The thermal range of the cushion sea star, *Culcita novaeguineae,* distribution and its behavioral response to warmer waters

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Overproduction of greenhouse gases is driving climate change and increasing the average temperature of oceans worldwide. As a result, organisms are exhibiting behavioral changes and species are shifting their natural distribution. This study aimed to assess the effects of temperature on *C. novaeguineae* distribution and movement in order to predict the effects of rising sea temperature on this echinoderm's behavior and ecology. The distribution study measured the temperature gradient of the cushion star's current habitat in order to determine how temperature changes with respect to depth. Additionally, the cushion star's distribution range in relation to depth and sea temperature was examined to demonstrate how temperature influences cushion star range. The field experiment was conducted to determine the effects of increased temperature on *C. novaeguineae* behavior. Movement, a common mechanism used by ectotherms to escape heat stress, was measured as the response variable in cushion stars heat shocked in ocean waters 3°C above their expected upper thermal limit and in control organisms kept in ambient ocean waters of 31°C. The results of the distribution survey found that temperature decreased as depth increased. And cushion stars were generally found at 1, 2, and 3 meters and in temperatures between 29°C and 31°C. The field experiment revealed that the heat shocked individuals moved 3.2 times further than the control organisms and twice the number of heat shocked cushion stars moved into deeper waters than control organisms. This study suggests that temperature is the major factor affecting cushion star distribution and increased temperature promotes movement into greater depths. Consequently, as the ocean continues to warm, cushion stars may move into deeper waters to find relief from the heat stress, altering the structure of the shallow, coral reef ecosystem in which cushion stars are currently abundant.

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Abstract. Overproduction of greenhouse gases is driving climate change and increasing the average temperature of oceans worldwide. As a result, organisms are exhibiting behavioral changes and species are shifting their natural distributions. This study aimed to assess the effects of temperature on C. novaeguineae distribution and movement in order to predict the effects of rising sea temperature on this echinoderm's behavior and ecology. The distribution study measured the temperature gradient of the cushion star's current habitat in order to determine how temperature changes with respect to depth. Additionally, the cushion star's distribution range in relation to depth and sea temperature was examined to demonstrate how temperature influences cushion star range. The field experiment was conducted to determine the effects of increased temperature on C. novaeguineae behavior. Movement, a common mechanism used by ectotherms to escape heat stress, was measured as the response variable in cushion stars heat shocked in ocean waters 3°C above their expected upper thermal limit and in control organisms kept in ambient ocean waters of 31°C. The results of the distribution survey found that temperature decreased as depth increased. And cushion stars were generally found at 1, 2, and 3 meters and in temperatures between 29°C and 31°C. The field experiment revealed that the heat shocked individuals moved 3.2 times further than the control organisms and twice the number of heat shocked cushion stars moved into deeper waters than control organisms. This study suggests that temperature is the major factor affecting cushion star distribution and increased temperature promotes movement into greater depths. Consequently, as the ocean continues to warm, cushion stars may move into deeper waters to find relief from the heat stress, altering the structure of the shallow, coral reef ecosystem in which cushion stars are currently abundant.

Introduction

Since the industrial revolution, fossil fuel emissions have continued to escalate, altering the concentration of greenhouse gases in the atmosphere and causing irreversible damage to the climate system (Soloman et al., 2009). These unnatural levels of carbon dioxide contribute to an increase in global average temperatures, which in turn, raises the amount of heat and carbon absorbed by the ocean (Pörtner et al., 2014). Although ocean warming, acidification and lower oxygen levels are interacting factors associated with climate change in the marine environment (Pörtner et al., 2014), this paper will focus on ocean temperature as the main driver of spatial distribution and behavior of marine organisms.

As oceans continue to warm, marine environments are experiencing physical and biological changes (Pörtner et al., 2014). Despite visible ramifications from an increase of 0.25°C in global ocean temperature since 1971, sea surface temperature is projected to continue to warm 1°C to 3°C more in the 21st century (Rhein et al., 2013). These ocean temperature anomalies trigger ecological response and disrupt the natural distribution and behavior of marine organisms worldwide (Walther et al., 2002).

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Biological responses to ocean warming have gained a great deal of scientific interest in recent years as biodiversity and ecosystem goods and services become increasingly threatened (Pörtner et al., 2014). Tropical marine ecosystems are of particular interest due to the high biodiversity and vulnerability to change (Pörtner et al., 2014). Many organisms inhabiting these tropical oceans exhibit sensitivity to temperature increases because they are already living close to their upper thermal limits or the maximum temperature in which they can adequately function (Compton et al., 2007). Understanding ways in which these shifts in temperatures affect organismal responses is essential in projecting the future state of tropical marine ecosystems.

Temperature delineates geographic distribution and response for many species (Pörtner et al., 2014). Increased temperatures that go beyond an organisms' thermal tolerance results in temperature-induced hypoxia, affecting the functional capacity responsible for energy and behavioral traits (Pörtner, Langenbuch, & Michaelidis, 2005). One study examining the effect of temperature on *Pisaster* sea star feeding rates found that an increase in temperature by just 3° C, resulted in a 29% increase in feeding rates, suggesting that sea stars are sensitive to temperature and require more energy at higher temperatures (Sanford, 2002). Additionally, fish have been observed to respond to temperatures above their thermal tolerance through immediate movement in order to evade the temperature-induced hypoxia zone (Pörtner, 2002). These organismal responses allow species to adapt to increased temperatures, often contributing to large scale range changes (Pörtner et al., 2014). Large scale species distribution shifts and ecosystem transformations in response to ocean warming are already occurring and have been reported across all ocean basins (Pörtner et al., 2014).

