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NUDIBRANCH NEIGHBORHOOD: THE DISTRIBUTION OF TWO NUDIBRANCH SPECIES (*CHROMODORIS LOCHI* AND *CHROMODORIS* SP.) IN COOK'S BAY, MO'OREA, FRENCH POLYNESIA

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Abstract. Benthic invertebrates are vital not only for the place they hold in the trophic web of the marine ecosystem, but also for the incredible diversity that they add to the world. This is especially true of the dorid nudibranchs (family Dorididae), a group of specialist predators that are also the most diverse family in a clade of shell-less gastropods. Little work has been done on the roles that environment and behavior play on distribution patterns of dorid nudibranchs. By carrying out habitat surveys, I found that two species of dorid nudibranchs (*Chromodoris lochi* and *Chromodoris* sp.) occupy different habitats in Cook's Bay. Behavioral interaction tests showed that both species orient more reliably toward conspecifics than toward allospecifics. *C. lochi* has a greater propensity to aggregate than *Chromodoris* sp. These findings indicated that the distribution patterns are a result of both habitat preference and aggregation behaviors. Further inquiry into these two areas is needed to make additional conclusions on the forces driving distribution. Information in this area is necessary to inform future conservation decisions.

Key words: *dorid nudibranchs; Chromodoris lochi; behavior; environment*

INTRODUCTION

Nudibranchs (order Nudibranchia), a diverse clade of marine gastropods, are unique marine snails that have lost a crucial means of protection-- their shell. This loss, in many ways, has driven multiple evolutionary paths, resulting in an incredible diversity in the sea slug clade. For example, The Aeolidean nudibranchs feed specifically on Cnidaria and ingest their nematocysts, or stinging cells. Some of the species in this clade, such as *Spurilla neapolitana*- that feeds on sea anemones- reuse the nematocysts for their own defense (Conklin et al. 1977, Greenwood and Mariscal 1984). Another group, the dorid nudibranchs (family Dorididae) also steal their defense mechanisms from their prey. By feeding only on poisonous sponges, they concentrate toxic metabolites in their skin glands and secrete them in order to deter predators (Cimino et al. 1983). The dorids are not only the most speciose group of nudibranchs, but also the most colorful. Their colors stem from the ability to retain pigments from their sponge diet. These resultant bright colors work as a passive defense mechanism- as they are a form of aposomatic, or warning coloration (Faulkner and Ghiselin 1983, Rudman 1991). Therefore, dorid nudibranchs

rely on sponges for survival in three interconnected ways: as a food source and for their two major defense mechanisms. This dependence on specialized prey places dorid nudibranchs in an important role in the food web of many reef ecosystems (Todd 1983).

The dynamic coral reef ecosystem, where nudibranchs are found ubiquitously across the South Pacific, consist of a complex chain of interactions between organisms. This complex exchange of resources has historically allowed these biodiverse environments to thrive in the nutrient poor waters of the tropics. However, due to harvesting, pollution from terrestrial runoff, diseases, and climate change, coral reefs worldwide have undergone extensive degradation, resulting in an overall decrease in species richness and reef resilience (Bellwood et al. 2004). The dorid nudibranch's strict reliance on typically only one food item puts them in a precarious position in an unstable food web (Rudman and Bergquist 2007). Some of the extreme diversity and novel defense mechanisms found in this clade may be at risk of disappearing (Hay and Fenical 1996). In order to combat this widespread reef degradation, it is critical to have a more thorough understanding of the ecological processes that regulate the community structure of reefs. Spatial distribution of

organisms, as well as the environmental and behavioral factors that drive distributional patterns, are central processes that control the biodiversity across coral reef ecosystems. In order to sustain these species abundant systems, the interacting variables that influence reef structure must be better understood. A lack of data in this area has been a major impediment to effective reef management (Pittman and Brown 2011).

Nudibranchs, notorious for being difficult to monitor, clearly need more study. The disappearances of prevalent species from their ranges, as well as the appearance of species in areas distant from their range, have been described (Gosliner and Draheim 1996). However, the reasons behind these altered species compositions are not known. One such shift in the nudibranch assemblage has taken place in Cook's Bay on the island of Mo'orea, French Polynesia. The dorid nudibranch population in this area has been monitored regularly during the past 17 years as a result of UC Berkeley student projects. An overview of these projects shows a great fluctuation in the nudibranch species composition over time.

