

INVESTIGATING THE BEHAVIORAL ECOLOGY AND REEF HABITAT PREFERENCES OF *LIMARIA FRAGILIS* BIVALVES IN MOOREA, FRENCH POLYNESIA

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Abstract. This study set out to determine whether *Limaria fragilis* bivalves' burrowing behaviors and ecological interactions might be predictably characterized in its Mo'orea, French Polynesia habitat. Observations of morphological data, substrate selection preferences, and burrowing in the presence of a conspecific were conducted through separate experimental trials. Morphological observations determined positive correlations between *L. fragilis* shell size and tentacle length. Results from the substrate selection study do not support the hypothesis that *L. fragilis* exhibits predictable habitat preference as mediated by their tentacles. Conspecific interactions were found not to have significant effects on *L. fragilis* burrowing and substrate selection behaviors. This work guides future studies of *L. fragilis* to further investigate the effects of size on community interactions, characterize community composition and nest-building behavior, and better understand the physiology and sensory capabilities of *L. fragilis*' functional morphology.

Key words: bivalve; mollusk; conspecific behavior; habitat preference; *Limaria fragilis*; French Polynesia

INTRODUCTION

Coral reefs are home to marine organisms that interact in unique ways with their abiotic and biotic surroundings. Many organisms evolve morphological or behavioral adaptations to mediate these interactions, which often result in resource acquisition, habitat establishment, or beneficial symbiotic relationships (Glynn 1976, Sale 1977, Hughes and Hughes 2007). These interactions also shape community dynamics among organisms, and due to intense competition for resources in reef environments the selective pressures of coral reef ecosystems are amplified (Glynn 1976).

Predation is an interaction that pressures organisms to evolve mechanisms to defend and preserve their own livelihoods. These mechanisms often combine particular functional morphologies with specific behaviors (Werner et al. 1983, Lima and Dill 1990). For some animals, selective habitat preference is an effective way to avoid predators (Werner et al. 1983). Organisms that burrow or hide underneath reef substrate survive more encounters with predators than organisms that do not exhibit this behavior (Sale 1977). Bivalves are sessile without complex sensory organs or defensive appendages and, besides closing their shells,

cannot actively defend themselves from predators (Côte and Jelnikar 1998). As a result, most mature bivalves must burrow to protect themselves from threats (Haddon et al. 1987, Côte and Jelnikar 1998). Studies on bivalve ecology have found that greater burrowing depth affords more effective protection from local predation (Blundon and Kennedy 1982, Haddon et al. 1987). Bivalves therefore present interesting model organisms for understanding the evolution of defensive behaviors in sessile coral reef inhabitants.

Limaria fragilis is a bivalve mollusk found in the Indo-Pacific region (refs). In its Mo'orea, French Polynesia habitat (pers. obs.), *L. fragilis* is found burrowed underneath coral rubble and reef sediment. *L. fragilis* has bright red tapered tentacles protruding from its mantle, which it uses to defend itself and independently swim (Gilmour 1967, Donovan et al. 2004). Facing threats, *L. fragilis* autotomizes its tentacles and secretes a distasteful mucus (Morton 1979, Donovan et al. 2004). As a short-term defense mechanism, autotomy presents the immediate benefit of a quick escape, however it is unclear whether *L. fragilis* has evolved other strategies for longer-term protection and defense (Donovan et al. 2004, Fleming and Bateman 2007). Other strategies might include conspecific aggregation and nest-building, which have

been studied of the related bivalve *Lima hians*, which burrows when disturbed (Gilmour 1967, Moore 2000).

Little is known about whether *L. fragilis*' tentacles help identify surroundings, or if the animal prefers one type of habitat over others. Additionally, it is unclear whether the animal's size might affect how the organism interacts with its environment (Donovan et al. 2004). Greater bivalve size has previously been connected to high survival rates and conspecific density, and deep burrowing (Nicastro et al. 2012). These studies have only been conducted on sessile bivalves with different morphologies and habitats than *L. fragilis*, though they leave room to investigate whether bivalve behavior and ecological interactions differ with the presence of additional appendages.

