Beroe abyssicola Patterns of Predation: A Behavioral Analysis

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Abstract

Ctenophores play an important role in many marine ecosystems worldwide and affect multiple trophic levels. They consume large amounts of plankton while, in turn, are also consumed by fish. *Beroe abyssicola* is a carnivorous ctenophore that preys upon *Bolinopsis infundibulum*, a planktivorous carnivore. While many studies exist on the feeding behaviors of other ctenophore genera, research on the genus *Beroe* is lacking. This study aimed to discern the patterns of predatory behavior of *B. abyssicola* and found that size was a significant factor in feeding behavior. We also tested whether seawater conditioned with the chemical signature of *B. infundibulum* would cause a change in the behavior of *B. abyssicola* but found no significant effect. Lastly, we tested whether *B. abyssicola* would consume a species of *Pleurobrachia* but found no evidence for this.

Introduction

Pelagic and nearshore trophic systems are highly variable both temporally and spatially. Within these environments, certain groups of organisms create limits on population size which, left unchecked, could shift the ecological balance (Kozloff 1990). One such animal is *Bolinopsis infundibulum*, a planktivorous ctenophore. This species goes through annual cycles of population growth followed by rapid decline, consuming large amounts of copepods in the interim (Båmstedt & Martinussen 2015). Without this influence on copepod populations, it is possible that phytoplankton abundance could be severely negatively affected (McNamara et al. 2013). These ctenophores are also capable of negatively affecting fish populations; they are known to consume substantial amounts of ichthyoplankton such as eggs and larvae. The annual decline in *B. infundibulum* populations is likely due to predation via carnivorous ctenophores such as *Beroe abyssicola*. These Beroid ctenophores are considered specialists in that they prey on other ctenophores (Båmstedt & Martinussen 2015) but in turn are known to be eaten by many species of fish, creating a positive effect on fish populations worldwide (Purcell & Arai 2001).

The ctenophores within the genus *Beroe* are distinct from other ctenophores in that they lack tentacles throughout their entire lives (Laverack 1979, Haddock 2007). They also exhibit the unique behavior of "biting" their prey. This is possible because they contain unique variations of cilia around their mouth called macrocilia which are functionally used as teeth to remove pieces of prey which they cannot engulf entirely (Horridge 1965). Because these animals play an important and unusual role in marine ecosystems worldwide, understanding their foraging behaviors can advance our understanding of planktonic systems.

While numerous behavioral studies have been performed on several species of ctenophores, literature on the predatory behaviors of *Beroe* and *B. abyssicola* is sparse. This study aims to add to our understanding of ctenophore behavior and is comprised of three separate experiments. The first tests whether different sized *B. abyssicola* exhibit any discernable differences in their patterns of predatory behavior while in the presence of their prey, *B. infundibulum*. The second experiment examines whether there are any measurable differences in *B. abyssicola*'s behavior when exposed to seawater conditioned with the chemical signature of *B. infundibulum*. And the third tests whether *B. abyssicola* will consume a different species of ctenophore which shares the same habitat, *Pleurobrachia sp*., after a period of starvation.

Methods and Materials

Collection

Ctenophores were sampled from the Friday Harbor Laboratories dock located on San Juan Island, WA (48°32'42.3"N 123°00'43.8"W) during May 2021. They were gathered from the harbor using sampling devices comprised of plastic beakers attached to the ends of wooden rods approximately 2m long, also known colloquially as "jelly dippers". *Beroe* and *Pleurobrachia* were kept in 800mL plastic beakers with plastic mesh bottoms and *Bolinopsis* were kept in a larger plastic bin with mesh siding. All containers were kept in a sea table with locally sourced circulating sea water for at least 24 hours before testing. There were no criteria for selecting individuals from each genus to use in this study. Various sizes of *Beroe* were found throughout the sample which fell into 3 categories of length: small (2-3cm), medium (4-5cm), and large (6-7cm).

Treatments

<u>Experiment 1 – Predation of *B. infundibulum*</u>. A single *Beroe* was randomly selected and placed in a rectangular acrylic tank containing approximately 1L of seawater filtered through a

common cloth rag to reduce debris and increase visual clarity. After a 5-minute acclimatization period, filming began and a randomly selected *Bolinopsis* was introduced to the tank. The ctenophores were then left undisturbed in the tank for 20 minutes. At 20 minutes we removed the specimens, rinsed out the tank, and reset for another treatment with fresh, randomly selected ctenophores. This process was repeated 25 times using 9 individuals of *Beroe* (n = 9) over a 4-day period.