The three species that were most abundant according to previous student papers- *Risbecia imperialis*, *Glossodoris hikuerensis*, and *Glossodoris cincta* (Johnson 1994, Ghazali 2006)- have either decreased in number or disappeared completely. Currently, there are two closely related species that exist in relative high densities in the bay: *Chromodoris lochi* and *Chromodoris* sp. During preliminary observations, these two nudibranch species were found in specific areas throughout the bay. *C. lochi* was found only on the ridge running horizontal to the shoreline that marks the drop-off into the area of deeper water. *Chromodoris* sp. was only found in the area leading up to, but not including, the deepwater trench.

Many factors could contribute to these distributional patterns. As discussed previously, dorid nudibranchs have very specific diets; their concentration in a particular part of the bay might be a result of a habitat preference in relation to a food source. However, their distribution could also be a result of their aggregation behavior in order to facilitate the reproductive process. As a consequence of their aquatic larval stage, nudibranchs disperse far from their natal area and must use chemical cues to locate conspecifics with which to mate (Faulkner and Ghiselin 1983).

The first goal of this study was to determine if the distributional patterns observed during preliminary observation could be supported by data. I hypothesized that these two species of nudibranchs occur in different areas of the bay in relation to distance from shore. To test this hypothesis, I surveyed transects to document the depth and distance from shore where each species occurred.

The second goal of this study was to determine how environmental and behavioral factors contribute to the population distributions of these species in Cook's Bay. I hypothesized that both factors have an influence on where these species situate themselves in the bay.

For environmental factors, I wanted to determine if there were specific habitat differences between the two areas where these species were found. In order to test this, I compared substrate composition and current between the two different habitats. Based on preliminary observations, I hypothesized that there would be differences between substrate composition given that Cook's Bay is not uniform in habitat composition.

To assess the importance of behavior on distribution, I first wanted to determine if there were differences in nocturnal and diurnal activity for these species. I hypothesized that because these species are aposomatically colored, they would be less active at night because their colors would be less visible to predators. In order to test this hypothesis I conducted behavioral observations during both day and night. The outcome of this experiment would influence my transect methods.

To determine how intraspecific and interspecific interactions affect distribution, I carried out a variety of orienting and aggregation experiments in the laboratory. I hypothesized that individuals would orient more toward conspecifics than toward allospecifics. I also hypothesized that *C. lochi* would have a propensity to aggregate more than *Chromodoris* sp. because *C. lochi* had a more clumped distribution in the field.

This work provides an understanding of how both environment and behavior play a role in species distribution.

METHODS

Study site

All nudibranchs were observed and collected in Cook's Bay adjacent to UC Berkeley's Richard Gump Station in Mo'orea, French Polynesia (17°29'25.26"S, 149°49'34.42"W) (Figure 1).

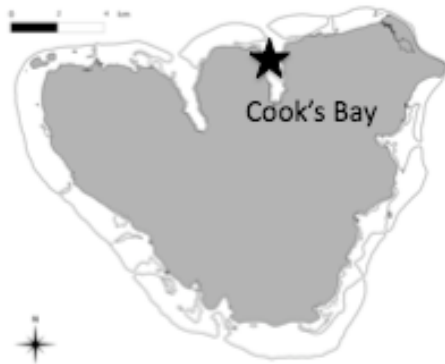


Figure 1. Map of Mo'orea, French Polynesia. Cook's Bay site marked by the star.