L. fragilis habitat selection and burrowing behavior might also be influenced by the presence of conspecific organisms. Sessile bivalves often cohabitate as aggregations in their intertidal communities (Côte and Jelnikar 1998). This behavior has been experimentally found to increase survival rates, reproductive success, and the maintenance of favorable environmental conditions (Okamura 1986, Haddon et al. 1987, Côte and Jelnikar 1998, Nicastro et al. 2012). *Lima hians* also utilize aggregate behavior and nest-building as a defensive strategy (Gilmour 1967, Moore 2000). These nests are constructed of byssal threads, contain multiple conspecifics and other nearby organisms, and bind surrounding sediment (Moore 2000). In tidal ecosystems, these reefs amount up to 10-20cm in height, spanning hectares (Moore 2000). This reef-building ability is uncommon among bivalves, who often burrow with conspecifics but do not construct such elaborate structures (Moore 2000, Bertolini et al. 2017). It is unclear how the animals determine what materials should make up their nests, and how animal size might affect their overall community composition (Moore 2000). Some field studies have found that adult *L. fragilis* organisms inhabit solitary nests, while smaller juveniles build larger reefs together (Jeffreys 1863, Step 1927, Moore 2000). Others suggest that nest-occupation patterns might not be so predictable (Gilmour 1967). Nonetheless, these biogenic reefs are of particular importance to conservation efforts. Their structures provide great protection from threats and contain high biodiversity, but are especially sensitive to anthropogenic mechanical disturbances (Sale 1977, Moore 2000). Given the benefits of

burrowing and the occurrence of aggregate behavior among related bivalve species, studying the influence of conspecifics on habitat selection and burrowing behavior might provide new insights to fundamental aspects of *L. fragilis* life history and ecological interactions.

This study investigated the relationship between behavior and morphology of the bivalve mollusk *Limaria fragilis* in Mo'orea, French Polynesia, to better understand community interactions and defensive strategies in its unique reef ecosystem. The first objective of this study was to determine whether *L. fragilis* exhibits predictable substrate preference in its burrowing behavior. The second objective of this study was to determine whether substrate preference and habitat selection might be affected by the presence of *L. fragilis* conspecifics and prior resident conspecifics. The third objective of this study was to determine whether *L. fragilis* shell size and tentacle length might be correlated, and whether organismal size influences burrowing behavior and defensive strategies. These objectives were tested by substrate preference trials under different conditions, cataloging and characterizing conspecific behavior, and quantitative analysis of *L. fragilis* morphology within a behavioral context.

METHODS

Study Site Description

This study took place on the island of Mo'orea, in French Polynesia. Mo'orea is one of many volcanic atoll islands in the Society Island chain, with an expansive fringing reef surrounding the greater perimeter of the island. *L. fragilis* individuals were collected at a shallow reef site on the Western side of Opunohu Bay, 17°29.28'S, 149°53.00'W (FIG. 1).



FIG. 1. Map of Mo'orea with field site indicated.

This site was visited twice a week; seven to ten organisms were collected each time depending on abundance of organisms at the site.

Study System

L. fragilis is a bivalve mollusk that burrows underneath reef rubble and sediment in Indo-Pacific coral ecosystems (refs., pers. obs.). *L. fragilis* is perhaps best recognized for its red and white-banded, tapered tentacles which protrude from its mantle and provide the animal with abilities of locomotion and self-defense (Donovan et al. 2004). These animals filter-feed to acquire nutrients from their surroundings, and primary predators are not known (pers. obs.). *L. fragilis* presents an intriguing study system for understanding diverse defense mechanisms employed by reef organisms.

Specimen Collection and Identification

Organisms were collected by turning over rocks and coral rubble, then grabbing the animal's shell with two fingers, careful to avoid excessive contact with the animal's tentacles. Contact with the animal's tentacles may result in autotomy, where the animal ejects its tentacles and secretes a sticky mucus. Gloves were worn while collecting to prevent coral scrapes and harm from nearby *Hermodice carunculata* or *Diadema*. Collected organisms were transported back to the Gump South Pacific Research Station and kept in a large holding tank with continuous flow and coral rubble, rock, and algae. Individuals were tagged with an identifying number written in pencil on a 0.5cmx0.5cm square of Rite-in-the-Rain notebook paper super-glued to the animal's shell. One number per individual was written with pencil on a 0.5cmx0.5cm square of Rite-in-the-Rain notebook paper. Next, each square was cut using a pair of scissors. Then, tweezers were used to hold the square in one hand, and a dot of super glue was applied to the unmarked side of the square by the other hand. After this, the same hand was used to pick up a *L. fragilis* individual by the shell. The animal was held so that its tentacles and mantle remained submerged in the water, but part of its shell could be quickly wiped dry and the

identification square could be affixed to the shell by the tweezers. This procedure was repeated for all 45 collected individuals. Size quartiles were identified using the size data within R (Table 1, R Core Team 2018).