Much of the research on the impact of sea temperature changes conducted thus far tends to focus on coral and macro vertebrates, due to their obvious ecological and commercial significance (Przeslawski, 2008). However, little attention is given to tropical benthic marine invertebrates, which may exhibit unique responses to heat stress due to their inherently slow nature. Tropical Echinodermata, specifically cushion sea stars (*Culcita novaeguineae*), are of distinguished interest due to their niche in shallow (<25m), warm waters and slow-moving behavior (Goreau et al., 1972). *Culcita novaeguineae* are ectothermic asteroid corallivores (Dubinsky & Stambler, 2011) that exist on outer reef slopes, reef flats, and on patch reefs in the eastern Indian Ocean, as well as the western, central, and south Pacific Ocean (Glynn & Krupp, 1985). Cushion stars have been observed in loose aggregates (Goreau et al.,1972) at depths of up to 20 meters (Glynn & Krupp, 1985). They feed on a variety of organisms including algae, sponges, bryzoans, and coral (Bell, 2008) and due to this feeding behavior, it can be inferred that the presence and abundance of *C. novaeguineae* have an impact on coral reef communities and ecosystem structure (Glynn & Krupp, 1985). Past studies conducted on cushion stars have focused on their feeding preference in the presence of crown of thorns (Bell, 2008) and their symbiotic relationship with the sea star shrimp (Olliff, 2011). While the substrates in which they occur have been recorded, little is known about the exact depth and temperature that they prefer to thrive in. Additionally, no studies have investigated the effect of changing sea temperature on their behavior.

Cushion stars and their associated ecosystems are vulnerable to ocean warming. As tropical ectotherms, *C. novaeguineae* are sensitive to changes in temperature due to their presence in shallow reefs, where temperatures are already close to their upper thermal limit, (Compton et al., 2007) and their inability to self-regulate body temperature (Bicego et al., 2007). Consequently, exposure to higher temperatures is likely to affect their ability to optimally function, driving the species into cooler and deeper waters and altering the structure of their current ecosystem.

This study will provide insight into the possible shifts in local distribution of cushion stars that may occur as climate change persists. The overarching goal of this project is to determine how temperature affects the distribution and behavior of cushion stars. Depth will also be examined as a covariate of temperature. This study aims to determine the (1) the variance in temperature at different depths, (2) the depth at which cushion stars are in greatest abundance, (3) the temperature range in which cushion stars are most commonly found, (4) and the effects of ocean warming on cushion star movement. The associated hypotheses consist of: (1) As ocean depth increases, water temperature of the benthic layer will decrease. (2) Cushion stars will be at greatest abundance in moderately shallow waters (2m). (3) Cushion stars will most commonly be found in temperatures ranging from 29°C to 31°C. (4) Cushion stars exposed to higher than average temperatures will display increased movement and move into deeper waters. *Culcita novaeguineae* are expected to respond to ocean warming through movement into deeper waters as a mechanism to escape heat stress and find an environment that corresponds with their thermal tolerance.

Methods

Study site

Distribution surveys and collections of *C. novaeguineae* were conducted on the reef flat and reef slope just off shore of the public beach in Opunohu, Moorea, French Polynesia (17°29′28.2″S 149°51′02.4″W) and on the reef flat and reef slope slightly North of the UC Berkeley Gump Station in Cook's Bay, Moorea, French Polynesia (17°29′21.7″S 149°49′33″W) (Fig. 1). The field experiment portion of this study was conducted just off the dock of UC Berkeley Gump Station (Fig.1). These sites were chosen due to the high abundance of *C. novaeguineae* individuals present in the area in addition to the reef slopes present at all three sites, which provided varying depths to observe the organisms.

Collection and accommodation of Culcita novaeguineae

All of the cushion stars used in the field experiments described below were encountered while strategically snorkeling and searching around substrates in which they can burrow, along the reef flat and slope. *Culcita novaeguineae* and any algae or coral rubble they were feeding on at the time of detection was collected using 1liter Ziploc bags. After being transferred back to the Gump Station wet lab, the organisms were placed in a large, circular tank. The tank was supplied with sand, coral rubble, algae, rocks to burrow under, and a constant flow of ocean water in order to resemble their natural habitat. Cushion stars were collected in densities of two to four organisms at a time and housed in the tank for 18 to 24 hours before conducting the experiment in order to minimize any effects of transportation stress.

Distribution Survey

In order to assess the variance of temperature at different depths and the depth and temperature range in which cushion stars are most commonly found, distribution surveys were taken from October 25th, 2016 until November 2nd, 2016 between 3:00pm and 5:00pm. The survey consisted of 18 transects along Opunohu Public Beach and 24 transects along Cook's Bay. The difference in number of transects between the two sites was due to a limited area of cushion star habitat in

Opunohu Bay. In Opunohu Bay, six transects were conducted at each of the three chosen depths. And in Cook's Bay, eight transects were conducted at each of the three chosen depths.

