Intertidal sand dollar *Dendraster excentricus* larvae are resilient to high temperatures in early development and at settlement.

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REU Blinks Research Program 2025

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Keywords: Sand dollars, Settlement, Thermal tolerance, Larval development, Echinoderms, *Dendraster excentricus*

Abstract

Understanding how different stages in the life cycles of benthic marine invertebrates respond to environmental stressors is essential for predicting future population dynamics and can be critical to the management and conservation of species. With the rise of global warming and its effects on the ocean, this study examined the effects of temperature and chemical cues on early larval development and settlement success in the sand dollar *Dendraster excentricus*. Adults collected from an intertidal population on Orcas Island, WA. Individuals were spawned, and embryos and larvae were cultured under controlled laboratory conditions across a range of temperatures representative of typical intertidal field conditions. Data on early development and settlement under temperature and chemical cues were recorded. Results showed that elevated temperatures for 24 hours starting at fertilization accelerated developmental rates and produced abnormalities starting at 25°C. In contrast, temperatures as high as 30°C had no detectable effect on larval settlement but were lethal at 35°C. Additionally, the presence of sand as a cue for settlement had a significant effect on settlement decisions. These findings highlight *D. excentricus* as a model for thermal resilience and underscore the importance of thermal variability and extremes and the different sensitivities found at different stages in the life cycles of benthic marine invertebrates. More broadly, this work provides insight into how rising ocean temperatures may influence recruitment dynamics in benthic communities.

Introduction

Increasing sea temperatures in response to global warming are a growing critical pressure on marine organisms. High temperatures can lead to prolonged periods of stress, and this exposure can promote alterations in marine species composition and ecosystem functionality (Venegas et al., 2023). Temperature stress in marine invertebrates strongly shapes their development. Among the most sensitive processes are early developmental stages, which often exhibit narrow thermal tolerances and are at risk of mortality under warming thermal conditions (Byrne, 2011). Environmental warming can accelerate growth, but associated increased stress and shifts in developmental rates frequently cause abnormalities and can ultimately lead to premature death and failure of individuals, populations, and even species to survive. Since larval survival determines dispersal and recruitment, potentially lethal thermal conditions can become strong limiting factors that may shape population and species geographic distributions (Andrikov, 1975).

In species with complex life cycles, like echinoderms, metamorphosis is one of the most critical stages. Larval settlement marks the transition from planktonic to a benthic juvenile stage. Dispersal occurs largely in the larval phase of benthic marine invertebrates, and so, they can be key drivers of population dynamics and distribution in the long term (Prado et al., 2012). In free-spawning echinoderms, embryos and larvae are the primary stage to cover large distances, as the benthic juvenile and adult do not move as extensively. After being carried by currents and evading predation, their settlement decision affects long-term population dynamics and larval recruitment. Larval readiness for settlement is referred to as “competence”, the stage in which larvae lose some larval features in exchange for metamorphosis when exposed to the appropriate chemical cues. (Hadfield et al., 2001; Hodin et al., 2015; Pawlik, 1992). In echinodis, turbulence has been found to be one of the physical factors that can induce the developmental shift to settlement from a competent larva (Hodin et al., 2018; Gaylord et al, 2013).

Temperature effects are well-documented for echinoderm development, with studies showing changes in growth, morphology, reproduction, and survival across thermal ranges. For instance, sea urchins reared at higher temperatures (14°C vs. 18°C) exhibited larger body size (Wilkins et al., 2024). However, the intersection between the effect of temperature stress and settlement cues is understudied. Like echinoderms, corals have a biphase lifecycle with planktonic larval and benthic adult stages, and their larvae have been shown to change settling behaviour when ambient seawater temperature was increased by 3℃ (Putnam et al., 2008). This work suggests that temperature could disrupt settlement in echinoderms as well, and understanding its impacts could help predict future recruitment dynamics as the temperature rises.

Sand dollars, specifically *D. excentricus,* represent a unique model to explore the intersection of these different temperature effects. Despite their ecological importance and ecosystem engineers, few thermal studies have been done on them. Existing work reveals that thermal tolerances in *D. excentricus* are much higher than other echinoderms in the same geographic region (Bingham, 1997; Podolsky & Emlet, 1993; Abdel-Raheem and Allen, 2019). It has been shown that their larvae survive and develop rapidly at high thermal limits, of 20- 25 °C, with higher temperatures even increasing the fertility of the adults (George, 2008; Leuchtenberger et al., 2022). Other studies have found that environmental cues that induce settlement are turbulence and sand from adult populations (Hodin, 2015; Highsmith, 1992; Strathmann, 1987).