Morphological Data

Once in the laboratory, I measured the shell size and tentacle length for each collected individual. A caliper was used to measure the shell lengthwise (mm), parallel to the animal's adductor muscle edge. Next, the caliper was used to measure the length of a second-row tentacle protruding from the central bisecting point of the animal's shell (mm). Linear regression was used to test correlations between shell size and tentacle length using R software and with alpha = 0.05 (R Core Team 2018).

Burrowing Time and Preference Alone

To explore whether animals demonstrated substrate preference and to determine how long it took for animals to burrow, I conducted a study to measure these objectives. Specifically, 41 animals were introduced to a new container of size 20.32 x 20.32 centimeters with one 12.00 x 5.08 x 1.27 centimeter piece of fungia rubble ("Fungia"), collected from Gump Station property, and one 10.16 x 7.62 x 5.08 centimeter rock ("Rock") inside, 6 centimeters apart at opposite sides of the tub. At the start of each trial, one animal was introduced alone to this substrate selection arena, its identification number was noted, and a stopwatch was started. The animal was observed for three minutes. The substrate chosen and time to burrow underneath the substrate were recorded for each clam. Individuals that did not burrow during the three-minute window were noted ("Does Not Burrow"). After three minutes, the individual was removed from the substrate selection arena and placed back into its tank habitat. Water in the tub was changed, and each substrate rinsed, between each trial.

TABLE 1. Size quartiles as determined by specimen identification and R software.

Size Group	Size Range	Individuals
1	1.2-1.9cm	6, 13, 20, 26, 27, 35
2	1.9-2.2cm	7, 15, 16, 19, 28, 29, 30, 36, 37, 43, 44, 45
3	2.2-2.5cm	3, 4, 10, 11, 17, 23, 34, 40, 41, 42
4	2.5-3.2cm	1, 2, 9, 14, 22, 38, 39

Burrowing Time and Preference in the Presence of a Conspecific

In a separate experiment, I tested the animals' behavior in the presence of a conspecific. In this case, animals were separated into different tanks according to size quartiles.

Two animals from the same quartile were randomly selected and placed into the substrate selection arena together, with one available *Fungia* and one available Rock substrate for burrowing. Time to burrow, preferred substrate, and other observations of the animal's behavior were recorded for each animal over a three-minute observation period.

Burrowing Time and Preference in the Presence of a Prior Resident Conspecific

In another round of trials, animals were separated into different tanks according to size quartiles as before. Size quartiles were determined using R software to identify range of animal size, collected as morphological data (Table 1, R Core Team 2018). Each animal was introduced to the preference selection arena while one other animal from the same size quartile remained underneath the available *Fungia* substrate. Substrate preference, time to burrow, and other observations of the animal's behavior were recorded for each animal over a three-minute observation period.

A one-way ANOVA test was used for analysis of mean burrowing time for the three conducted burrowing trials using PAST statistical analysis software.

RESULTS

Morphological Data

Of 45 measured *L. fragilis* individuals, shell sizes ranged from a minimum of 1.20cm to a maximum of 3.20cm. Mean shell size for these 45 individuals was 2.13cm. Tentacle length ranged from 0.5cm to 2.40cm, with mean tentacle size of 1.50cm. A linear regression analysis performed for this data found a positive correlation of 0.8 between shell size and tentacle length, indicating a positive relationship between shell size and tentacle length. A regression line to fit this data had an R^2 value of 0.64 (FIG. 2), and this correlation data was found to be statistically significant ($p=4.14E-11$).

