

# A Study of the Feeding and Predatory Behavior of the Ctenophore *Beroe abyssicola*

Andrew Paley<sup>1,2,3</sup>, Jacob Beemer<sup>1,2</sup>

FHL 470 A Spr 21: Research in Marine Biology  
Spring, 2021

<sup>1</sup>University of Washington, Friday Harbor Laboratories, Friday Harbor, WA 98250

<sup>2</sup>Department of Marine Biology, University of Washington, Seattle, WA 98195

<sup>3</sup>Department of Oceanography, University of Washington, Seattle, WA 98195

Keywords: *Beroe abyssicola*, *Pleurobrachia sp.*, *Bolinopsis infundibulum*, feeding behavior, predator-prey interactions

Contact Information:

Andrew C. Paley

UW Marine Biology, UW Oceanography

(425) 736-9676

[apaley@uw.edu](mailto:apaley@uw.edu)

## Abstract

Beroid ctenophores such as *Beroe abyssicola* are found in many marine habitats and serve as critical predators in planktonic food webs, often consuming other grazing ctenophores such as *Bolinopsis infundibulum*. Despite this critical relationship, comparatively little study has been conducted on the specific and complex feeding behaviors these animals display, which could expand the current understanding of the complexity in nektonic/planktonic food webs and their interactions. This study aimed to rectify this gap in the scientific literature by studying the patterns in the feeding behavior of *B. abyssicola* in the presence of its prey *B. infundibulum*, in addition to examining the impact of the prey item's chemical cues alone on the behavior of *B. abyssicola* and this ctenophore's willingness to feed on alternative prey items such as *Pleurobrachia sp.* We found noticeable patterns in the time spent in certain behavioral states across size ranges of *B. abyssicola*, with large and small ctenophores spending comparatively higher amounts of time in sedentary states compared to medium-sized ctenophores, which were much more active hunters. These relationships are likely behavioral adaptations to variations in metabolic rate and likelihood to encounter prey and suggest that these Beroid ctenophores have far more complex behaviors than widely believed. In addition, we found evidence suggesting that *B. abyssicola* is statistically unlikely to consume or even attack, *Pleurobrachia sp.* even when hungry likely due to the inability to perform such action or due to the lack of a chemical trigger.

## Introduction

Ctenophores are carnivorous, nektonic organisms that serve as an integral part of planktonic food chains, helping to regulate the standing crop of phytoplankton in many marine

ecosystems (Fraser, 1962). Ctenophore species derive their name from complex rows of fused cilia plates, or "ctenes," on which they rely for locomotion, moving slowly through the water column to feed on swarms of plankton. Ctenophores can take many different forms, with some genera, such as *Bolinopsis sp.*, relying on complex lobes to feed, while others, such as *Pleurobrachia sp.*, use a simple array of two tentacles to "fish" for prey (Ruppert, 1987).

Regardless of the genus, most ctenophores employ sticky cells, called colloblasts, to capture their quarry, which fire upon contact and trap prey items like the cnidocytes found in cnidarians (Kozloff, 1990). Even members of the order Platyctenida, benthic ctenophores that "walk" along the benthos using an eversible pharynx and can be mistaken for nudibranchs, employ this same feeding strategy, with long strands of colloblasts aiding in the capture of their prey. Amongst common patterns seen among taxa of ctenophore, the genus *Beroe* deviates rather dramatically and has instead evolved to feed on other ctenophores.

*Beroe*, such as *B. ovata* or *B. abyssicola*, serve a unique role in planktonic food chains by assuming the role of a predator—feeding on grazers such as *Bolinopsis sp.* Given their unusual position in the food chain, it is not surprising that their morphology would be equally disparate compared to other ctenophores. Featuring a long, tube-shaped body and eight comb-rows culminating in a set of distinct "lips," *Beroe* is genuinely an oddity among members of their taxa (Laverack, 1979). These seemingly simple organisms, however, are, in fact, complex predators with a suite of unique adaptations that help them survive and feed. Large concentrations of mitochondria are found in the cells under the comb rows of *Beroe* and allow these organisms to make rapid, fine movements within the water column. Unique and specialized "macrocilia" allow them to grab and tear chunks from their gelatinous prey, maximizing the lethality of the attacks (Kozloff, 1990). In addition to these adaptations, Beroid ctenophores also exhibit

comparatively “advanced” behaviors not seen in many other nektonic organisms. They have been known to exhibit stereotypical hunting behaviors, including utilizing a circular pattern while searching for food, and demonstrate both positive and negative geotaxis when the aboral organ and statocysts are stimulated (Kozloff, 1990). However, despite these intriguing and complex search behaviors, research on ctenophores in the genus *Beroe* and their feeding behavior is still lacking in the modern literature.