The effects were examined by using a Salish Sea population of *D. excentricus* that has adapted to an intertidal environment, exposed to a daily fluctuation in temperatures, conditions that can change adult behaviours, and would have great effects on the larvae. Bingham et al. (1997)

studied this same population and compared the intertidal early embryonic thermal resilience with a subtidal population. They found that both populations had similar normal development from 7-26 °C. However, higher temperatures (22-26 °C) had drastic effects on the rate of embryonic cleavage, where the subtidal population rate decreased with increasing temperature. Overall, their findings suggested that the differences they saw between populations were a result of the environmental phenotypic plasticity rather than genetic differentiation. This study expands on the use of sand dollars as a valuable comparative model to study temperature effects and larval development.

The primary objective of this study was to determine how temperature affects development and settlement in intertidal *D. excentricus* from fertilization to different larval stages, to settlement. We gathered data on 1) early development of embryonic stages exposed to a range of temperatures, and 2) evaluated if the larval decision to settle and undergo metamorphosis was affected by chemical cues and/or temperature. These experiments test our hypotheses that high temperatures will accelerate the development of embryos and larvae and that high temperatures will cause larvae to decide against settlement when temperatures are at an upper limit.

Methods

Collection and maintenance

D. excentricus were collected from Crescent Beach, Orcas Island, WA (48°41'41.9"N 122°53'44.8"W) on May 5 and July 12, 2025. Animals were kept in open-air sea tables with constant water flow. Food was provided by a constant water flow coming from the ocean.

Temperature Loggers

We used two HOBO TidbiT v2 Water Temperature Data Loggers (Onset Company, Bourne, MA) placed at the upper intertidal edge of the Sand Dollar bed in Crescent Beach. Loggers were strapped to bricks that were buried in the sand and served to hold the loggers at the sand surface for extended periods. Data was extracted from the loggers in the field 12 days later, covering 24 tidal cycles, going from July 13 to July 25, 2025. HOBOware application. We assume that these temperatures are the ones that *D. excentricus* is exposed to in the summer months and were used for the experimental design. Data was run through R to make the graph.

Spawning and fertilization

A. Thermotolerance Experiments

Under guidance of Dr. Jason Hodin, adult Crescent Beach sand dollars were spawned and fertilized, with two adults used for each thermotolerance experiment. In brief: A syringe needle containing 0.5 M KCl was used to inject 0.5-0.8 ml into the gonad, going through the mouth (and perivisceral coelom) at an angle. After injection, individuals were gently shaken and placed on the table, making sure to keep them moist while they released eggs or sperm from their gonopores, located on the aboral side. When a female released eggs, (transparent with red/pink pigment vesicles surrounding egg jelly) they were placed aboral side down on a 250 ml beaker filled to the brim with 1μm sand-filtered seawater. On the other hand, when males released sperm, concentrated sperm was collected by extracting a “notch” using a 1.5 ml glass pipette. A single notch of sperm was later added to a 15 ml test tube and diluted with 10 ml of filtered seawater to use for fertilization.

To prepare for fertilization, we cut the tip off of a plastic pipette to avoid damaging the eggs when pipetting and filled a 600 ml beaker with 400 ml of filtered seawater. We then took a plastic 2 ml pipette full of the eggs and added them to the beaker, plus 20 drops of the diluted sperm solution. With the same pipette, we mixed the eggs and sperm around to increase the chances of fertilization (Hodin et al., 2015). Fertilization was allowed to proceed for 10 minutes without disturbance, allowing the eggs to settle to the bottom of the beaker. Washed the eggs with fresh filtered seawater to avoid polyspermy. To evaluate fertilization success, an aliquot of embryos was visually evaluated on a dissecting microscope. Shortly after spawning, sand dollar adults were returned to their tanks to ensure their health and well-being.

B. Settlement Experiment

Under guidance of Dr. Sophie George, we spawned and fertilized embryos for the settlement experiment. Five sand dollar adults were used for spawning: three females and two males. We induced spawning by injecting approximately 0.2 ml of 0.55M KCL into the mouth cavity of the individual and laid each of them aboral-side-down in a bowl filled to the brim with filtered seawater. These techniques are widely used to spawn echinoids. Sand dollars started spawning within 5 minutes. We collected and imaged spawned eggs using a HAYEAR digital camera attached to a trinocular compound microscope Nikon Eclipse Ci, Remaining eggs were combined, rinsed twice through a 300µm Nitex mesh to remove debris, and poured into a 1000 ml beaker containing approximately 900 ml of 0.45µm fresh filtered seawater. Sperm were also rinsed through a 75µm Nitex mesh into a 20 ml beaker. Eggs were fertilized by adding 6 drops of sperm with a 1.5 ml glass pipette. Fertilization success was 90% (Fig.1).