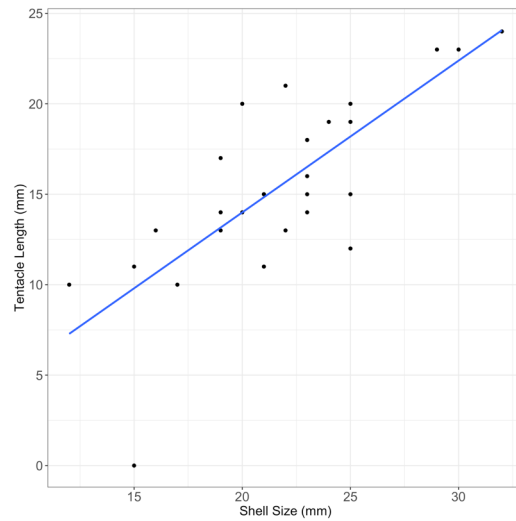


FIG. 2. Scatter plot displaying single measures from each organism's shell size and tentacle length.

Burrowing Time and Preference Alone

A total of 41 individuals participated in a solitary burrowing trial, where 19 burrowed underneath the *Fungia* substrate and 19 burrowed underneath the Rock substrate. 3 animals did not burrow (FIG. 3). A Chi-Squared Goodness-of-Fit test showed that observed substrate selection preferences were not significant ($X^2 = 0.1097$, 1 d.f., $p = 0.7400$).

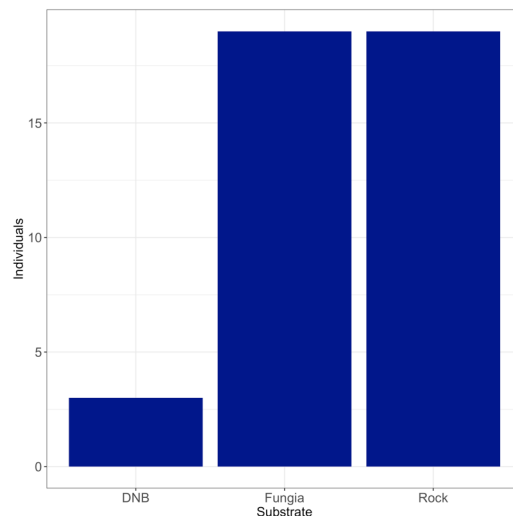


FIG. 3. Bar plot showing substrate selection by 41 organisms in a solo burrowing trial.

The minimum time to burrow under substrate was 5.00 seconds, and the maximum time to burrow was 162.00 seconds. Mean time to burrow was 42.95 seconds (FIG. 4).

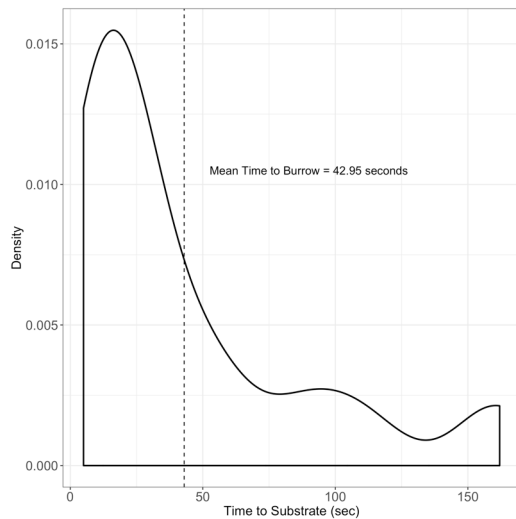


FIG. 4. Kernel density plot based on a cumulative frequency distribution of total time to burrow during solo trials.

Burrowing Time and Preference in the Presence of a Conspecific

For 35 individuals who underwent the conspecific burrowing trial, 21 burrowed under the same substrate as their conspecific partner and 10 burrowed alone. 4 animals did not burrow at all (FIG. 5). A Chi-Squared

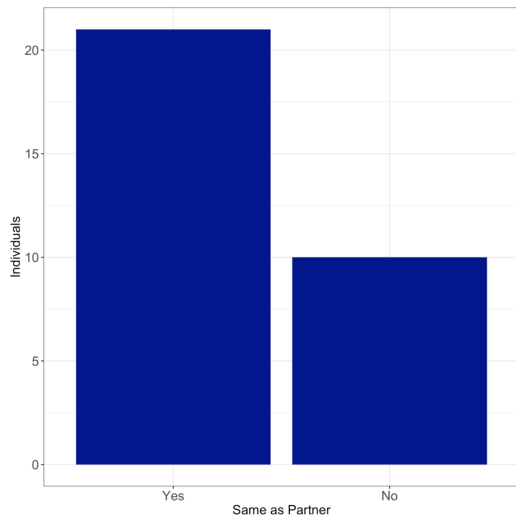


FIG. 5. Bar plot of burrowing in the presence of a conspecific. 21 individuals burrowed with their partner and 10 individuals did not.