*B. abyssicola* is one member of this understudied genus. Found throughout the northeast Pacific, *Beroe abyssicola*, like other members of its order, lacks tentacles during any stage of its life history and grows to seven centimeters in length, making it comparatively one of the shortest members of the order (Norekian, 2019). It plays a critical role in many planktonic food webs across a large oceanographic area, making the paucity of literature on its feeding behavior and the nature of its interactions in one of the largest marine ecosystems even more puzzling. This study aims to begin filling in some of those gaps by examining the feeding behavior of both *Beroe abyssicola* and its prey *Bolinopsis infundibulum*, which are found throughout the Northern Pacific. Through careful observational study and experimentation, we hope to better characterize patterns in the "hunting" behavior of these organisms and examine their willingness to consume other prey species such as *Pleurobrachia sp.*, as well as possible physiological mechanisms that may drive such behaviors. By seeking to understand the feeding behavior of *Beroe abyssicola* better, as has been done with other species such as *B. ovata*, this study hopes to elucidate further the often-overlooked role that *Beroe* ctenophores might play in large planktonic ecosystems.

## **Methods**

### *Animal Collection and Preparation*

Specimens of *Pleurobrachia* sp., *Bolinopsis infundibulum*, and *Beroe abyssicola* were collected from May 10, 2021, to May 25, 2021 from the docks of Friday Harbor Labs. Individuals of all species were gathered, without limits on size, using jars and "dippers" before being carefully placed into buckets of seawater from the surrounding area. They were then moved to the laboratory for permanent housing. Species were separated into different containers, with plankton mesh on the sides to allow adequate flow into the container, and left in a sea table to allow for the circulation of fresh seawater. Specimens of *Bolinopsis* and *Pleurobrachia* are suspension feeders and thus do not require constant feeding because they receive adequate nutrition from the circulation of seawater in their containers; however individual *B. abyssicola* were placed on a strict feeding schedule. Given the nature of this experiment, specimens of this species were not fed for 24 hours before the start of the first experiment to ensure they would be hungry, and thus willing to search for food during behavioral trials. Outside of this period, when supply allowed, specimens of *B. abyssicola* were given one *Bolinopsis* a day if they did not already consume an individual during the testing period.

### *Feeding Behavior and Observational Trials*

We made observations of the interactions between *Beroe abyssicola* and its prey species of *Bolinopsis infundibulum*. Behavioral trials were conducted and filmed in a specially constructed black box and a small acrylic aquarium with lighting that allowed for adequate capture of the feeding behavior of *B. abyssicola* on digital video in spite of the transparent appearance of these animals. For every trial, a single individual *Beroe* was moved from its housing container and carefully transported to the filming aquarium, where it was then allowed

to acclimate for five minutes before experimental testing. Once the acclimation period concluded, a single specimen of *Bolinopsis infundibulum* was moved from the housing container into the filming aquarium, and a video of its interactions was recorded via an iPad. The entire setup within the black box was then covered with a tarp to prevent human disturbance and glare during filming and checked periodically for progress. The trial was allowed to continue until either 20 minutes had elapsed, or until the *Beroe* had consumed the prey item. In the case of the latter, two minutes were allowed for initial digestion and sealing of the prey item in the *Beroe*. At the end of filming, one or both specimens were moved back to their holding containers in the sea table, and the filming aquarium was cleaned and re-filled with fresh, filtered seawater. Trials were repeated for a total of 27 replicates. After filming of all trials was completed, videos of each were scrutinized, and time-series observations of the observed behaviors were made according to a pre-determined list (see Table 1). We recorded the behavior displayed and the time elapsed doing said action out of the 20 minutes according to a pre-defined list of possible behaviors before recording the observed results in a spreadsheet for later analysis.

Table 1: The below table displays the list of possible behaviors taken by the predatory *B. abyssicola* during the hunting behavior trials. These nine actions were recorded in a datasheet from the video of the encounter between the individual *Beroe* and its prey.

	Possible Actions of <i>B. abyssicola</i> during prey encounter.		*Indicates open mouth
<b>Sedentary</b>	The animal is not moving and is stationary. The mouth can be closed or open	<b>*Engulfing</b>	Completely swallows prey item
<b>*Horizontal Searching</b>	They are rotating/swimming about a fixed horizontal axis in a circular pattern with an open mouth.		
<b>*Vertical Searching</b>	They are rotating/swimming about a fixed vertical axis in a circular pattern with an open mouth.		
<b>*Helical Searching</b>	Swimming in a helical pattern combines vertical and horizontal axes in a spiral swimming pattern with an open mouth.		

<b>Rotating</b>	Spinning without any positional change, mouth closed.		
<b>Swimming</b>	Mouth closed, just swimming.		
<b>Bobbing</b>	Moving up and down the water column continuously, mouth closed.		
<b>*Contorted/ Lunge Strike</b>	Contorted entails a strike that causes the animal to bend its body, a lunge is simply a straight strike at the prey item.		

### *Pleurobrachia sp. Feeding Trials*

This sub-experiment was carried out overnight between trials conducted for the feeding-behavior trials. The objective was to gauge the willingness of *Beroe abyssicola* to feed on a prey item other than its typical target species, in this case, *Pleurobrachia sp.* To accomplish this, a single specimen of *Pleurobrachia sp.* was moved into the housing containers of individual *Beroe* which had been deprived of food for the previous 24 hours to ensure that they would be both hungry and willing to feed if given the opportunity. Prey items were matched to the individual *Beroe*, ensuring that they were all smaller than the specimen of *B. abyssicola* they would be housed with. Once preparations were completed, specimens were left overnight and re-examined in the morning to assess the results of the interactions. For each trial, *Pleurobrachia sp.* was examined for evidence of attack by *B. abyssicola*, and the results recorded to indicate whether the *Beroe attempted* to consume the prey item.

