



Effects of capture surface morphology on feeding success of scyphomedusae: a comparative study

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ABSTRACT: Predation by feeding-current foraging medusae can have detrimental effects on prey populations. Understanding the mechanics that control prey selection and ingestion rates with different types of prey enables us to better predict the predatory impact of these medusae. We quantified the outcomes of each post-entrainment stage of the feeding process in multiple scyphozoan jellyfish species to understand how post-entrainment feeding events influence feeding patterns. Using 3-dimensional video, we observed and quantified the fate of both passive and actively swimming prey that were entrained in the feeding current of 5 different scyphomedusan species belonging to the orders Semaestomeae and Rhizostomeae. Less than 65 % of entrained prey contacted the capture surfaces (termed contact efficiency) of the semaestome medusae, while the rhizostome medusae came into contact with less than 35 % of the prey entrained in the feeding current. However, when contacted, prey were very likely to be ingested (>90 %) by all species examined. These results suggest that prey capture by oblate medusae appears to be largely limited by the probability that prey entrained in the feeding current will contact a capture surface. As a passive process, this contact stage of the feeding process is directly affected by the morphology of the contact surfaces. The importance of the contact stage of the feeding process suggests that differences in prey selection patterns observed among oblate medusan taxa are likely dominated by the morphology of contact surfaces as opposed to traits which influence the other stages of the feeding process, i.e. bell shape and nematocysts.

KEY WORDS: Predator–prey interactions · Prey selection · Mechanistic ecology · Post-encounter

INTRODUCTION

Understanding scyphozoan jellyfish predation patterns and behaviors has gained importance due to increases in population sizes of jellyfish over recent years (Purcell et al. 2007). Some scyphozoan populations have expanded their ecosystem boundaries in response to ecosystem disturbances, such as overfishing (Utne-Palm et al. 2010), and are forming more frequent and massive blooms. Consequently, some of these scyphomedusan populations may be able to out-compete zooplanktivorous fish (Richardson et al. 2009). Our ability to understand and pre-

dict impacts of jellyfish populations on local marine communities largely depends upon our understanding of the mechanics which govern their predatory impact.

Some scyphomedusae, e.g. *Periphylla periphylla*, *Catostylus mosaicus*, and *Nemopilema nomurai* (Dong et al. 2010, Uye 2014), have been shown to have significant negative impacts on prey standing stocks and biodiversity (Behrends & Schneider 1995, Graham et al. 2014). Zooplankton most influenced by these significant scyphozoan blooms include hydromedusae (Matsakis & Conover 1991), decapod larvae (Sullivan et al. 1994), ciliates (Stoecker et al. 1987),

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and fish eggs/larvae (Titelman & Hansson 2006). In cases where scyphomedusan predation is important, their predatory success has been attributed to factors including their high population densities, their inflated gelatinous bodies, and feeding currents which result in high encounter rates (Acuña et al. 2011, Pitt et al. 2013, Gemmell et al. 2015). Most studies aiming to understand medusan feeding have focused primarily on the pre-encounter (for scyphomedusae, an encounter is initiated when prey are entrained in the feeding current) capture process, e.g. feeding-current mechanics (Dabiri et al. 2005), or the end result of the feeding process, e.g. clearance rates (Matsakis & Conover 1991, Ford et al. 1997, Brodeur et al. 2002, Titelman & Hansson 2006) and prey capture maps (Ford et al. 1997, Nagata et al. 2016). From these studies we know that the feeding currents of scyphomedusae provide medusae with high encounter rates with surrounding prey but that clearance rates are considerably lower than encounter rates. With the exception of Suchman & Sullivan (1998, 2000), few studies have quantified post-encounter/entrainment capture processes associated with the feeding surfaces of medusae. This lack of information is most likely the result of the inherent difficulties associated with quantifying such capture processes. One consequence is the potential to overestimate prey capture rates, especially for larger adult stages.

Scyphomedusae include 2 major orders, Semaestomeae and Rhizostomeae. Both use similar feeding currents to entrain prey but differ considerably in their feeding patterns and prey selection. Semaestomes, such as *Aurelia aurita*, possess 4 distinct oral arms with tentacles around the bell margin. Semaestomes have diverse diets consisting primarily of mesozooplankton and macrozooplankton (Båmstedt et al. 1994, Behrends & Schneider 1995, Brodeur et al. 1999). In contrast, Rhizostomeae, such as *Phyllorhiza punctata*, have 8 oral arms fused to make up an oral disk, no tentacles, are limited mainly to tropical seas, and feed primarily on microplankton (Dawson et al. 2005, Peach & Pitt 2005, Pierce 2005). These differences in feeding patterns presumably derive from the different capture surface morphology between semaestomes and rhizostomes, which interact differently with feeding currents and contribute to different prey encounter and capture patterns.

By comparing morphologies and post-encounter feeding processes, our intent was to evaluate the importance of post-encounter events in determining prey selection and how medusan morphology contributes to different feeding patterns. Several scyphomedusae were examined to represent both semaestomes (*Aurelia aurita* Linnaeus, 1758, *Chrysaora plocamia* Lesson, 1830) and rhizostomes (*Cassiopea xamachana* Bigelow, 1892, *Catostylus tagi* Haeckel, 1869, *Phyllorhiza punctata* Lendenfeld, 1884). Using 3-dimensional (3D) video observations we quantified the outcome of each stage of the feeding process of the medusae fed both *Acartia hudsonica* and *Artemia* sp. These data were used to establish the role of each stage of the feeding process in determining predatory patterns.

