**Hermit crab predator avoidance based on shell type: *Suberites domuncula* symbiont or gastropod shell**

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## ABSTRACT

Hermit crabs are ecosystem engineers, decomposers, and a prey source for many larger predators such as the red rock crab, *Cancer productus*. All of these ecosystem factors are affected by interactions between species, especially predator-prey interactions. Some subtidal hermit crabs live in symbiosis with *Suberites* sponges that dissolve and replace the calcareous gastropod shell the hermit crab initially inhabits and continues to grow with the hermit crab. Sponges produce anti-predatory chemicals which could protect the hermit crab. Despite these anti-predatory defenses, some nudibranchs (e.g. *Doris montereyensis*) specialize in eating *Suberites domuncula*, a sponge species that often lives in symbiosis with hermit crabs. Predatory avoidance behavior is quantified by the time it takes the hermit crab to come out of its shell (in this study referred to as emergence time), after it has retracted into its shell in response to a stimulus. Emergence time gets shorter when running away is more beneficial to its survival, such as when a hermit crab has a weak shell, or a slow and shell crushing predator is near. It was hypothesized that Sponge shelled hermit crabs would have a longer emergence time when exposed to *C. productus*, and a shorter emergence time when exposed to a *D. montereyensis*, compared to gastropod shelled hermit crabs. Emergence time of hermit crabs was measured after being dropped from 20cm above the water surface of three treatment tanks: *C. productus*, *D. montereyensis*, and control, to explore the effects of having a sponge shell on predatory avoidance behavior of hermit crabs. Hermit crabs inhabiting sponge shells were found to have shorter emergence times overall but responded similarly to gastropod shelled hermit crabs: longer emergence time when exposed to *C. productus* than *D. montereyensis* or control. Knowledge of symbiotic and predator-prey interactions are crucial in understanding food webs and ecosystem dynamics.

## INTRODUCTION

Hermit crabs are scavenger decomposers of a multitude of food types and are important organisms in connecting terrestrial and aquatic habitats in coastal areas (Gorman et al. 2019). They are an important part of the food web, as they are prey to many animals such as the red rock crab, *Cancer productus* (Rosen et al. 2009). Hermit crabs can detect predator crabs from chemicals present in seawater (Rosen et al. 2009), and their behavior has been shown to change accordingly. This is demonstrated by a longer time spent in shell (in this study referred to as emergence time) if predator is unlikely to crush their shell, and shorter emergence times if fleeing is more beneficial and a shell crushing predator is detected (Mima et al. 2003, Rosen et al. 2009). Shell selection by hermit crabs has also been shown to affect behavior, as they are selective of their shells depending on environmental and biotic conditions (Mima et al. 2003). Most hermit crabs inhabit gastropod shells (hereafter referred to as GSCs), but some species live in symbiosis with sponges in the genus *Suberites* (hereafter referred to as SSCs; Caruso et al. 2005). Some sponges are capable of bioerosion (Wisshak et al. 2014), which is how sponges dissolve the calcareous shells of gastropods that hermit crabs inhabit and allows them to grow along with the host crab. Bioerosion rates by sponges are predicted to increase as ocean temperatures rise with climate change, and oceans become more acidic (Wisshak et al. 2014), which could potentially increase the amount of sponge shells available to hermit crabs. Sponges have few natural predators, as they produce chemical defenses which deter predators (Thoms and Schupp 2008), so they also provide this same protection to the hermit crabs they grow on (Wilson et al. 1999). However, some nudibranch species (order Nudibranchia), are specialized predators of sponges, like *Doris montereyensis* which specialize in eating *Suberites domuncula*, which often lives in symbiosis with hermit crabs (Turner et al. 2024). It is unknown if SSCs exhibit defensive behavior meant to protect their sponge symbionts.

Interactions between SSCs and sponge-eating predators are not well-studied. In a similar study done by Mima and colleagues in 2003, they found that GSCs had shorter emergence times in response to predator stimulus. Due to this finding, it was expected that in the present study all hermit crabs would have shorter emergence times when detecting a *C. productus*, and SSCs were predicted to respond the same way to the *D. montereyensis*, if they had defensive behavior for conserving their sponge symbionts. This study is based on the following two hypotheses: (1) SSCs will have a longer emergence time vs. GSCs when exposed to *Cancer productus*, and (2) SSCs will have a shorter emergence time vs. GSCs when exposed to *Doris montereyensis*.

