

# How temperature affects nudibranch partial predation of *Dendrobeatia lichenoides* bryozoan

Santiago Ledesma

University of Washington, Seattle, WA, 98195

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## KEYWORDS

Bryozoan  
Brown body  
*Dendrobeatia lichenoides*  
*Dirona*  
Partial predation  
Polypide  
Zoid

## ABSTRACT

Bryozoan colony structure (*Dendrobeatia lichenoides*) of degenerated parts known as brown bodies helps determine the grazing pattern and partial predation by nudibranchs (*Dirona albolineata* and *Dirona pellucida*). Although previous studies have explored the facets of partial predation of bryozoan colonies from various nudibranch species, the temperature is not often considered an external factor affecting their consumption of colonies. Three feeding trials under increasing temperatures (14 °C, 18 °C, and 20 °C) were run in Friday Harbor Laboratories, Friday Harbor, WA. *Dirona albolineata* and *Dirona pellucida* nudibranchs were fed *Dendrobeatia lichenoides* colonies in laboratory conditions to determine if being introduced to increasing temperature levels affected their partial predation. Results showed a positive correlation between increased colony consumption and increased temperature with nudibranchs grazing closer to the center of the bryozoan colonies up until 18 °C, after which that correlation decreased. Statistical analysis showed no significant difference between the overall means of each trial, but there was a significant decrease in bryozoan colony consumption after 18 °C. Nudibranchs are resilient to temperature, but 18 °C could be the threshold they can reach before their activity is affected by temperature. This study indicates that increases in seawater temperature do not necessarily dictate that nudibranchs stop partially consuming bryozoan colonies. However, they suggest that nudibranchs have a temperature tolerance ceiling that, if breached, will affect their behavior.

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## 1 Introduction

Nudibranch species are all alike; every nudibranch diet is different in its own way. Using some form of highly specialized toothed structures as a tongue to rasp off their prey from the substrate or break it down (Behrens et al., 2005), nudibranchs display a wide range of variability in how that feeding apparatus is shaped and what they consume with it (Cheney & Wilson, 2018). Headshield slugs (Cephalaspidea) can be either herbivores, carnivores, or cannibalistic. Sea hares (Aplysiida) only feed on algae, and members of Dendronotoidea feed on a wide variety of prey, including soft corals, sea anemones, hydroids, worms, juvenile fish, and bryozoans (Behrens et al., 2022). Nudibranch diet diversity has made it one of the most intriguing aspects of these opisthobranchs and the focus of a large portion of scientific literature. The variability of how these sea slugs feed does not stop there, as depending on their food preference, nudibranchs display selective behaviors on what parts of their prey they consume. Partial predation is the consumption of parts of prey without killing, and it is a common practice of many organisms, particularly those that graze on colonies (Jackson & Palumbi, 1979, D. Harvell, 1984). Colonial organisms are rarely killed by predators thanks to their regenerative body structure, making them regular victims of partial predation by nudibranchs.

Viewed briefly, bryozoans might be taken for a coral or hydroid. However, if examined with more care, it would become clear that they are multifaceted collections of zooids, reproductive and defensive organisms that all vary in age and condition depending on their distributions within the colony (Yoshioka, 1982). Zooids are constructed of polypides, feeding units within each zoecium, and a structural frame for the zoid (Drynda, 1981). When closely examined, zooids can sometimes reveal the presence of one or more dark sphere shapes inside them; these are products of degenerated polypides and are known as brown bodies (Ryland, 1970). Brown bodies help determine the age of a bryozoan colony, and the number of brown bodies is higher with older regions in the colony that have gone through more degeneration-generation cycles (Gordon, 1977; Drynda, 1981); these regions are found at the center end of the colony. Every colony is different in its quantity of brown bodies and not evenly constructed, which can explain to some degree why they are only partially predated. There is still no knowledge of what determines partial predation by a predator on a colony beside the content of brown bodies. However, the answer remains whether brown bodies are disregarded for consumption because they offer no nutritional value or palatability. Bryozoans are sessile organisms, and they are capable of colonizing any free natural or anthropogenic surface in the sea, so long as nutrient-rich water is available to satiate their filter feeding (Ryland, 1970). This range in their distribution across the water makes them a regular choice of predation by nudibranch species.

