Symbiosis with Sponge: Differential Predator Response with Hermit Crab Shell Types

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Abstract

Hermit crabs are important marine detritivores, and characteristically use discarded gastropod shells to cover their exoskeleton. However, some species use toxic symbiotic sponge shells instead, where the sponge dissolves and replaces their gastropod shell. The impact these mutualistic sponges have on hermit crab ecology remains poorly understood. In the present study, the behavioral responses of gastropod-shelled (GSCs) and sponge-shelled (SSCs) hermit crabs to two different predators was examined, with the goal of determining if the type of hermit crab shell influences the duration of their predator avoidance response. GSCs and SSCs were individually dropped into experimental tanks containing either a known hermit crab predator or a sponge predator, and the time it took for crabs to emerge from their shells after being dropped (refuge time) was recorded. It was found that hermit crabs of both shell types spent more time refuging from the hermit crab predator (a red rock crab - *Cancer productus*) compared to the sponge predator (lemon nudibranch - *Doris montereyensis*) or control treatments. However, compared to GSCs, SSCs spent (non-significantly) less time refuging from the hermit crab predator, relative to the control. The difference between SSC and GSC predator response could indicate behavioral changes due to sponge protection, size, or hermit crab species, such as increased protection due to sponge toxicity or less room to shelter in the sponge due to smaller aperture size. Shorter refuge time in sponge shells could also result in less predation by hermit crab predators if the SSCs escape faster or the sponge acts as a toxic barrier. Further research, such as larger sample sizes or more species of hermit crabs, is needed to determine the significance and mechanism behind this altered behavior.

Introduction

Hermit crabs (superfamily Paguroidea) are a common intertidal and subtidal group of organisms, characterized by their tendency to live in empty gastropod shells for protection due to a soft abdominal exoskeleton. Hermit crabs are generally omnivore scavengers, playing an ecological role in recycling detritus (Hazlett, 1981), and are important prey for many other predator species (such as larger crabs, fish, and birds). The shells they inhabit also provide habitats for other organisms such as polychaetes, anemones, bryozoans, algae, protozoa, and flatworms (Williams & McDermott, 2004). One of their more unique community interactions is with symbiotic sponges (Phylum Porifera), which can replace the gastropod shell in some hermit crab species. The exact mechanism of this replacement is debated, as some sponge species are thought to completely dissolve and replace the gastropod shell, and other species are thought to simply cover the shell (Sandford & Brown, 1997; Williams & McDermott, 2004). Regardless of the process, this is considered a mutualistic relationship, with the hermit crab providing a mobile substrate and oxygenated water, while the sponge provides a shell that grows with the hermit crab (Williams & McDermott, 2004). The latter point is critical, as shell availability has been found to drive behavior and population dynamics in hermit crabs, serving as one of the limiting factors to population growth (Hazlett, 1981). Additionally, certain sponges associated with

hermit crabs, such as *Suberites domuncula*, are highly toxic to larger predator crabs, and could thus provide more protection (Cariello & Zanetti, 1979). However, other studies found that certain species of hermit crabs show no preference for sponge shells (Sandford, 1995). Sponge shells can also provide challenges to hermit crabs, such as being heavier than gastropod shells, or the inability to go out of water, as sponges would get filled with air and cause the crab to float. However, little literature beyond shell-choosing behavior exists on the ecology of these relationships. As such, filling this gap in knowledge will help gain a better understanding of the dynamics of hermit crab-sponge shell relationships.

The present study aims to fill this gap by studying predator-response behavior of gastropod-shelled crabs (GSC) vs. sponge-shelled crabs (SSC). In doing so the influence of shell type on behavioral patterns of hermit crabs was assessed, as was the implications on hermit crab spatial distribution and time spent responding to predators, as opposed to foraging, molting, mating and other behaviors. Specifically, the present study will test if GSCs and SSCs each react differently to the presence of a hermit crab predator (red rock crab, *Cancer productus)* vs. a sponge predator (lemon nudibranch, *Doris montereyensis*). Predator reaction behavior was defined as time spent refuging in the shell after being dropped from a standard height into a water tank containing a predator (referred to as refuge time), as described in Mima et al. (2003). When housed in a stronger gastropod shell, hermit crabs have been observed to spend less time refuging in their shell vs crabs with weaker shells (Mima et al., 2003). Combining the concepts in the above study, and the idea that toxins in sponges might provide more defense, we hypothesize that 1.) GSCs will spend more time refuging in their shell when exposed to a hermit crab predator (*C. productus*) compared to a sponge predator (*D. montereyensis*) 2.) SSCs will spend less time refuging in their shell when exposed to a hermit crab predator (*C. productus*) compared to a sponge predator (*D. montereyensis*), and 3.) SSCs will spend less time refuging in their shells compared to GSCs when exposed to *C. productus*, and more time refuging compared to GSCs when exposed to *D. montereyensis*.