### *Bolinopsis Chemical Cue Trials*

The goal of these trials was to examine if searching/hunting behaviors of *B. abyssicola* occur, at least in part, as a result of the presence of chemical cues in the water originating from target prey, *Bolinopsis infundibulum*. Before trials began, ten specimens of *B. infundibulum* were

left in a container filled with fresh seawater overnight to “condition” the seawater in their container with chemical cues that might potentially trigger hunting behavior in species of *Beroe*. After 24 hours, a single specimen of *Beroe abyssicola* was moved into a 1-gallon jar of unconditioned or fresh seawater and allowed to acclimate for five minutes. Once acclimation was completed, the amount of time spent by the specimen of *B. abyssicola* "searching" for food, or moving in circular patterns, was recorded for five minutes and recorded. Thereafter, water was "conditioned" by adding 50 mL of seawater from the previously conditioned container with *Bolinopsis* housed in it. The same behaviors were then assessed to see determine the addition of conditioned seawater with the chemical cues of the prey species had any noticeable impact on the searching behavior of *Beroe abyssicola*. The process was then repeated with different *Beroe abyssicola* using the same conditioned water for the desired number of trials.

### *Statistical Analysis*

Statistical analysis of the feeding behavior and observational trials was conducted in a multipart process to yield adequate results from the time trials. First, observed behaviors were grouped by the "mood" or "state" the animal was in during the exhibited behavior. We classified these as "aggressive state," which indicated the animal was actively searching for food, with the mouth open, "passive state" in which the animal had its mouth closed and was not actively hunting, and finally "sedentary state" in which the mouth could be open or closed but the animal was not actively moving or exhibiting any complex behavior. Differentiation between passive and aggressive states was derived from observations made during feeding trials. On multiple occasions, an individual *B. abyssicola* did not strike a prey item even if its “lips” made direct contact with it when its mouth is closed, suggesting that the animals cannot/are not actively

looking for food, and can only strike prey when the mouth is open. Once these distinctions had been made, time series data from each trial was used to calculate the time spent in each of the three states by *Beroe* during the period encompassing all trials, before visually analyzing them for interesting patterns and consistencies across trials. When no such patterns could be found, trials were regrouped in accordance to the size of the *B. abyssicola*, with ctenophores between 2-3 cm in length classified as “small”, those between 4-5 cm as “medium”, and finally those between 6-7 cm as “large.” Once the data was regrouped in this manner, the above process was repeated and revealed more intriguing visual patterns that we thought warranted statistical analyses. To accomplish this, for every size category, we created three new observation series for each size group of *Beroe* and measured the average amount of time they spent in a particular behavioral state, per minute, over the 20-minute testing period. Doing so allowed us also to create consistent time intervals across size categories and trials (Sponaugle, 1990). These calculations permitted the creation of visual representations for the distribution that each size group of ctenophore, on average, spent in a given behavioral state across the observational period, and were informative in determining how to proceed with further analyses. Initially, a 2-factor ANOVA employed in attempt to examine statistical differences in time elapsed between size groups. Autocorrelation testing, however, revealed a non-parametric alternative to be more appropriate; thus, it was decided to utilize Wilcoxon Rank Sum Tests for each behavioral state comparing size groups (Wild, 1997). Once statistical testing was completed, results were compared with the visual patterns for each group to determine if the analyses were accurate.

For the *Pleurobrachia sp.* feeding trials and the *Bolinopsis* chemical cue trials, a simple two-sample T-test assuming unequal variances was determined sufficient for analyzing both data sets. For the *Pleurobrachia* experiment, the test examined statistical differences between the

number of instances in which an attack on the presented prey item occurred versus the number in which the prey item escaped unscathed. For the *Bolinopsis* experiment, the T-test examined statistical differences between the time an individual swam in the tank unconditioned with *Bolinopsis* cues versus the time they spent swimming in a tank that had been conditioned with the chemical cues of their preferred prey item.