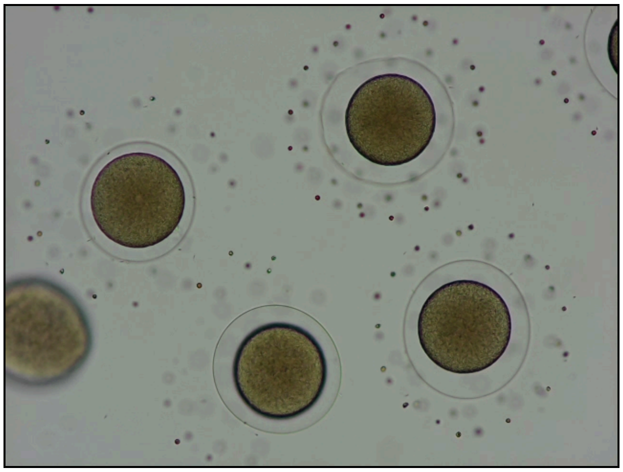

Fig.1. *Successful fertilization of Dendraster excentricus*. Fertilization membranes rose after exposure to sperm, marking successful fertilization.

C. *Tolerance Experiment*

Following fertilization, embryos were uniformly suspended in 600 ml of filtered seawater and 50 ml aliquots were distributed into 27 bowls, resulting in three replicates for each of nine temperatures (5, 8, 10, 15, 20, 25, 28, 30, 35°C). Bowls of embryos were maintained in incubators calibrated to each of the 9 temperatures. Subsamples of embryos per replicate were fixed at one hour and at twenty-four hours in PFA fixative (4% paraformaldehyde in PBS). Pictures and videos were collected at the time of fixation.

D. *Larval Culturing*

Larval growth and development were followed using fertilized eggs from previous fertilization (section B). Two treatments were performed: Ambient temperature conditions (CA) of 10-16°C and high temperature (MHW) conditions of 20°C. To determine the total number of embryos, we obtained five 1 ml samples from one of our stock jars and counted the number of embryos per sample using a trinocular compound microscope Nikon Eclipse Ci. We estimated an average of 38.4 embryos per ml, or 38,400 embryos per 1000ml. Based on this calculation, we added 15.6

mL of stock jar embryos to each culture jar filled with 1500ml of filtered seawater, with three replicate jars per treatment. High temperature treatment culture jars were placed in a sea table at 20°C, while ambient treatment culturing jars were placed in a second water table that varied between 10 °C and 16°C, as determined by local ambient seawater conditions at the time.

Three heating rods were used to maintain sea table temperature for the high-temperature 20°C treatment (MHW). INKBIRD sensors were used to monitor and record ambient and treatment temperatures and to ensure heating rods were functioning correctly. In addition, HOBO Tidbit MX2202 Temperature 400' Data Loggers were placed in each tank to record the temperature. To distribute algal food in larval culturing jars, a paddle was placed in each jar. A system of paddles swung gently from side to side in each jar throughout the duration of the experiment, driven by a small electric motor. Larvae were fed every two days, and water was changed twice a week. Each jar was given a mixture of cultured algae: 3.0 ml of *Dunalliela tertiolecta*, 1.5 ml of *Rhodomonas* spp, and 1.0 ml of *Isochrysis galbana.* This was equivalent to between 1000-2000 cells of Dunaliella and Rhodomonas and up to 10,000 cells of Isochrysis. As larvae developed, algal concentration was increased with a maximum of 5000 cells per ml of Dunaliella.

Settlement

To prepare the settlement experiment, we collected sand from adult sand dollar tanks to provide a chemical cue or cues of adult habitat to induce larval settlement. Specifically, we sieved the sand down to <150µm so that it would be smaller than larvae and newly-settled juveniles, the small sand size allowing us to identify and collect animals after treatments. We also leached 50 ml plastic tubes with RO H_20 for 24 hours before use in the experiment.