Study organisms

I focused on two closely related dorid nudibranchs species, which were the most abundant nudibranchs in the bay during the time of this study. They are both in the genus *Chromodoris*, known for having extremely specific sponge diets (Rudman and Bergquist 2007). The first, *Chromodoris lochi* (Rudman, 1982) (Figure 2), has three dark longitudinal lines that run down its primarily white mantle. In Cook's Bay, the rhinopores and gills of this species are light orange or light pink although these colors vary in other parts of the world. The individuals observed in this study had an average length of 2.5 cm. *C. lochi* has been documented in the bay since 2001 and studied twice since then (Lee 2001, Smith

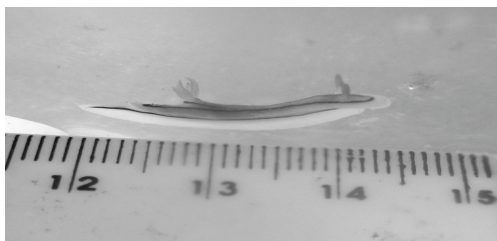


Figure 2. *Chromodoris lochi*

2005).

The second species, referred to as *Chromodoris* sp. (Figure 3), has been documented in the bay only once and is thought to be a close relative of *Chromodoris virbrata* (Ghazali 2006). *Chromodoris* sp. has a yellow and white spotted mantle and a dark

purple border, rhinopores, and gills. This species was found to have an average length of 1.9 cm.

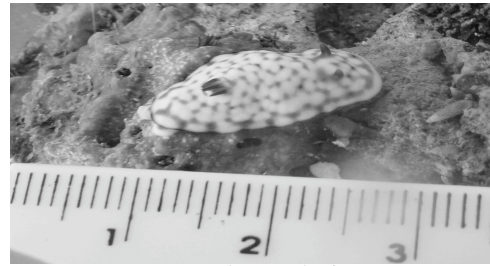


Figure 3. *Chromodoris* sp. 1

Distribution

To address my first question on whether or not these two species occupy different areas of the bay, I carried out 43 systematic timed-search transects throughout Cook's Bay. Each transect was placed 5 m apart and ran east to west from the shoreline to the deepwater drop off. Since transects varied in length depending on how far from the shoreline the drop off started, 20 seconds of search time was allotted for every meter in length. Searching method consisted of visual scanning and close inspection of substrate and crevices in coral head and rubble. No materials were disturbed or flipped during searches. Species, general habitat, substrate, depth, and distance from shore of nudibranch found were recorded.

Habitat

With the data obtained from the transects, I found the average depth of each. In order to answer the question of whether or not the habitats of *C. lochi* and *Chromodoris* sp. differ, I returned to these average depths at 14 of the transects. At these sites, I photographed three 0.25 m² quadrats. These quadrats were placed sequentially, east to west. I later analyzed these photos, paying particular attention to substrate composition. I considered a total of ten factors - five algal species, one living coral species, and four abiotic substrate factors. To measure current, I used plaster of Paris (calcium sulfate). Easily prepared in a standard ice cube tray, plaster of Paris cubes measure water movement since they dissolve at a rate relative to the strength of the current (Thompson and Glenn 1994). I used 28 cubes, 14 for the shallow points and 14 for the deep points. I weighed each cube and then placed them at the correct depths along the 14

transects. After 48 hours of being undisturbed, they were collected and dried for 12 hours. I then re-weighed them and took the difference in weight pre- and post-placement. These values were used as a proxy for current strength.

Behavior

To determine if activity of these two nudibranch species is related to time of day, I repeated six transects at night, three at spots of abundant diurnal activity and three where nudibranchs were not previously found. If I found a nudibranch, I would observe it for five minutes. The total amount of active time was recorded. Four categories were used as a proxy for activity: visibility, crawling, not crawling, and head waving. "Visibility" was defined by the ability to see the individual from directly overhead. "Crawling" means the nudibranch had its foot in contact with the substrate and made any directional movement. "Non-moving" was when the animal was anchored to the substrate by its foot but did not move. "Head-waving" was when the individual held its head above the substrate and moved it from side to side in a wide arc (Figure 4). This took place while the individual was "not moving" (Leonard and Lukowiak 1984).

