RELATIONSHIP BETWEEN NEMATOCYST DISTRIBUTION AND PREY CAPTURE IN HYDROMEDUSAE

by

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THESIS ABSTRACT

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We analyzed the relationship between prey capture and nematocyst distribution in the tentacles of the ambush predators, *Aglantha digitale* and *Proboscidactyla flavicirrata*, and the filter feeders, *Clytia gregaria* and *Mitrocoma cellularia*. we used video observations to compare capture locations of *Artemia salina* nauplii relative to the bell margin of each species. Tentacle pictures were analyzed to determine if nematocyst abundance changes along their length. By analyzing behavior and morphology simultaneously, we found that the ambush predators *A. digitale* and *P. flavicirrata* plus *Sarsia tubulosa* have higher nematocyst density at the tentacle tips and tend to capture more prey toward the tips. In contrast, the filter-feeders *Aequorea victoria*, *C. gregaria* and *M. cellularia* capture most of the prey close to the body, where they also show a slight increase in nematocyst densities. This thesis includes unpublished coauthored material.

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A mi familia y a Karla. A pesar de la distancia y la soledad, siempre estuvieron en mi mente y en mi alma.

MAN AND SEA

Man-a free man- always loves the sea
and in its endlessly unrolling surge
will contemplate his soul as in a glass
where gulfs as bitter gape within his mind.

Into this image of himself he dives,
his arms and eyes wide open and his heart
sometimes diverted from its own dead march
by the tides of that untamable complaint.

How grim their combat, and yet how discreet
-who has sounded to its depths the human heart?
and who has plucked its riches from the sea?-
so jealously they guard their secrets, both!

Countless the ages past and still to come
in which they wage their unrelenting war
for their sheer delight in carnage and in death,
implacable brothers and eternal foes!

Charles Baudelaire

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CHAPTER I

INTRODUCTION

Hydrozoa is the most diverse medusozoan class (Colin et al., 2005, Zapata et al., 2015) and comprises organisms with a wide range of morphologies, which relate to their feeding behavior (Costello et al., 2008). For instance, the cycles of bell contraction and relaxation in oblate (disc-shaped) medusae generate vortices for propulsion as well as for entraining prey and direct them to the tentacles (Ford et al., 1997; Colin and Costello, 2002; Katija et al., 2011; Gemmell et al., 2015). Medusae that feed and swim in this way are called filter feeders. However, in prolate (bullet shaped) medusae, swimming and feeding are decoupled processes (Colin and Costello, 2002).These organisms feed by extending their tentacles while remaining stationary in the water column (Greene, 1985) and capture occurs when prey collide with the tentacles; thus they are considered ambush predators (Greene, 1986; Madin, 1988; Hansson and Kiørboe, 2006; Regula et al., 2009).

In addition to umbellar shape, other morphological features such as size, arrangement and spacing of the tentacles determine the region where medusae are likely to encounter prey (Madin, 1988). Although medusae can encounter prey at several locations on the body, capture may be more frequent in certain regions of the organism. Ford et al. (1997) determined that the scyphozoan filter-feeder *Chrysaora quinquecirrha* captures most prey at the proximal part of the tentacles, closer to the bell margin. It is not known, however, how capture frequencies are distributed along the tentacle of ambush feeding medusae.

Once the medusa encounters prey, specialized cells in the tentacles called nematocysts capture the prey and retain it (Purcell and Mills, 1988). Previous morphological descriptions of hydromedusae have recognized different patterns of nematocyst distribution and density in the tentacles. For instance, nematocysts can be more concentrated to one side of the tentacle or at the tentacle tips, and can be either evenly distributed or arranged in clusters (Bouillon, 1985, Purcell and Mills, 1988). Nematocyst density is a relevant factor that can determine capture efficiency, since adherence force between the predator tentacles and prey increases with the number of nematocyst fired (Thorington and Hessinger, 1996). It is unclear, however, if the patterns of nematocyst distribution are related to prey capture locations.

In addition to prey capture, prey selectivity in hydromedusae is attributed in part to nematocyst properties such as identity, spatial arrangement and density in the tentacles (Purcell and Mills, 1988; Thorington and Hessinger, 1996; Regula et al., 2009). For instance, the ambush feeders *Cladomena californicum* and *Leuckartiara sp*. have different transfer efficiencies for variable prey types, and these changes are related to differences in nematocyst densities and arrangements in the tentacles (Regula et al., 2009). Since ambush and filter-feeding medusae capture different prey types (Costello and Colin, 2002), it is likely that hydromedusae with different feeing mechanisms have different nematocyst densities in the tentacles.

In this study, we analyzed the relation between prey capture and nematocyst distribution in the tentacles of the ambush-predators *Aglantha digitale* (O.F. Müller, 1776) and *Proboscidactyla flavicirrata* (Brandt, 1835) and the filter-feeders *Clytia gregaria* (Agassiz, 1862) and *Mitrocoma cellularia* (Agassiz, 1862). First, we used video

observations to compare capture locations of *Artemia salina* nauplii relative to the bell margin in these species. Second, tentacle pictures of these hydromedusae plus *Sarsia tubulosa* (M. Sars, 1835) and *Aequorea victoria* (Murbach and Shearer, 1902) were analyzed to determine 1) if nematocyst densities change along the tentacle length and 2) if these densities differ between species with different feeding modes.