We distinguished between three categories of behavior displayed by *Beroe*: passive, active, and sedentary. Passive behavior included any movement with the mouth closed, active behavior included any movement with the mouth open, and sedentary behavior included any time the ctenophore was stationary, mouth open or closed. Passive behaviors were further defined: “bobbing” – moving up and down the water column relatively quickly (twice per minute), “swimming” – any vertical, horizontal, or helical movement, and “rotating” – spinning while stationary. Active behaviors were also further defined: “horizontal searching” – any lateral movement (including circling, rotating, or straight paths), “vertical searching” – the same as horizontal but only up and down the water column, “helical searching” – a combination of both horizontal and vertical searching, “strike” – either a lunge (straight on) or contorted (having to bend its body to orient its mouth toward prey), and “engulfing” – complete capture of prey.

Experiment 2 – Water Conditioning. A single *Beroe* was selected and placed in a large glass jar with approximately 1L of fresh seawater filtered through a common cloth rag. After an acclimatization period of 5 minutes, we recorded its behavior for 5 minutes. We then added 50mL of sea water conditioned with the chemical signature of *B. infundibulum* and recorded its behavior for another 5 minutes. To condition the water, we left several *Bolinopsis* in a container for at least one hour. This experiment was replicated for a total of 5 trials.

Experiment 3 – *Pleurobrachia* Consumption. After a starvation period of at least 24 hours, we placed a single *Pleurobrachia* in each of the *Beroe*–containing beakers in the sea table where it was kept overnight for 24 hours and recorded any consumption events.

Statistical Analysis

Experiment 1 – Predation of *B. infundibulum*. To determine whether there existed any discernable patterns of behavior from the ctenophore *B. abyssicola*, we performed a non-parametric Wilcoxon rank-sum test. We also created several visual representational graphs of the data (Sponaugle & Lawton 1990) and compared them to the statistical results to show possible patterns in behavior over time.

Experiment 2 – Water Conditioning. In testing whether seawater conditioned with the chemical signature of *B. infundibulum* had a significant impact of *B. abyssicola* behavior, we performed a two-tailed *t*-test assuming unequal variance.

Experiment 3 – *Pleurobrachia* Consumption. To test the significance of *B. abyssicola* consuming *Pleurobrachia* we performed a two-tailed *t*-test assuming unequal variance.

Results

Experiment 1 – Predation of *B. infundibulum*. We found no significant differences in behaviors displayed by small- and medium-sized *Beroe*. Large *Beroe* differed from small- and medium-sized *Beroe* in time spent in aggressive behavior and differed from medium-sized *Beroe* in time spent in passive and sedentary behavior (Table 1). We found no overall patterns in behavior when all samples from all size groups were combined (Figure 1a). However, relationships were found when grouping ctenophores based on size (Table 1) and behavioral states (Figure 1b). We also found the results from our statistical analysis coincide with the visual representation of the data (Figure 2).