## Results and Analysis

### *Patterns in Feeding Behavior when in the Presence of B. infundibulum*

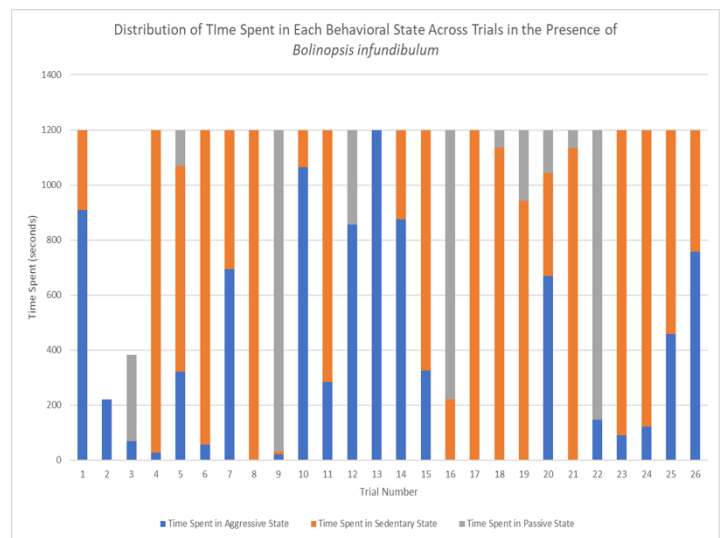
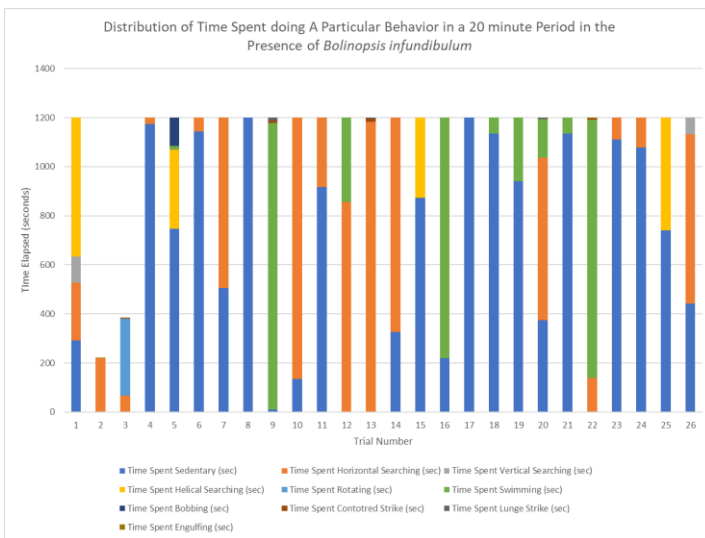


Figure 1: The above figure illustrates the distribution of time an individual *Beroe* spent executing a particular behavior during the observational period. Note the lack of distinct patterns across all trials.

Figure 2: The above figure illustrates the distribution of time an individual *Beroe* spent in a behavioral state during the observational period. Again, there are no actual discernable patterns across all trials.

Across all *B. abyssicola* examined, when in the presence of a preferred prey item, in this case, is *Bolinopsis infundibulum*, there were no large, observable patterns in the specific actions performed across all ctenophores, as evidenced by Figure 1. Even when behaviors were grouped by state (i.e., aggressive vs. passive state), very little, if any, consistency was found throughout all the trial periods, as shown in Figure 2 above. This outcome does not mean there were no interesting results across all trials, however. In Figure 3, we can see that out of all possible

actions, on average, when in the presence of its typical prey *B. infundibulum*, the predatory ctenophore *B. abyssicola* will spend most of its time sedentary, and simply maintaining its position in the water column. Our observations had *Beroe* spending, on average, 600 seconds sedentary over a 20-minute interval. The three subsequent most common behaviors observed were horizontal search patterns, helical search patterns, and finally, passive swimming with the mouth closed, spending approximately 290, 70, and 150 seconds, on average, over 20 minutes respectively. Across all trials, all other observed behaviors were comparatively rare, with a mean time spent during the observational period of fewer than 20 seconds for all remaining behaviors. This would seem to suggest that there is indeed a standard set of actions most *B. abyssicola* will perform during a hunting encounter.

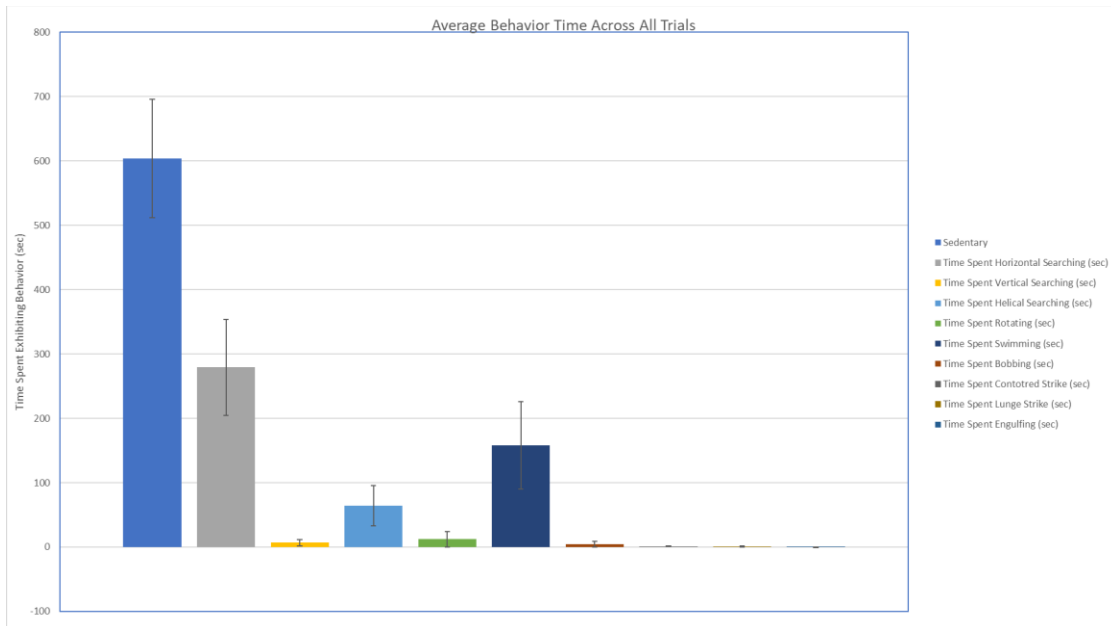


Figure 3: The above figure illustrates the average time all specimens of *B. abyssicola* spent executing a particular action or behavior during the observation period.