Methods

Specimen Collections

To test differential predator response of gastropod-shelled and sponge-shelled crabs, six individuals of both shell types were collected from a ~100m trawl near Roche Harbor, San Juan Island, WA (48.5952195 N, 123.0675733 W) on April 18th, 2024. Of the 12 hermit crabs that were collected, four GSCs were determined to be *Elassochirus tenuimanus*, two GSCs were *Pagurus kennerlyi*, four SSCs were *Pagurus stevensae*, and two SSCs were *Pagurus kennerlyi*. All SSCs had *Suberites domuncula* as their symbiotic sponge. A red rock crab (*Cancer productus)* was collected from Argyle Lagoon, WA (48.5206500 N, 123.0129357 W), and a lemon nudibranch (*Doris montereyensis)* was collected from the docks at Friday Harbor Labs, WA (48.5455368 N, 123.0126299 W). *C. productus* has been shown to eat hermit crabs, and *D. montereyensis* has been shown to eat *Suberites* sponge (Rosen et al., 2009; Turner et al., 2024), and were thus suitable to use as predators in the experiment. All organisms were then acclimated

to sea tables with flowing fresh seawater for two weeks. During acclimation and after each trial, the hermit crabs were fed crushed scallops or urchins every 2-3 days to reduce stress.

Experimental Design and Data Collection

We employed experimental methods described in Mima et al. (2003) to effectively test differential predator response. The experimental setup consisted of 3 treatment tanks contained within one sea table, each filled with 13 liters of seawater. Since the presence of predators could be detected via visual and/or chemosensory cues, the fixed volume of water in each treatment tank ensured that the "scent" of each predator was dispersed thoroughly and in equal concentrations, serving as the predator stimulus for the hermit crabs. The sea table was also partially filled with constant flowing water to keep the treatment tanks at the same temperature (around 11°C). Oxygen bubblers were used in all treatment tanks to ensure sufficient dissolved oxygen concentrations for all organisms used in the experiment, and so that the crabs and nudibranch would stay alive for the necessary time without the need for flowing water that would wash out the predator scent (Figures 1 & 2).

To begin the experiment, *D. montereyensis* and *C. productus* were each placed in one of the three treatment tanks (one was empty for a control) and left for 20 minutes to ensure their scent percolates through the water in the tank. The GSCs and SSCs were then arranged in alternating rows of jars and assigned different drop orders into the different treatment tanks to ensure the number of times/orders dropped did not impact our results (Figure 1). For example, GSC #1 was dropped in the control, then *C. productus*, then *D. montereyensis* treatments, while GSC #2 was dropped in the *C. productus*, then *D. montereyensis*, then control treatments, and so on in a different order for each individual to ensure that drop order had no influence on crab behavior. Predator response was measured using refuge time, which was the time between when the crab was dropped into the treatment tank (causing it to retract into its shell) and when both claws fully emerged (Mima et al., 2003). To measure this, each individual was picked up by hand and dropped from a standard height of 20 cm above the water surface into a small plastic container with holes that had previously been placed in each treatment tank, where the crab would retract into its shell (Figure 1 & 2). These small containers within the treatment tanks were 14x14x8.5 cm and had rocks to weigh them down (Figure 2). They were used to prevent *C. productus* from attacking any of the hermit crabs, while still allowing hermit crab behaviors to be observed. To standardize behavioral measurements, a timer was started when the hermit crab reached the bottom of their container after being dropped, and the elapsed time (in seconds) was recorded when both front clawed appendages of the crab had fully emerged from its shell. Test subjects were then removed and placed into a separate holding tank for approximately 2 minutes between drops. Following the 2-minute period, each individual was then dropped into the other treatment tanks and refuge time recorded using the same methods. This routine was repeated 6 times for all 6 GSCs, then all 6 SSCs, to get a total of 6 trials per individual. Any crabs with refuge times above 60 seconds were dropped again in the same treatment, as long delays in emergence were assumed to be anomalous behavior due to being incorrectly dropped, such as air

being stuck in the shell, or injury to the crab. If two successive drops resulted in emergence times of over 60 seconds, the data point was declared an outlier and was eliminated from analysis. After all refuge times were measured, the species of hermit crab, aperture width, and max width of the shell were recorded (in cm) for all 12 individuals. These were measured after all drops were finished to ensure handling did not impact results.