The transects were executed by snorkeling in a straight line parallel to the shore for 100 meters at a depth of 1 meter, 2 meters, and 3 meters. At every occurrence of *C. novaeguineae* an Onset HOBO data logger was placed in the sand directly next to the cushion star and left there for 1 minute to allow time for the logger to record the temperature in which the cushion star was stationed in addition to the temperature of that specific depth. The time in which the data logger was planted and the number of stars in that particular patch was recorded. If no stars were found during a transect, the data logger was placed into the sand next to a substrate to determine the temperature of that specific depth.

Field Experiment

In order to determine the effect of temperature on cushion star behavior, a series of 20 trials were run, in which heat shocked individual *C. novaeguineaes'* behavior was observed in comparison to individuals' behavior who did not receive the heat shock treatment. Trials were run from October 12th, 2016 until November 9th, 2016 between 8:00am and 10:00am. Each trial consisted of two cushion stars; one control organism and one experimental organism. The experimental organism was randomly chosen by assigning each cushion star heads or tails and flipping a coin.

Before the start of each trial, ocean water was collected directly off the dock at UC Berkeley Gump Station using two buckets and a 1liter thermos. Ocean water from the thermos was placed in a pot and heated over a gas stove to approximately 60°C and then poured back into the thermos. Ocean water from bucket one was placed in a pot and heated over a gas stove to 34°C, simulating the projected increase in sea surface temperature. The heated ocean water from bucket one was then poured back into the bucket and the temperature was measured again. If the temperature fell below 34°C, ocean water from the thermos was added and stirred into the bucket until the water temperature reached 34°C. Bucket two of sea water was unchanged and kept at 31°C, corresponding to the upper limit temperature of current cushion star distribution. Then, the experimental organism was placed in bucket one of 34°C ocean water and the control organism was placed in bucket two of 31°C ocean water. The cushion stars and water temperatures of the buckets were constantly monitored for 45 minutes and heated ocean water from the thermos was added as needed. After the treatment, both cushion stars were placed next to markers on the ocean floor of the reef slope. The distance each organism moved was determined by using transect tape to measure the cushion star's distance from the marker after 5 minutes, 20 minutes, and 30 minutes. The total distance moved over 30 minutes was calculated. The direction each organism moved was determined by measuring the depth in which the cushion star was found after 30 minutes using transect tape. All individuals found in depths greater than 1 meter was classified as moving into deeper water and all individuals found in in depths of 1 meter or less was classified as remaining in shallow water.

Statistical Methods

In order to determine if the data collected in this study was normally distributed, Shapiro-Wilk normality tests were performed in R (R Core Team, 2013). All response variables were tested and results found that the data from the distribution survey and the field experiment does not follow a normal distribution. Therefore, nonparametric tests were used to analyze the results of this study (Ambrose, 2007) (R Core Team, 2013).

First, a Kruskal-Wallis test was used to test differences in temperatures at different depths. And in order to determine if the number of stars at varying depths was different, a Chi-square test was conducted between the number of stars found at each depth. Additionally, data from both sites was combined into 1 plot to determine the distribution of cushion stars across different temperatures. Finally, differences in the average total movement after 30 minutes between the control and heat treated cushion stars was determined using a Wilcoxon Signed-Rank test and a Chi-square test was conducted to determine if the number of heated and control stars that remained in shallow waters and moved into deeper waters was different (Ambrose, 2007) (R Core Team, 2013).

Results

Sea temperature gradient

Although both sites had significant differences in temperatures at different depths ($H^2 = 13.69$, $p < .001$), Opunohu Bay had a higher ratio of change between temperature and depth ($b = -1.52$, $H^2 = 8.53$, $p = .01$) when compared to Cook's Bay ($b = -0.36$, $H^2 = 6.88$, $p = .03$) (Fig. 2). Additionally, Opunohu Bay exhibited higher average temperatures than Cook's Bay, most notably at 1 meter, where the average temperature in Opunohu Bay was approximately 2.3°C higher ($M = 32.29$, $SD = 2.03$) than the average temperature at 1 meter in Cook's Bay ($M = 29.93$, $SD = .74$) (Fig. 2).

Distribution based on depth and temperature

Cushion stars were evenly distributed throughout the different depths and the number of stars at each depth was not different, $c^2(2, N = 48) = 1.39$, $p = .50$ (Fig. 3). On the other hand, the number of cushion stars at different temperatures exhibited a right skewed distribution, where stars were observed between 29°C and 31°C and cushion star abundance was highest at 29°C (Fig. 4).

Behavioral experiment: total distance moved

The average total distance moved (cm) after 30 minutes by the cushion stars that received heat treatment ($M = 79.29$, $SE = 20.71$) was different than the average total distance moved (cm) after 30 minutes by the cushion stars that did not receive heat treatment ($M = 24.70$, $SE = 10.91$) ($T = 332$, $p < .001$). And the cushion stars that received heat treatment moved on average 3.2 times further than the cushion stars that were not heated shocked (Fig. 5).