MATERIALS AND METHODS

Medusae collection and care

Medusae including *Aurelia aurita* (N = 12), *Chrysaora plocamia* (N = 7), *Cassiopea xamachana* (N = 7), *Catostylus tagi* (N = 7), and *Phyllorhiza punctata* (N = 7) were supplied by the New England Aquarium, Boston, Massachusetts, USA (Table 1). All medusae were housed in 37 l closed system kreisel aquariums with 12 h light:12 h dark cycles under varying temperatures: *A. aurita* at 18°C, *C. plocamia* at 10°C, *C. xamachana* at 25 to 28°C, and *C. tagi* and *P. punctata* at 25°C. Experiments were conducted either at Roger Williams University, Rhode Island, or the Marine and Biological Laboratory, Massachusetts. All medusae were starved for 1 to 2 d (depending on species) before feeding trials.

Table 1. Summary of the scyphomedusae used in this experiment including; (D) averaged bell diameter, (F) average medusae fineness, (T) average tentacle length, (O) average oral arm length. Values are \pm SD

Species	Body dimensions (cm)			
	D	F	T	O
<i>Aurelia aurita</i> (N = 12)	2.03 \pm 0.40	1.33 \pm 0.10	0.51 \pm 0.09	2.52 \pm 0.20
<i>Chrysaora plocamia</i> (N = 7)	3.56 \pm 0.75	3.49 \pm 0.20	8.12 \pm 0.10	7.11 \pm 0.41
<i>Cassiopea xamachana</i> (N = 7)	2.54 \pm 1.20	3.33 \pm 0.15		0.50 \pm 0.10
<i>Catostylus tagi</i> (N = 7)	1.27 \pm 0.30	1.54 \pm 0.10		3.04 \pm 0.12
<i>Phyllorhiza punctata</i> (N = 7)	1.77 \pm 0.20	1.25 \pm 0.10		2.03 \pm 0.53

Video recording

A 3D video setup was used to accurately identify when prey were entrained in the feeding current and the location around the medusae where entrainment occurred. To get a 3D view of the interaction, medusae were placed in a right-triangle shaped filming vessel ($21 \times 15 \times 15$ cm) with the hypotenuse side constructed out of a mirror (Fig. 1; Colin et al. 2015). A cold, collimated LED light source was placed perpendicular to the camera. The light entering the filming vessel created a silhouette of the medusa and its reflection. Both of these were recorded simultaneously using a video camera (SONY HVR-77U Digital HD Video Camera Recorder, 30 frames per second) equipped with a standard lens (50 mm Nikon). A ruler was placed in the field of view of each recording to determine the spatial scale.

Individual medusae were tethered in the center of the filming vessel with a glass micro-sampling pipet (25 μ m), attached to the uppermost part of the ex-umbrella of the medusa using aquarium-safe super glue (Corrales-Ugalde et al. 2017). For each individual, video recording commenced after 5 to 20 min when 'normal' swimming behavior was observed. Live prey of either cultured *Artemia* sp. nauplii (0.6 mm, 1 to 2 d) or wild *Acartia hudsonica* (male/female ranging from 0.9 to 1.1 mm) were introduced into the filming vessel in high enough concentration to initiate medusan feeding ($\sim 0.5 \text{ ml}^{-1}$). Each feeding medusa was recorded individually for 30 to 45 min. Recordings of medusae were stored and observed on

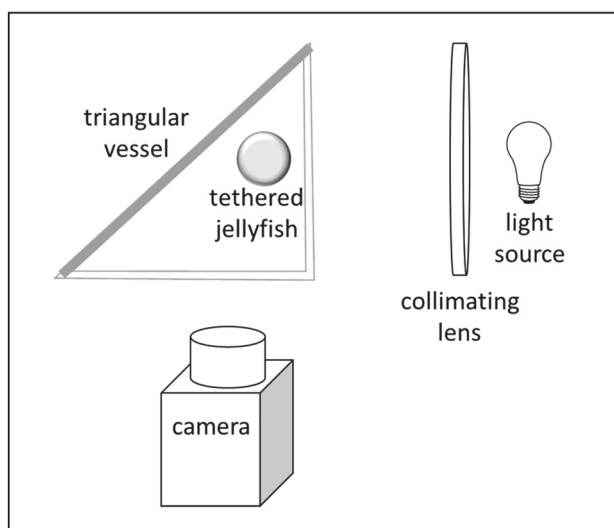


Fig. 1. Schematic of 3-dimensional video set-up. The tethered medusae were placed into the right-triangle shaped filming vessel ($21 \times 15 \times 15$ cm) with the hypotenuse side constructed out of a mirror

Vegas Pro (version 13.0, 64 bit), where entire video sequences were examined and predator–prey interactions were quantified.