Two species of SSCs (*Pagurus kennerlyi, Pagurus stevensae*) with sponge *Suberites domuncula* shells, and two species of GSCs (*Elassochirus tenuimanus, Pagurus kennerlyi*) were used as the test subjects in the present study to determine their predatory avoidance behavior. One data collection of emergence times was measured after dropping each hermit crab in three treatments to quantify response to presence of a predator crab *Cancer productus* and a sponge predator *Doris montereyensis*.

## METHODS

### *Specimen collection*

Six GSCs and six SSCs were used in this experiment. They were collected from a trawl on the San Juan Channel in Washington state, between Friday Harbor Labs and Roche Harbor at 48.5952195 N, 123.0675733 W (Figure 1), on April 18$^{th}$, 2024. The trawl was done at approximately 100m deep. A map (Figure 1) of the trawl location was made using Google Maps. The specimens were selected based on maturity (all individuals were adults) and having similar sizes of gastropod (3-4.5cm width) and sponge (4-4.5cm width) shells, as well as to have as many of the same species as possible in common between GSCs and SSCs. All hermit crabs and sponge shells were identified to species, and the gastropod shells were identified to family (due to all species in this family being morphologically similar, it is not expected that each species would affect hermit crabs differently) using the book Marine Life of the Pacific Northwest by Andy Lamb and Bernard Handby (Lamb et al. 2005). Each crab had measurements of aperture and width taken and recorded (Figure 2). Each crab was kept track of by separating them into jars during the experiment and assigned a unique ID label based on their shell type: G1, G2, G3, G4, G5, G6, and S1, S2, S3, S4, S5, S6. If one escaped, it was identified by combination of pictures taken during the first trial, species, and measurements of aperture and width. Two predators that were used in this experiment were one *Doris montereyensis*, collected from the Friday Harbor Labs dock (48.5455368 N, 123.0126299 W), and one *Cancer productus* collected from Argyle Bay (48.5206500 N, 123.0129357 W) on the San Juan Island, Washington. All hermit crabs were housed together in a holding tank with flowing sea water of 10-11˚C (variation reflected current sea temperature). Sponges filter fed from the sea water and the hermit crabs were fed 2 crushed up scallops and sea urchins every 2-3 days. Data was collected on May 5$^{th}$, 16$^{th}$, and 17$^{th}$, and two rounds of data collection were performed each day, with 2-4 hours between rounds for hermit crabs to recover after being dropped.

*Experimental setup*

Three treatment tubs varied in size of approximately 25x40x20cm, and were filled with 13L sea water each, and a smaller (14x14x8.5cm) perforated container that the hermit crabs were dropped in was placed on the bottom of each treatment tub (Figure 3). A weight was added to each smaller container to keep it from floating. The tubs were placed in a sea table (59x127x26cm) with the sea water covering 5-10cm of the bottom of the sea table which kept the treatment tubs at the same temperature of 10-11C. Each treatment tub had an air stone that was connected by a hollow tube to an air pump which supplied oxygen into the water, keeping the *C. productus* and *D. montereyensis* alive, in addition to eliminating hypoxic conditions from affecting predator avoidance behavior of the hermit crabs. The *C. productus* and the *D. montereyensis* were placed in their own tubs for 20 minutes prior to running the experiment, with no in or outflow of water, so the scent of the predators gets concentrated and disperses throughout the treatment tub.