Behavioral experiment: direction moved

The number of heat shocked cushion stars that moved into deeper water and remained in shallow water is different than the number of control cushion stars that moved into deeper water and remained in shallow water, $c^2(1, N = 40) = 4.91$, $p = .02$. The number of heat shocked stars that moved into deeper waters (14) was 2 times greater than the number of control stars that moved into deeper waters (7) (Fig. 6). Likewise, the number of control stars that remained in shallow waters (13) is approximately 2.2 times greater than the number of heated stars (6) that remained in shallower waters (Fig. 6).

Discussion

The results of this study indicate that there is a sea temperature gradient in the cushion star habitat and ocean water is cooler at greater depths. In addition, cushion stars were found at all three depths and only found at intermediate temperatures between 29°C and 31°C, suggesting that temperature is the main factor affecting cushion star distribution. Finally, the results from the behavioral experiment suggest that cushion stars respond to heat stress through increased movement into deeper waters.

Culcita novaeguineae distribution

Considering the inverse correlation between temperature and depth in both Cook's Bay and Opunohu Bay and the temperature range in which cushion stars were typically found, a relationship between cushion star abundance and depth would be expected. However, results suggest there is no relationship between depth and number of cushion stars. This result may be due to the small scale changes in temperature that occurred between each depth in Cook's Bay, which is likely undetectable to cushion stars. On the other hand, Opunohu Bay exhibited a detectable rate of change in temperature at each depth, yet there was no relationship between depth and abundance of stars. This result could be due to the sample size, which was limited by cushion star habitat in Opunohu Bay. Therefore, a higher sample size could be beneficial in explaining the relationship between depth and number of stars when there is a detectable difference between temperatures among increasing depths.

Given that cushion stars were evenly distributed among the three depths, but only found in temperatures between 29°C and 31°C, it can be inferred that temperature defines the distribution range of cushion stars and temperatures between 29°C and 31°C are within their thermal tolerance. Based on these interpretations and the projected increase in ocean temperature, the cushion star's current niche in shallow coral reefs will be outside of their thermal tolerance. As a result, cushion star distribution may shift into deeper waters, where their thermal range can be found. This possible range change is indicative of the ramifications associated with warming waters due to climate change.

Behavioral response to heat

Cushion stars exposed to higher than average temperatures exhibited increased movement compared to control individuals, suggesting that cushion stars respond to higher temperature through movement. This response suggests that the heat shocked cushion stars were exposed to temperatures that surpassed their thermal tolerance. Past studies have observed fish behavior at temperatures greater than their thermal tolerance and found that they experience temperature-induced hypoxia, which alters their ability to function and promotes movement (Pörtner, 2002). Therefore, the increased movement in cushion stars immediately after heat exposure is indicative of the organism reacting to temperature-induced hypoxia or sensing the potential threat. Furthermore, the cushion star's response to heat could be an attempt to escape the heat-stressed situation that limits their functional capacity (Pörtner, 2002).

A greater number of heat shocked cushion stars moved into deeper water compared to control organisms, suggesting that the heat stressed individuals respond to increased temperatures by moving away from the warm water. Given that temperature decreases as depth increases, the heat shocked cushion star's movement into deeper waters could be indicative of them searching for a cooler environment. Therefore, as ocean temperature continues to rise, cushion stars are likely to experience heat stress that goes beyond their thermal tolerance, causing them to retreat to deeper, colder waters in order for them to properly thrive.

Implications of higher sea temperatures

Past studies have confirmed that ectotherms are unable to maintain a constant body temperature at environmental extremes, thus rely on behavioral mechanisms for thermoregulation (Bicego et al., 2007). As an ectothermic species, cushion stars appear to be greatly affected by external temperatures. With that being said, results of this study imply that cushion stars chose to inhabit areas where temperatures are within their thermal tolerance and they respond to heat stress through immediate movement into deeper waters. Although the average sea surface temperature is projected to surpass *C. novaeguineae's* thermal tolerance within the 21st century, their ability to move under environmental pressure suggests that they may respond to climate change through a distribution shift. Cushion stars may find refuge from increased sea temperature at greater depths, meaning that they will no longer be found in shallow reef flats as climate change progresses into the future.

Implications of Culcita novaeguineae response to heat

Cushion star's inability to acclimate to increased temperatures may result in the disappearance of the species from their current habitat, which in turn could affect the entire structure of the coral reef ecosystem. Since *C. novaeguineae* feed on a variety of organisms (Glynn & Krupp, 1985), loss of this species may affect the current composition of the ecosystem. More specifically, a decrease in cushion stars could lead to an increase of prey that cushion stars typically feed on. For example, the absence of algae eating *C. novaeguinea* (Glynn & Krupp, 1985) could contribute to an overgrowth of algae within the coral reef and ultimately an ecosystem phase shift.

Not only is the cushion star's response to heat indicative of the future species distribution and coral reef health, but *C. novaeguinea's* stress response can serve as a model to predict the responses to climate change of similar tropical marine ectotherms, who are unable to regulate internal temperatures (Bicego et al., 2007) and are already living at temperatures near their thermal optimum (Colwell et al., 2008). Thus, it is likely we see significant changes in tropical marine ectotherm distribution and behavior with increasing ocean temperatures. This study provides a glimpse of the possible outcomes of global warming and sheds light on the susceptibility of the ocean environment. As climate change persists, seas continue to warm, threatening not only the fate of individual species, but the natural structure of tropical marine ecosystems as a whole.