The results become far more interesting when examined in the context of distinct size groups of *B. abyssicola*. As seen in Figure 4, clear patterns in

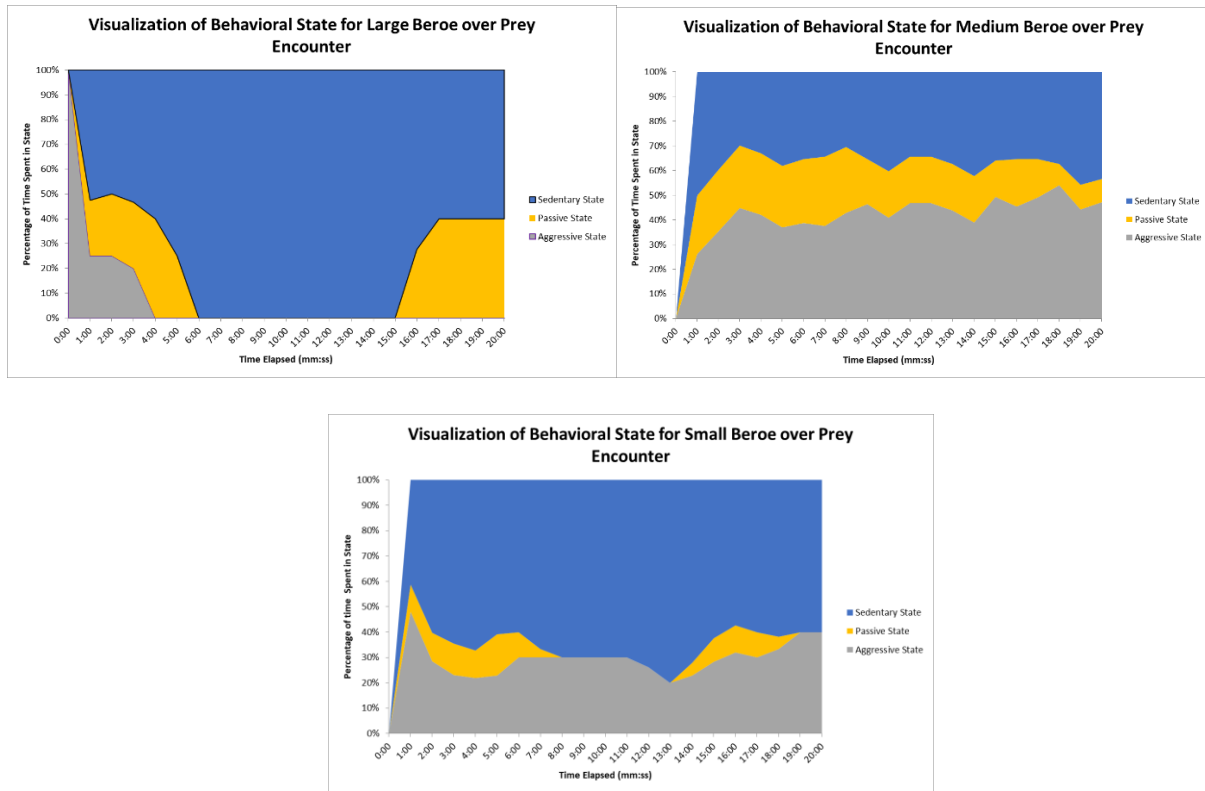


Figure 4: The above figure illustrates the percentage of time spent in a behavioral state (aggressive, passive, or sedentary) by an individual ctenophore when in the presence of its prey item for each size category examined.

present for every group examined, and similarities between the groups also begin to emerge. Examining behavioral patterns in the large *B. abyssicola* (individuals between 6-7 cm), the majority of their time across the observational period is spent sedentary, with 100% of their time spent in a sedentary state between the 7-minute and 15-minute period of the 20-minute trial representing a considerable amount of their time. In addition to this preference towards a sedentary feeding behavior, on average, they spent the second largest percentage of their time in a passive state with their mouth closed (meaning they are unable to feed in the event of an encounter with the prey item), with 40-50% of their time per minute at specific periods spent in this behavioral state. Finally, out of all three size groups examined, large *Beroe* spent by far the least amount of time in an aggressive state, meaning they were actively searching for food with a

maximum of only 25% of their time spent in an aggressive state at any given point in the observational period. Examining medium-sized *Beroe*, there is a far more interesting distribution regarding the percentage of time spent at a given time across behavioral states.