*Data collection*

During data collection, each crab was dropped from 20cm above the water surface into each of the smaller containers within the three treatment tubs. The three treatment groups are control (no predator in tank, set up otherwise identical to other treatments), *C. productus* (a *C. productus* in a treatment tank), and *D. montereyensis* (a *D. montereyensis* in a treatment tank). A 20-cm drop ensures the hermit crab retracts into its shell (Mima et al. 2003). The emergence time was defined as the time in seconds it took for the two front claws to come out of the shell and was recorded using a stopwatch. To avoid bias in the number of times a hermit crab was dropped, they were dropped in sets of three (Set 1: G1, S1, G2. Set 2: S2, G3, S3. Set 3: G4, S4, G5. Set 4: S5, G6, S6). Each crab in a set of three would start with a different treatment and rotate through all three treatments (control, *C. productus*, and *D. montereyensis*) in a different order. While one crab was being dropped, the rest were in the holding tank. The first crab in a set of three was dropped in its assigned treatment, followed by the other two in their treatments, then it would be repeated so all crabs go through all treatments. The next set of crabs would go in different order than the first set to go through all possible combinations of orders dropped. In the case that a hermit crab did not emerge within 60 seconds, it was dropped one more time. The second time was accepted if it was under 60 seconds, otherwise this data point was discarded from data analysis. 60 seconds was determined the cut off point because most crabs emerged in under half (30 seconds) of that time. SSC5 and GSC6 were not included in analysis due to having five or more discarded data points.

*Data analysis*

Emergence time values were input into Microsoft Excel where all calculations were made. Average emergence times were calculated for each hermit crab using the =AVERAGE (number1, [number2], …) command, where emergence times for each of the six runs were used as number1, number2, etc. Then all the individual averages were used to calculate average emergence times for GSCs and SSCs in each treatment (Figure 4). To eliminate bias due to testing multiple species of hermit crabs, the average emergence times for each crab were used to calculate differences between emergence times for each treatment, this is called treatment time difference (TTD, Table 3, 4). The TTDs were: control treatment emergence time subtracted from *C. productus* emergence time (rr-c), control emergence time subtracted from *D. montereyensis* emergence time (n-c), and *D. montereyensis* treatment emergence time subtracted from *C.*

*productus* treatment emergence time (rr-n). A table was made with columns for: ID, emergence time, TTD, shell type, and TTD + shell type (G for gastropod and S for sponge, followed by TTD). This table was used in RStudio (RStudio Team, 2020) to perform an ANOVA, comparing emergence time (dependent variable) with TTD + shell type (independent variable). This way the significance between TTDs can be tested. This ANOVA was analyzed using a TukeyHSD test that provided any significant differences in TTDs between all possible groups. Bar graphs were made comparing TTDs with gastropod versus sponge shelled hermit crabs (Figure 5). GSC6 and SSC5 were excluded from all calculations, as they exhibited opposite trends to all other hermit crabs and were thus treated as outliers.


**Figure 1.** Trawl was performed at coordinates 48.5952195 N, 123.0675733 W, indicated by the red marker. The trawl path is shown by the red line. The red box in the smaller map shows the location of the large, more precise map in the San Juan Islands, Washington.

**Figure 2.** Blue line shows how width (left) and aperture (right) of shells were measured.

**Figure 3.** Experimental setup (left) has three treatment tubs placed in a sea table. The sea table has water covering the bottom and each treatment tub has 13L of water each. A *C. productus* is placed in one of the treatment tubs and a *D. montereyensis* is in another treatment tub, the control tub has no predator. All treatment tubs include a smaller tub with a weight, and an air stone

connected with a tube to an air pump. Hermit crabs were separated into jars during data collection, and the jars were kept in the holding tank (right).

## RESULTS

### *Species and measurements*

The species of crabs used were: two *Pagurus kennerlyi* (S1 and S6) and three *Pagurus stevensae* (S2, S3, and S4) with sponge shells (*Suberites domuncula*), and three *Elassochirus tenuimanus* (G1, G2, and G4) and two *Pagurus kennerlyi* (G3 and G5) with gastropod shells belonging to the family Nalicidae. The widths for GSCs ranged from 3-4.5cm (sd: 0.63, average: 3.42cm), and aperture ranged from 1.9-2.8cm (sd: 0.34, average: 2.32cm, Table 1). For sponge shelled crabs, the width ranged from 4-4.5cm (sd: 0.20, average: 4.18cm), and aperture ranged from 0.9-1.7cm (sd: 0.39, average: 1.18cm, Table 2).