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Figure 1

Map of of Mo'orea, French Polynesia with selected study sites.

Map of Mo’orea, French Polynesia with the Opunohu field site, Cook’s field site, and experimental site (Gump Station) noted.

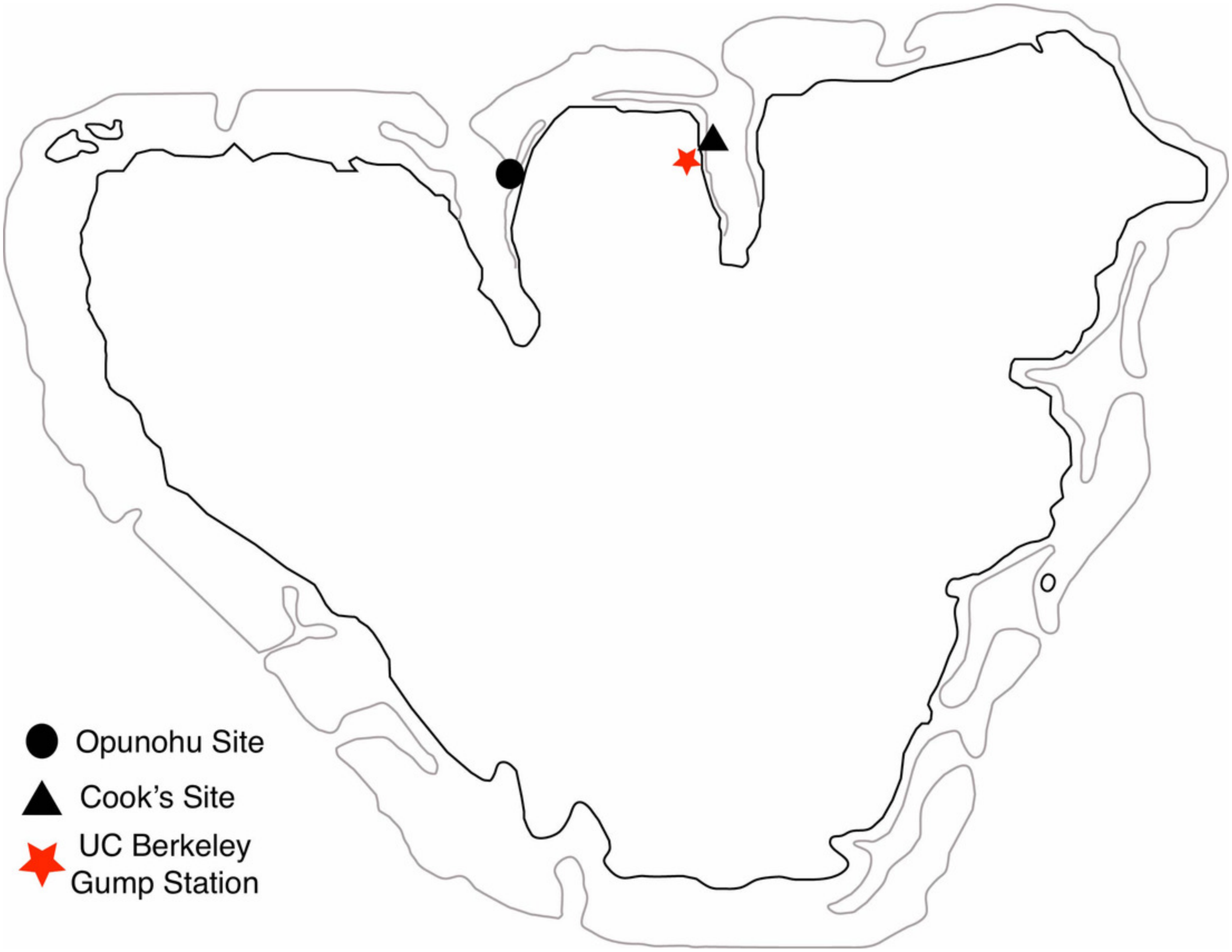

Figure 2

Measured temperature at different depths.

Temperature recorded at 1, 2, and 3 meters in Cook’s and Opunohu Bay.