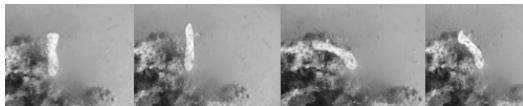


Figure 4. *Chromodoris* sp. exhibiting the head-waving movement

Orienting behavior

To test how the presence of a conspecific and an allospecific impacted behavior, I brought 20 nudibranchs, 10 of each species, into the wet labs at the Gump Station. I set up a 1 m x 2.5 m flow tank (12cm in depth) as the test space (Figure 5). Each test subject (TS) was involved in two tests. In the first, the stimulus was a conspecific, and in the second, the stimulus was an allospecific. The stimulus, held in a Tupperware container with holes through it, sat in the tank five minutes before a trial began to allow a stable current and odor plume to form. A brick, similar in volume to the stimulus container, acted as a control. The TS was then placed in the test space and allowed free movement for ten minutes. I then

determined if the TS oriented. Between trials, I scrubbed the tanks to remove the mucus pathways left by the TS. Each TS performed three trials for both tests, for a total of six trials per individual.

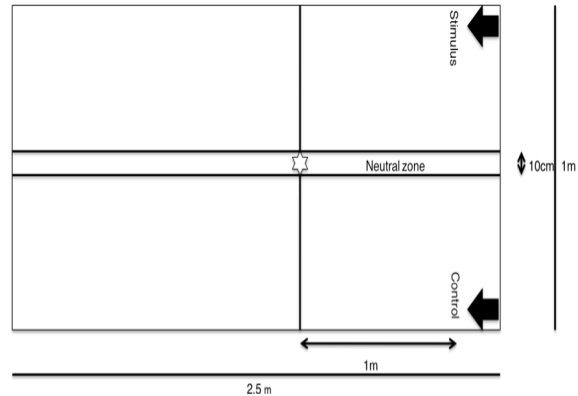


Figure 5. Test space for orienting behavior. The two black arrows at the top indicate incoming current. The placement of the stimulus and the control were randomized. The star indicates where TS began a trial. If the TS left the neutral zone, the trial was counted. If the TS ended in the stimulus quadrant, this was considered "orienting". If the TS ended in any other area, the trial was considered "not orienting".

Aggregation behavior

In the lab, I also tested the ability for these two species to aggregate. All aggregation tests were carried out in smaller flow tanks measuring 30cm x 20cm x 20cm (Figure 6). I placed pieces of bleached coral rubble in each corner of the flow tank. Each piece was approximately the same volume and weighed between 50g and 70g. The placement of the stimulus (always a conspecific) was randomly placed in one of the four corners of the test area. The TS was placed in the center of the test area. I monitored each test every hour for four hours. When the two individuals were found within 5 cm of each other and remained within this distance for two consecutive hours, I considered this "aggregation". Six trials for each species were carried out.

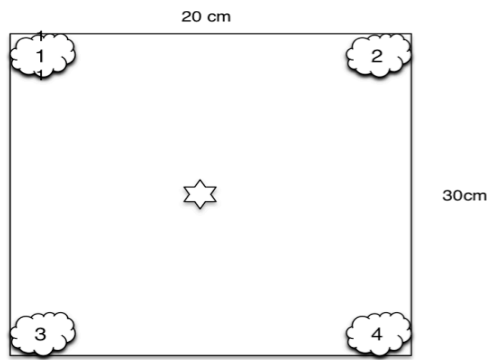


Figure 6. Aggregation test area. In the corner are four pieces of bleached coral rubble. The star indicates where the TS was placed at the beginning of a trial. For each trial, a stimulus (a conspecific nudibranch) was placed in one of the four corners.

Aggregation vs. depth

In order to separate the influence of environment and aggregation behavior on distribution, I took the lab nudibranchs back into the bay and released them at the depths and substrates associated with the opposite species. *Chromodoris lochi* was placed at a depth of approximately 1 m in areas with higher amounts of dead coral and algae. *Chromodoris* sp. was placed at a depth of approximately 2 m where the substrate was primarily coral conglomerate platform. This procedure was carried out at three different transects. At each transect, I placed three individuals of each species for a total of 18 nudibranchs. I returned to these areas three times in 36 hours and monitored the presence and mobility of the test subjects. To ensure that the procedure of handling the nudibranchs was not causing the changes observed, a procedural control was also carried out on two individuals of *C. lochi* found at their preferred habitat. I monitored this site as well.