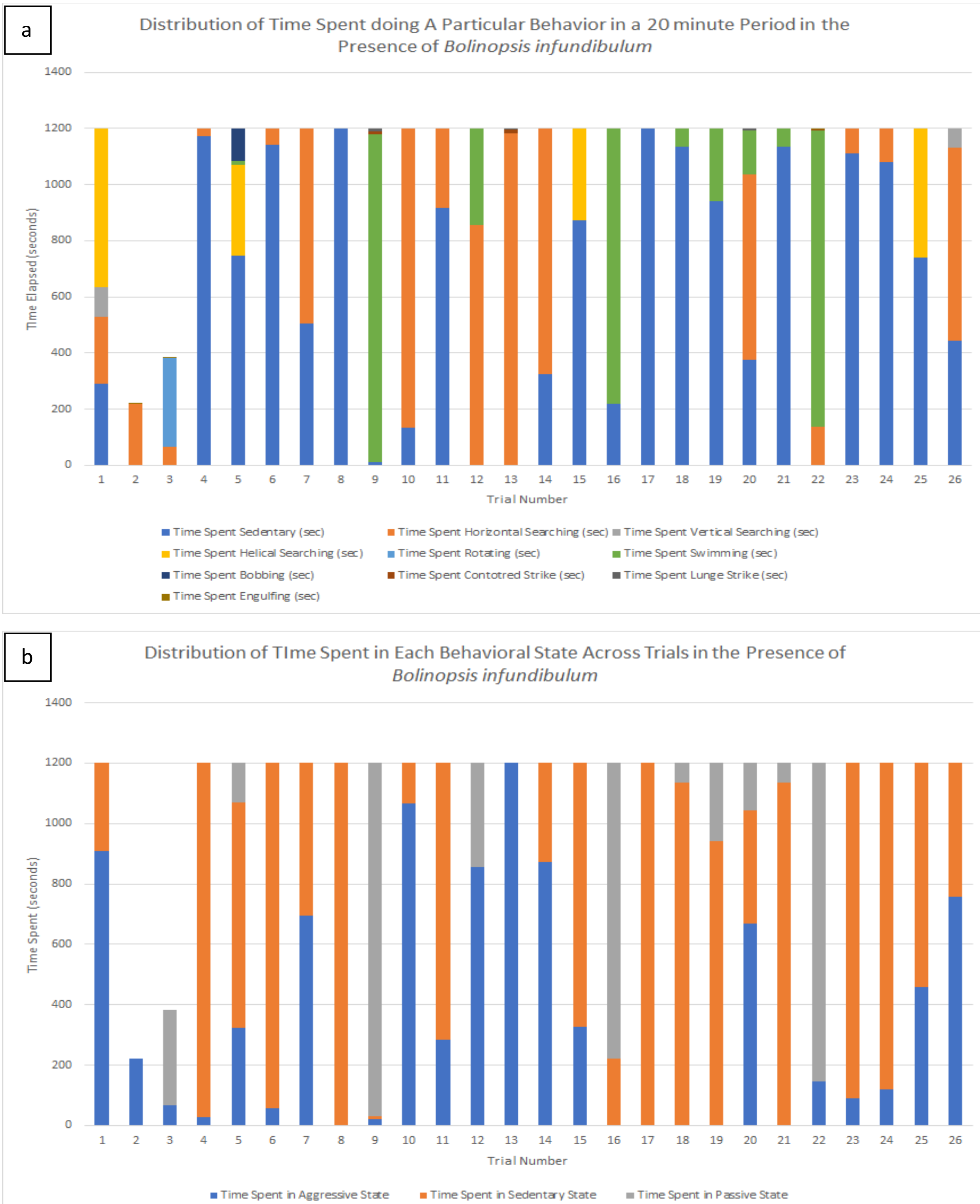
Table 1

Test values for Wilcoxon rank-sum statistical tests across behavioral categories comparing size groups.

	Aggressive		
	Small Beroe	Medium Beroe	Large Beroe
Small Beroe	-	98	-68*
Medium Beroe	-	-	-51.5*
Large Beroe	-	-	-
	Passive		
	Small Beroe	Medium Beroe	Large Beroe
Small Beroe	-	84	-12
Medium Beroe	-	-	-32*
Large Beroe	-	-	-
	Sedentary		
	Small Beroe	Medium Beroe	Large Beroe
Small Beroe	-	97	-9
Medium Beroe	-	-	-31.5*
Large Beroe	-	-	-

Note. Asterisk indicates statistical difference.

Figure 1.



Note. Trials 2, 3, and 22 end after successful engulfing events.