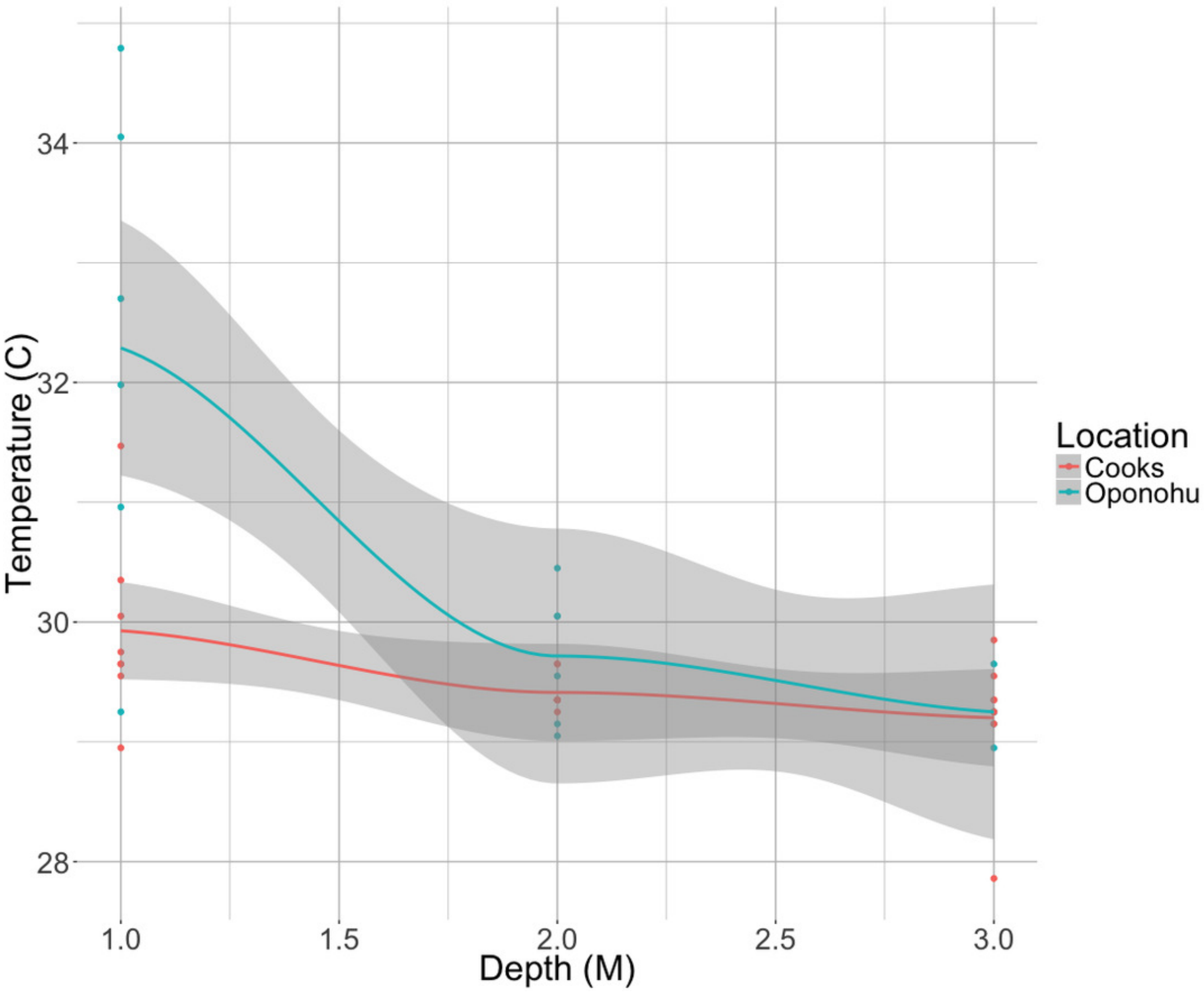

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Figure 3

The abundance of *Culcita novaeguineae* at different depths.

The number of *Culcita novaeguineae* per 800 m in Cook's Bay and 600 m in Opunohu found at 1, 2, and 3 meters.