Competent larvae (see section D) were used in the experiment. Given differences in time to competence for settlement at different temperatures, high temperature treatment (MHW) larvae were used at 12 days post-fertilization, while ambient treatment larvae (CA) were used at 22 days post-fertilization. Each treatment consisted of sand present vs absent and temperatures of 10°C vs 20°C vs 30°C. Leached 50 ml tubes were filled with 18ml of filtered seawater, 1.5ml of seawater containing 15 larvae, and either 2ml seawater with sand or no sand. Tubes were placed at treatment temperatures for 8 hours and then returned to their original culturing temperature until 24-hours post-settlement induction. All larvae/juveniles were PFA fixed at 24 hours after the treatment. Fixed samples were washed with phosphate-buffered saline (PBS), and larvae were extracted.

To determine the number of *Dendraster excentricus* individuals that had successfully settled and metamorphosed into juveniles versus those that remained as swimming larvae, the contents of each test tube were placed into a counting tray and counted using a hand counter and a stereo microscope. Each treatment consisted of 15 individuals with three replicates per condition. Due to an error in measuring competence during the initial marine heatwave (MHW) treatment(12 days post fertilization), a second MHW exposure was conducted after 22 days to compare larval response at the same developmental stage as the constant ambient treatment. However, this follow-up trial included only one replicate due to limited larval availability. Proportion of juveniles out of 15 was calculated, and statistical analyses were performed using R.

Mortality testing of competence larvae was performed using a mixed leftover culture. We separated 50 larvae into 1000ml beakers and put them into incubators at 10, 20, 30, and 35°C for 8 hours. We counted larvae that survived or died.

Results

Temperature

Temperature logger data indicated that sand dollars experience a broad range of temperatures in the intertidal. Temperatures were recorded from two sample sites at Crescent Beach at the edges of the sand dollar bed. Temperatures at the tidal flat fluctuated considerably over a 13-day period from July 13 to July 26, 2025. The temperatures ranged from 11.71℃ to 32.02℃, with rapid declines associated with incoming water of daily tidal cycles, plus 4-5 cloudy days in the middle of the sampling period (Fig. 2). These helped us understand the range of temperatures that the tidal flat and the sand dollars are exposed to. If the adults spawn at all of these temeperature ranges, the larvae will also be exposed. Based on field observations, we realized that individuals would bury themselves in the sand as the tide went out, possibly protecting themselves from the high heat. We were not sure what larval strategies are during low tides but assume here that they would stay in the pools of the tidal flats, exposed to the recorded temperatures.

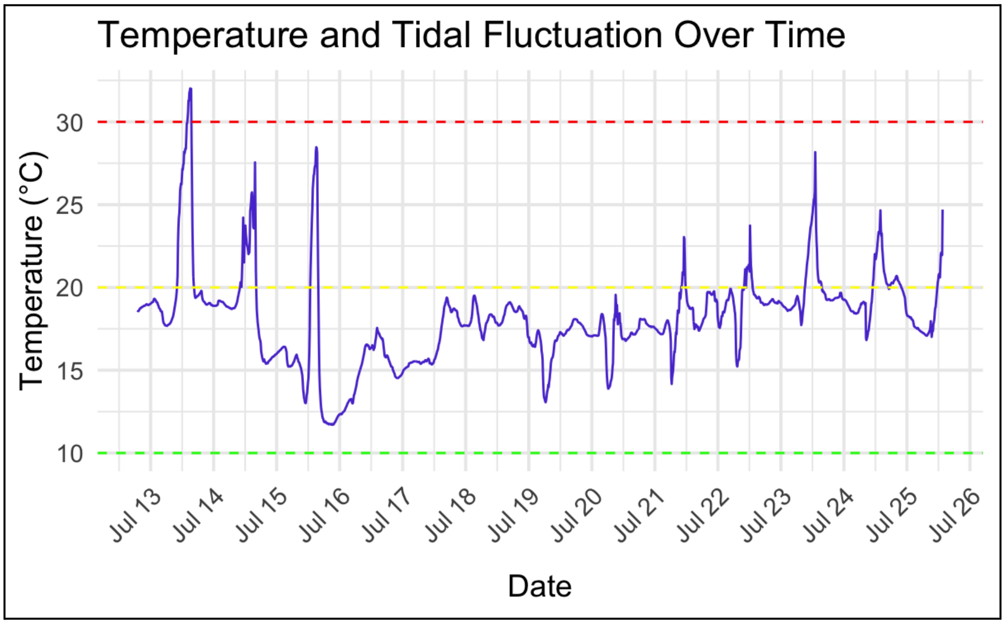

Fig.2. *Temperature fluctuations in Crescent Beach, Orcas Island, WA, over a period of 2 weeks in July, 2025.* Dotted lines show ranges that were used in Settlement experiments to simulate field data.