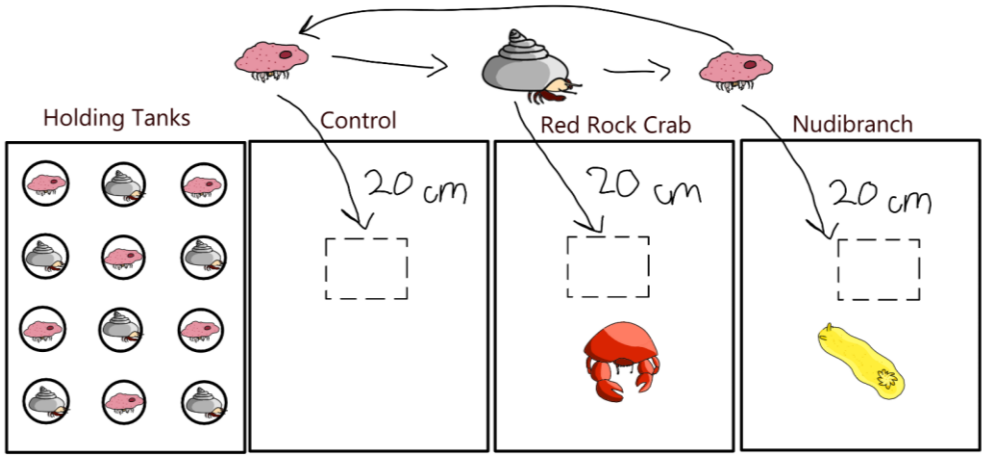

Figure 1: Experimental design (top-down view) showing the three different treatment tanks with gastropod (gray) and sponge-shelled (pink) hermit crabs. Crabs were dropped into a water-permeable small container (dotted square) in each tank from a 20cm height.

Figure 2: Hermit crab holding tank (left) and treatment tanks (right). Crabs were dropped into small containers within the treatment tanks, which were held down by rocks, due to the tendency of the containers to float. Each treatment tank had the same volume of water (13L).

Data Analysis

Data analysis was performed in R version 4.2.1 (R Core Team, 2022) using refuge times of GSCs and SSCs in each treatment. The mean refuge time across all trials (n = 6) per individual crab was calculated for each treatment (control, *C. productus*, *D. montereyensis*). Using this, the difference in refuge times between the predator and control treatments were then found for each crab (i.e. how much more/less time an individual spent refuging from a predator relative to their control). This was necessary because there were multiple species for each shell type, so by finding the predator refuge time for each individual relative to their control refuge time, the possibility that species react differently to being dropped was controlled for. These predator responses relative to controls for each crab (called relative refuge times) were run through ANOVA and TukeyHSD tests, with alpha values of 0.05 to find any significance between predator reactions and shell types.

To test differences within shell types (hypotheses #1 & #2), an ANOVA was run using relative refuge times as the dependent variable and predator type as the independent variable for GSCs, then for SSCs. To test differences between shell types (hypothesis #3), another ANOVA was run with relative refuge time from *C. productus* as the dependent variable, and shell type (GSC and SSC) as the independent variable, and then again with relative refuge time from *D. montereyensis* as the dependent variable. For hypothesis 3, the one species that had both sponge and gastropod shells (*P. kennerlyi*) was also examined to further determine if shell type influenced behavior within a single species, though no statistics were performed due to low sample sizes. Lastly, bar graphs showing relative predator responses within and between shell types, with standard error bars, were made in Microsoft Excel.

Results

Gastropod-Shelled Hermit Crabs

Within GSCs , there was a significant increase of relative refuge times in the *C. productus* treatment compared to *D. montereyensis* treatment (Figure 3, ANOVA, Tukey test, $\alpha = 0.05$, $p = 0.017$). There was also a significant increase of relative refuge times in the *C. productus* treatment compared to the control (ANOVA, TukeyHSD, $\alpha = 0.05$, $p = 0.006$). There was no significant difference in relative refuge times between the *D. montereyensis* and control treatments (ANOVA, TukeyHSD, $\alpha = 0.05$, $p = 0.846$).