CHAPTER II

MATERIALS AND METHODS

Specimen collection and handling

For the behavioral and morphological studies, we collected specimens of the ambush predators *Aglantha digitale* (O.F. Müller, 1776), *Proboscidactyla flavicirrata* Brandt, 1835, *Sarsia tubulosa* (M. Sars, 1835) and the filter feeders *Aequorea victoria* (Murbach and Shearer, 1902), *Clytia gregaria* (Agassiz, 1862) and *Mitrocoma cellularia* (Agassiz, 1862), from surface waters off the dock at Friday Harbor Marine Laboratories, Washington, USA during June and July of 2015. Organisms used for the behavioral analyses were maintained in a sea table for a period of 24 hours before the video recording. Prior to dissection for morphological analyses, medusae were placed in a solution of $MgCl{\bullet}6H_2O$ in fresh water (~5% $\frac{m}{v}$) for 5 minutes to relax the tentacles.

Analysis of prey capture locations

Videos for the behavioral analyses were made using a Sony HD Digital Video Camcorder recording at 30 frames per second. Filming vessels were filled with sea water and contained a single hydromedusa plus hatched *Artemia salina* nauplii as a prey item. This larva has been used as prey in studies where the main goal is to analyze the effect of the predator's behavior on feeding mechanics (Ford et al., 1997; Colin et al., 2015). The 12.5 ×6.5 ×2.5 cm rectangular filming vessel was placed between the camera and the light source. A LED collimated white light was pointed directly in front of the camera lens, and to create uniform illumination and enhance contrast of the predator and prey

bodies, a light diffuser filter was located between the vessel and the light source. When the hydromedusa was small (<5 mm diameter), we placed a 10X magnifying lens between the camera and the tank to better visualize the capture behavior. Since *A. digitale* consistently swam away from the filming area, the medusae were tethered to a capillary pipette; based on our observations, this procedure did not inhibit feeding behavior. Due to the larger size of *M. cellularia,* the experiment was conducted in a 22.5 ×16.5 ×7.5 cm vessel.

Capture was defined as prey attaching to the tentacles for more than 1 second (Hansson and Kiørboe, 2006), and we limited our measurements to events that happened within the focal plane. To determine the location relative to the bell margin where prey capture occurred, we measured the distance from the bell margin where the prey was captured (*d*) using ImageJ 1.50b. This distance was standardized by the equivalent spherical diameter (ESD) of each hydromedusa individual. ESD is defined as the diameter of a sphere with the same volume of an animal (Pitt et al., 2013); this standardization is used when comparisons between planktonic animals with different morphologies are made (Hirst et al., 2003; Pitt et al., 2013). To obtain an ESD for each predator individual, the volumes of the hydromedusae were estimated as half the volume of an ellipsoid ($(\frac{4}{3}\pi hr^2) \div 2$) where *h* is the bell height and *r* is the bell radius.

Nematocyst density and distribution in the tentacles

To measure nematocyst distribution within a tentacle, we dissected the relaxed medusae and removed the tentacles from the umbellar margin. The extended tentacle was placed on a glass slide and was photographed from the base toward the tip using a Nikon E 600 microscope equipped with phase and differential interference optics. Tentacle

bulbs were excluded from the analysis since nematogenesis has been shown to happen in this region (Denker et al., 2008). Images were compiled using Adobe Photoshop CS5. Next, we divided the full tentacle picture in sections that had a length equal to 10% of the full tentacle length, with the purpose of obtaining 10 measurements per tentacle with different distances from the bell margin; thus 0% of the tentacle length stands for the tentacle base and 100% of the tentacle length is the tip. This method provided a comparative estimate of how nematocyst densities change along the tentacle length. Using ImageJ, we measured a minimum of 5000 μm^{-2} of tentacle area and counted the number of nematocysts in each section to obtain $\#\ nematocysts\ \cdot 1000\ \mu m^{-2}$. We performed general linear regressions to quantitatively describe how nematocyst abundance changes according to the percent of total tentacle length in each species. In some cases more than one tentacle was analyzed per individual, thus, the number of individuals analyzed per species are reported as "N" and tentacle sample sizes are reported as "n".

Morphological and behavioral data analysis

A non- parametric Kruskal- Wallis (KW) test was used for comparing the mean standardized capture distance (*d/ESD*) and the mean nematocyst density ($\#\ nematocysts\ \cdot 1000\ \mu m^{-2}$.) in the species analyzed. If the differences among rank means were significant, post- hoc comparisons between species were made by a Bonferroni-Dunn test. All analyses were performed in RStudio 0.98.1091. KW and Dunn tests were made using the "dunn.test" package (Dinno, 2016) following Dunn (1964)**.** Dunn´s z statistic and probability values for the interspecific comparisons of prey capture locations and nematocyst densities are presented in Appendix C.

CHAPTER III

RESULTS

Prey capture locations

Artemia were captured at different locations relative to the bell margin of the hydromedusa species (KW $X^2(3)=83.18$, $p<0.0001$, Figure 1). Although most of the captures by *A. digitale* and *P. flavicirrata* also occurred close to the bell margin in relation to the farthest capture in each species, in these ambush-feeding medusae more captures happened further from the bell margin (Dunn´s z= 1.02, p=0.923 ; Figure 1 and Figure 2A, B). In the filter-feeders *C. gregaria* and *M cellularia* however, captures far from the swimming bell were rare, and in *C. gregaria* more captures happened further from the bell margin compared to *M. cellularia* (Dunn´s z= -4.53, p<0.0001; Figure 1 and Figure 2A, B).