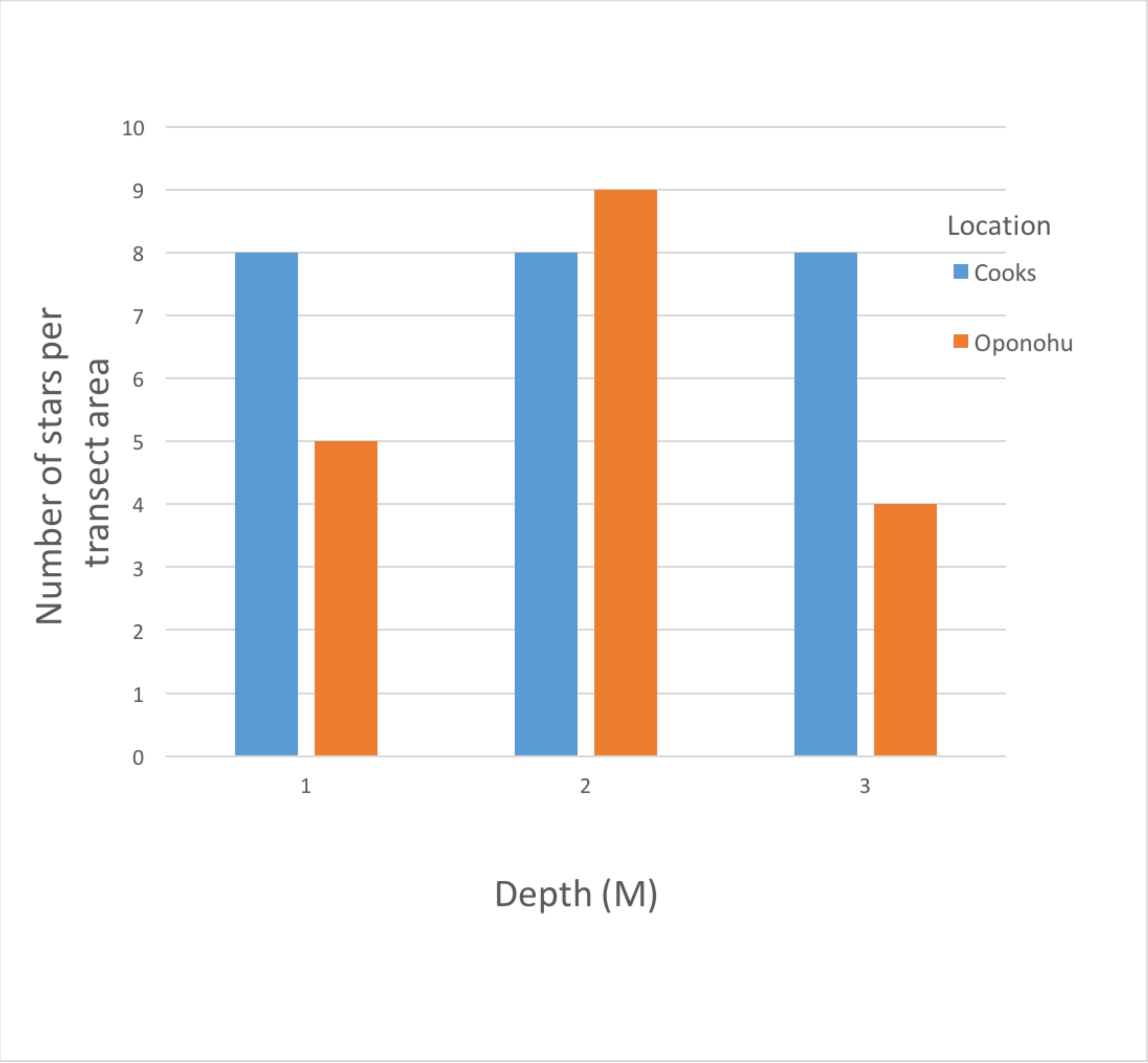

Figure 4

The abundance of *Culcita novaeguineae* at different temperatures.

The number of *Culcita novaeguinea* per 4,200 m found between 27.5°C and 34.5°C.