Although previous studies have explored the facets of partial predation of bryozoan colonies from various nudibranch species (D. Harvell, 1984; C. Harvell & Suchanek, 1987), the temperature is not often considered as an external factor that affects their consumption of colonies. *Dirona albolineata* and *Dirona pellucida* can be found from Alaska down to the Pacific Northwest Coast (Behrens & Hermosillo, 2005). They are known to feed on various species of prosobranchs (Robilliard, 1971) and bryozoan species *Bugula* and *Dendrobeatia*, of which they only partially prey (Behrens et al., 2022; D. Harvell, 1984). With partial predation being a common practice amongst colony grazers, what will be examined in this research is how increasing temperature affects partial predation by *Dirona* nudibranch species on the bryozoan *Dendrobeatia lichenoides*. If introduced to increasing temperature levels under experimental conditions, will nudibranch species be inclined to consume more than they usually do as partial predators? Climate change in the form of rising ocean temperatures and lowering pH levels concern all living organisms. Any slight change to these variables can have massive effects on their physiology, and opisthobranchs are not out of harm's way. Ocean acidification can affect the plasticity of nudibranchs as they need to adapt to higher temperatures increases (Armstrong et al., 2019). This study hopes to gain insight into the impacts of rising temperatures on nudibranch behavior, particularly their prey consumption. It is predicted that if nudibranchs are introduced to increasing temperature levels under experimental conditions, they will showcase higher prey consumption than they would usually in normal conditions and possibly shed off partial predation. They will consume entire colonies, including areas with more brown bodies present.

## 2 Methods

### 2.1 Specimen collection and maintenance

I collected 2 *D. albolineata* and 4 *D. pellucida* specimens from the tires and pilings in the dock of Friday Harbor Laboratories, Friday Harbor, WA, via jars, dip nets, and sticks from depths no lower than 1.5 meters between November 8th and November 11<sup>th</sup> of 2022. The collected nudibranchs were in environments with ample *D. lichenoides* colonies on which they were likely feeding. I placed the nudibranchs in individual mesh-sided containers in the control sea table in laboratory three at Friday Harbor Laboratories. They were treated to shallow seawater baths with continuously running fresh seawater at the temperature they were found (~10 °C). *D. lichenoides* colonies were collected from the exact locations before the beginning of each feeding trial. Colonies were removed from the substrate using forceps, chisel, and pocketknife and placed in jars with fresh seawater from laboratory 3.

### 2.2 Sea table Layout

The control table remained set up the way it was described above for the entirety of the experiment. The experimental table was set up differently to compensate for the large size of the sea table and the need to maintain higher temperatures than the running fresh seawater at a constant rate. A smaller container was placed inside the sea table with two titanium heaters at the bottom connected to two digital temperature controllers and a water pump attached to the side to help maintain the current water temperature inside the container. Inside the container, nudibranchs were placed in individual mesh-sided containers with a constant flow of fresh seawater (Figure 1).



**Figure 1.** Feeding trial sea table layout. A larger container was placed inside the sea table with two heaters at the bottom and a water pump attached to the side. Where nudibranchs were placed in individual mesh-sided containers with a constant flow of fresh seawater.