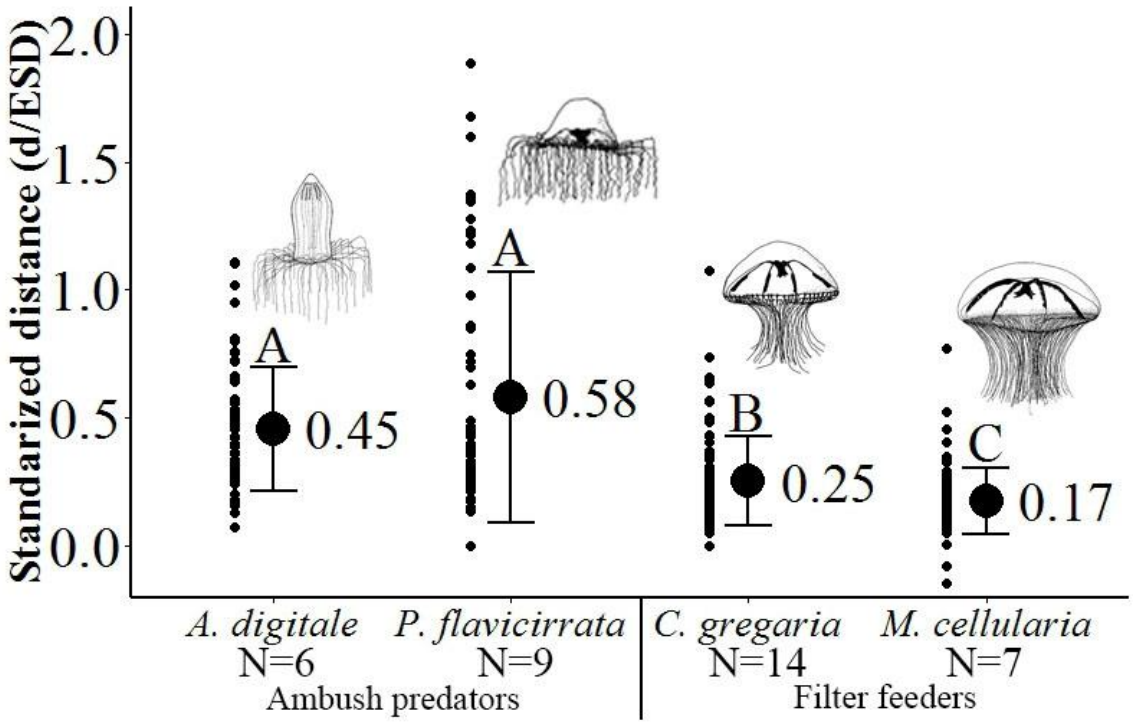


Figure 1. Standarized distance along tentacle (d/ESD) where prey were captured, measured from videos of medusae feeding (N=number of medusae recorded). Big dots indicate mean standardized distance, error bars represent standard deviation. Different letters above error bars represent significant differences across rank means (Bonferroni-Dunn test, Appendix C), small dots represent each capture location measurement.

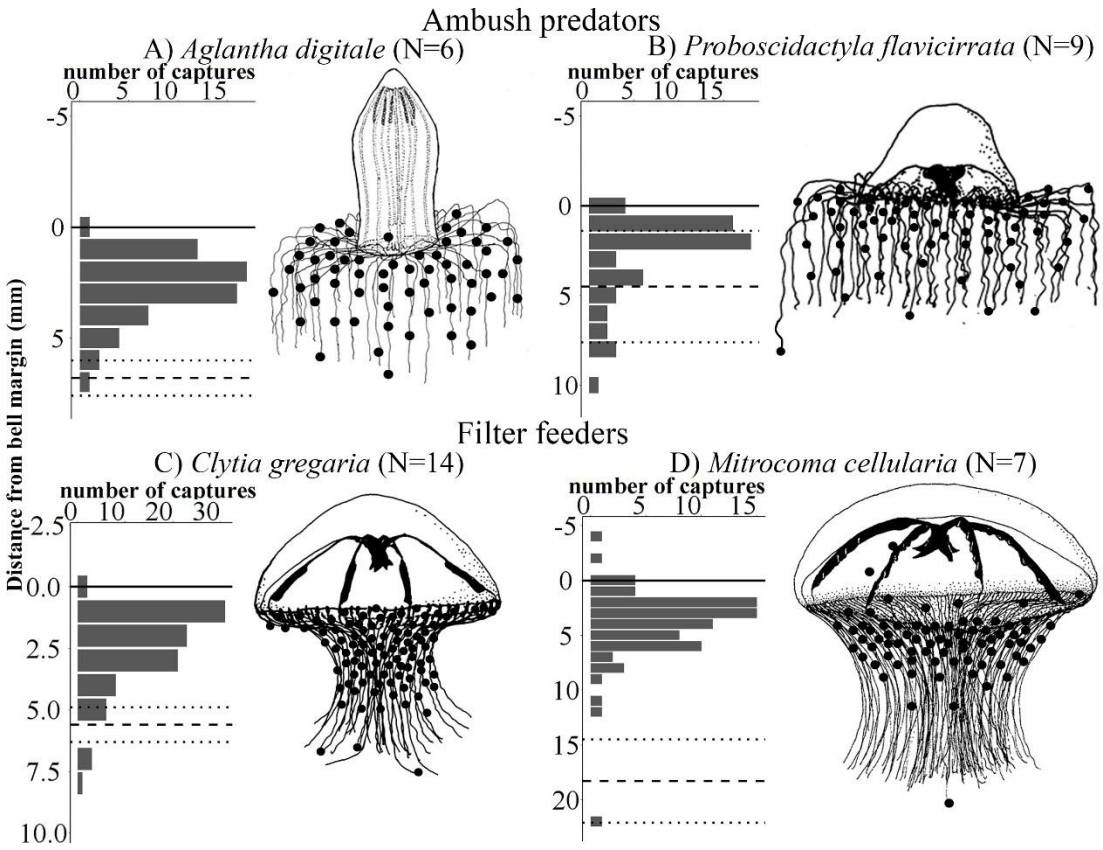


Figure 2. Cumulative prey capture locations of all hydromedusae individuals feeding on *A. salina* nauplii. N= number of individuals recorded. Solid line represents the bell margin, dashed line represents the mean tentacle length of the recorded individuals and dotted lines represent the standard deviation of the mean tentacle length. Black dots in the drawings show all observed capture locations from all individuals (horizontal positions of the dots are arbitrary).