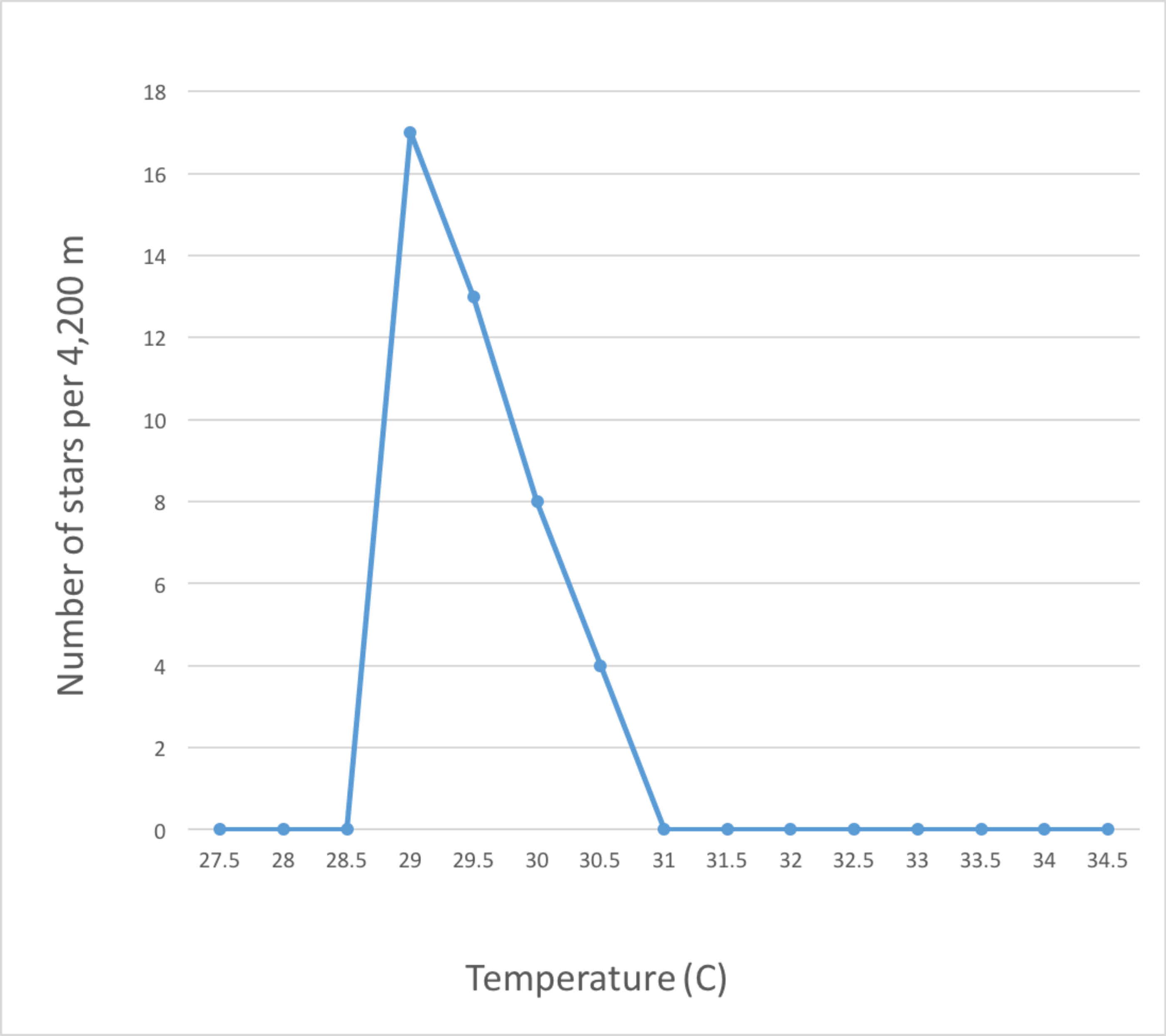

Figure 5

The total distance moved of heat treated and control cushion stars.

The average total distance moved in centimeters of the heat treated and control group after 30 minutes (+/-standard error).

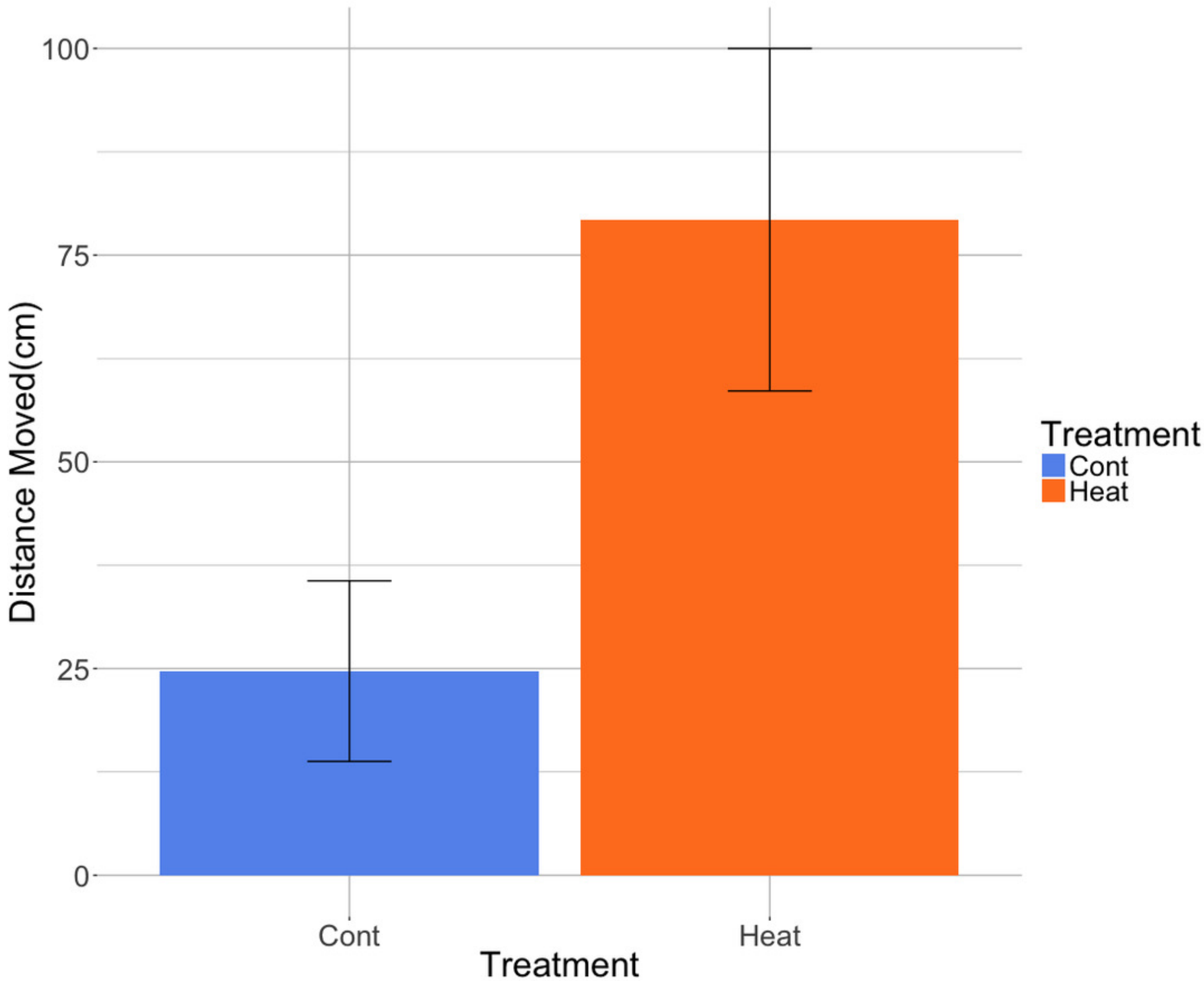

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Figure 6

The number of heat treated and control cushion stars that remained in shallow water or moved deeper.

The number of *Culcita novaeguineae* that remained in shallow water and the number of *Culcita novaeguineae* that moved into deep water for the heat treated and control group.