### 2.3 Temperature treatment

Three feeding trials were recorded over a week at temperatures 14 °C, 18 °C, and 20 °C. While a single *D. albolineata* and 2 *D. pellucida* remained on the control table, the other *D. albolineata* and 2 *D. pellucida* were taken out and placed on the experimental sea table on November 12<sup>th</sup> at a temperature of 11 °C. Every eight hours, the container temperature was increased by .5 °C to account for specimen acclimation for temperature conditions until the container reached 14 °C on November 14<sup>th</sup>. The exact process was repeated for the other two temperatures. Once the feeding trials were over, the temperature was slowly lowered to help acclimate nudibranchs back to the original water temperature they were found in.

### 2.4 Bryozoan measurements

*D. lichenoides* colonies were collected in the morning before each feeding trial from tires at the dock in Friday Harbor Labs using forceps, a chisel, and a pocketknife. They were put into jars sealed airtight, which were then brought back to laboratory 3. In the lab, they were placed into separate Petri dishes submerged in fresh seawater. Two methods of weighting colonies were applied to account for water weight that could affect correct bryozoan measurements. First, the desired number of bryozoans to feed each nudibranch according to their size was weighted in grams on a dried petri dish. Second, a beaker with 50 ml of water was weighed in grams. A petri dish with the desired number of bryozoans I wanted to feed a nudibranch was picked, and those bryozoans were submerged into the water. The difference between the original weight and the final weight was recorded. The dry weight and beaker weight were then averaged, and the final weight was recorded. These steps were repeated for each nudibranch portion. Accounting for the brown body mass of *D. lichenoides* was done by observing each individual colony's anatomical characteristic through a magnifying glass (TRIPLET 18 mm – 10x) and under a microscope to recognize which parts of the colony held the brow bodies. Distance between the center of a colony and its perimeter and total area (L x W) were measured using the microscope's ocular micrometer at 10x. Colonies were also photographed (Nikon D750) before and after feeding trials to compare visual differences in mass.

### 2.5 Feeding trials

From the time they were collected to the beginning of the feeding trials on the morning of November 14<sup>th</sup>, nudibranchs were starved to allow for the best chances of observing feeding habits under experimental conditions. Each feeding trial began when the desired amount of *D. lichenoides* colonies weighed for each nudibranch were put into their containers and given a 24-hour period to be consumed by their respective nudibranch. Once the trial period was over, the remaining portions of the bryozoan offered were collected and weighted the same way as the initial amount described above. Just as nudibranchs were not fed before the first feeding trial, they were not fed between feeding trials. This feeding process was repeated for trials at all three temperatures; the second feeding trial (18 °C) took place from Thursday morning to Friday morning and the third feeding trial (20 °C) from Sunday to Monday. Aside from collecting bryozoan consumption rates at each trial, changes in behavior, length, width, and coloration were recorded throughout

the experimental period to observe if temperature changes affected more than just how much bryozoan colonies nudibranchs consumed. Containers were also cleaned before and after every feeding trial to get rid of accumulating mucus from nudibranchs.

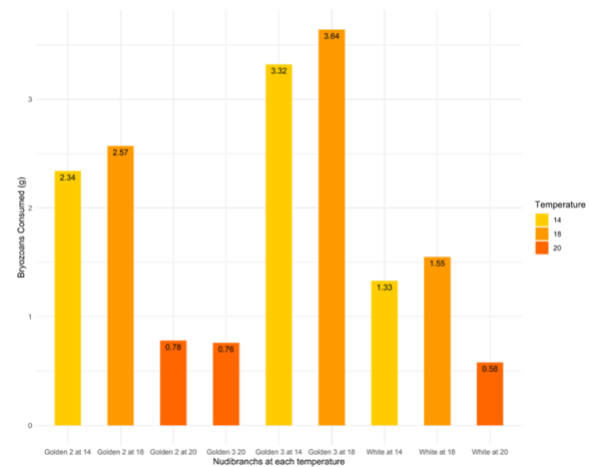
### 2.6 Data Analysis

Once all the data needed was collected and organized, a one-way ANOVA analysis was conducted to determine whether there was any significant difference between the mean values of bryozoans consumed at each temperature treatment. Paired T-tests between bryozoan consumption at 14 °C and 18 °C, at 18 °C and 20 °C, and at 14 °C and 20 °C were also used to see if there was any significant difference between paired trials in all orders. All tests were set to be significant at  $P < 0.05$ , and all data analyses and graphs were done in R Studio.

