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Prey capture by the cosmopolitan hydromedusae, *Obelia* spp., in the viscous regime

Kelly R. Sutherland,*[1] Brad J. Gemmell,[2] Sean P. Colin,[3,4] John H. Costello[4,5]
[1]Oregon Institute of Marine Biology, University of Oregon, Eugene, Oregon
[2]Department of Integrative Biology, University of South Florida, Tampa, Florida
[3]Department of Marine Biology and Environmental Science, Roger Williams University, Bristol, Rhode Island
[4]Whitman Center, Marine Biological Laboratory, Woods Hole, Massachusetts
[5]Biology Department, Providence College, Providence, Rhode Island

Abstract

Obelia spp. are cnidarian hydromedusae with a cosmopolitan distribution but very little is known about their feeding. The small size of *Obelia* (bell diameter ~ 1 mm, tentacle width ~ 0.05 mm) suggests that feeding occurs in a viscous regime characterized by thick boundary layers. During feeding observations with a natural prey assemblage the majority of prey were captured at the tentacle tips during the contraction phase. Swimming kinematics from high speed videography confirmed that swimming was a low Re number process ($Re < 50$) and showed that maximum tentacle velocities occurred at the tentacle tips midway through a bell contraction. Flow visualizations from particle image velocimetry demonstrated that fluid motion between the tentacles was limited and that velocities were highest at the tentacle tips, leading to a thinning of boundary layer in this region. The highest nematocyst densities were observed in this same region of the tentacle tips. Taken together, the body kinematics, flow visualizations and nematocyst distributions of *Obelia* explain how these predators are able to shed viscous boundary layers to effectively capture microplanktonic prey. Our findings help explain how other small feeding-current medusae whose feeding interactions are governed by viscosity are able to successfully forage.

Cnidarian medusae are significant and sometimes dominant predators in coastal and open ocean ecosystems and are capable of substantially reducing standing stocks of prey (Purcell et al. 1987; Purcell and Grover 1990). The class Hydrozoa is the most diverse group of the medusazoa, with around 1000 species of Hydrozoan medusae (Bouillon and Boero 2000). Individual hydromedusae species are highly selective in the prey types they consume (Purcell 1997); these differences are driven in part by specialized feeding mechanisms including body morphology and behavior (Costello and Colin 2002; Costello et al. 2008). Cnidarian medusae have been broadly categorized as either filter-feeders or ambush predators. Cruising, filter-feeding predators spend the majority of the time swimming and ambush predators spend the majority of the time motionless and rely on direct contact with motile prey (Colin et al. 2003).

In addition to behavior, predation is also mediated by physical factors. For small hydromedusae operating at low Reynolds numbers ($Re = lU/\nu$, where l is body length, U is velocity, and ν is kinematic viscosity) viscosity dominates, limiting flow around the tentacles. Most species of hydromedusae (> 60%) are less than 1 cm in size (Costello et al. 2008) with tentacles that are tens of microns in diameter and therefore swim and feed in a viscous regime. How do small medusae overcome viscous forces to achieve high enough feeding rates for survival? Previous work with the small hydromedusa *Aglaura hemistoma* (bell diameter < 4 mm) showed that motile protistan prey comprised the majority of the diet (Colin et al. 2005). *A. hemistoma* is considered an ambush predator and can take advantage of prey motility to increase encounter rates. For small filter-feeding medusae, however, direct interception of prey particles on the tentacles may be ineffective because viscous boundary layers push potential prey items away (Kiørboe 2011).

To understand the mechanics of filter-feeding by small hydromedusae, we studied feeding by *Obelia* spp., cruising cnidarian hydromedusae, with a cosmopolitan distribution in shallow, coastal areas. Because there are discrepancies in

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*Correspondence: ksuth@uoregon.edu