Goodness-of-Fit test showed that these preference results were not significant ($\chi^2 = 0.0482$, 1 d.f., $p = 0.8263$). The minimum time to burrow was 0.00 seconds. The maximum time to burrow (excluding 4 DNB values of 180.00 seconds) was 104.46 seconds. Mean time to burrow was 26.40 seconds (FIG. 6).

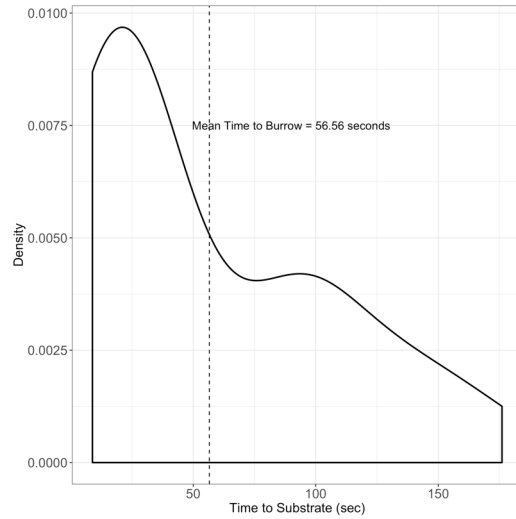


FIG. 6. Kernel density plot based on a cumulative frequency distribution of total time to burrow during conspecific trial.

Burrowing Time and Preference in the Presence of a Prior Resident Conspecific

A total of 32 individuals underwent a prior resident conspecific burrowing trial. During these trials, 18 individuals burrowed with the conspecific underneath the Fungia substrate, and 14 burrowed under the Rock (FIG. 7). A

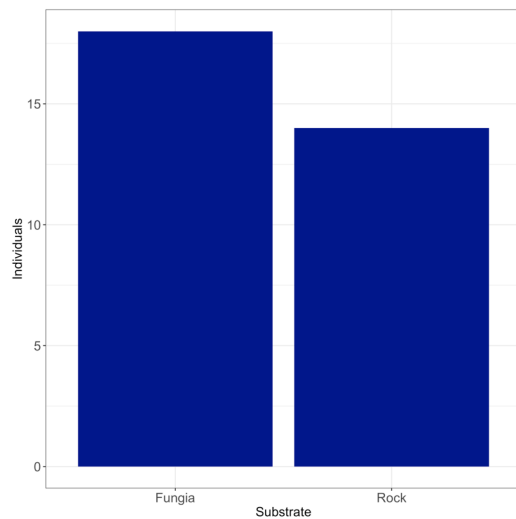


FIG. 7. Bar plot of burrowing with a prior resident. 18 individuals burrowed with the prior resident and 14 did not.

Chi-Squared Goodness-of-Fit test showed that these selection results were not significant ($\chi^2 = 0.0253$, 1 d.f., $p = 0.8736$).

The minimum time for an animal to burrow was 0.00 seconds. The maximum time to burrow was 145.32 seconds. The mean time to burrow was 47.10 seconds (FIG. 8).

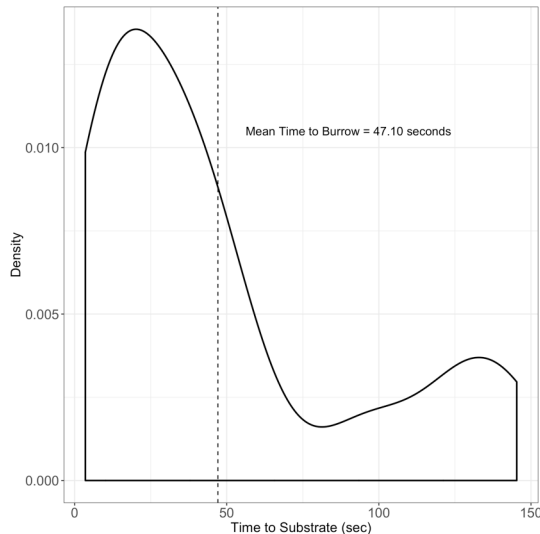


FIG. 8. Kernel density plot based on a cumulative frequency distribution of total time to burrow underneath substrate during prior resident conspecific trial.