Figure 2

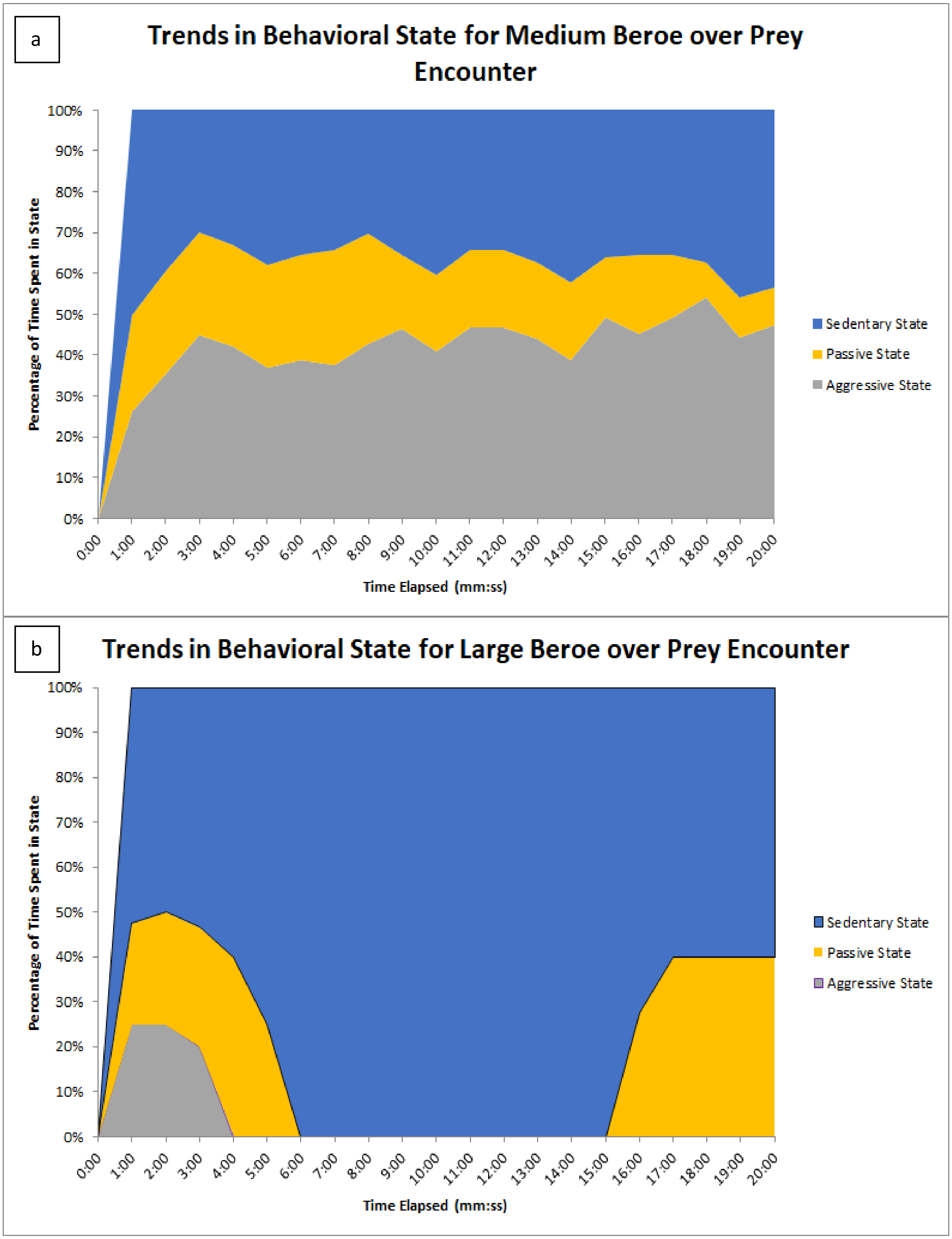
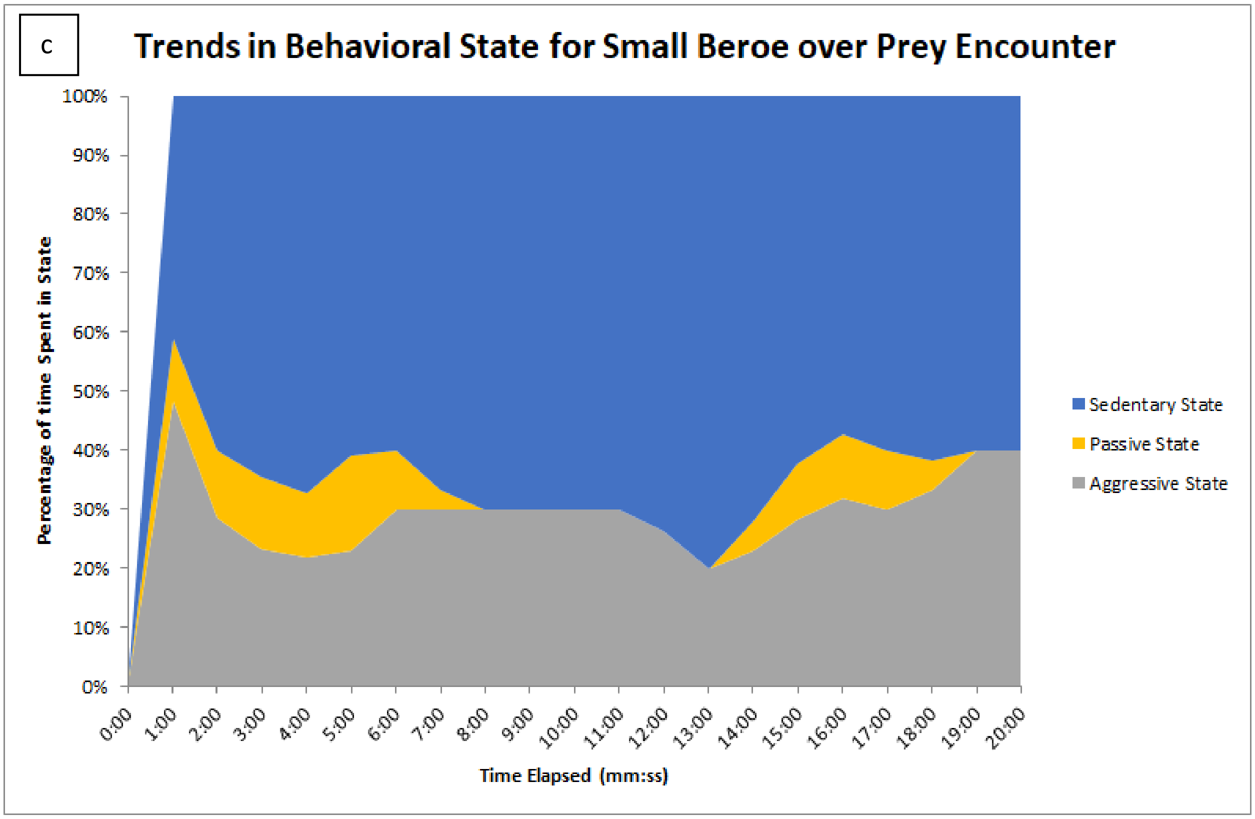