Nematocyst density across species

The hydromedusae species present different total nematocyst densities (KW $X^2(5)=179.77$, $p<0.0001$, Table 1, Figure 3). The ambush feeders *A. digitale* and *S. tubulosa* and the filter feeder *A victoria* show similar nematocyst densities (Appendix 3), the latter species however, presents maximum nematocyst densities > 15 cells• 1000 μm^2

, similar to the other filter feeding medusae (Figure 3). Overall, filter-feeding medusae have higher nematocyst densities than ambush-feeding medusae.

Table 1. Weighted means by individuals with repeated measurements (±std. deviation) of nematocyst densities (*no • 1000 μm^{-2}*) in the hydromedusae species analyzed (n=number of tentacles, N=number of individuals)

Species	Desmonemes	Isorhizas	Microbasic euryteles	Mastigophores	Stenoteles	Total
Ambush predators						
Aglantha digitale (n=9,N=4)	-	-	2.8±1.2	-	2.9±1.9	5.7±2.8
Probosidactyla flavicirrata (n=6,N=5)	2.1±0.8	-	-	2.3±1.0	-	4.4±1.8
Sarsia tubulosa (n=7,N=3)	4.9±1.7	-	-	-	1.0±0.5	5.8±2.0
Filter feeders						
Aequorea victoria (n=7,N=6)	-	0.9±0.4	-	6.1±3.9	-	7.0±4.1
Clytia gregaria (n=6,N=5)	-	-	-	11.1±2.1	-	11.1±4.7
Mitrocoma cellularia (n=5,N=4)	-	-	-	15.4±2.2	-	15.4±4.3

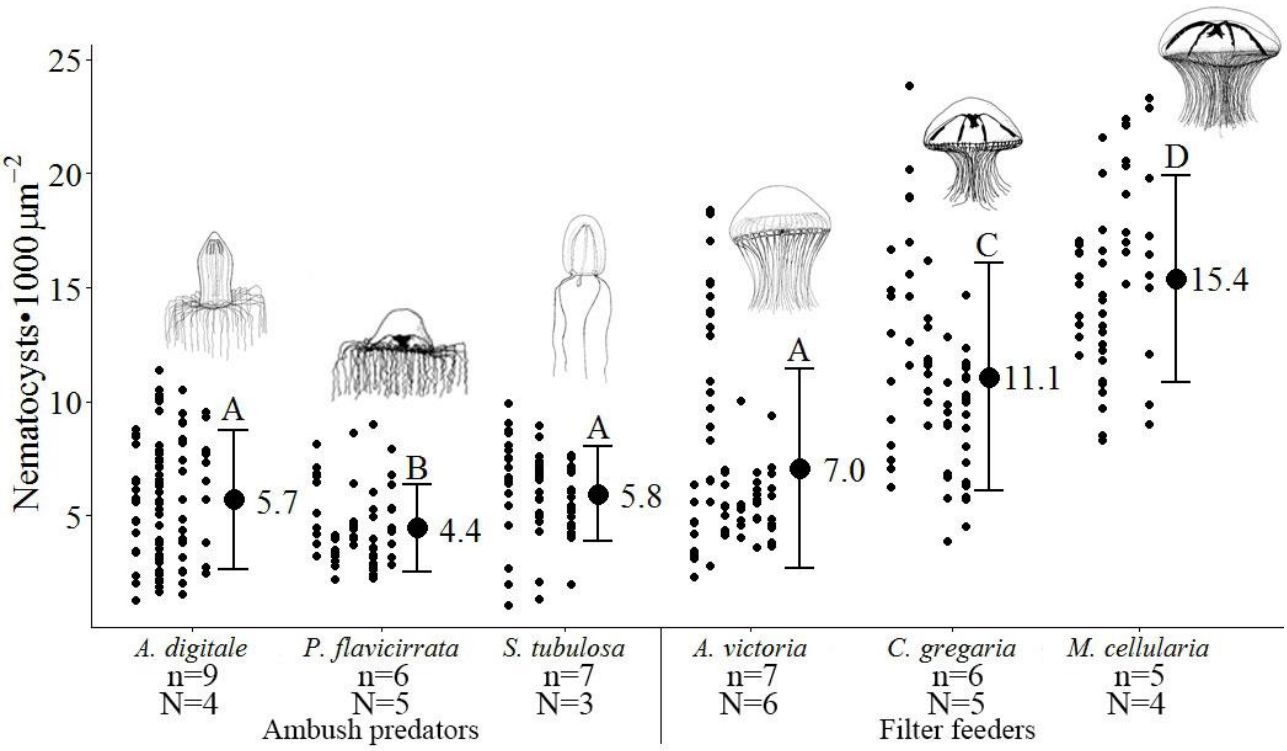


Figure 3. Nematocyst densities for the six species analyzed. Each small circle represents a single density measurement from one section of the tentacle and these are grouped in vertical lines for each individual. N is the number of hydromedusae per species and n is the total number of tentacles analyzed for all individuals of that species. Big circles represent mean nematocyst density for each species, error bars represent standard deviation. Different letters above error bars represent significant differences across rank means (Bonferroni-Dunn test, Appendix C).