Tolerance

Embryonic development rate of *D. excentricus* showed strong temperature dependence when tested over the first 24 hours after fertilization (Fig. 3). At low temperatures (5°C), embryos displayed mortality and failed to reach the 32-cell stage, whereas development appeared successful and at a normal rate between 8°C and 20°C, even reaching the early two-arm stage. However, at 25°C, morphological abnormalities became apparent with arms at disparate lengths and abnormally shaped bodies. Embryos exposed to even higher temperatures (28°C, 30°C, 35°C) failed to develop normally and mortality was observed, where cells seemed to disintegrate and become a "soup" by 24 hours post-fertilization.

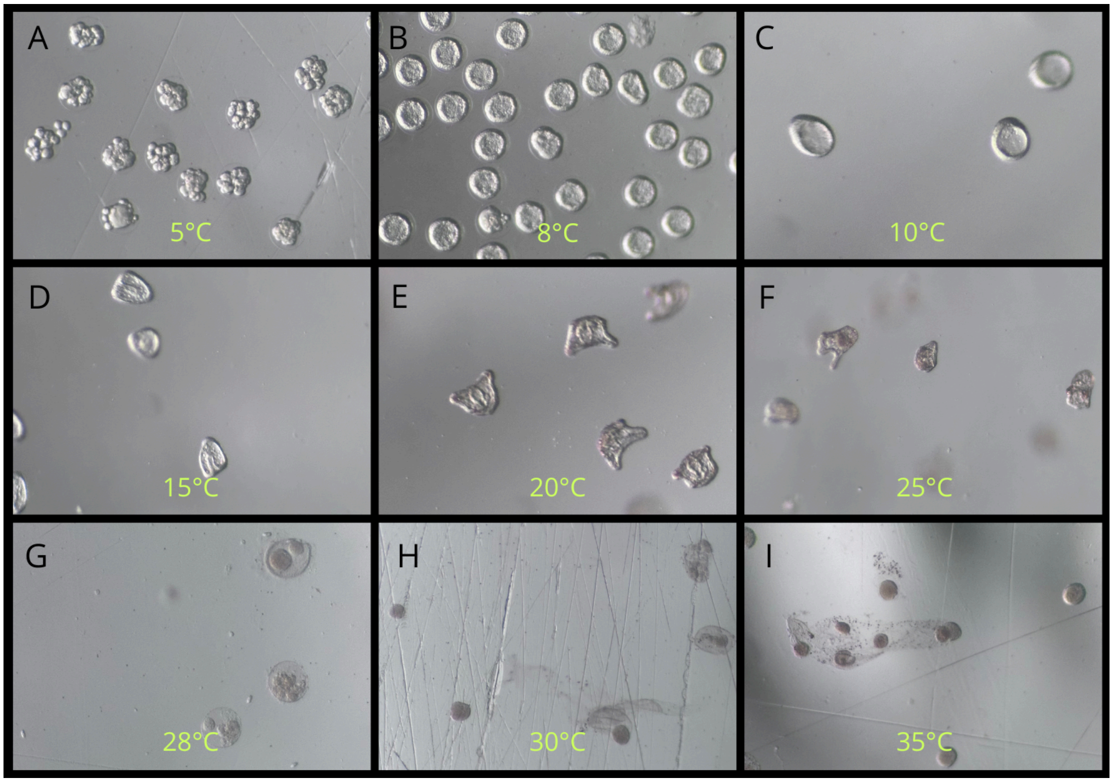

Fig.3. *Temperature Tolerance of Embryos after 24 hours.* Treatments included: A) 5°C, B) 8°C, C) 10°C, D) 15°C, E) 20°C, F) 25°C, G) 28°C, H) 30°C, I) 35°C. At 25°C, physiological abnormalities started to present and after 28°C embryo did not reach 32-cell stage.

Settlement

Test done to rectify that the experimental temperatures used were not deadly to the larvae and we could have results and not account for mortality. There was no mortality for the 10°C, 20°C, and 30°C but as soon as the temperature was 35°C , all larvae perished.

Temperature	Live	Dead
10°C	50	0
20°C	49	1
30°C	50	0
35°C	0	50

Fig.4. *Mortality of competent D. excentrius after 8 temperature treatments at 10C, 20C and 30C.* We foud that 100% of larvae perished at 35C while 98-100% survived in all the other treatments.