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the identification of distinct *Obelia* species with similar morphologies (Govindarajan et al. 2006) and there are three common species in our study region (*O. dichotoma*, *O. geniculata* and *O. longissima*; Light and Carlton 2007), we simply refer to the genus in this study. The small size of *Obelia* (bell diameter ~ 1 mm, tentacle width ~ 0.05 mm) suggests that feeding occurs in a viscous regime characterized by thick boundary layers. Though *Obelia* are ubiquitous, the trophic role of the medusa stage is not understood. Previous studies have been hampered by its cryptic nature in the field—it is small and transparent—and challenges with maintaining medusae in the laboratory (Boero et al. 2007). Like other cnidarians, *Obelia* have nematocysts along their tentacles for prey capture and limited studies suggest that *Obelia* can consume a variety of prey ranging from crustacean zooplankton to bacteria (Kubota 1981; Boero et al. 2007). However, gut contents from field-collected *Obelia* are typically unrecognizable (pers. obs.) and during laboratory studies natural prey assemblages have not been offered to feeding medusae. Direct observation of prey capture and selection using a natural prey assemblage is therefore required to understand the trophic role of *Obelia*.

Here, we used a combination of feeding observations, high-speed videography, flow visualization and microscope visualization of nematocyst distributions to gain a mechanistic understanding of predation by the cosmopolitan hydromedusa *Obelia*.

Methods

Obelia were hand-collected in beakers from the dock at Friday Harbor Laboratories, Washington, USA in June of 2014 and 2015 and maintained in unfiltered seawater at ambient field temperature (10–12°C). A natural prey assemblage (30–440 μm) was obtained from the same location by gently pouring field-collected seawater through 30 μm and 440 μm meshes.

Prey capture observations

Feeding behavior sequences (2–10 min) with a mixed prey assemblage were recorded at 30 Hz or 60 Hz under a dissecting microscope with a Sony HD camcorder (1920 × 1080 pixels) to analyze individual prey encounters and captures. Size scale was provided with a plastic ruler. For each prey encounter, the diameter of the *Obelia* (with and without tentacles), the length of the prey (longest dimension), the location of prey encounter (tentacle tip, center or base), timing of encounter during pulse cycle (contraction, relaxation, still), and the prey transfer time (time to transfer prey from the tentacle to the manubrium) were measured using ImageJ (NIH). All parameters could not be measured in all prey encounter events.

Swimming kinematics

Individual *Obelia* and field-collected prey were placed in glass cuvettes (H × W × D = 45 × 12.5 × 22.5 mm) and swimming motions were recorded at 500 Hz using high speed videography. Brightfield illumination was provided by placing a collimated LED light source behind the cuvette, directed into the camera lens. To minimize wall effects, sequences where the medusa was in the center of the tank, and at least two body lengths from the walls were selected for measurements of body and tentacle kinematics using ImageJ. Bell and tentacle velocities were determined based on the x, y positions of the apex of the bell and points along a tentacle (base, middle and tip), respectively, and the time interval between frames. The whole-body Reynolds number ($\mathrm{Re_b}$) was calculated as: $\mathrm{Re_b} = l_b U_b / \nu$, where l_b is relaxed bell diameter, U_b is bell velocity, and ν is kinematic viscosity of seawater at 12°C ($\nu = 1.28 \times 10^{-6}\ \mathrm{m^2{\cdot}s^{-1}}$). The tentacle Reynolds number ($\mathrm{Re_t}$) and the boundary layer thickness (δ) were calculated at three locations along the tentacle based on the respective length scales and velocities. $\mathrm{Re_t} = l_t U_t / \nu$, where l_t is tentacle diameter and, U_t is tentacle velocity. The boundary layer thickness, δ, around the bell was approximated as δ around a flat plate: $\delta = 1/\sqrt{\mathrm{Re_t}}$ (Nawroth et al. 2010). The boundary layer around a tentacle was approximated as δ around a cylinder in laminar flow: $\delta = l_t/\sqrt{\mathrm{Re_t}}$ (Sumer and Fredsoe 2006).

Fluid mechanics of feeding

Fluid motion during swimming was visualized using micro-scale particle image velocimetry (μPIV; Gemmell et al. 2014). A fiber optic light with a collimator was directed through the tank to provide bright field illumination and *Isochrysis galbana* cells (~ 5 μm) served as neutrally buoyant tracer particles. The motion of the particles was imaged at 500 Hz using a high speed camera (1024 × 1024 pixels) with a ×4 plan objective lens. Sequences where the animal was swimming in the field of view over several pulse cycles were analyzed using PIV software (DaVis) to produce velocity and vorticity flow maps.