Data analysis

To quantify prey capture and encounters with the feeding structures, we recorded the outcome of each stage of the feeding process (Fig. 2). Since medusae are not visual predators and they use a feeding current to encounter their prey, we define an encounter as occurring when a prey item is clearly entrained (being transported) by the feeding current of the medusae. Consequently, we will use the term 'entrainment' throughout the rest of the manuscript to denote an encounter. The definition for feeding efficiency has been variously defined by previous authors, so for this study we defined different feeding efficiencies based on 3 sequential steps (Fig. 2): contact (Eq. 1), capture (Eq. 2), and retention (Eq. 3). For this experiment we defined contact efficiency as the proportion of entrained prey particles that made contact with the feeding structures of the medusae. Capture efficiency was the proportion of contacted prey that were captured, i.e. stuck to the capture surface. Retention efficiency was the proportion of entrained prey that were ultimately ingested. We did not track prey into the guts and assumed if they remained captured for >30 s that they were eventually ingested.

$$\text{Contact efficiency} = \frac{\text{no. prey contacted}}{\text{no. prey entrained}} \times 100 \quad (1)$$

$$\text{Capture efficiency} = \frac{\text{no. prey captured}}{\text{no. prey contacted}} \times 100 \quad (2)$$

$$\text{Retention efficiency} = \frac{\text{no. prey captured}}{\text{no. prey entrained}} \times 100 \quad (3)$$

Capture maps were generated from the 3D videos. During video analysis, individual prey were tracked in relation to the medusae and the medusa's reflection to observe points of contact. Points of contact

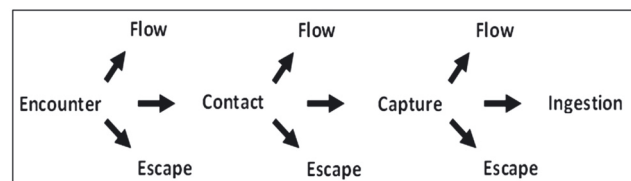


Fig. 2. Post-entrainment stages of the predator–prey interactions that occur during the feeding process. At each stage, prey may avoid capture by actively escaping or being passively transported away by flow

were recorded on line maps generated by averaging the size ratios of the medusae using dimensions recorded in ImageJ (64 bit, Java 1.8.0_66).

Nematocyst distribution and density

Nematocysts were identified and recorded using a Nikon Eclipse TE2000-U inverted microscope equipped with a Fastcam mini UX50/100 camera. Nematocyst patterns were determined by observing the distribution and density at equal distances along the length of the feeding appendages. Nematocysts were identified based on their volume and extracellular morphology following procedures and methods described by Colin & Costello (2007) and Corrales-Ugalde et al. (2017).

Statistical analysis

Statistical analyses were performed using Sigma Plot® statistical software. Analysis of variance tests were performed to compare post-entrainment events among medusan species and prey type and nematocyst distributions. Between-group comparisons were made between the 5 medusan species and within-group comparisons were made for the 2 prey types. Holm-Sidak tests were used to make post-hoc comparisons to compare efficiencies between the semaeostome and rhizostome species (significance level, $\alpha = 0.05$). All of the data conformed to the assumptions of homoscedasticity (Browne-Forsythe test) and normality (Shapiro-Wilk test).

RESULTS

Feeding efficiencies of scyphomedusae

Feeding efficiencies were quantified to determine the proficiency of morphologically distinct medusae in contacting, capturing and retaining prey that were entrained in their feeding current. Both species types (2-way ANOVA, $F_{4,63} = 65.0$, $p < 0.001$) and prey type (2-way ANOVA, $F_{2,63} = 34.9$, $p < 0.001$) affected contact efficiencies with no interaction ($F_{8,63} = 2.0$, $p > 0.05$; Fig. 3A). Post-hoc comparisons between each species type showed that all the semaeostome species contacted a significantly greater proportion of the prey entrained in their feeding current (contact efficiency) than did rhizostome species (Fig. 3A; Holm-Sidak post-hoc test, $p < 0.001$). Specifically, mean se-