Sponge-Shelled Hermit Crabs

For the SSCs, there was a significant increase of relative refuge times in the *C. productus* treatment compared to the *D. montereyensis* treatment (Figure 3, ANOVA, TukeyHSD, $\alpha = 0.05$, $p = 0.004$). There was also a significant increase of relative refuge times in the *C. productus* treatment compared to the control (ANOVA, TukeyHSD, $\alpha = 0.05$, $p = 0.005$). There was no significant difference in the relative refuge times between the *D. montereyensis* and control treatments (ANOVA, TukeyHSD, $\alpha = 0.05$, $p = 0.999$).

Sponge-Shelled vs Gastropod-Shelled Hermit Crabs

On average, GSCs spent more time refuging in their shell relative to the control in the *C. productus* treatment than did SSCs (Table 1 & Figure 3). However, this difference was not significant (ANOVA, Tukey test, $\alpha = 0.05$, $p = 0.070$). There was also not a significant difference in relative refuge time between GSCs and SSCs in the *D. montereyensis* treatment group (ANOVA, Tukey test, $\alpha = 0.05$, $p = 0.975$).

Table 1: Average refuge time, relative to the control, with standard deviations (in seconds) of gastropod vs sponge shelled hermit crabs across different predator treatment groups. Values represent how far away predator refuge times are from control refuge times (a refuge time of 0 would represent the control). Average aperture width of both shell types (in cm) is also given.

	Gastropod Shell		Sponge Shell	
Treatment	**Average (s)**	**Standard Deviation (s)**	**Average (s)**	**Standard Deviation (s)**
***C. productus* (sec)**	9.238	5.582	3.838	1.962
***D. montereyensis* (sec)**	1.345	3.575	-0.015	1.741
Aperture Width (cm)	2.383	0.343	1.133	0.367

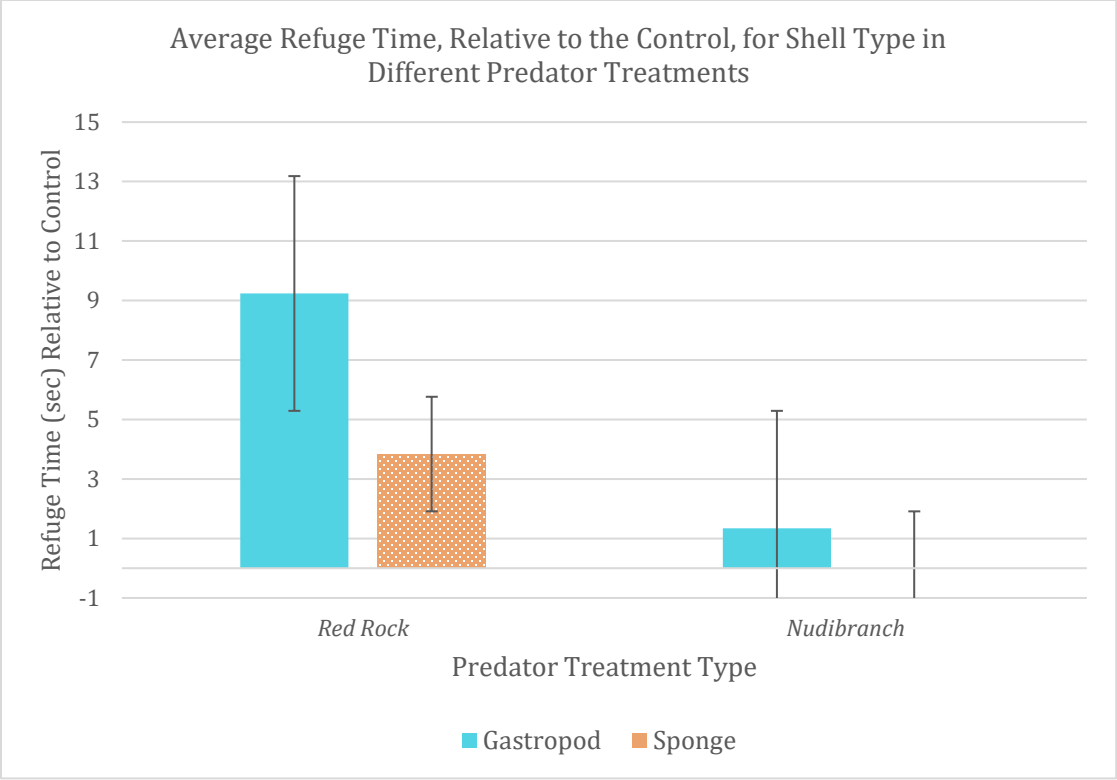

Figure 3: Average relative refuge time (in seconds) between shell type and predator treatment groups, with standard error bars. A refuge time of 0 represents the control, and any value above/below 0 is a difference from the control. The solid blue bar is relative refuge time of all GSCs in the different predator treatments, and the dotted orange bar is relative refuge time of all SSCs in the different predator treatments.