a
Trends in Behavioral State for Medium Beroe over Prey Encounter
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Percentage of Time Spent in State
0:00
1:00
2:00
3:00
4:00
5:00
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
Time Elapsed (mm:ss)
Sedentary State
Passive State
Aggressive State
b
Trends in Behavioral State for Large Beroe over Prey Encounter
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Percentage of Time Spent in State
0:00
1:00
2:00
3:00
4:00
5:00
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
Time Elapsed (mm:ss)
Sedentary State
Passive State
Aggressive State

Figure 2 (continued)



Note. Visual representation of time spent in categories of behavior per size group, medium (a), large (b), and small (c).

Experiment 2 – Water Conditioning. We found no significant difference in behavior in conditioned and unconditioned water ($p = 0.8$).

Experiment 3 – *Pleurobrachia* Consumption. We found that none of the *Pleurobrachia* left overnight in the presence of *B. abyssicola* were consumed ($p = 0$).

Discussion

Small and medium sized *B. abyssicola* exhibited similar patterns of sedentary, passive, and aggressive behavior while in the presence of *B. infundibulum* but larger *B. abyssicola* shared fewer patterns across behavior states. This may be the result of physiological differences between sizes influencing individual behavior. Rather than actively searching for prey, it might be metabolically more efficient for large carnivorous ctenophores to simply remain still and wait for prey to come to them as it has been shown that *Beroe* respiration rates are positively correlated to size (Svetlichny 2004). Contrary to sedentation behavior in large *Beroe*, medium and smaller individuals may exhibit more aggressive behaviors as they maintain lower rates of respiration coupled with a having a lower probability of contacting their prey solely by chance while sedentary based on their smaller size.