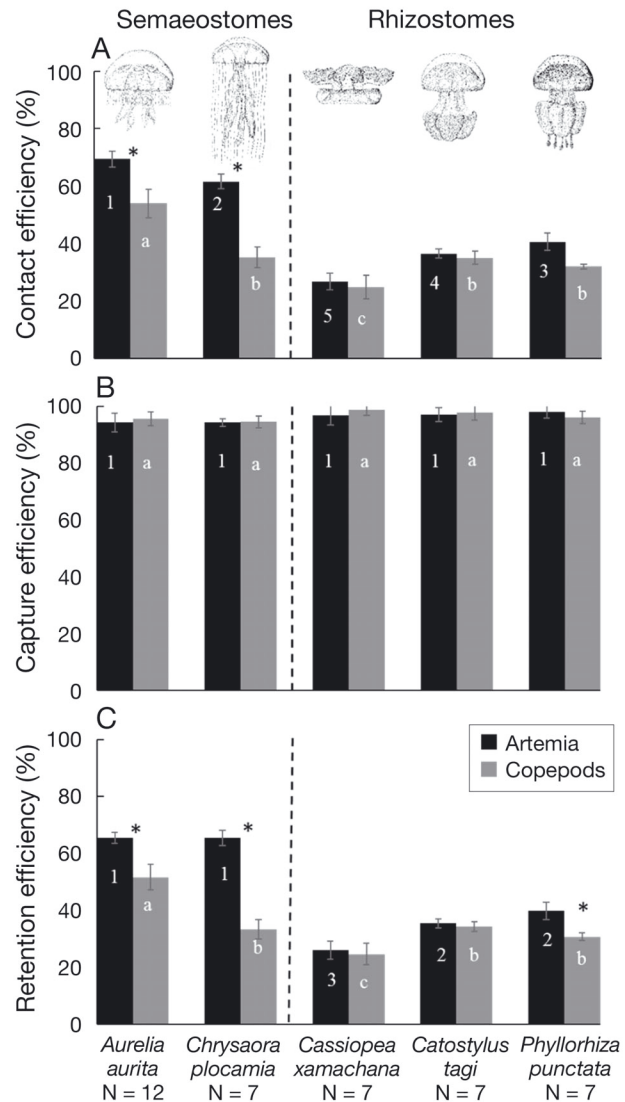


Fig. 3. Percent success of each stage of the post-entrainment feeding stages. (A) Contact, (B) capture, and (C) retention efficiencies for 5 species of Scyphozoa (*Aurelia aurita*, *Chrysaora plocamia*, *Cassiopea xamachana*, *Catostylus tagi*, and *Phyllorhiza punctata*) provided different types of prey, *Artemia* sp. or the copepod *Acartia hudsonica*. Asterisks indicate significant differences in efficiencies between prey types. Different numbers and letters indicate significant differences among medusa species for *Artemia* and copepod prey, respectively. Significance was based on Holm-Sidak post-hoc comparisons ($p < 0.05$). Error bars are SD

maeostome contact efficiencies were 65% (*Artemia* prey) and 45% (copepod prey) compared to only 35% (*Artemia* prey) and 32% (copepod prey) for the rhizostomes. Mobile prey such as *Acartia hudsonica* could actively avoid contact using evasive jumps and, as a result, entrained copepods contacted semaeostome medusae less than the non-evasive prey, *Artemia* sp. (Fig. 3A; Holm-Sidak post-hoc test, $p < 0.001$).

Once contacted, neither prey type was successful at escaping and both were caught with high capture efficiencies (>90%; Fig. 3B). As a result, most of the prey contacted were ultimately ingested, and this is reflected by retention efficiencies (which indicate the overall success of the encounter process) that were only slightly lower than contact efficiencies (Fig. 3C).

As mentioned, a lower proportion of entrained prey contacted the oral arms of rhizostome medusae and, consequently, contact efficiencies were lower for rhizostome than for semeanostome medusae (Fig. 3A). Prey that did contact the oral arms of the rhizostomes were typically captured, which resulted in high capture efficiencies (>95%) that were similar to those of the semeanostomes (Fig. 3B). Prey escapes after contact were mainly the result of the feeding current dislodging prey. However, prey would often be recaptured shortly after the initial dislodgement. Because fewer prey were retained relative to those entrained, rhizostome medusae were characterized by lower overall retention efficiencies than semeanostome me-

dusae (Fig. 3C). Specifically, the mean retention efficiencies among all the semeanostomes were 63% (*Artemia* prey) and 42% (copepod prey) compared to only 34% (*Artemia* prey) and 30% (copepod prey) for the rhizostomes. Of the tested rhizostomes, *Cassiopea xamachana* experienced the lowest contact and retention efficiency of all the medusan species. An overall comparison of contact, capture, and retention rates for both the semeanostome and the rhizostome medusae indicates that initial contact between the medusan capture surface and prey appears to be the rate-limiting step for prey selection and ingestion rates.

Capture maps

To compare the role of different capture surfaces in the encounter process, we constructed capture maps displaying the percentage of prey contacts over the length of the medusae (Fig. 4). Capture maps of