**Table 1.** Widths of gastropod shells and size of apertures in GSCs. GSC6 was excluded from data analysis (including SD and average on this table), highlighted in red.

| Gastropod shelled hermit crabs | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Crab 1 | Crab 2 | Crab 3 | Crab 4 | Crab 5 | Crab 6 | SD | average |
| Width (cm) | 3 | 3 | 4.5 | 3.4 | 3.2 | 4 | 0.63 | 3.42 |
| Apperature (cm) | 2.4 | 2.1 | 2.8 | 2.4 | 1.9 | 2.7 | 0.34 | 2.32 |

**Table 2.** Widths of gastropod shell and size of aperture in SSCs. SSC5 was excluded from data analysis (including SD and average on this table), highlighted in red.

| Sponge shelled hermit crabs | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Crab 1 | Crab 2 | Crab 3 | Crab 4 | Crab 5 | Crab 6 | SD | average |
| Width (cm) | 4 | 4.5 | 4 | 4.2 | 4.1 | 4.2 | 0.20 | 4.18 |
| Apperature (cm) | 1.5 | 0.9 | 0.9 | 0.9 | 0.9 | 1.7 | 0.39 | 1.18 |

### *Emergence times*

The averages for gastropod shelled crab emergence times were 9.85s in control treatment, 19.09s in *C. productus* treatment, and 11.20s in *D. montereyensis* treatment (Figure 4). The average emergence times for sponge shelled hermit crabs were 14.05s in control treatment, 17.97s in *C. productus* treatment, and 13.91s in *D. montereyensis* treatment (Figure 4).

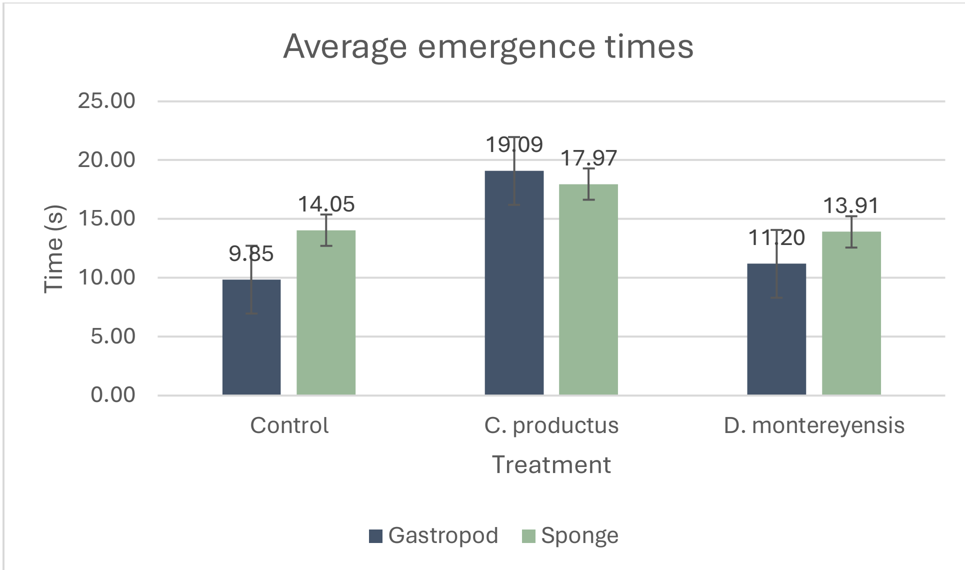


**Figure 4.** Average emergence times were more uniform for SSCs than GSCs. Dark blue bars show GSC, and light green bars show SSC average emergence times in each of the three treatment groups. Y-axis shows time in seconds (dependent variable) and x-axis shows the treatment groups: control, *C. productus*, and *D. montereyensis* (independent variable). Error bars indicate standard error.

*Hypothesis 1.*

Srr-c emergence values compared with Grr-c emergence values were statistically insignificant (ANOVA, TukeyHSD, a = 0.05, p-value = 0.22). SSCs spent on average 17.97s in their shell before emerging when exposed to *C. productus* stimulus, while GSCs spent an average of 19.09s. Average emergence times were lower in *D. montereyensis* (11.20s) and control (9.85s) treatments than in the *C. productus* treatment (Figure 4). The same pattern was exhibited by SSCs as their emergence times for *D. montereyensis* (13.91s) and control (14.05s) were lower than their emergence time in the *C. productus* treatment (Figure 4). These groups had a difference of 1.12s, which is insignificant due to p-value > 0.05 signifying no difference between emergence time.