To assess the effects of environmental conditions on settlement, the contents of each test tube were counted to determine the number of *Dendraster excentricus* individuals that had successfully settled and metamorphosed into juveniles versus those that remained as swimming larvae. Each treatment consisted of 15 individuals with three replicates per condition. Since the competence of the CA and MHW (Fig. 5&6) was different, they cannot be compared. Instead, a second MHW culture was used that was as old as the CA, but its significance cannot be knownk as there was only one replicate (Fig.7).

This experiment revealed that the absence of sand substrate resulted in no settlement (Fig.5), indicating that the presence of sand is a necessary environmental cue for metamorphosis. We found that temperature did not have a significant effect on settlement under constant ambient conditions. However, within the MHW treatment, there was a significant difference between 10 °C and 20 °C exposures, suggesting that temperature variation may influence settlement success under short-term thermal stress. Across all treatments where sand was present, settlement proportions were consistently high, with at least 50% of individuals metamorphosing into juveniles (Fig. 5,6,7).

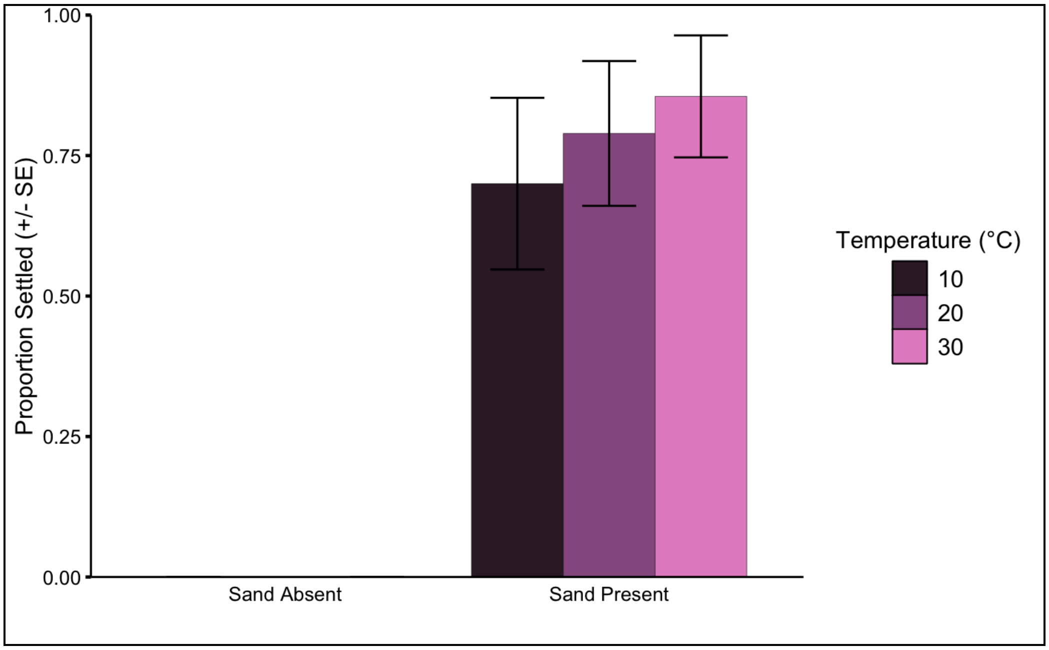

Fig.5. *Settlement proportions of Sand Dollars from 22-day old CA larvae after 24 hours.* There were no settlement occurrences (juveniles present) when sand was absent. Temperature did not have a significant effect on settlement proportion (p=0.730). Bars represent proportion settled ± SE (n=3)