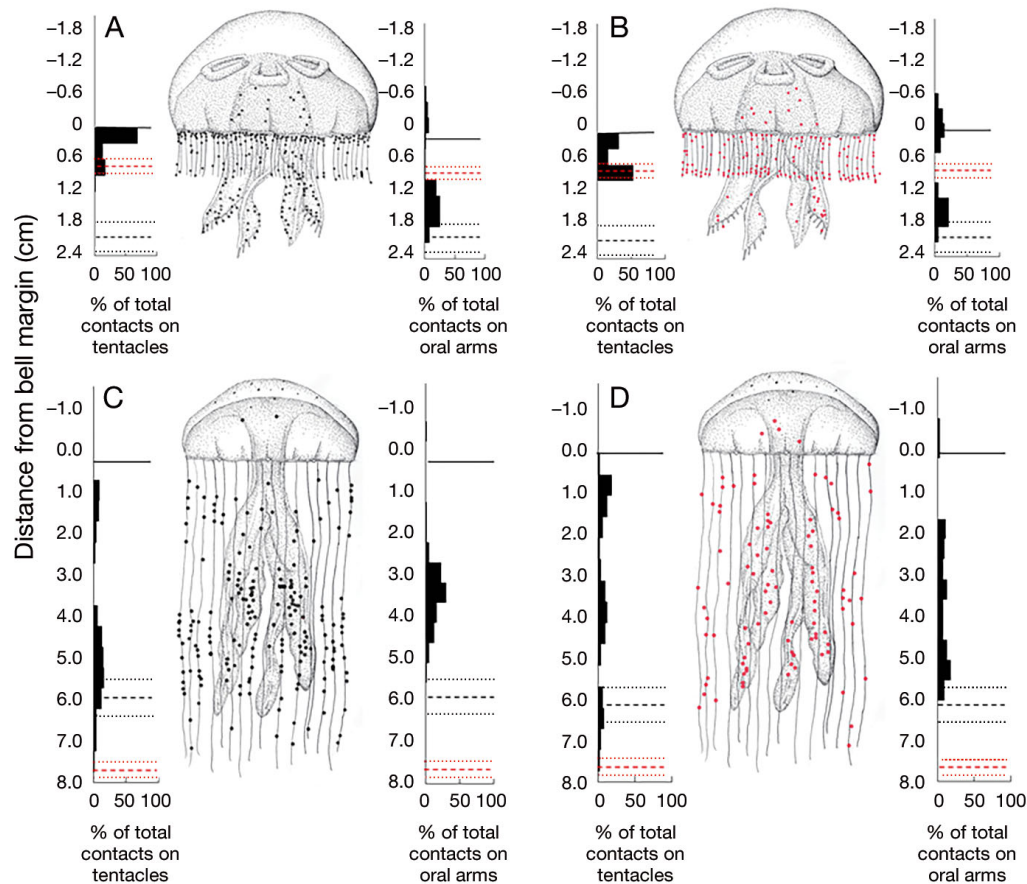


Fig. 4. Distribution of captures by the semeanostomes (A,B) *Aurelia aurita* (N = 12) and (C,D) *Chrysaora plocamia* (N = 7) when exposed to (A,C) *Artemia* sp. (black dots) and (B,D) the copepod *Acartia hudsonica* (red dots). Bold lines: bell margin; black dashed lines: average oral arm length; black dotted lines: size variation of the oral arms; red dashed lines: average tentacle length; red dotted lines: size variation of the tentacles

semaeostome medusae revealed that similar quantities of *Artemia* sp. were captured on both the tentacles (*Aurelia aurita* $n = 168$ captures, *Chrysaora plocamia* $n = 215$ captures) and the oral arms (*A. aurita* $n = 217$, *C. plocamia* $n = 223$), indicating no clear advantage of either capture surface. Likewise, *Acartia hudsonica* was captured similarly on either the tentacles (*A. aurita* $n = 202$, *C. plocamia* $n = 103$) or the oral arms (*A. aurita* $n = 222$, *C. plocamia* $n = 144$).

Capture maps revealed that *A. aurita* medusae caught the less responsive prey, *Artemia* sp., closer to the bell margin, while they caught faster-moving copepods further down the tentacles, closer to the tentacle tips (Fig. 4A,B). *C. plocamia* captured both

prey types in similar locations (Fig. 4C,D). Interestingly, captures for *C. plocamia* occurred in bands moving away from the bell margin where the prey clustered at specific distances. These clusters seemed to alternate between tentacles and oral arms (Fig. 4C,D). This could be the result of varying nematocyst distributions or patterns of how the wake transported prey to the surfaces.

Unlike the semaeostomes, the rhizostomes *Catostylus tagi* and *Phyllorhiza punctata* experienced horizontal variations in capture on the oral arms. *C. tagi* captured greater concentrations of prey on the edges of the external wings of the oral lobes where the feeding currents are most prevalent (Fig. 5A,B).