Microscopy of nematocysts and gut contents

Freshly collected *Obelia* were mounted on microscope slides with a cover slip and photographed using Differential interference contrast (DIC) microscopy. Images of the tentacles, gut and manubrium were examined for nematocyst densities and gut contents. Nematocyst counts along the length of individual tentacles were made from the tip to the base of the tentacle. Subsamples of the prey assemblage used in prey capture videos were examined under a compound microscope to determine the dominant prey types.

Results

Prey capture

Though *Obelia* were offered a mix prey assemblage (30–440 μm), prey in the microplankton size range (mean length ± SD = 70 ± 40 μm, $n = 25$) were consistently selected. Prey were actively swimming and included dinoflagellates, tintinnids, and ciliates. Nonswimming items, primarily diatoms, were never observed to adhere to the tentacles. Regardless of the direction of approach, prey were ultimately captured

Fig. 1. Encounter and capture of a tintinnid (circled in red) by *Obelia*. At $t = 0$, the tintinnid is near the bell surface. Over several pulses, the tintinnid becomes entrained in the boundary layer surrounding the bell ($t = 8$ s) and then the tentacles ($t = 24$ s). The tintinnid directly contacts a tentacle ($t = 26$ s) during a contraction and is transferred to the manubrium ($t = 30$ s). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

on the tentacles and subsequently transferred to the manubrium (Fig. 1, Supporting Information video 1). Observations indicated that larger plankton that were present in the prey assemblage—for example, copepod nauplii, polychaete larvae, echinoderm bipinnariae, the large dinoflagellate *Noctiluca* sp., and rotifers—were not successfully captured, though in some cases they became attached to the tentacles for several pulse cycles. In these cases, there was no attempt to transfer the prey to the manubrium and eventually the prey actively broke free or became detached from the tentacle.

Obelia spent most of the time swimming and foraged as a feeding-current medusa. After a prey item contacted a tentacle, initiation of prey transfer to the manubrium was rapid (median = 0.9 s, mean = 5.6 ± 12.5 s, $n = 19$). Completion of transfer of the particle to the manubrium took longer due to handling (median = 4.1 s, mean = 5.4 ± 5.1 s, $n = 19$). Prey capture did not occur equally throughout a pulse cycle ($\chi^2_2 = 6.42$, $p < 0.05$) and usually occurred during the contraction phase (11 of 19 or 58% of captures). Prey capture also did not occur uniformly at all capture surfaces ($\chi^2_3 = 12.35$, $p < 0.01$) and, most frequently, prey were captured on the middle or outer portion of the tentacle (27 of 34 or 79% of captures). Though the standard capture mode involved capture on the tentacles (29 of 34 or 85% of captures) followed by transfer to the manubrium, prey were also occasionally captured directly on the manubrium (5 of 35 or 15% of captures). The highly maneuverable manubrium and oral lips oriented toward prey and "grabbed" these items as they moved past. In some cases, the currents generated by the pulsing medusa helped sweep the prey item toward the manubrium. Guts of freshly collected *Obelia* viewed under a light microscope contained green-pigmented, amorphous material and lacked exoskeletons suggesting consumption of chlorophyll-containing cells or grazers that had recently ingested chlorophyll-containing cells. The observation of green-pigmented material was consistent with feeding observations of microplanktonic grazers as the dominant prey.

Swimming kinematics

The average bell diameter of *Obelia* in this study was 1.77 ± 0.38 mm and 3.21 ± 0.7 mm including tentacles. The mean tentacle width was 0.05 ± 0.01 mm. *Obelia* swimming occurred in an intermediate to low Re regime where viscous forces dominate ($\mathrm{Re_b} < 50$ and $\mathrm{Re_t} < 0.5$, Fig. 2). Over the course of a contraction the bell transitioned from a concave-upward configuration with tentacles extended in the same two-dimensional plane as the bell margin to a concave-downward, almost hemispherical configuration with tentacles oriented roughly in the same direction as the oral-aboral pole (Fig. 2). Because viscosity dominates over inertia, forward momentum ceased during the recovery stroke and net motion was slightly backward (Fig. 3). Tentacle velocity was always higher at the tip than at the base because the tip traveled further than the base over a given time period (only data from tentacle tip are shown in Fig. 2). The highest tentacle velocities coincided with the highest bell velocities and occurred during the mid-point of a contraction.