Statistical methods

To examine distributional differences between the two species in relation to depth and distance from shore, one-way analysis of variance (ANOVA) tests were used. To test the significance of the differences between the substrates found at the two different depths, I first did a discriminant analysis. To look more specifically at these data, I also did one-way ANOVA tests to compare the factors that made up the substrates at the two different depths. This same test was used to compare levels of activity during the day and the night. Lastly, to test for significance in orienting trials and aggregation trials, Pearson Chi-

square tests were utilized. JMP 9 © was used for all statistical analysis.

RESULTS

Distribution

Chromodoris sp. and *Chromodoris lochi* were found in at significantly different depths (one-way ANOVA $F_{1,28}=61.3679$, $P=0.0001$). *Chromodoris* sp. was found at an average depth of $1.1\text{m}\pm 0.37\text{m}$ while *C. lochi* was found at an average depth of $2.2\text{m}\pm 0.37\text{m}$. Likewise the two species occurred at different distances from shore (one-way ANOVA $F_{1,28}=54.8107$, $P=0.0001$). *Chromodoris* sp. was found at an average distance of $27.4\text{m}\pm 32.2\text{m}$ from shore, while *Chromodoris lochi* was found at an average distance of $85.9\text{m}\pm 9.9\text{m}$ from shore (Figure 6).

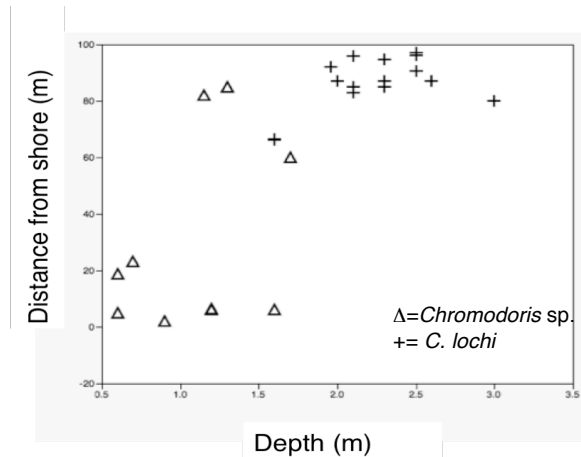


Figure 7. The distribution of *Chromodoris* sp. and *C. lochi* in relation to depth and distance from shore. The two different shapes represent the two species studied. The grouping of the shapes indicate that the species occur in different regions of the bay.

Habitat

I found significant differences between the two areas inhabited by *Chromodoris* sp. and *Chromodoris lochi*. The current strength was much stronger at the shallower areas associated with *Chromodoris* sp. than at the deeper sites (oneway ANOVA, $F_{1,26}=25.2271$, $P=0.0001$).

The substrate composition was also distinct between these two habitats. This divergence was the result of four factors shown to be significantly different between

Table 1: The four factors determined to be different between the shallow habitat and deep habitat. The stars indicate significance.

Factor	Habitat (shallow / deep)	Test	F _{1,82} =	P-value
dead coral	shallow	one-way ANOVA	7.4194	< 0.0079*
coral conglomerate platform	deep	one-way ANOVA	8.6199	< 0.0043*
<i>Padina boryana</i>	shallow	one-way ANOVA	27.2217	< 0.0001*
<i>Dictyopta</i> sp.	shallow	one-way ANOVA	8.1543	< 0.0054*

the areas: the presence of dead coral, coral conglomerate platform, and the two algae *Padina boryana* and *Dictyopta* sp. (Table 1). Despite these documented differences, discriminant analysis showed only a minor amount of clustering based on substrate composition occurring at the shallow and deep depths.

Behavior

On average, both *Chromodoris* sp. and *C. lochi* were more active during the day than at night (Figure 8). *Ch* Sp. was 61.8% more active during the day (one-way ANOVA F_{1,18}=18.3101, P=.0005). Sp. 2 was 42.7% more active during the day (one-way ANOVA F_{1,18}=18.3, P=.0005).