Nematocyst distribution along the tentacles

The distributions of nematocysts on the tentacles are different in ambush-predators, which might have the nematocyst arranged in clusters like *P. flavicirrata* and *S. tubulosa* (Figure 4B,C), compared to the filter-feeding medusae, that have these cells dispersed uniformly along the tentacles (Figure 4D-F). Figure 5 shows the nematocyst density along the tentacle length, which tends increases in a distal direction along the

tentacles of *A. digitale*, *P. flavichirrata* and *S. tubulosa*. *Aequorea victoria* presents a similar nematocyst density throughout the tentacle length (R^2=0.06, p=0.236), but the filter feeders *C. gregaria* and *M. cellularia* present higher nematocyst densities in the first half of the tentacle length (Figure 5E, F).

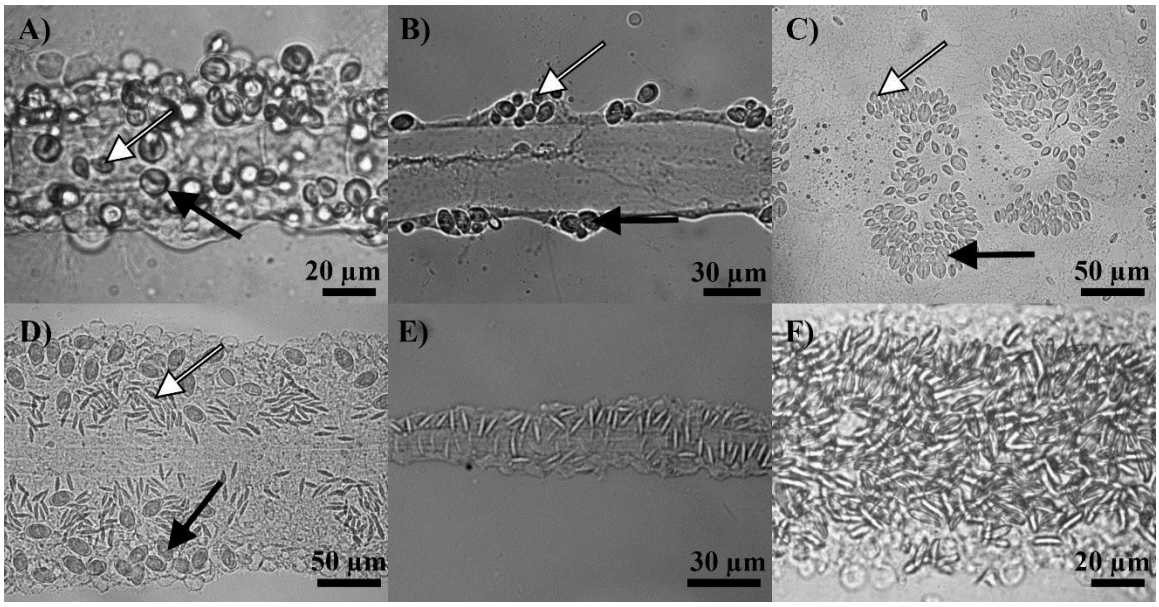


Figure 4. Nematocysts in the tentacles of ambush-feeding (A-C) and filter-feeding (D-F) hydromedusae. A) *A. digitale:* stenoteles (black arrow) and microbasic euryteles (white arrow). B) *P. flavicirrata,* desmonemes (black arrow) and macrobasic mastigophores (white arrow). C) *Sarsia tubulosa:* stenoteles (black arrow) and desmonemes (white arrow). D) *Aequorea victoria:* isorhizas (black arrow) and microbasic mastigophores (white arrow). E) *C. gregaria* and F) *M cellularia* microbasic mastigophores only.

