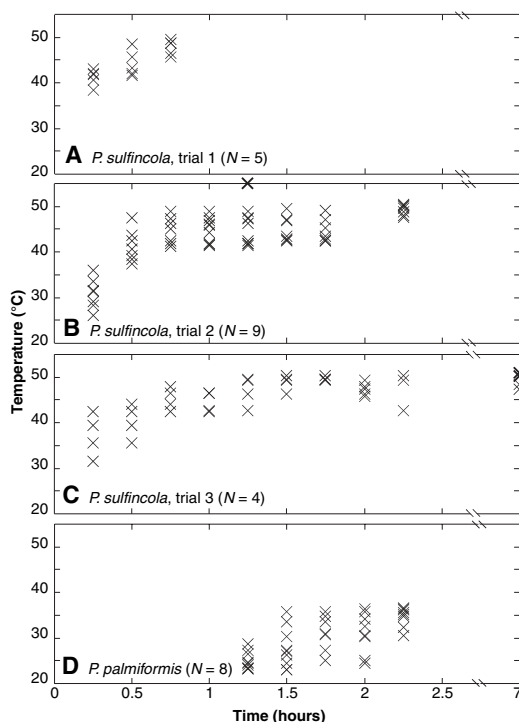


Fig. 1. Distribution of *P. sulfincola* and *P. palmiformis* worms in temperature-gradient experiments. Worms were uniformly dispersed within the aquaria before establishing the temperature gradient. (A to C) Plots of *P. sulfincola* distributions over time within a 20° to 61°C gradient; $N = 5, 9,$ and 4 individuals, respectively. (D) Plot of *P. palmiformis* distributions over time within a 20° to 55°C gradient; $N = 8$ individuals.