In contrast to the other two size categories, medium-sized individuals spent the least amount of time in a sedentary state over the trial period, with a maximum of approximately 40% of time spent in a sedentary state at any given period. Individuals in this size class spent by far the most time in aggressive and passive behavioral states, with 50% at specific periods of their time spent in an aggressive state and between 20-30% of their time spent in a passive state throughout all periods. The patterns in the behavioral state for small *Beroe* (between 2 and 3 cm in length) fall between those observed for large and medium-sized individuals. Small individuals spent the second-largest amount of time in a sedentary state out of all size groups examined, with as much as 80% of their time allocated to passive behavior at the 13-minute mark of the observational period. In addition, they also spent the second-largest amount of time in an aggressive/searching behavioral state out of all *B. abyssicola* examined, with 20-40% of their time spent actively searching for food with the mouth open across the entire trial period. Finally, they spent a comparatively small amount of time in a passive state, with only 10-15% of their time maximum spent in this type of behavioral state across the observational period making it the smallest amount of time out of any group examined.

Table 2: The below table lists the output values from the Wilcoxon Rank Sum Tests (either *W* or *W'*), used to compare the time spent across trials in a behavioral state by *Beroe* of different size classes. Note that green indicates statistical differences.

	Test- Values for Wilcoxon Rank Sum Tests for Aggressive Behavior		
	Small <i>Beroe</i>	Medium <i>Beroe</i>	Large <i>Beroe</i>
Small <i>Beroe</i>	-	98	-68
Medium <i>Beroe</i>	-	-	-51.5

Large <i>Beroe</i>	-	-	-
	<b>Test- Values for Wilcoxon Rank Sum Tests for Passive Behavior</b>		
	Small <i>Beroe</i>	Medium <i>Beroe</i>	Large <i>Beroe</i>
Small <i>Beroe</i>	-	84	-12
Medium <i>Beroe</i>	-	-	-32
Large <i>Beroe</i>	-	-	-
	<b>Test- Values for Wilcoxon Rank Sum Tests for Sedentary Behavior</b>		
	Small <i>Beroe</i>	Medium <i>Beroe</i>	Large <i>Beroe</i>
Small <i>Beroe</i>	-	97	-9
Medium <i>Beroe</i>	-	-	-31.5
Large <i>Beroe</i>	-	-	-
	Indicates Not Statistically Different, (Populations are the Same)		
	Indicates Statistically Different, (Populations are Different)		

Statistical analyses of these behavioral patterns served to confirm these results further. Large ctenophores were found to spend significantly less time in an aggressive behavioral state as compared to both small and medium ctenophores with W' values of -68 and -51.5 (see Table 2). Medium ctenophores and small ctenophores were noted to form statistically similar populations in the test context, meaning that they statistically spent the same amount of time in an aggressive state. When examining sedentary behavior, small *Beroe* were found to spend a statistically similar amount of time as did medium and large individuals in a sedentary state. In contrast, large individuals were found to spend significantly more time in a sedentary state than medium *Beroe*. Finally, similar patterns were demonstrated between sedentary and passive behaviors, with small individuals spending statistically the same amount of time in a passive state as the other two size groups. In contrast, members of the medium category spent

considerably more time in passive states, in the presence of their prey, than did large ctenophores.

*Pleurobrachia sp. Feeding Trials*

The feeding trials to test whether *B. abyssicola* would consume an alternative prey item, such as *Pleurobrachia*, were the most conclusive of all experiments performed. Out of the twenty trials conducted, not a single instance of an attack by *Beroe* on the prey item occurred, with all 20 individuals ignoring the prey item entirely. Statistical testing served to confirm these results with a two-sample, two-tailed T-test yielding a statistically significant difference in the data when comparing the number that attacked *Pleurobrachia*, and the number that ignored this alternative prey item (Table 3).

Table 3: The above table shows the outputs of statistical tests, (2-sample t-tests), for both the *Pleurobrachia sp.* feeding trials as well as the chemical cue conditioning experiments. In this case only one result was statistically significant, that being the results of the feeding study.

Output of t-Test: Two-Sample Assuming Unequal Variances for <i>Pleurobrachia</i> Feeding Study	Output of t-Test: Two-Sample Assuming Unequal Variances for <i>Chemical</i> Cue Study
<b>P = 0.00</b>	<b>P = 0.81</b>

*Bolinopsis Infundibulum* Chemical Cues

In testing a variety of *B. abyssicola* to examine the swimming time in conditioned seawater, versus water that had not been conditioned with cues from *Bolinopsis infundibulum*, no conclusive results could be extrapolated from the resulting data. A preliminary T-test on the first five trials comparing the time spent swimming by *B. abyssicola* in conditioned seawater versus unconditioned seawater yielded no statistically significant results (Table 3). This lack of significance was deemed the result of a poor choice of the metric "swimming time" as a

dependent variable because it did not account for nuanced differences in behavior types for species of *Beroe* and thus further testing was abandoned due to time constraints.

Table 4: The above table illustrates the results for the preliminary five trials of the experiment to determine the effects of chemical cue conditioning on the swim time of *Beroe abyssicola*.