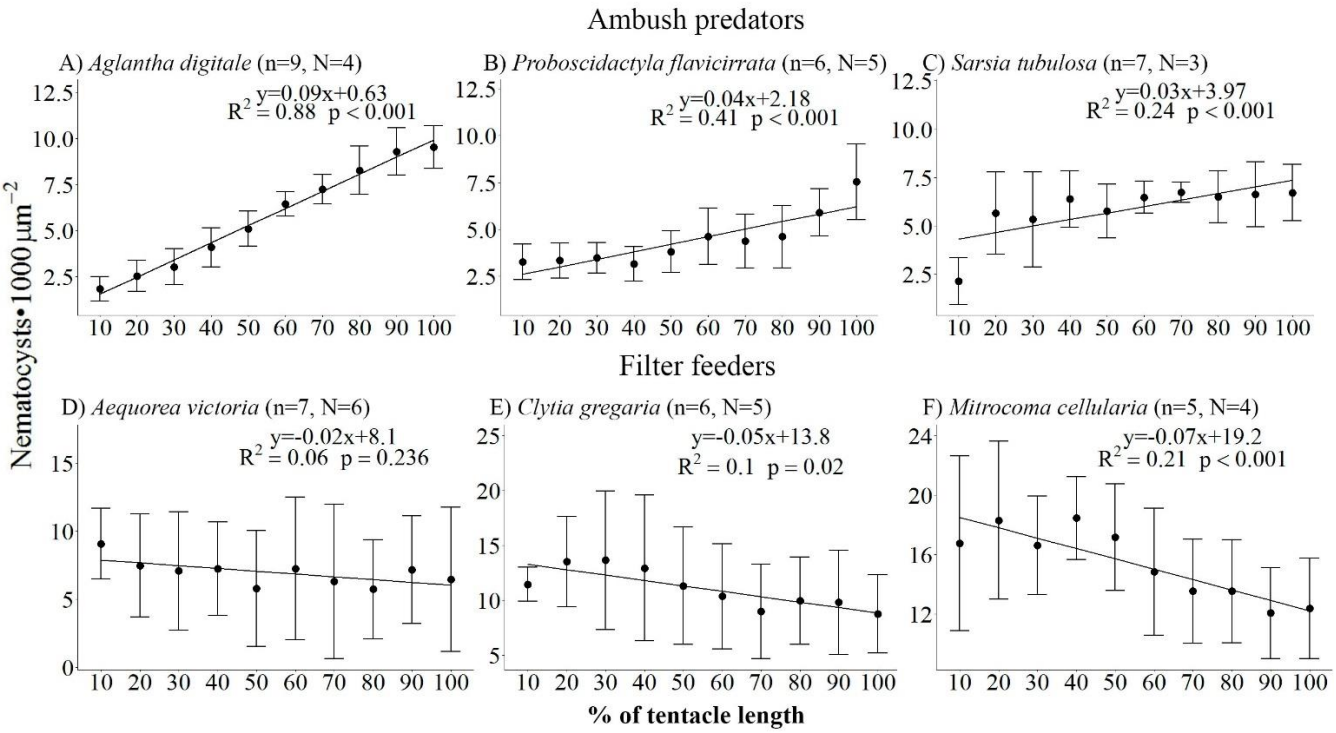


Figure 5. Nematocyst densities through the percentage of tentacle length, where 0% is the tentacle base and 100% is the tentacle tip. Error bars represent standard deviation. n= number of tentacles analyzed, N= number of individuals analyzed. General linear regressions with equation, R^2 values and p-values are shown on each plot,

CHAPTER IV

DISCUSSION

We determined that ambush predator medusae capture more prey further from the swimming bell compared to filter-feeding medusae (Figure 2). In addition, our quantitative descriptions of nematocyst densities within the tentacles show an increase of nematocysts toward the tentacle tips of ambush-feeding medusae (Figure 5 A-C). In filter feeders however, nematocyst distribution throughout the tentacle length is either constant or shows maximum densities closer to the bell margin (Figure 5 D-F). Overall, both capture locations and nematocyst distribution and density are related to the different feeding modes of hydromedusae.

Comparative prey capture locations

Although the prey encounter region in hydromedusae is determined by their morphology (Madin, 1988), capture within that volume is affected by each species behavior (Madin, 1988; Ford et al., 1997; Colin et al., 2005). Thus, the interaction between morphological and behavioral traits involved in feeding determine prey capture locations. For instance, oblate medusa with disc-shaped umbrellas are considered "filter feeders"; with each bell contraction and relaxation they create a starting and stopping vortex respectively, that move fluid through the tentacles (Colin and Costello, 2002; Dabiri et al., 2006; Katija et al., 2011). The starting vortex directs fluid away from the medusa body (Katija et al., 2011), and produces captures further away from the medusa body compared to the stopping vortex, which directs fluid inside the subumbrellar cavity (Katija et al., 2011) and results in captures close to the bell margin (Ford et al., 1997).

Overall, filter-feeding behavior clusters capture locations in specific regions of the feeding structures, as in *M. cellularia,* where most captures happened at less than 4 mm from the bell margin (Figure 2D).

As mentioned above, prey capture locations in filter feeders are determined by the phase of the swimming cycle in which prey is encountered (Ford et al., 1997). We found, however, that prey capture locations in *C. gregaria* happen further from the bell margin compared to *M. cellularia*, (Figures2C and 2D, respectively). Prey that are captured far from the bell margin in the scyphozoan *Chrysaora quinquecirrha* are entrained by a pulsed but continuous flow which makes prey capture location unpredictable (Ford et al., 1997). Although *C. gregaria* is considered a filter-feeder and eats similar prey as other oblate medusae (Costello & Colin, 2002), bell contraction and vortex formation happens faster compared to other filter-feeders (Colin and Costello, 2002), which might produce a steadier flow further from the bell margin and make captures happen at random locations.

Captures by the ambush-feeding medusae also occurred randomly at several distances from the bell margin, including even the tentacle tips (Figure 1, Figure 2A-B). Ambush-predator medusae feed by remaining stationary in the water column with their tentacles extended (Colin et al., 2003) and capture occurs when prey collide with the tentacles (Gerritsen and Strickler, 1977; Greene, 1985; Costello, 1992). This category, however, does not consider some specialized feeding mechanics of ambush-feeding medusae, which might have an important effect on determining capture locations. At least two species of rhopalonematid hydromedusae, including *A. digitale*, move their tentacle tips and simultaneously create a small feeding current by ciliary action, (Mackie et al., 1989; Colin et al., 2005). In *Aglaura hemistoma*, this behavior has been directly related to

the species ability to feed on variable prey types, since the flow manages to entrain small, non-motile prey, but encounters with large crustacean prey happened when these motile prey items collided with the tentacles (Colin et al., 2005). It is likely then that the interaction between prey and predator behavior has a considerable effect in determining capture locations.