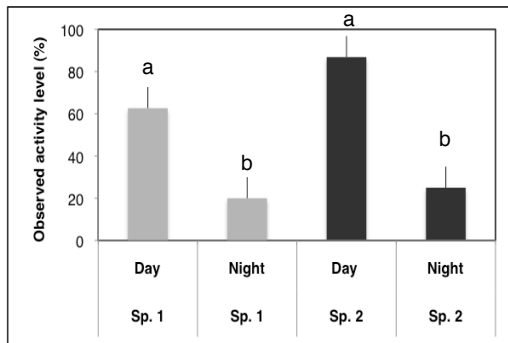


Figure 8. The average observed activity levels during day and night for both species. Sp. 1 is *Chromodoris* sp. and sp. 2 is *Chromodoris lochi*. The level of activity during the day is significantly higher than during the night for both species.

Orienting Activity

In the tests where a conspecific stimulus was used to test for intraspecific orientation, both species did not orient in the majority of the trials. In the allospecific trials, both species significantly did not orient (Table 2).

Table 2: Results of the Pearson Chi-square applied to the orientation trials of four different tests. CS means conspecific and AS means allospecific. The stars indicate significance. In the two allospecific tests the test subjects significantly did not orient.

Species	Stimulus	X	P
<i>Chromodoris</i> sp.	CS	0.1333	0.7150
<i>C. lochi</i>	CS	2.1333	0.1441
<i>Chromodoris</i> sp.	AS	19.2000	0.0001*
<i>C. lochi</i>	AS	13.3333	0.0003*

However, when comparing the data from the allospecific trials to the conspecific trials it is clear that when test subjects did orient, they did so more toward a conspecific than toward an allospecific. In total, test subjects oriented toward conspecifics 43% of the time and toward an allospecific 13% of the time (Figure 9).

Aggregation

Out of six trials for each species, *Chromodoris lochi* aggregated five times and

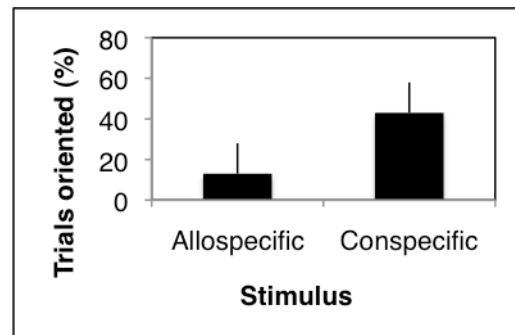


Figure 9. Comparison of the total percent of trials oriented during allospecific tests and conspecific tests. The graph shows the total percent for both species combined. Test subjects oriented more frequently to a conspecific than toward an allospecific.

Chromodoris sp. aggregated one time. A Pearson Chi-squared analysis showed that *C. lochi* aggregated more frequently than *Chromodoris* sp. ($X^2=4.412$, $DF=1$, $P<0.0357$).

Depth vs. Aggregation

Of the 18 nudibranchs used in this experiment, only five were monitored for the entire 36 hours (Figure 10). Of the five test subjects monitored for the whole experiment, all were *C. lochi*. All five of these individuals moved from where they were placed back toward the area of deeper habitat, where they were originally found.

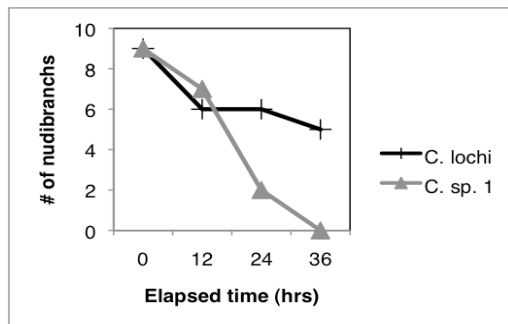


Figure 10. Number of nudibranchs monitored over a 36-hour period. At the beginning of the experiment there were nine of each species present. By the end of the experiment, I could not find any *Chromodoris* sp. individuals. I could only locate five *C. lochi* individuals.

DISCUSSION

Taken together, my results show that *C. lochi* and *Chromodoris* sp. are found in distinctly different locations and habitats in Cook's Bay. Environment and behavioral interactions both affect where these nudibranchs situate themselves in the bay.

My hypotheses- that the distribution of these two species is not random and that they occurred at different distances from shore- were supported. The transects showed their occurrences at different depths as well. Specifically, *C. lochi* was found at distances further away from shore and at deeper depths than *Chromodoris* sp. These patterns could be explained by a number of non-mutually exclusive factors. For this reason, I considered both habitat composition and behavior.