## 3 Results

### 3.1 Feeding trials

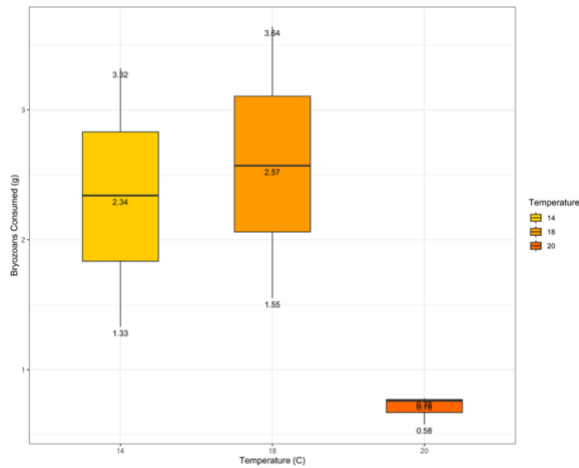
From November 14<sup>th</sup> to the 21<sup>st</sup>, 59 % of all bryozoan colonies offered to the three nudibranchs had been grazed (Figure 2).



**Figure 2.** Bar graph displaying the number of bryozoans (g) consumed for each nudibranch at each temperature treatment (14 °C, 18 °C, and 20 °C).

The first feeding trial (14 °C) had an average consumption of *D. lichenoides* colonies of 2.34 grams (74 %), the second feeding trial (18 °C) 2.57 grams (81 %), and the third and final feeding trial had the lowest consumption of *D. lichenoides* for all nudibranchs at 0.71 grams (22 %) (Figure 3). Control groups had an overall average of 2.37 grams accounting for all three trials. There was no significant difference between the mean values of all three feeding trials (One way ANOVA,  $F = 4.428$ ,  $P > 0.05$ ). However, the unpaired T-tests found that there was a significant difference between 18 °C and 20 °C ( $T = 3.07$ ,  $P < 0.05$ ) and between 14 °C and 20 °C ( $T = 2.825$ ,  $P < 0.05$ ), but not between 14 °C and 18 °C ( $T = 0.276$ ,  $P > 0.05$ ). Across the 24 hours they were allowed to consume the colonies, nudibranchs showed no particular scheduled behavior regarding grazing colonies. On average, it took them ~1-2 hours to find the colonies after they had been placed in

their containers. However, from there, the three nudibranchs varied on how much they consumed at a time and how many times they revisited the colonies offered to them. By the last hour of the feeding trials, all nudibranchs were found separated from the colonies.



**Figure 3.** ANOVA plot of minimum, mean, and maximum values for each feeding trial, averaged for all three nudibranchs.