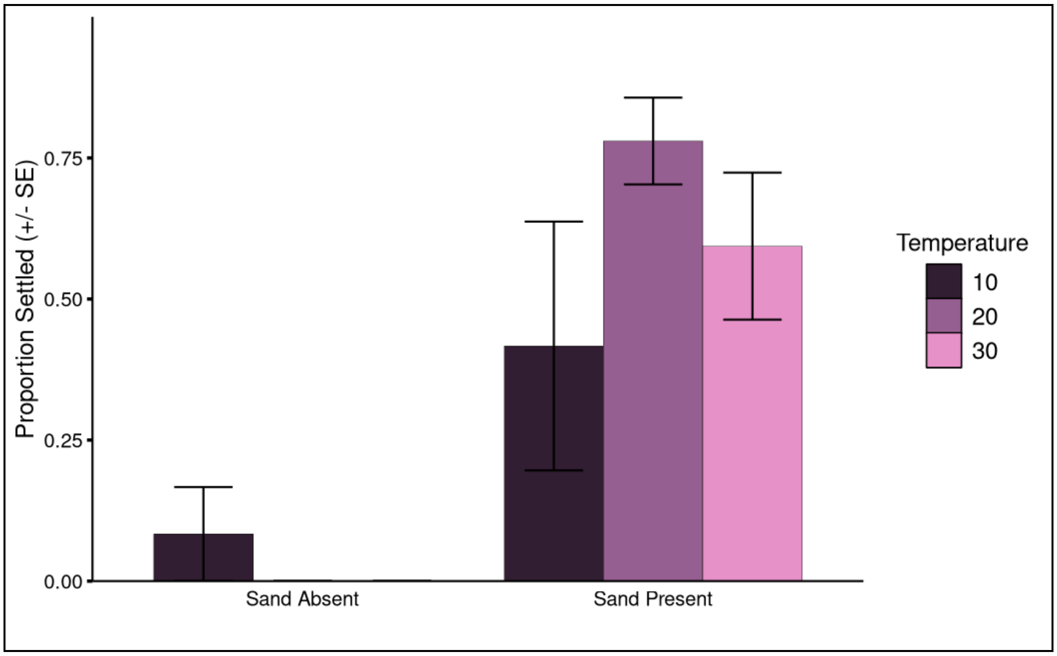

Fig.6. *Settlement proportions of Sand Dollars from 12-day old MHW larvae after 24 hours.* There were no settlement occurrences (juveniles present) when sand was absent, except for one at 10 °C. Temperature did not have a significant effect on settlement proportion (p=0.283). Bars represent proportion settled ± SE (n=3)

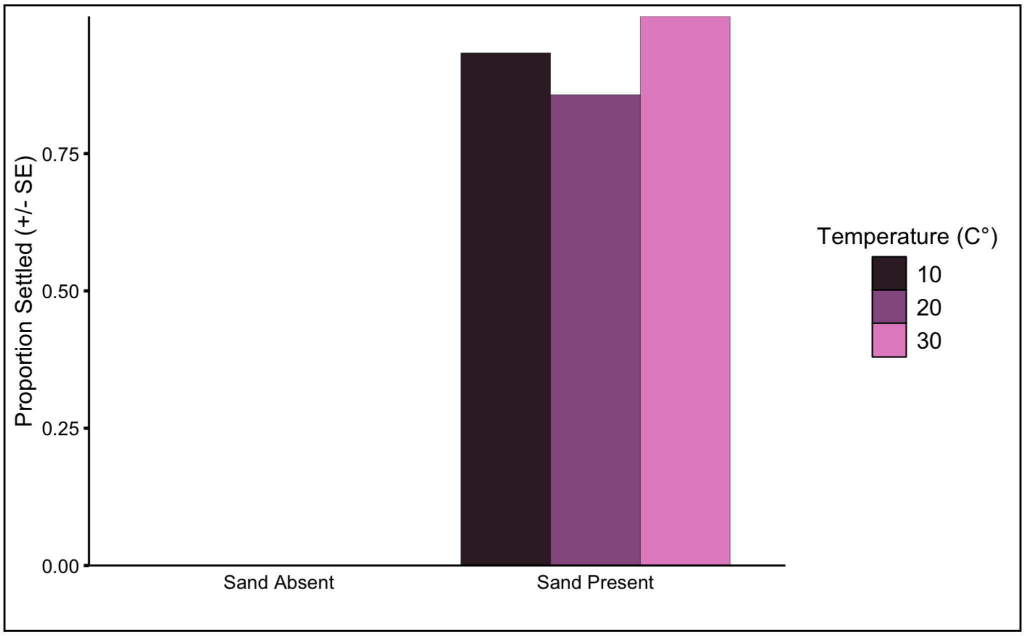

Fig.7. *Settlement counts of 22-day old MHW larvae after 24 hours.* There were no settlement occurrences in the absence of sand. Temperature did not have a significant effect on settlement proportion (p=0.678). No bars due to only one replicate.

Discussion

The study demonstrates that the intertidal sand dollar *D. excentricus* exhibits strong thermal resilience during both early embryonic development and later settlement. Embryos tolerated temperatures up to 25 °C, with normal development occurring between 8 °C and 20 °C, consistent with Bingham (1997), who found similar thermal thresholds for this same population. Beyond this range, developmental abnormalities and mortality increased, suggesting that 25 °C represents a physiological limit for early developmental processes. Additionally, at low temperatures (5°C), embryos displayed mortality and failed to reach the 32-cell stage, whereas development appeared successful and at a normal rate between 8°C and 20°C, even reaching the early two-arm stage (Strathman, 1987; Ozaki, 1965).