To further examine hypothesis 3 (differences between shell types), differences of relative refuge time within the *P. kennerlyi* species that had both gastropod and sponge shells were examined. For this species, the individuals with sponge shells spent, on average, less time refuging in predator treatments compared to control than those with gastropod shells (Fig. 4). However, there were only two individuals of *P. kennerlyi* per shell type, and as such no statistical analysis of this difference could be conducted. As for shell size, all SSCs had consistently smaller shell apertures than GSCs (Table 1). All GSCs in the experiment were residing in moon snail (family Naticidae) shells of approximately the same size (Table 1).

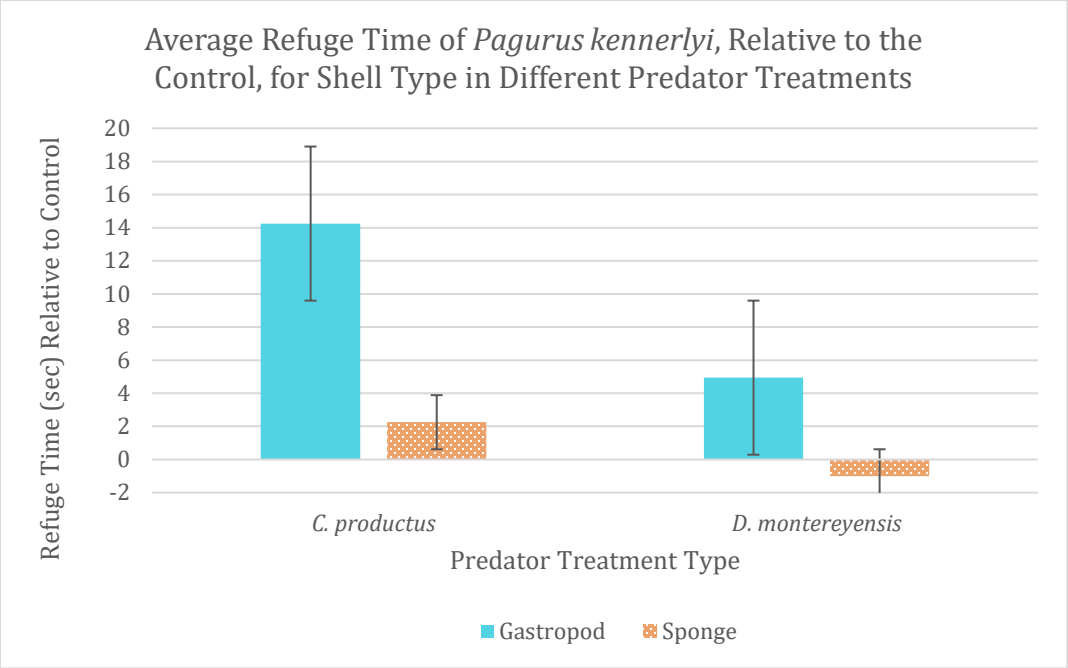

Figure 4: Average time spent refuging in shell from predators, relative to control for *Pagurus kennerlyi* hermit crabs between shell type and treatment group, with standard error bars. The solid blue bar is the relative refuge time of just *P. kennerlyi* GSCs (n = 2) and the dotted orange bar is relative refuge time of just *P. kennerlyi* SSCs (n = 2).

Eliminations from Analysis

One GSC and one SSC were eliminated from analysis due to consistently extreme refuge times. When gently set in a tank, these individuals would emerge quickly, but when dropped, would stay in their shells for 1+ minutes at a time, which was a large outlier when compared to all other crabs. We believe this was an aversion to being dropped, rather than a reaction to a predator, and as such these crabs were eliminated from analysis (in accordance with the process outlined in the methods).