Spatial nematocyst distribution in the tentacles and prey capture

Tentacle traits such as high nematocysts densities at capture locations in medusae could increase capture efficiency. In fact, several studies have noticed increased nematocyst densities in the regions of the medusan body where prey are captured. For instance, in *Cyanea capillata* the relative importance of different anatomical structures used in prey capture can change during the ontogeny due to mechanical constraints, and nematocyst density is higher where prey captures are more frequent (Higgins et al., 2008). One *Obelia* sp. presents nematocyst clusters at the tentacle tips: due to its small size, feeding occurs at small Reynolds numbers, and bell contraction decreases the boundary layer at the tentacle tips which allows prey capture in that region (Sutherland et al., in review). Cruising medusae such as *Solmissus incisa* place their tentacles to the front of the animal, and this "tentacle first" swimming behavior maximizes stealthy prey capture (Raskoff, 2002). It has been noted that all the nematocysts are located only on the upper side of *S. incisa* tentacles, which was interpreted as an indication of where the prey was captured (Mills and Goy, 1988).

We found that both capture locations and nematocyst distribution along the tentacles (measured as nematocyst density per area) are different between feeding modes of hydromedusae (Figures 2 and 5). The ambush-feeders *A. digitale*, *P. flavicirrata* and *S.*

tubulosa had their highest nematocyst densities at the tentacle tips (Figure 5A-C), and at least in two of those species, we found that prey are captured along the tentacle length including the tips (Figure 2 A-C). In *C. gregaria* and *M. cellularia*, the differences in nematocyst density were not as evident, however there were slightly more nematocysts in the first half of the tentacles than in the second half (Figure 5E, F), which corresponds to the regions where most *Artemia* nauplii are captured by these species (Figure 2C-D). *Aequorea victoria* did not present any significant changes of nematocyst density along the tentacle length (Figure 5D). The differences in nematocyst distribution and density described here for these species could have a significant effect on their transfer efficiencies of variable prey types, since adherence force to the capture surface of a predator is determined, in part, to the number of nematocyst fired in each encounter (Thorington and Hessinger, 1996).

Differential nematocyst densities and prey selectivity

Co-ocurring hydromedusae species such as the ones analyzed in this study show distinct prey selectivity patterns, which overlap according to their feeding mode (Colin and Costello, 2002). Prey selectivity in hydromedusae is due to variable capture and handling efficiencies of prey types (Costello and Colin, 2002; Hansson and Kiørboe, 2006; Regula et al., 2009; Katija et al., 2011). These efficiencies have been related to the prey retention capabilities of the tentacles (Regula et al., 2009), which, as mentioned above, might be affected by the number of nematocyst discharged in each prey capture event. For instance, adherence force between a prey item and the tentacles of the sea anemone *Apistasia pallida* increases with the number of mastigophores fired (Thorington

and Hessinger, 1996). However, tentacle traits that maximize prey capture can be dependent on the size of prey selected (Regula et al., 2009).

One such tentacle trait that can be related to selectivity according to prey size is nematocyst density in the tentacles of hydromedusae. For instance, siphonophores that feed on large prey tend to have fewer nematocyst batteries per tentacle (Purcell, 1984). We found that ambush predators, which feed on relatively large sized prey present low nematocyst densities compared to the filter feeders that eat small prey (Table 1, Figure 3). Both ambush-feeding *A. digitale* and *S. tubulosa* ingest copepodites and adult copepods (Purcell and Mills, 1988; Colin and Costello, 2002) and present similar nematocyst densities (Dunn´s z=-0.62, p=1.000, Figure 3). *Proboscidactyla flavicirrata*, which eats mostly veliger larvae (Mills, pers. comm.; Colin and Costello, 2002), shows a slightly lower nematocyst density (Figure 3) than the other ambush predators. The filter feeders *C. gregaria* and *M. cellularia* presented the highest nematocyst densities of all the species analyzed (Table 3). Both of these species prefer smaller prey items such as invertebrate eggs, which together with appendicularians and small medusae, are ingested by *A. victoria* (Purcell and Mills, 1988; Colin and Costello, 2002), this species also had high nematocyst densities in at least one individual, but overall, its densities were similar to the ambush predators (Figure 3).

Nematocyst identity and interaction with prey surfaces

Although it is widely known that the cnidome (i.e. the type of cnidae that a cnidarian species has) changes within hydrozoan species (Purcell, 1984; Purcell and Mills, 1988; Östman, 2000; Kass-Simon and Scappaticci, 2002; Costello et al., 2008) we found when a species has two or more types of nematocysts, the ratios of each type can

be different within a species (Table 1). Nematocyst such as desmonemes usually adhere to the surface of hard-bodied prey, whereas isorhizas and mastigophores penetrate soft-bodied prey (Purcell and Mills, 1988). Purcell and Mills (1988) noted that medusae that feed on hard bodied prey usually had two types of nematocyst, however *A, digitale* and *P flavicirrata* have a ~1:1 ratio of nematocyst densities, while *S. tubulosa* has five times more desmonemes than stenoteles, and *A. victoria* has 6 times more microbasic mastigophores than isorhizas.

Although our study does not address the interaction between fired nematocysts and different types of prey surfaces, this factor is relevant for understanding prey selectivity. For instance, prey-specific mechanical and chemical cues are sometimes needed to trigger nematocyst discharge (Thorington and Hessinger, 1988; Watson and Hessinger, 1991).In addition to this, the adherence force between tentacle and prey can change according to the number and the kind of discharging cnidae (Thorington and Hessinger, 1996). Hardness of the prey body is also relevant to determine the adherence force (Thorington and Hessinger, 1996) and adherence mechanics of nematocysts, since it has been noticed that stenoteles and mastigophores can either adhere to or penetrate different types of prey (Purcell and Mills, 1988). Differential densities of each nematocyst type could then produce variable adherence force between the prey and the tentacle surface, which would either prevent or facilitate attachment to the tentacles.