My results demonstrated specific differences between the habitat types of these two species. *Chromodoris* sp. occurs in areas with a more intense current than *C. lochi*. The habitat associated with *C. lochi* was comprised of a coral conglomerate platform substrate, while the habitat of *Chromodoris* sp. can be described as a substrate of dead coral, covered with two types of algae- *Padina boryana* and *Dictyota* sp. Although these differences were significant, a discriminant analysis looking at all ten of the factors that I measured did not show an overall difference between these two sites. A closer analysis of these areas that examines a greater number of variables could yield more conclusive results.

These findings, however, do support the hypotheses that the environment throughout Cook's Bay is not uniform and that these two species occupy different habitats. As it stands, the methods used in this study were not comprehensive enough to make any conclusions about why these nudibranchs occur in these areas. The most convincing speculation for the different distribution patterns in relation to environment focuses on diet. The first possibility is that these two species specialize on two different sponges. The species in Chromodorididae, the family to which both *C. lochi* and *Chromodoris* sp. belong, have extremely specific diets (Rudman 1991). If this is the case, the areas where each nudibranch species was found might best reflect the habitat preference of the sponges that they are consuming. The second possible explanation is that both species feed exclusively on the same sponge. In this instance, the distribution patterns documented would then likely reflect resource partitioning; the species occupying different locations in the bay to avoid direct competition (Bloom 1981, Nakayama et al. 2011). A diet choice experiment might shed light on the question of whether or not the distribution patterns are related to food preference. An assessment of the sponges occurring in the two habitats would also help answer this question.

Behavior also plays a role in the spatial distribution of *C. lochi* and *Chromodoris* sp., according to my results. Both *Chromodoris* sp. and *C. lochi* were shown to be more active during the day than the night. This indicates that these two species are most likely diurnal and that the distribution patterns observed during the day transects were an accurate representation of population size during the time of this study.

In the lab experiments, although neither species consistently oriented, both species did orient toward a conspecific more frequently than toward an allospecific. This tendency indicates that they may stick to specific areas of the bay because of their drive to aggregate.

Aggregated spatial distributions are a trade-off between spacing to optimize food acquisition and having regular contact with conspecifics for mating purposes. Most benthic invertebrates choose the second strategy and increase the opportunity for mating at the expense of resource acquisition (Heip 1975, Luttmann et al. 2006). Further tests on the aggregation behavior of *C. lochi* and *Chromodoris* sp. however, showed that these each of these species might be choosing different strategies. *C. lochi* exhibited a stronger propensity to aggregate in the lab than *Chromodoris* sp. This phenomenon was observed in the field as well—the former was often found in groups of two to six individuals, while the latter was typically found alone. This indicates that these two species are making different trade-offs: *C. lochi* for increased mate interaction and *Chromodoris* sp. for increased resource acquisition.

The inability to reliably move toward a conspecific in the orienting trials may be a result of the sensory mechanisms used for orientation and aggregation. The experiments I performed only tested the subject's ability to follow a smell gradient. These nudibranchs may rely on the slime trails left by conspecifics, a potentially more permanent cue than an odor gradient, for orientation (Nakashima 1995). Further tests with intact slime trails might give more consistent results.

Results from the depth versus aggregation experiment were inconclusive because of the inability to track test subjects for the duration of the trial. However, the movement of the five *C. lochi* individuals that I was able to monitor indicated that even when surrounded by conspecifics, these nudibranchs still moved towards their original habitat. This suggests that there is something in this area, perhaps a critical food source. This experiment should be repeated with a larger sample size to show a statistically sound trend and to draw more specific conclusions.

As a whole, this study provides a basis for understanding how both environment and behavior influence the distribution process of marine gastropods. It also shows the complexity and the interrelatedness of these factors. My results generate a new list of questions that prompt

further research on this multifaceted system. A thorough examination on the food preferences and the orientation abilities of these two species would contribute further to the knowledge of the ecological processes at work. Increased understanding is necessary for further ecological work that must take both types of factors into consideration when making conservation decisions (Guichard et al. 2004).

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