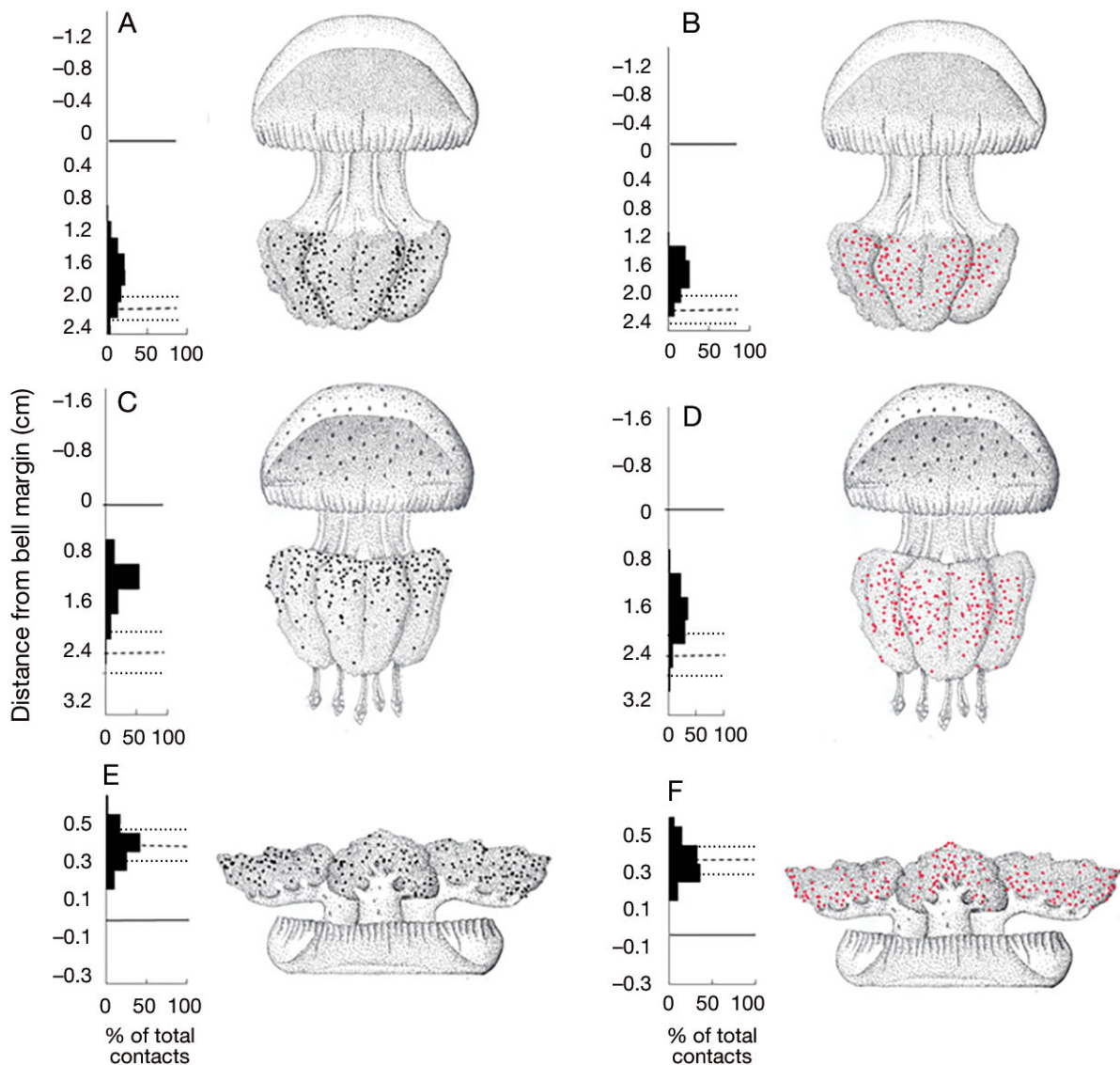


Fig. 5. Distribution of captures by the rhizostomes (A,B) *Catostylus tagi* ($N = 7$), (C,D) *Phyllorhiza punctata* ($N = 7$) and (E,F) *Cassiopea xamachana* ($N = 7$) fed with (A,C,E) *Artemia* sp. (black dots) and (B,D,F) the copepod *Acartia hudsonica* (red dots).

Bold lines: bell margin; black dashed lines: average oral arm length; black dotted lines: size variation of the oral arms

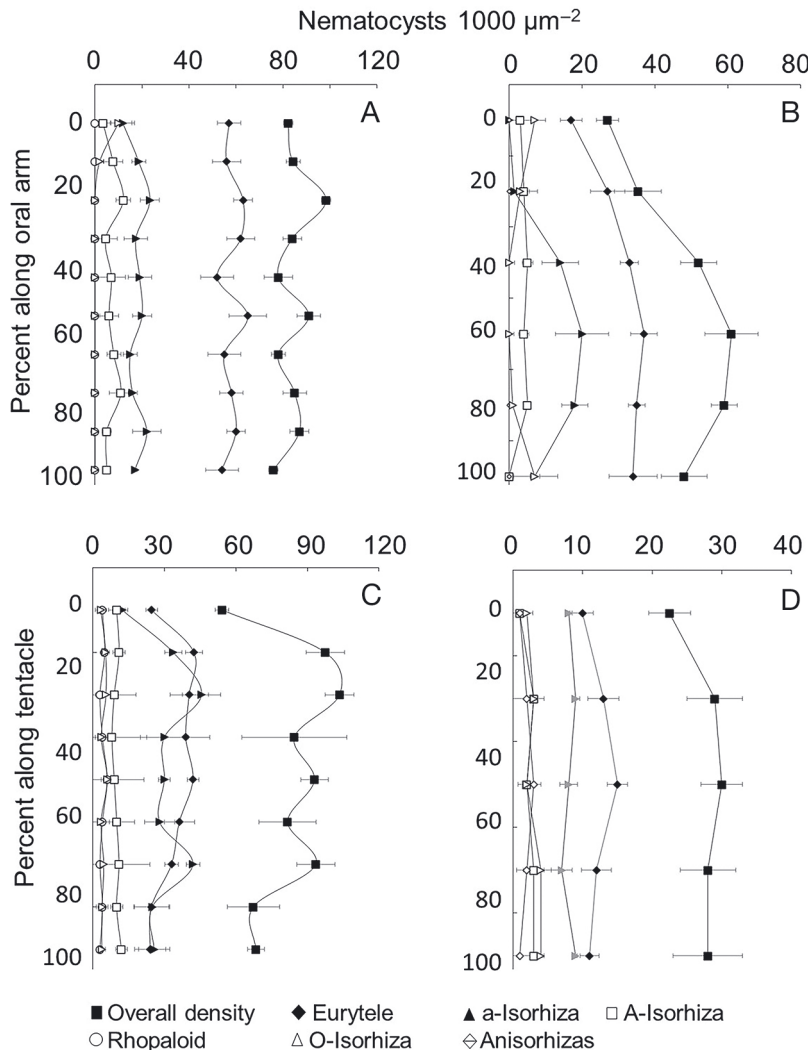


Fig. 6. The distribution and density of nematocysts on (A,B) the oral arms and (C,D) tentacles of the sennaeostomes (A,C) *Chrysaora plocamia* and (B,D) *Aurelia aurita* (N = 3). Error bars represent standard deviations

P. punctata captured prey closer to the bell margin on top of the outer wings of the oral arms (Fig. 5C,D). For both medusae, prey were evenly captured along the length of the oral arms with zonation only occurring along the width of the structures. Capture maps of *Cassiopea xamachana* revealed no clear pattern in the distribution of captures on the feeding appendages for either prey (Fig. 5E,F).