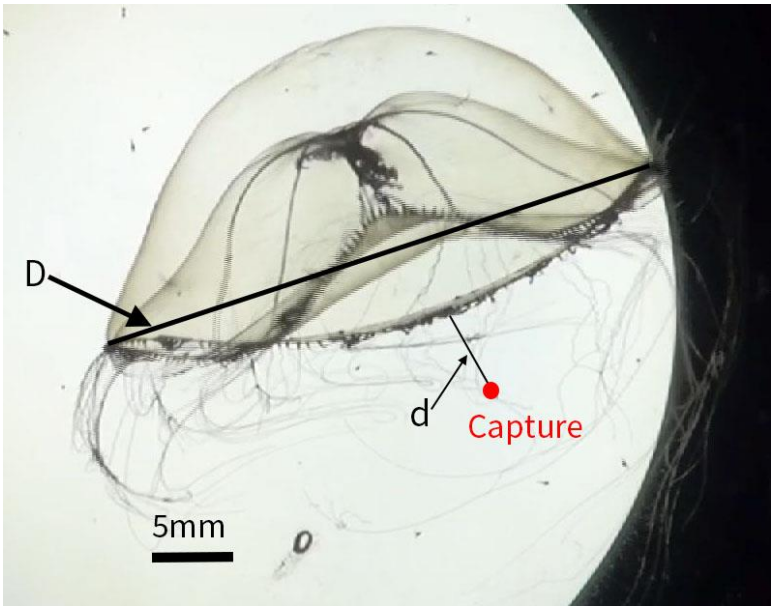
Behavioral and morphological traits relate to trophic patterns in hydromedusae

The relationships among functional morphology and dietary niches of medusae are key for understanding the ordering principles that determine trophic patterns in

hydromedusae (Costello and Colin, 2002). Here we have demonstrated that locations of prey capture and nematocyst distribution in the tentacles change according to guild associations of hydromedusae. Differences among these traits, such as nematocyst density, might also be related to the distinct prey selectivity patterns within species with similar feeding modes. Thus we hypothesize that differential capture efficiencies within prey types might be related, amongst other factors, to differences in nematocyst densities through the surfaces in which the predator encounters prey.

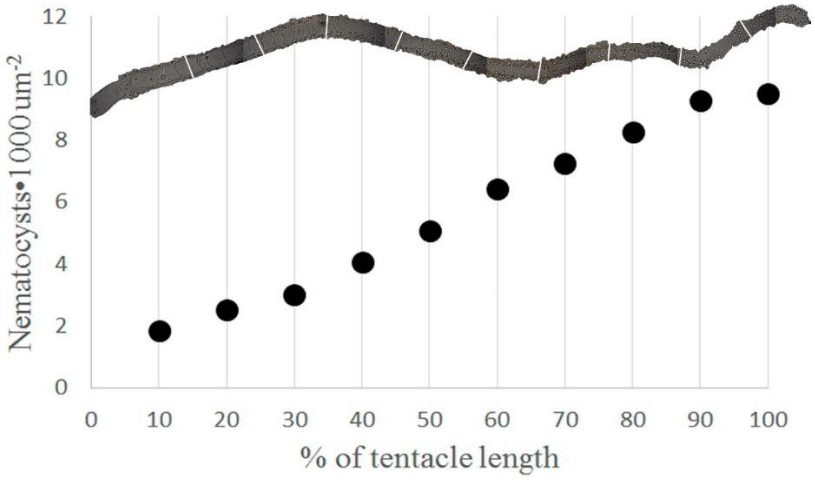
APPENDIX A

Measurements from the feeding behavior videos. Distance of capture from bell margin(d) and bell diameter (D).



APPENDIX B

Method for obtaining nematocyst densities at different regions of an *Aglantha digitale* tentacle. It is divided into 10 sections, in which the number of nematocyst in a minimum area of 5000 μm^2 were counted to obtain # cells • 1000 μm^2



APPENDIX C

Bonferroni-Dunn test results for comparisons between species of hydromedusae

Variable	Species pair	Dunn´s *z*	probability
Relative capture distance	Cly-Agl	5.49	**<0.0001**
	Mit-Agl	7.61	**<0.0001**
	Mit-Cly	2.62	**0.0257**
	Pro-Agl	0.50	1.0000
	Pro-Cly	-4.88	**<0.0001**
	Pro-Mit	-7.00	**<0.0001**
Nematocyst density	Agl-Aeq	1.10	1.0000
	Cly-Aeq	-5.36	**<0.0001**
	Cly-Agl	-6.71	**<0.0001**
	Mit-Aeq	-8.09	**<0.0001**
	Mit-Agl	-9.48	**<0.0001**
	Mit-Cly	-2.89	**0.0287**
	Pro-Aeq	3.60	**0.0024**
	Pro-Agl	2.75	**0.0444**
	Pro-Cly	8.64	**<0.0001**
	Pro-Mit	11.13	**<0.0001**
	Sar-Aeq	0.45	1.0000
	Sar-Agl	-0.62	1.0000
	Sar-Cly	5.80	**<0.0001**
	Sar-Mit	8.50	**<0.0001**
	Sar-Pro	-3.17	**0.0114**

Aeq: *Aequorea*, Agl: *Aglantha*, Cly: *Clytia*, Mit: *Mitrocoma*, Pro: *Proboscidactyla*, Sar: *Sarsia*

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