Trial Number	Time Swimming Unconditioned (Seconds)	Time Swimming Conditioned (Seconds)
1	5	0
2	300	300
3	228	252
4	300	300
5	110	190

## Discussion

### *Patterns in Feeding Behavior Exist across a Size Gradient in B. abyssicola*

Like other Beroid ctenophores such as *B. ovata*, *Beroe abyssicola* are complex nektonic predators typically found in areas where populations of their preferred prey item, *B. infundibulum*, are present (Swanberg, 1974). Despite proximity to their prey, successful encounters are still rare because for an individual *Beroe* to “strike” its prey item for consumption, contact between the lips and the prey item must occur (Haddock, 2007). Furthermore, personal observations from this study on feeding *B. abyssicola* suggest that the mouth must also be open during this correctly oriented collision as on multiple occasions, the *Beroe* made direct contact with a prey item but pushed it out of the way. Such an outcome is likely due to the need to expose the chemokinetic and mechanoreceptors hidden on the “lips” of *B. abyssicola*, which must contact the prey to trigger the strike response (Norekian, 2019 and Tamm, 1987). This suggests that in addition to maximizing the value, (nutritional gains such as tissue pieces), of encounters with prey via the use of macrocilia, *B. abyssicola* must also likely

exhibit specific behavior patterns across the species to help maximize the chance of such encounters happening, as had been observed in other studies with *B. ovata* (Swanberg, 1974). Such a thought process was the driving hypothesis behind this study. Although the behavioral observations suggest that across all members of the species, there are no clear behavioral patterns shared, when we examined the species in different size categories, specific behavioral patterns did emerge.

Larger *B. abyssicola* were shown to spend a statistically greater amount of time in a sedentary state than any other size group, meaning that while their mouth could be open or closed, they were ultimately not performing any elaborate actions/behaviors and simply maintaining their position in space. In addition, large individuals spent the statistically smallest amount of time actively hunting or searching for prey as compared to any other group in an aggressive behavior state, while spending more time in a passive state simply moving around without the mouth open and the receptors needed for prey-encounters active. These behavioral patterns are potentially due to a direct proportional relationship between respiratory rate and wet weight in Beroid ctenophores (Svetlichny, 2004). As the length of Beroid ctenophores increases, so too does the wet weight, which consequently adds to existing energy requirements that allow the animal to simply function as supported by a complex network of mesoglea, muscles, nerves, and epidermis that comprise the animal (Kozloff, 1990). Thus, it would be beneficial for an animal who's "hunting" strategy is to bump into prey at a correct orientation to behave in specific ways that minimize energy expenditure. In the larger animals, as the animal grows, its respiratory demand to actively search for food increases, but so too does the probability of colliding with a prey item even while sedentary. This relationship could mean that it would be beneficial for larger *B. abyssicola*, who already have an inherent increase in the probability of

encountering prey, to rely on a sedentary feeding strategy. This hypothesis is, of course, only speculative and would require further substantiation. However, in this way the animal can still support triggering of a strike response rather than expending additional energy in active search patterns. This same line of thinking can explain patterns in passive states of behavior, which consist of moving to a new area where prey is located as the mouth is often closed during these behavioral states, and thus, strike responses cannot be triggered. Thus, it may not be advantageous for larger *Beroe* to expend energy moving to new areas when a more sedentary feeding strategy works, explaining the high degree of passive movement, as compared to aggressive movement observed in larger specimens.

Medium individuals, on the other hand, were by far the most active out of all groups during encounters with *Bolinopsis infundibulum*, perhaps because this size range represents a “sweet spot” in which respiration rate and energy demand are balanced by the size of prey they can consume, and the increased likelihood of an encounter due to size (Svetlichny, 1997 and Haddock, 2007). Medium-sized *B. abyssicola* can afford to exist in an aggressive behavior state, and actively search for food, due to increased energy reserves; thus, it is beneficial for them to maintain the circular searching patterns as much as possible. Compared to larger and smaller ctenophores, this allows medium-sized *Beroe* to maximize the chances of an encounter that is distinctly advantageous over ctenophores of other sizes, as seen in *B. ovata* (Swanberg, 1974). Finally, in small *Beroe abyssicola*, the increase in time spent sedentary could reflect a lack of suitable prey for this size of ctenophore to consume, and reduced energy gains from such interactions, in addition to a decreased likelihood of encounter due to their small size (Hoving, 2018). Smaller ctenophores (like larger ones) cannot afford to be active hunters, despite reduced respiration costs, due to a lack of energy reserves. Therefore, encountering prey of the correct

size is a smaller likelihood than other individuals (Hosia, 2011). To summarize, the observed feeding behaviors across size ranges of *Beroe abyssicola* are likely behaviors tailored to maximize energy efficiency while searching for food due to varying energy requirements and probabilities of successful prey encounters.

*B. abyssicola* does not Exhibit Willingness to Feed on *Pleurobrachia* sp.

Although all Beroid ctenophores may be equipped with macrocilia that allow them to tear chunks of tissue from prey such as *Bolinopsis* sp, likely, the observed lack of willingness to feed on alternative prey items such as *Pleurobrachia* is either because *B. abyssicola* cannot do so, or the feeding response is never triggered in the first place. *Pleurobrachia* is known as one of the most physically tough genera of ctenophores, able to maintain its spherical shape even out of the water, unlike other species such as *Beroe* and *Bolinopsis*, which cannot be harvested using plankton nets due to their delicate nature (Hoving, 2018 and Tamm, 2014). This resistance could render *Pleurobrachia* sp. immune to attacks from *B. abyssicola* if they occur, as even the macrocilia of the delicate *B. abyssicola* may not be able to harm this genus of ctenophore. Much more likely, however, is that the chemical cues of *Pleurobrachia* do not trigger the complex network of cues and receptors that evolved in *B. abyssicola* to be triggered by prey items as seen in other species of *Beroe*; thus, an attempted strike is never made in the first place (Norekian, 2019).