Nematocyst distribution and density

Nematocyst densities were measured for the sennaeostomes to determine whether nematocyst density patterns corresponded to prey capture patterns. The density of the nematocysts on the tentacles of *A.*

aurita (ANOVA, $F_{4,26} = 1.51$, $p = 0.23$) and *C. plocamia* (ANOVA, $F_{8,26} = 0.96$, $p > 0.4$) did not change with distance from the bell.

Nematocyst types distributed along the length of the feeding appendages did not vary greatly in *A. aurita*, with only a greater abundance of a-isorhiza near the tips of the oral arms (Fig. 6B). No pattern in the distribution of nematocysts could be seen in either the oral arms or tentacles of *C. plocamia* (Fig. 6A,C). Therefore, it is most likely that the patterns of capture locations for *C. plocamia* are the result of flow patterns rather than nematocyst distributions.

DISCUSSION

Understanding the mechanics of prey encounter and capture is fundamental to predicting the ecological role of predators because the feeding process determines which prey, and how many of them, are ingested. The feeding process can be broken down into multiple events where prey may avoid predation (either actively or passively) at each stage of the process (Fig. 2). For oblate feeding-current producing medusae, prey encounters are primarily initiated by prey entrainment within a feeding current followed by prey transport to medusan capture surfaces. Subsequent prey

capture depends upon contact of the entrained prey with capture surfaces and prey retention by nematocysts embedded within the capture surface. The entrainment-encounter process has been well studied and it is clear that oblate medusae process large fluid volumes, enabling high encounter and capture rates (Costello & Colin 1994, 1995, Dabiri et al. 2005, Peng & Dabiri 2008, Acuña et al. 2011, Katija et al. 2011, Santhanakrishnan et al. 2012). However, post-entrainment events are also important in determining prey selection (Suchman & Sullivan 2000), yet few studies have quantified the post-entrainment success rates of oblate medusae. Our current study demonstrates that scyphozoan medusae capture and retain $\leq 63\%$ prey transported past their capture surfaces. Captures appear to be most limited by the probability

of entrained prey coming into contact with trailing capture surfaces (i.e. contact efficiency), but if contacted, prey are very likely to be retained and ingested (capture efficiency >95%). This has important implications on the predatory impact, prey selection and evolution of feeding-current foraging medusae.

Determinates of prey selection

Previous research on prey selection by feeding-current foraging medusae has held that prey selection is largely determined by prey escape speeds relative to the velocity of the medusan feeding current (Costello & Colin 1994, 1995). Based on this notion, slow or non-swimming prey are more vulnerable to predation by oblate medusae because of their inability to escape from the feeding current (Costello & Colin 1994, 1995). Consequently, oblate medusae largely select vulnerable prey such as eggs, fish larvae, and other gelatinous zooplankton (Purcell & Grover 1990, Sullivan et al. 1994, Costello & Colin 2002, Purcell & Decker 2005). Consistent with this, our study showed that slow-swimming *Artemia* were more vulnerable to predation by the semaeostomes than fast-swimming copepods. However, there are important inconsistencies with the entrainment-dominated prey selection model. For example, fast-swimming adult copepods are often consumed by oblate medusae (Sullivan et al. 1994, Suchman & Sullivan 1998) and are, in fact, more vulnerable to predation than smaller, slower nauplii and copepodites (Purcell 1992, Sullivan et al. 1994, Suchman & Sullivan 1998, Hansson 2006). Small prey, such as juvenile copepod stages and bivalve veliger larvae, are readily entrained in the feeding current of medusae but generally pass through the tentacles and oral arms of the medusa without being contacted (Suchman & Sullivan 1998, 2000). The latter prey selection studies suggest that although the feeding current of oblate medusae is highly effective at entraining a large variety of prey (even fast-escaping copepods; Suchman & Sullivan 2000), post-entrainment events are perhaps more influential in determining prey selection (Suchman & Sullivan 1998, 2000). Furthermore, the current study shows that of the post-entrainment events, the contact stage is the greatest rate-limiting step. Therefore, of the different stages of the feeding process that influence prey selection, it appears that while entrainment and capture by nematocysts play a role in determining prey selection, they serve as less influential factors than the probability that prey will contact capture surfaces.

This is a revision to the conventional entrainment-dominated prey selection model (Costello & Colin 1994, 1995) and helps explain *in situ* prey selection patterns. A contact-dominated model means that prey selection depends primarily on the probability that a contact occurs between entrained prey and capture surfaces. For semaeostome medusae, which have a relatively low density of capture surfaces (i.e. tentacles and oral arms) compared to rhizostome medusae, larger prey are more likely to contact capture surfaces than small prey (Madin 1988). As a result, studies have found that large gelatinous zooplankton, larvaceans, and fish eggs are more abundant in the guts of *Chrysaora* spp., *Cyanea* spp., *Pelagia* spp., and *Phacellophora* spp. (Fancett 1988, Purcell & Sturdevant 2001, Suchman et al. 2008). But we still see large copepods in these medusan guts because if copepods are not able to escape entrainment, their larger size makes them vulnerable to capture and ingestion. *Aurelia* spp., which have more finely spaced tentacles lining the bell margin, have been shown to select mid-sized prey such as small copepods, while they do not readily capture the larger, fast copepods or small nauplii (Sullivan et al. 1994, Suchman & Sullivan 1998, Graham & Kroutil 2001, Purcell & Sturdevant 2001). This suggests that the largest copepods avoid entrainment while smaller copepods and nauplii do not (Graham & Kroutil 2001). However, of the prey entrained, the small copepods are more likely than nauplii to contact capture surfaces due to their larger size. Therefore, a contact-dominated prey selection model suggests that small changes to capture surface morphology can have large effects on prey selection.