Our trials testing *Beroe* behavioral changes in response to conditioned water yielded no significant results. This may be due to a limitation of our experimental setup; subtle changes in behavior could not be properly assessed. Our test on *Beroe* consumption of *Pleurobrachia*, however, indicate that they can discern prey type and will not consume this particular species of ctenophore even after a starvation period which supports our prior understanding (C. Mills, personal communication, May 2021). There were, however, interesting observations made outside of these analyses throughout the first experiment. We recorded several instances of *B. abyssicola* while in a passive behavior state swim mouth first into its prey, *B. infundibulum* and merely push it out of the way. It could be that some sort of sensory inhibition could have occurred by damaging them during transfer between tanks. Damage to their aboral sensory organ could also affect their vertical movement, thus changing their natural behavior (Greve 1970). Another notable instance was when a large *Beroe* performed a contorted strike towards the surface of the water as a *Bolinopsis* was being lowered a few centimeters above the water in a jar. While likely coincidence, this instance might inspire one to question what level of photosensory capabilities these animals may possess (Horridge 1964).

All our large specimens were asymmetrical at their aboral end with two exhibiting visible holes in this region where bits of food could escape. This could have possibly affected our data as these individuals may have been damaged throughout testing. It is also notable that larger *Beroe* were observably deteriorating at a faster rate than smaller specimens. Within a window of 48 hours, large *Beroe* would turn pale and create what appeared to be mucus after transfer which we interpreted as possible sloughing of tissue. Similar observations were made for medium sized *Beroe* but only after 3 or more days. The smallest *Beroe* were the most robust and showed no signs of deterioration over the course of the trials (approximately 4 days).

This study found that differences in the size of *Beroe abyssicola* affect its pattern of behavior when in the presence of its prey, *Bolinopsis infundibulum*. This finding could be used as supplementary information when predicting changes in nearshore ecosystems. Because lobate ctenophores such as *Bolinopsis* can alter the composition of coastal planktonic communities (Colin 2010), understanding how size impacts the hunting behavior of their top-down controlling predator may provide insight into how ecosystems could change when *Beroe* are restricted, or not, in their growth.

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References

Båmstedt, U., & Martinussen, M. B. (2015). Ecology and behavior of Bolinopsis infundibulum (Ctenophora; Lobata) in the Northeast Atlantic. *Hydrobiologia*, *759*(1), 3–14. https://doi.org/10.1007/s10750-015-2180-x

Colin, S. P., Costello, J. H., Hansson, L. J., Titelman, J., & Dabiri, J. O. (2010). Stealth predation and the predatory success of the invasive ctenophore Mnemiopsis leidyi. *Proceedings of the National Academy of Sciences*, *107*(40), 17223–17227. https://doi.org/10.1073/pnas.1003170107

Greve, W. (1970). Cultivation experiments on North Sea ctenophores. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, *20*(1), 304–317. https://doi.org/10.1007/BF01609908

Haddock, S. H. D. (2007). Comparative Feeding Behavior of Planktonic Ctenophores. *Integrative and Comparative Biology*, *47*(6), 847–853.

Horridge, G. A. (1964). Presumed Photoreceptive Cilia in a Ctenophore. *Journal of Cell Science, s3-105*(71), 311–317. https://doi.org/10.1242/jcs.s3-105.71.311

Horridge, G. A. (1965). Macrocilia with Numerous Shafts from the Lips of the Ctenophore Beroe. *Proceedings of the Royal Society of London. Series B, Biological Sciences, 162*(988), 351–364.

Kozloff, E. N. (1990). *Invertebrates*. Saunders College Pub.

Laverack, M. S. (1979). *Essential invertebrate zoology* (2d ed.). Wiley.

McNamara, M. E., Lonsdale, D. J., & Cerrato, R. M. (2013). Top-down control of mesozooplankton by adult Mnemiopsis leidyi influences microplankton abundance and composition enhancing prey conditions for larval ctenophores. *Estuarine, Coastal and*

Shelf Science, *133*, 2–10. https://doi.org/10.1016/j.ecss.2013.04.019

Purcell, J. E., & Arai, M. N. (2001). Interactions of pelagic cnidarians and ctenophores with fish: A review. In J. E. Purcell, W. M. Graham, & H. J. Dumont (Eds.), *Jellyfish Blooms: Ecological and Societal Importance* (pp. 27–44). Springer Netherlands. https://doi.org/10.1007/978-94-010-0722-1_4

Sponaugle, S., & Lawton, P. (1990). Portunid crab predation on juvenile hard clams: Effects of substrate type and prey density. *Marine Ecology Progress Series*, *67*(1), 43–53.

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