*Hypothesis 2.*

Sn-c values compared with Gn-c values were statistically insignificant (ANOVA, TukeyHSD, a = 0.05, p-value = 0.99). SSCs spent an average of 13.91s in their shell when exposed to *D. montereyensis* stimulus, and GSCs spent 11.20s (Figure 4). These groups differ by 2.7s which is insignificant due to a p-value > 0.05.

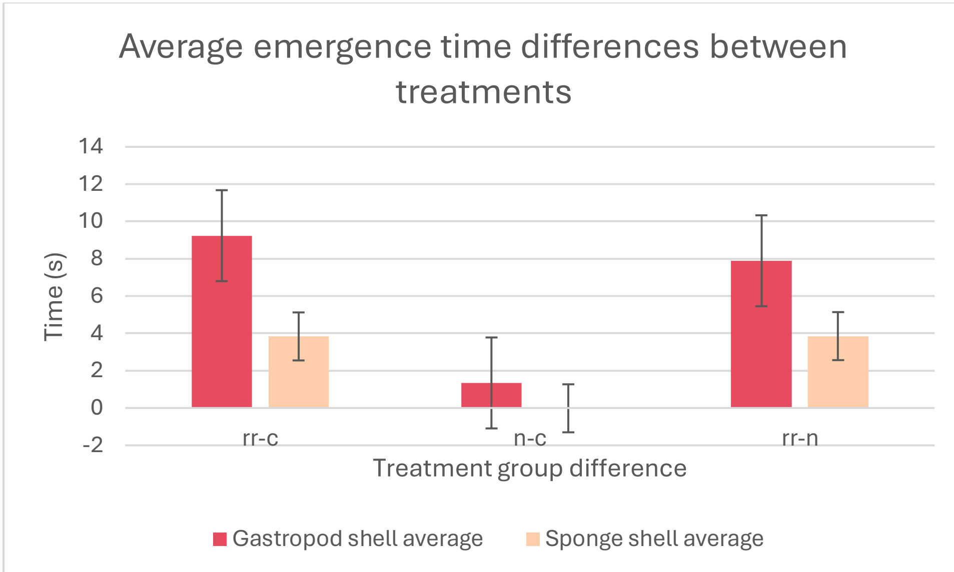


**Figure 5.** The difference in emergence times between groups was smaller for SSCs than GSCs. Y-axis shows time in seconds (dependent variable), and x-axis shows treatment group differences (independent variable). Red bars indicate results for GSCs, and light orange bars show results for SSCs. Error bars show standard error.

**Table 3**. Time differences (dependent variable) between treatments (independent variable) are shown for each GSC crab and averaged in the last column. GSC6 was eliminated due to conflicting data, it is not included in the averaged values.

| Differences in time between treatments (Gastropod shell) | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Crab 1 | Crab 2 | Crab 3 | Crab 4 | Crab 5 | Crab 6 | Average |
| rr-c | 7.011667 | 6.426667 | 9.961667 | 4.255 | 18.535 | -11.3293 | 9.238 |
| n-c | -2.07167 | -1.17333 | 6.62 | 0.083333 | 3.265 | -1.42583 | 1.344667 |
| rr-n | 9.083333 | 7.6 | 3.341667 | 4.171667 | 15.27 | -9.9035 | 7.893333 |

**Table 4.** Time differences (dependent variable) between treatments (independent variable) are shown for each SSC crab and averaged in the last column. SSC5 was eliminated due to conflicting data and not included in the averaged values.

| Differences in time between treatments (Sponge shell) | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Crab 1 | Crab 2 | Crab 3 | Crab 4 | Crab 5 | Crab 6 | Average |
| rr-c | 3.106667 | 4.975 | 3.19 | 6.521667 | -1.60667 | 1.398333 | 3.838333 |
| n-c | -1.5625 | -1.02833 | 2.9 | 0.078333 | -1.30833 | -0.46333 | -0.01517 |
| rr-n | 4.669167 | 6.003333 | 0.29 | 6.443333 | -0.29833 | 1.861667 | 3.8535 |