These findings support the hypothesis that intertidal *D. excentricus* populations are adapted to withstand substantial short-term temperature fluctuations typical of their habitat, which can exceed 30 °C in the field. Nonetheless, initial work done by Lagmay-Alonso (2025) at much lower culturing densities for embryos and larvae suggested a thermal threshold of 28°C for the onset of abnormal development. Further work exploring temperature vs. culturing density is required to address this interesting discrepancy.

Settlement assays revealed that the adult sand, as a chemical cue, rather than temperature, was the key factor influencing the switch to metamorphosis. No individuals settled in the absence of sand, except for one in the 12-day-old MHW, which could be an error or a factor of earlier competence. Replications of this experiment at multiple larval ages and morphological measurements with them could give us a clearer idea of the reason for this one settled individual.

In addition, due to cultures at mismatched competence stages (12 days vs. 22 days), experiments need to be replicated to ones that maintain an equal measure of competence percentages. However, these results emphasize the importance of benthic cues as triggers for metamorphosis, aligning with earlier work showing that chemical and physical cues from conspecific adults and sediment are essential for settlement (Highsmith, 1982; Hodin et al., 2015).

Furthermore, temperature did not significantly alter settlement success, suggesting that once larvae reach competence, the decision to metamorphose may be primarily governed by chemical cues. This population is exposed to high temperatures at the same time as their spawning season, which might push for the employment of strategies to make their larvae extra resilient in case they confront these high temperatures in intertidal pools or sand flats. This result can support the idea that *D. excentricus* has mechanisms that allow to decouple settlement decisions from temperature conditions, an ability potentially useful for an intertidal environment, providing an adaptive advantage. A version of this trade-off between thermal resilience and development can be seen in killfish, where they developed faster at unstable temperatures but had a weaker survival overall (Blanchard et al., 2025). These results suggest that as the temperature in the ocean increases, the balance of trade-offs between temperature and metamorphosis will also change.

The resilience of both embryos and larvae to elevated temperatures indicates that this population of *D. excentricus* may possess local adaptations or environmentally induced plasticity to heat stress. Bingham et al. (1997) proposed that such thermotolerance differences between intertidal and subtidal populations likely result from environmental phenotypic plasticity rather than fixed genetic divergence. It is possible that adults exposed to prolonged heat stress produce offspring with enhanced thermal tolerance through epigenetic mechanisms. Understanding whether this resilience is heritable or plastic is key to predicting how sand dollar populations will respond to accelerating ocean warming. Furthermore, this can aid conservation and management strategies of the intertidal zone by exploring the mechanisms of sand dollars.

Future research directions include determining whether the thermal resilience observed in this intertidal *D. excentricus* population is driven by genetic adaptation over generations or environmentally-induced plasticity within individual lifecycles. Cross-breeding experiments between intertidal and subtidal populations could help reveal whether thermotolerance is heritable or reflects phenotypic responses to local conditions, as suggested by Bingham et al. (1997). Nevertheless, the population used for that study was no longer found. Additionally, future studies can explore how food availability interacts with temperature to influence growth, competence, and settlement. Because sustenance is critical for successful metamorphosis, fluctuating food conditions could either amplify or buffer the effects of thermal stress or, perhaps, reduce competence response to chemical cues. Together, these studies would deepen our understanding of how environmental stress and habitat context interact and help us predict the future of sand dollar populations in a changing ocean.

Acknowledgements

This work was supported by the REU-Blinks Fellowship in the incomparable Friday Harbor Labs. As an international student, this is a rare opportunity. I would like to thank Eric Edsinger for his guidance and introducing me to the magnificent *Dendraster excentricus*. Sophie George for showing me patience and meticulous work. Jason Hodin and Lab 8 for spawning sand dollar methodology. Augie Kalytiak-Davis and Kaitlyn Tonra, for the best day of snorkeling, and for saving me with R analysis. Willem Weertman, Joey Ullman, and Ken Sebens for taking us on a great boat day. Olivia Graham for the temperature loggers. All the REUs - Brody, Alexander, Ciera, Gaby, Jayson, Emma, Ellie, Alex, Izzie, and Khrista for making this program a place where I felt safe to be myself. Heidi Dobson for encouraging me to apply to this opportunity, as well as Whitman College for providing me with an ocean of opportunities since I decided to study away from home. And once again, to the marvelous Friday Harbor Labs that enabled me to conduct scientific research for the first time in my life, something that had only existed in my dreams.

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