DISCUSSION

The overarching objective of this study was to better understand the relationships between *Limaria fragilis*' functional morphology and the reef environment it inhabits in Mo'orea, French Polynesia. This objective was met by designing experiments to better understand community behaviors and defensive strategies of these unique organisms. Data gathered from these experiments show that *L. fragilis* does not exhibit predictable, significant substrate preference, nor is the organism's habitat preference significantly influenced by the presence of conspecific organisms or prior residents. Additionally, these findings, along with observations made during experimental trials, provide insight to the ways an organism's size influences its individual behavior and shapes its interactions with the surrounding environment.

The first objective of this study sought to determine whether *L. fragilis* exhibits substrate preference when establishing a habitat. It was hypothesized that *L. fragilis*' tentacles might facilitate tactile recognition of surrounding substrates, and that this substrate recognition

would enable the organism to prefer one habitat to another. To test this hypothesis, I exposed the animals to substrates found in their typical reef environments, made observations of their behaviors and interactions with the substrates, then recorded which substrate each animal had chosen to burrow under. Statistical analysis of experimental findings determined no significance between where the animal had chosen to burrow during trials. However, considering these statistical findings alone misrepresents what qualitative behavioral observations of the organisms suggests about substrate selection. During trials, animals touched available substrate with their tentacles, swam around the selection tank before burrowing, moved from one substrate to another before making a decision, and in some cases abandoned one habitat for another altogether. These observations might indicate that *L. fragilis* undergoes some sort of substrate identification, or deliberation about the kind of habitat it might want to establish. However, quantitatively, half the organisms burrowed underneath each of two available substrates. This suggests that the organisms do not habitually prefer one type of substrate to another.

Consequently, the results of individual substrate selection trials offer new avenues for further studies of *L. fragilis* behavior and ecology. Future studies might incorporate more molecular or physiological work on *L. fragilis* tentacles to investigate and understand their sensory abilities. It is possible that the *L. fragilis* tentacles are not at all physiologically capable of identifying and differentiating substrates. It is also possible that substrate type does not matter as much to *L. fragilis*' life history and survival as protection and shelter altogether. Given the intense competition for space and resources in coral reef ecosystems, *L. fragilis* may have evolved generalist behaviors, taking advantage of whatever resources are immediately accessible and available. That is, *L. fragilis* does not seek a specific kind of substrate for burrowing as much as it seeks to burrow altogether. Because so few studies have been conducted on this species and its ecological interactions, my own understanding of their burrowing behavior might have been incorrect to begin with. A larger field study that meticulously surveys the type of sediment *L. fragilis* burrows underneath, and investigates the construction and maintenance of these burrows or nests, would have proved useful even in preliminary experimental design for

this project. Again, future research that analyzes not only the microscopic aspects of *L. fragilis* physiology, but also classifies the distinct niche that the organism occupies would help provide a more thorough foundation for the questions that guided this study. Lack of literature in this area leaves ample room for more definitive answers.

The second objective of this study was to determine whether the presence of *L. fragilis* conspecifics might influence an individual's habitat selection behavior. It was hypothesized that, even if *L. fragilis* did not use its tentacles to identify and differentiate possible substrates, the presence of a conspecific would influence habitat selection behaviors. It was hypothesized that *L. fragilis* would burrow with conspecifics, forming an aggregation underneath substrate together. This hypothesis was based on previous studies of sessile bivalve behavior that found positive correlations between high conspecific density and greater survival rates (Nicastro et al. 2012, Bertolini et al. 2017). Two separate trials were carried out to explore this objective.

In the first of these trials, animals were introduced to substrate selection conditions with a size-matched conspecific. In the second, animals were introduced to the same conditions while another size-matched conspecific remained underneath one of the substrates. Statistical analysis via Chi-Squared Goodness-of-Fit tests did not indicate a significant difference for either trial between observed and hypothesized substrate preference outcomes in the presence of conspecifics. Based on these statistical results alone, one cannot conclude that the presence of a conspecific might affect or influence another organism's substrate preference or habitat selection.