Discussion

Null and Alternative Hypotheses

Our results suggest that we reject null hypothesis #1 (that predator type will have no impact on refuge time of GSCs), since GSCs spent significantly longer refuging from *C. productus* compared to the control or *D. montereyensis*. We fail to reject null hypothesis #2 (that the presence of a sponge shell would not affect refuge time from *D. montereyensis*), as SSCs did not react differently in the *D. montereyensis* compared to the control, but did spend significantly longer refuging from *C. productus*. We also fail to reject null hypothesis #3 (that shell type will have no impact on refuge time from *C. productus* or *D. montereyensis*), since SSCs did not spend a significantly different amount of time refuging from *C. productus* or *D. montereyensis* when compared to GSCs. However, the difference between GSCs and SSCs in the *C. productus*

treatment was almost significant ($p = 0.070$), where SSCs spent less time refuging than GSCs. Considering individuals of the same species with different shells reacted differently to *C. productus* (Fig. 4), larger sample sizes may have revealed a clearer pattern. Overall, it seems as though *C. productus* induced higher refuge time compared to the *D. montereyensis* or control groups for GSCs and SSCs. Since the average difference in refuge times between the *D. montereyensis* and control treatments was near 0 for both shell types, the presence of *D. montereyensis* has no impact on refuge time for sponge or gastropod shelled hermit crabs.

Other Studies and Broader Implications

The finding that *C. productus* induces a longer predator response is consistent with previous studies that found differential refuge time in the presence of hermit crab predators vs. a control (Rosen et al., 2009). Interestingly, it has been found that crushing crabs, such as *C. productus*, induce a shorter refuge time when compared to a control, which is opposite to the results of the present study (Rosen et al., 2009; Alcaraz & Arce, 2017). However, those contradictory results were obtained using different species of hermit crabs than were used here, which could indicate that species of hermit crab can react differently to the same predator. The results of the present study also indicate that SSCs have no clear predator response to *D. montereyensis*, meaning these nudibranchs likely do not pose a natural threat to SSCs, possibly because hermit crabs are able to evade a slow-moving nudibranch.

Additionally, there could be numerous explanations for why SSCs spent less time refuging in the *C. productus* treatments compared to GSCs, including species, protection provided by sponge, size of shell, and random variation. For each crab used, we measured aperture widths, and found that the aperture of gastropod shells was larger than that of sponge shells. While both crabs appeared to fully retract into their shell when dropped, it is possible that SSCs had less room in their shell due to a smaller aperture or internal space, and thus came out sooner. Alternatively, the SSCs could be reacting differently due to increased protection provided by the sponge. As mentioned previously, *Suberites* sponge contains toxins that would harm most predators of hermit crabs (Cariello & Zanetti, 1979; Wiens et al., 2003), possibly causing SSCs to be less threatened by the *C. productus* crab, and thus came out of their shell sooner. Since this difference in refuge time between SSCs and GSCs was not significant, however, it is possible that this pattern is due to random chance. As such, a larger sample size would be needed to confirm any differences between GSC and SSC predator reaction.

The results of this study show that the symbiotic sponge-hermit crab relationship could have an impact on hermit crab ecology and behavior. Less time refuging could mean more time foraging and roaming, and as such, altered behavior with sponge shells may provide some benefit to hermit crabs due to the decreased refuge times in the *C. productus* treatment. This altered behavior could also indicate that SSCs are less threatened by predators since they spend less time refuging. The presence of sponge shells could therefore decrease the amount of hermit crabs that are being preyed upon by *C. productus* crabs and other predators. As such, predation patterns could change, increasing pressure on other prey species if a large proportion of hermit

crabs have sponge shells. Additionally, this study confirms that the methods used in Mima et al. (2003) are effective in testing predator response, as we found a significant difference in shelter time from *C. productus* for both shell types, which is what we expected from examining other studies.

Conclusion and Future Research

Overall, the present study found that both SSCs and GSCs refuge more in the presence of hermit crab predators, but do not change refuge time in the presence of sponge predators. Between GSCs and SSCs, SSCs spent non-significantly less time refuging from *C. productus*. To better understand the reasoning behind why SSCs have different predator responses, and confirm if this difference could be significant, more research is needed on how different species and sizes of SSCs react differently, as well as if the species of sponge has an impact. Larger sample sizes and more species/shell diversity could help answer this. Observing *C. productus* predation behavior on GSCs and SSCs would also provide insight into how much the presence of sponge can influence predation patterns.

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