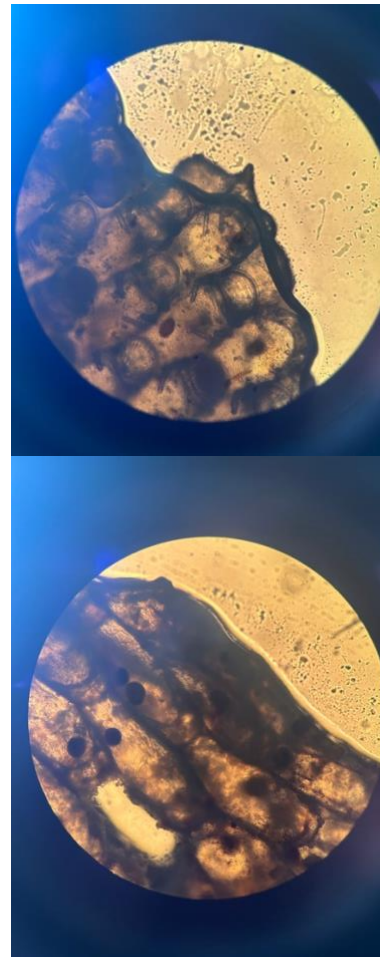
### 3.2 Bryozoan measurements

While nudibranchs were not found to consume more bryozoan colonies, at least not statistically, there is still the possibility of finding out they consume more brown bodies. Brown bodies increase with proximity to the center of the colony, and in the *D. lichenoides* colonies given to the nudibranchs, brown bodies were seen to follow the same trend. In the control group, nudibranchs were seen eating the perimeter of the colonies and never progressing to the center of the colonies. Before and after images and microscope observations of the colony remains after the first feeding trial (14 °C) revealed nudibranchs to consume the perimeters of the colonies offered to them, just like the control group did, and no visible interactions with the center of the colonies were found. At the second feeding trial (18 °C), however, the remains of the colonies were not as intact as in the first feeding trials. Using the ocular micrometer on the microscope to compare the remains of the first and second trials revealed that the nudibranchs did not consume zooids at the center of the colonies, but they did get closer to it. The average distance between the colony's center and the spineless margin for all colonies was 18.5 mm, with an average colony area of 244 mm<sup>2</sup>. At the first feeding trial, nudibranchs grazed colonies and reduced the distance to an average of 16.8 mm and the area to 212 mm<sup>2</sup>. The second trial values were 15.9 mm and 191 mm<sup>2</sup>. The third feeding trial values were 17.6 mm and 238 mm<sup>2</sup>. It is possible that in those differences, the nudibranchs consumed more brown bodies, but visual examinations of the colonies before being served and after showed that the center of the colonies was left undisturbed (Figure 4).

### 3.3 Observations

Besides observing feeding rates with changing temperatures, and consumption of bryozoan brown bodies, observations in other aspects of nudibranchs were made. There were no noticeable changes in coloration for all nudibranchs throughout

the experiment. However, behavioral observations and size showed changes as the experiment continued. At the beginning of the first feeding trial (14 °C), nudibranchs were active and constantly moving around their containers. From the time the temperature treatment began on November 12<sup>th</sup> to after the first feeding trial ended, no behavioral differences between the control and experimental groups of nudibranchs were noticed. That changed after November 16<sup>th</sup> when temperatures were around the 16 °C - 17 °C range. At that range, nudibranchs began to show subtle signs of being affected by the temperature. They became more inactive and spent most of their time hanging from the side of their container. The second feeding trial (18 °C) took place on November 18<sup>th</sup>; nudibranchs continued to be inactive by that day. However, more interestingly, daily size measurements on that day showed that the nudibranchs had decreased in size by an average of 14 % from their original size measured before the start of the temperature treatment. By the end of the last feeding trial (20 °C), the nudibranchs had decreased in size by an average of 16 %. They did not move throughout the day and fed at night.



**Figure 4.** *Dendrobeatia lichenoides* colony remains under microscope after 14 °C, and 20 °C feeding trials. Colony remains from White 1 (Left) and Golden 3 (Right). Brown bodies are clearly visible inside zoecium units.

## 4 Discussion

### 4.1 Feeding trials

The statistical analysis reveals that *Dirona pellucida* and *Dirona albolineata* mean consumption of *Dendrobeatia lichenoides* colonies did not have an overall significant difference, but that there was a significant difference when comparing two means at a time: 14 °C and 20 °C, and at 18 °C and 20 °C. The lack of an overall significant difference is a possible result of the decrease in bryozoan consumption that occurred after the second feeding trial. Up until 18 °C, *Dirona* species were consuming more bryozoan colonies. However, after the second feeding trial, they were too distressed when the temperature went above 18 °C and only consumed a small portion of the bryozoans offered to them. Nudibranchs are resilient to temperature to a certain point (Armstrong et al., 2019), and 18 °C may be the threshold of heat tolerance that nudibranchs can support, and anything past that will impede them from properly functioning. Therefore, inactivity at higher temperatures could be one of the ways that future increases in ocean temperature could affect nudibranchs. These results could offer more concrete conclusions if more time, replicates, and resources were available to examine the connection between nudibranch feeding performance and increased temperature.