Evolutionary consequences

The rate-limiting stage in the feeding process, the contact stage, is primarily determined by the size of the prey in relation to the capture surface morphology (Madin 1988). Interestingly, capture surface morphology is the least conserved trait among scyphomedusan taxa. In contrast, the traits that control entrainment and retention—bell shape and nematocysts, respectively—are highly conserved among scyphomedusae. The aspect ratio of scyphomedusan bells (fineness ratio) is the primary factor determining the feeding-current dynamics (Dabiri et al. 2005, 2010), and most scyphomedusae have very similarly shaped oblate bells with a fineness ratio of approximately 0.4 ± 0.1 (Costello et al. 2008). Similarly, the nematocyst complements of 29 species of

scyphomedusae (those for which nematocysts have been identified) are all characterized by primarily the same 2 types of nematocysts, heterotrichous microbasic euryteles and holotrichous isorhizas. A third nematocyst type, heterotrichous anisorhizas, additionally occurs in many of the species (Weil 1934, Calder 1983). Bell pulsations by oblate bells are highly effective at initiating encounters, and nematocysts appear to be highly effective at retaining contacted prey. This may explain why these traits have been evolutionarily conserved.

Diversity in capture surface morphology enables different medusan taxa to exploit different niches by altering prey selection patterns. This is illustrated by the comparison between semaeostomes and rhizostomes. The tentacles and oral arms of semaeostome medusae are more effective at contacting and capturing larger prey. In contrast, rhizostomes primarily select and feed on small nauplii and veliger larvae (Larson 1991, Peach & Pitt 2005, Álvarez-Tello et al. 2016). The prey used in our study, *Artemia* sp. and adult copepods, are much larger than those typically selected by rhizostomes (1 vs. 0.25 mm). Consequently, we observed lower contact efficiencies for the rhizostomes than the semaeostomes (but similarly high capture efficiencies). This suggests that the digitata on the oral disk of rhizostomes are not as likely to contact entrained large prey as the tentacles of semaeostomes, and this difference alters prey selection patterns. However, a more detailed study tracking and quantifying the interactions of rhizostome capture surfaces with different-sized prey is required to better understand why digitata are more effective at capturing small rather than large prey. Nevertheless, it is the differences in capture surface morphology which explains the difference in prey selection patterns between semaeostomes and rhizostomes rather than bell shape and nematocyst complement.

Passive feeding and trophic impact

Medusae such as scyphozoans are often grouped with another predatory gelatinous group, the ctenophores. However, there are critical differences in the predation mechanics of the 2 groups that influence their community impact. The capture of entrained prey by feeding-current foraging medusae is a passive process determined by the probability that prey in the current will contact passively trailing capture surfaces. In contrast, the lobate ctenophore, *Mnemiopsis leidyi*, actively scans its feeding current using

its sensory capabilities to detect and actively capture prey in its feeding current (Colin et al. 2015). Consequently, *M. leidyi* retains greater than 90% of the prey entrained in its feeding current (Waggett & Costello 1999, Colin et al. 2015). By comparison, oblate medusae feed less efficiently, retaining less than 63% of the prey they entrain. Interestingly, oblate medusae retention efficiencies are more comparable to, and in many cases higher than, visual fish predators feeding on copepods (O'Brien et al. 1976, Swift 1981, Gemmell & Buskey 2011). The feeding strategy of *M. leidyi* is based on generation of an undetectable, continuous feeding current that efficiently retains entrained prey (Costello & Coverdale 1998, Costello et al. 1999, Waggett & Costello 1999, Colin et al. 2010). This strategy relies on stealth. In contrast, the strategy of oblate medusae relies on a feeding current that bulk processes large volumes of fluid (Dabiri et al. 2005, Peng & Dabiri 2008, Acuña et al. 2011, Katija et al. 2011). This strategy appears to rely on high encounter/entrainment rates offsetting lower retention efficiencies. In the end, both strategies result in high size-specific clearance rates (Acuña et al. 2011 and reference therein). However, sensory scanning appears to enable the lobate ctenophore *M. leidyi* to have a greater size-specific clearance rate, and consequent trophic impact, than oblate medusae (Colin et al. 2015). Nevertheless, when medusae abundances are sufficiently high, their passive capture mechanism is sufficient to enable oblate medusae to impact the standing stocks of prey species (Purcell & Arai 2001, Costello et al. 2008 and reference therein).

Conclusion

Prey capture by oblate medusae appears to be largely limited by the probability that prey entrained in the feeding current will contact a capture surface. As a passive process, this contact stage of the feeding process will be directly affected by the morphology of the contact surface. Consequently, we find great diversity among oblate medusan taxa in the shape of contact surfaces, while traits which influence the other stages of the feeding process, bell shape and nematocysts, have remained relatively conserved in the evolution of scyphomedusae.

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