Despite the seemingly consistent results of the twenty trials conducted in this study, it is also possible that at the time of testing, more time was needed for the individual *B. abyssicola* to be hungry enough to attempt to consume *Pleurobrachia*, and that the willingness would have increased as time without food increase. Future studies, in addition to a larger sample size,

should also compare the chemical cues in *Bolinopsis* and *Pleurobrachia*, which likely trigger the strike response in *B. abyssicola*, to understand this relationship more fully.

*Chemical cues from B. Infundibulum may Influence Behavior in B. abyssicola.*

Initial statistical results from this experiment revealed no significant relationship between the swim time of *Beroe abyssicola* in areas that had been conditioned with *Bolinopsis infundibulum* cues and in water that had not been conditioned with those cues. This suggests that unlike other species, including *Beroe ovata*, cues from the prey item do not directly influence the searching behavior of *B. abyssicola*. This finding differs from those reported in current literature (Swanberg, 1974). Poor experimental design is likely the main issue with our study, and in our opinion is why the experiment proved inconclusive and was halted, in addition to time constraints. Future studies examining this relationship should better quantify searching behavior rather than swimming time, as that alone does not allow for adequate analysis of the impact of chemical cues on the induction of searching/hunting behavior in *B. abyssicola*. In addition, perhaps statistical results would have been more conclusive with larger sample size; however, due to time constraints, we decided our attention would be better spent in other areas.

**Acknowledgments:**

First, I would like to acknowledge the help of Dr. Tigran Norekian and Dr. Claudia Mills whose help and insight into the lifestyle of ctenophores laid the foundation for our ability to conduct this study and interpret the results. I would also like to acknowledge the help of Dr. Klinger, and finally, my research partner Jacob Beemer for helping read and suggest edits to this paper during the writing process. Finally a special thanks to Joe Dupreh whose insight into

statistical analysis was of great help in successfully analyzing and interpreting the results of this study.

## References

- Fraser, J. H. (1962). The role of ctenophores and salps in zooplankton production and standing crop. *Rapports et Proces verbaux des Reunions du Conseil permanent International pour l'Exploration de la Mer*, 153, 121-123.
- Haddock, S. H. D. (2007). Comparative Feeding Behavior of Planktonic Ctenophores. *Integrative and Comparative Biology*, 47(6), 847–853.
- Hosia, A., Titelman, J., Hansson, L. J., & Haraldsson, M. (2011). Interactions between native and alien ctenophores: *Beroe gracilis* and *Mnemiopsis leidyi* in Gullmarsfjorden. *Marine Ecology Progress Series*, 422, 129–138. <https://doi.org/10.3354/meps08926>
- Hoving, H.-J., Neitzel, P., & Robison, B. (2018). In situ observations lead to the discovery of the large ctenophore *Kiyohimea usagi* (Lobata: Eurhamphaeidae) in the eastern tropical Atlantic. *Zootaxa*, 4526(2), 232–238. <https://doi.org/10.11646/zootaxa.4526.2.8>
- Kozloff, E. N. (1990). *Invertebrates*. Saunders College Pub.
- Laverack, M. S. (1979). *Essential invertebrate zoology* (2d ed.). Wiley.
- Norekian, T. P., & Moroz, L. L. (2019). Neural system and receptor diversity in the ctenophore *Beroe abyssicola*. *Journal of Comparative Neurology*, 527(12), 1986–2008. <https://doi.org/10.1002/cne.24633>
- Ruppert, E. E. (1994). *Invertebrate zoology* (6th ed.). Saunders College Pub.
- Sponaugle, S., & Lawton, P. (1990). Portunid crab predation on juvenile hard clams: Effects of substrate type and prey density. *Marine Ecology-Progress Series - MAR ECOL-PROGR SER*, 67, 43–53. <https://doi.org/10.3354/meps067043>

Svetlichny, L. S., Abolmasova, G. I., Hubareva, E. S., Finenko, G. A., Bat, L., & Kideys, A. E. (2004). Respiration rates of *Beroe ovata* in the Black Sea. *Marine Biology*, 145(3), 585–593.

<https://doi.org/10.1007/s00227-004-1336-4>

Swanberg, N. (1974). The feeding behavior of *Beroe ovata*. *Marine Biology*, 24(1), 69–76.

<https://doi.org/10.1007/BF00402849>

Tamm, S. L. (2014). Cilia and the life of ctenophores. *Invertebrate Biology*, 133(1), 1–46.

Tamm, S. L., & Tamm, S. (1987). Massive actin bundle couples macrocilia to muscles in the ctenophore *Beroë*. *Cell Motility and the Cytoskeleton*, 7(2), 116–128.

<https://doi.org/10.1002/cm.970070204>

Wild, Chris. (1997). The Wilcoxon Rank-Sum Test. University of Auckland Department of Statistics. 1-10. [Ch10.wilcoxon.pdf \(auckland.ac.nz\)](#)