## DISCUSSION

*Hypothesis 1.*

SSCs were hypothesized to have a longer emergence time compared to GSCs when exposed to a *C. productus*. There was no statistically significant difference in emergence times between GSCs and SSCs when exposed to the *C. productus* (p-value > 0.05), thus the null hypothesis cannot be rejected. Since both shell types react with a similar time differential, and emergence time was higher when exposed to *C. productus* (G=19.09s, S=17.97s) than *D. montereyensis* (G=11.20s, S=13.91) or control (G=9.85s, S=14.05s), this hypothesis cannot be accepted (Figure 4). This behavior could indicate that SSCs either feel equally protected by their Sponge shells against a *C. productus*, or that the SSCs do not have a way of sensing that the amount of protection from a Sponge shell might be less than a gastropod shell. If *C. productus* are deterred by the chemical defenses, SSCs hiding in their Sponge shell does not come at a cost to the SSC. However, it is possible the Sponge shell does not deter the *C. productus*, as it will likely not be ingested by the *C. productus*, since the shell is crushed or picked apart (Zipser and Vermeij 1978) and is easier to break than a gastropod shell, not changing predator avoidance behavior will come at a fitness cost, and possibly an earlier death to the SSCs.

*Hypothesis 2.*

SSCs were hypothesized to have a shorter emergence time than GSCs when exposed to a *D. montereyensis*. No significant difference was found between GSC and SSC emergence times when exposed to a *D. montereyensis* (p-value > 0.05), therefore the null hypothesis cannot be rejected. This means having a Sponge shell did not affect SSCs behavior around a Sponge predator (*D. montereyensis)*, and therefore Sponge protective behavior was not exhibited during this study by the SSCs. This could be due to gastropod shells being more favorable to the hermit crabs than Sponge shells (Sandford 1995) or that the *D. montereyensis* are very slow and unlikely to reach the Sponge shells of SSCs, so no quicker fleeing behavior is needed.

*Broader implications and future studies*

Overall, the findings of this study indicating longer emergence time in all hermit crabs when exposed to *C. productus* stimulus is opposing the findings of Mima et al. (2003), where they found hermit crabs decrease emergence time in the presence of a predatory crab. However, Mima and colleagues in 2003 used different species of hermit crabs (*Pagurus filholi*) and predatory crabs (*Gaetice depressus*), which could be the reason for the opposing overall trend, as hermit crabs may decrease their hiding time when a predator is likely able to crush the hermit crabs shell, but might increase the hiding time if the shell will keep the hermit crab protected and the predator can catch the fleeing crab easily (Rosen et al. 2009). Although the *C. productus* is a shell crushing predator (Zipser and Vermeij 1978) which makes the opposite trend in emergence time strange. It is possible that the predator crab used by Mima and colleagues in 2003 has a different hunting style than the *C. productus* used in the present study, and therefore caused differing results (Rosen et al. 2009). This also disputes the hypothesis that SSCs exhibit Sponge shell protecting behavior, as the *D. montereyensis*s are slow moving and therefore shortening emergence time would be beneficial to protect the Sponge shell (Rosen et al. 2009). Since the emergence time was the same in *D. montereyensis* treatment and control treatment, it is indicative that the SSC species in the present study do not exhibit Sponge shell protective behavior.

Small sample size is the main factor contributing to insignificance of results and may be a contributing factor to results contradicting previous studied. In addition, the rest time between drops may not have been long enough, as crabs seemed to have increasingly long emergence times during the second trial of each day. Further research of how predator prey interactions are affected by shell type needs to be done. The possibility of differing predatory avoidance behavior of SSCs with sex and maturity should be explored, as Sponge shells are often inhabited by younger crabs due to competition for gastropod shells (Sandford 1995). Behavioral mpacts of having a Sponge shell in rising oceanic temperatures and acidic water hould be studied as well, as Sponges can erode shells quicker in more acidic conditions (Wisshak et al. 2014), the amount of Sponge shells compared to gastropod shells has the potential to increase as global warming progresses. The symbiosis between *Suberites* shells and hermit crabs is complicated and needs to be studied in more detail to see how predator-prey interactions shape the food web.

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