Fluid motion around body and tentacles

Fluid motion was governed by viscous forces: when the body motion stopped, the surrounding fluid also ceased moving within ~ 60 ms (Fig. 4, Supporting Information video 2). During contraction, fluid flow was orthogonal to the tentacles and velocities and vorticities were highest at the tentacle tips. Flow visualizations were consistent with calculations of the boundary layer around the tentacles (Fig. 2) and showed that the minimum boundary layer thickness occurred at the tentacle tip and during the time when the tentacle velocity was highest (Fig. 4, Supporting Information video 2). The minimum boundary layer thickness also

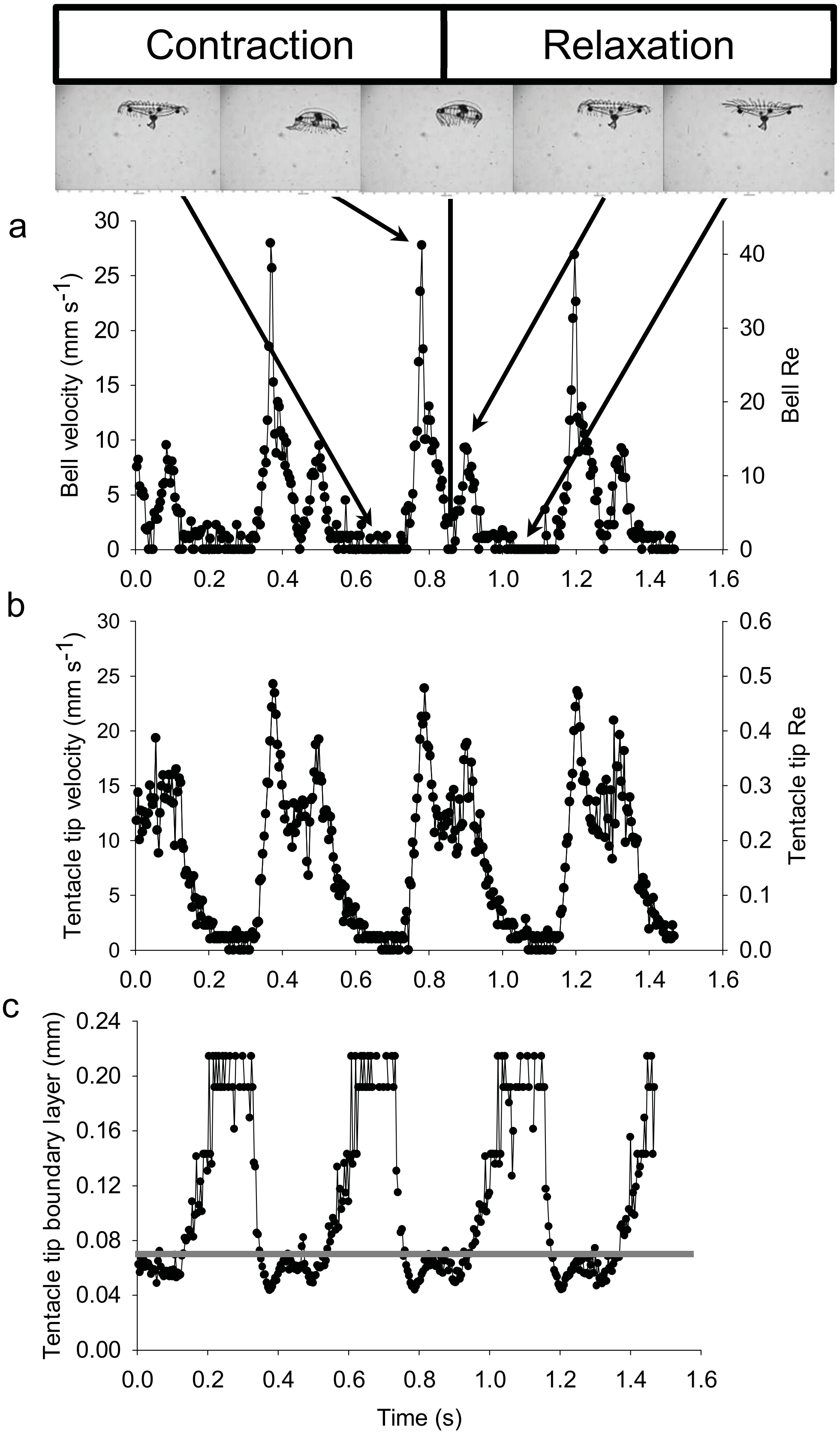

Fig. 2. Bell and tentacle kinematics through three full bell pulsation cycles. (**a**) whole-body velocity and Re, (**b**) tentacle tip velocity and Re and (**c**) boundary layer around the tentacle tip. Maximum velocity and Re and minimum boundary layer thickness occur midway through a contraction. Horizontal grey line in (c) indicates the mean size of prey captured during feeding experiments (70 μm).

corresponded with the size of particles captured (70 ± 40 μm; range = 30–200 μm, $n = 25$).

Nematocyst distribution

Nematocysts were distributed in rings, or annulae, along the length of the tentacle with the highest density of nematocysts at the tentacle tip (20.4 ± 2.1; Figs. 5, 6). The decrease in nematocysts along the length of the tentacle from tip to base was driven by two factors. First, moving from tip to base, the number of nematocysts per annule gradually declined (Fig. 6a). Second, the distance between annulae increased along the tentacle length so that after an initial gap between the tentacle tip and the first annule, annulae were closest