It is important to differentiate between habitat selection versus burrowing behavior in the presence of a conspecific. "Habitat selection" refers to the final result of an animal's substrate selection. "Burrowing behavior" refers to observations we might make of the ways the organism interacts with its environment and conspecifics. Conspecific organisms did not significantly influence habitat selection. Observations of conspecific interactions suggests, however, that the presence of a conspecific does affect *L. fragilis* burrowing behavior. Similar to individual substrate selection trials, observations of the organisms during experimental trials provides new insights that purely quantitative data cannot. When introduced to experimental

conditions, conspecifics interacted with each other for a long time before burrowing underneath available substrate. Individuals touched each other and available substrate using their tentacles, swam around and toward each other from opposite sides of the selection tank, and in some cases competed with each other for a specific hiding spot. An ANOVA test to compare burrowing times for the three separate trials did not find a significant difference between means for these data, however ($p > 0.05$, FIG. 9 and Appendix Table 2).

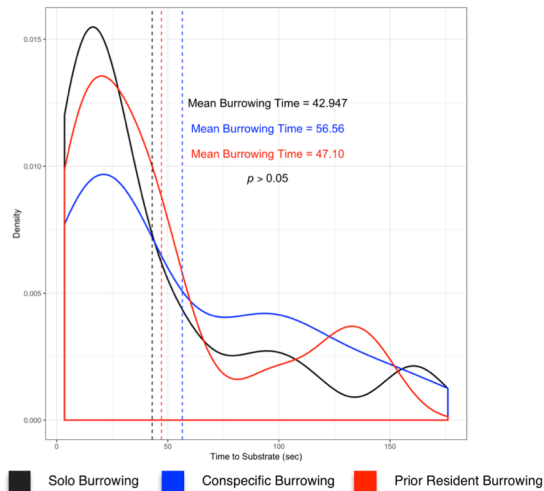


FIG. 9. Kernel density plot showing cumulative frequencies of mean time to burrow for all experimental trials.

Another factor for consideration with this experiment's data set is organismal size. Studies of sessile bivalve and other organismal ecology have determined behavioral trends linked to individual size (Gilmour 1974, Ridgway et al. 2011, Bertolini et al. 2017). Observations of size quartiles, combined with results of conspecific trials, show that burrowing behavior in the presence of conspecifics changes with size differences. Across both conspecific pairings and prior resident trials, one individual from the fourth quartile burrowed with a conspecific. Smaller individuals burrowed more often with conspecifics, however, behaving differently in conspecific pairings and prior resident trials. During conspecific pairing trials, 83% of individuals from the first size quartile burrowed with their partner. During prior resident trials, 55% of individuals from the first size quartile burrowed with a conspecific. This suggests that larger individuals are less

inclined to burrow with conspecifics (FIG. 10). The relationship between organismal size, age, and burrowing and community behavior has been discussed with regards to the related *Lima hians* species. Some studies hypothesize that only the smaller, juvenile *Lima hians* participate

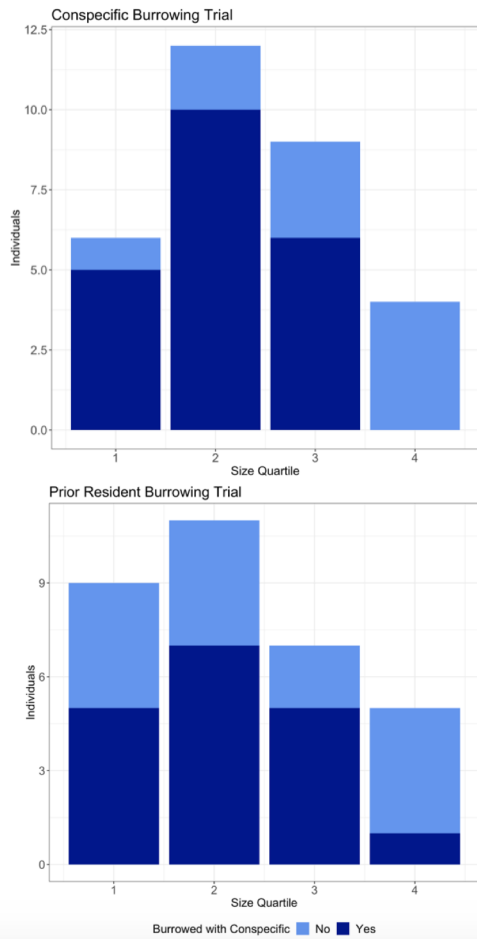


FIG. 10. Bar chart displaying number of organisms that burrowed with and without conspecifics during trials.

in aggregate behavior and nest-building behavior, while larger *Lima hians* burrow by themselves (Moore 2000). Other field surveys, however, assert that these trends are not so discernible (Gilmour 1967). Future work on *L. fragilis*, informed by or in conjunction with these studies of related systems, might specifically focus on how size impacts *L. fragilis*' ecological interactions.