### 4.2 Bryozoan measurements

As with bryozoan consumption, nudibranchs ceased eating zooids closer to the colony after 18 °C. Until then, the measurements revealed a decrease in distance between the center of the colony and the proximity of nudibranch feeding, which could result from the temperature increase and the necessity for more nutritional refinement. However, after 18 °C, the nudibranchs were affected and became more inactive, stopping them from proceeding further into the colony's center. Bryozoan structural organization is not homogenous (Palumbi & Jackson, 1983), and nudibranchs likely consume some brown bodies out of the colony's center every time they graze on it. Control groups showcased colony consumption mainly in grazing over the perimeter of the colonies. The center of colonies, where most brown bodies are present, did not seem to attract any consumption. Excluding the fact that nudibranchs under temperature treatment did get closer to the center up to a certain point, the same results were seen. It could be that the increase in the number of brown bodies in the center of colonies causes a decrease in palatability or that brown bodies hold no nutritional value for nudibranchs. However, these are just speculations with nothing to support them, as the literature on brown body's nutritional content is minimal.

### 4.3 Nudibranch behavior

While brown body palatability is only speculation, there are other possible explanations for *Dirona pellucida* and *Dirona albolineata* hesitation to reach the center of *Dendrobeatia lichenoides* colonies. As opposed to the consumption of a whole organism, partial predation is at the center of the primary form of colony predation. It raises questions on why predators would be inclined not to consume prey entirely and what stops them. As discussed above, the increase in brown bodies at the center of the colony likely stops the nudibranchs from entirely consuming a

colony. However, another hypothesis is that of "prudent predators" (Slobodkin, 1974). The term "prudent predator" is given to predators that avoid exhausting their prey resources, like only consuming portions of prey that do not reproduce. In the case of nudibranchs, slow gastropods who spend most of their time moving and searching for prey, prudent predation is not the reason for their lack of interest in total colony consumption.

Intentional abstinence from grazing an entire colony does not seem reasonable as it would require the predator to stop feeding, and it is unlikely that nudibranchs are actively deciding to do so. It is more likely that the cause of the shortstop of *Dirona pellucida* and *Dirona albolineata* towards the center of *Dendrobeatia lichenoides* colonies is the result of a response from within the colonies themselves. *D. lichenoides* colonies may respond to nudibranch grazing by utilizing inducible defenses (Harvell, 1984), releasing chemical attacks that fend off predators. Bryozoans produce defensive spines and reproduce immediately in response to grazing by partial predators (Yoshioka, 1982). The same could be possible in interactions between *Dirona* species and *D. lichenoides*, where the colonies could be actively deciding to begin reproduction and chemical defenses, decreasing the quality of the prey, and discouraging nudibranchs from continuing grazing. Nevertheless, as the results showed, at 18 °C, nudibranchs got closer to the colony's center. Whether they were not yet exposed to the chemical response of the colonies or some other phenomena, it cannot be discarded that just as higher temperatures affect nudibranch behavior and predation, they can also affect bryozoan inducible defenses.

It is also essential to consider the limitations that influenced these results. This research was conducted over a short period, limiting the number of trials, lengths, and replicates. More detailed conclusions about nudibranch partial predation under temperature treatments could have been achieved with better conditions. However, the results discussed above pose questions about the temperature tolerance of nudibranchs and how it affects their behavior and activity. Bryozoan temperature tolerance and chemical defenses should also be considered in future endeavors to understand these relationships.

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