Organismal size, however, did not significantly affect burrowing time during trials. A two-way ANOVA with factors of organismal size and trial type was carried out to compare the means from the three conducted trials. The differences between

mean time to burrow for different size groups, during aforementioned experimental conditions, were not significantly different ($p > 0.05$, FIG. 11 and Appendix Table A2). This suggests that size and experimental treatment do not affect burrowing time, and that their combined interactions do not significantly change what we might otherwise observe in solo burrowing trials.

It is unclear how *L. fragilis* exhibit social behavior or make determinations of

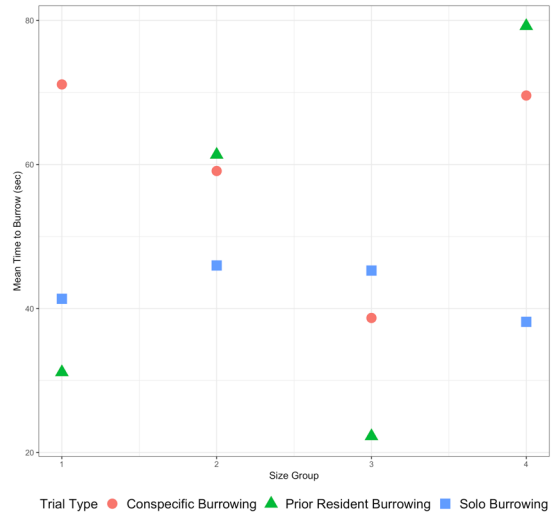


FIG. 11. Scatter plot showing mean times to burrow for three experimental trials.

surrounding substrate and the presence of conspecifics. This analysis invites future studies to investigate possible signaling mechanisms that *L. fragilis* might employ in community interactions, with special attention to molecular perspectives on *L. fragilis* tentacle physiology. The pursuit of these questions will provide new and deeper understandings of *L. fragilis* behavior and interactions with its reef home. This will additionally introduce new insights to the basis and efficacy of these interactions on three separate yet significant scales: individually, within groups, and as they pertain to a surrounding abiotic environment. This study provides further understanding of diverse defense mechanisms and insight to life histories of Mo'orea's coral reef inhabitants. While these results raise new questions about the evolution and enactment of *L. fragilis* behaviors, they introduce a new appreciation for their profundity within a complex ecosystem.

ACKNOWLEDGEMENTS

I would be remiss to overlook the plain truth that colonial and imperialist attitudes run rampant throughout the scientific community. Scientists have as much responsibility as anyone to educate, and to hold ourselves and our peers accountable for perpetuating ignorant and problematic mindsets. I hope future Gump scientists honor Mo'orea's history and culture, recognize the privilege of living and working there with an institution like UC Berkeley, and understand the sacrifices and losses that created this opportunity. I want to thank the volunteers at the Atitita Center for welcoming us with open minds and hearts. Mauruuru'Roa!

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APPENDIX

RESULTS OF STATISTICAL TESTS

TABLE A1. Result of One-Way Analysis of Variance (ANOVA) test of mean time to burrow for each trial condition.

	Sum of Squares	d.f.	Mean Square	F	p
Between Groups	3043.2	2	1521.6	0.6963	0.501
Within Groups	207609	95	2185.63		
Total	210653	97			

TABLE A2. Result of Two-Way Analysis of Variance (ANOVA) test of mean time to burrow, with factor of organism size and trial condition.

	Sum of Squares	d.f.	Mean Square	F	p
Size	6886.73	3	2295.58	1.048	0.3757
Trial	3043.2	2	1521.6	0.6946	0.5021
Interaction	12156.8	6	2026.14	0.9249	0.4813
Within	188393	86	2190.62		
Total	210653	97			