together at the distal end of the tentacle and the separation increased toward the base of the tentacle (Fig. 6b). Though a logarithmic regression best fit the nematocysts per annule data (Fig. 6a), a multiple linear regression based on location and distance between annulae is sufficient to explain 70% of the mean nematocyst count at a given location ($F_{2,14}$= 16.60, $R^2 = 0.70$, $p < 0.001$). Consistent with previous studies (Kubota 1981; Boero and Sarà 1987), nematocysts were not observed on the manubrium.

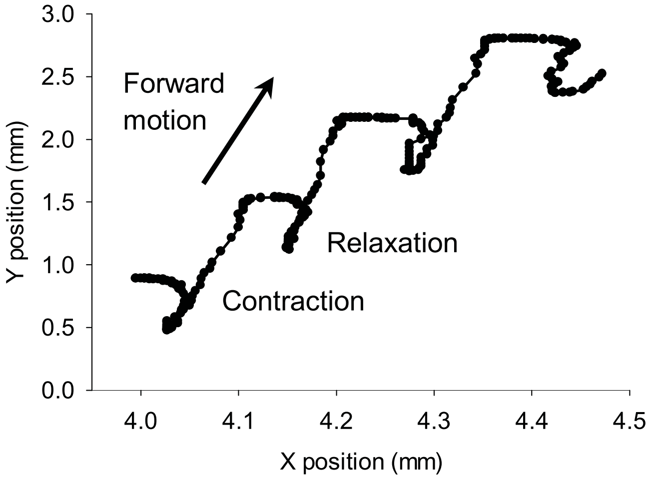

Fig. 3. *Obelia x, y* position through three full bell pulsation cycles showing forward motion during contraction and reverse motion during relaxation.

Discussion

Obelia medusae swim and feed in a viscous regime characterized by thick boundary layers around the body and tentacles. During feeding observations, *Obelia* captured motile microplankton on the outer portion of the tentacle, primarily during the contraction phase of a pulse (Fig. 1). Three separate lines of evidence—tentacle kinematics, fluid motion around the tentacles and nematocyst distributions—support that *Obelia* overcomes its viscous environment by accelerating prey capture surfaces in order to shed boundary layers along the tentacle tips and capture microplanktonic prey in the same region (Fig. 7). Kinematic data showed that the body and tentacles accelerate through a pulse cycle with maximum speeds occurring midway through a contraction (Fig. 2). The boundary layer, which was calculated based on the kinematic data, was thinnest during maximum tentacle acceleration (Fig. 2). The thinner the boundary layer, the higher the likelihood that potential prey can directly contact the tentacles and our results revealed that the minimum

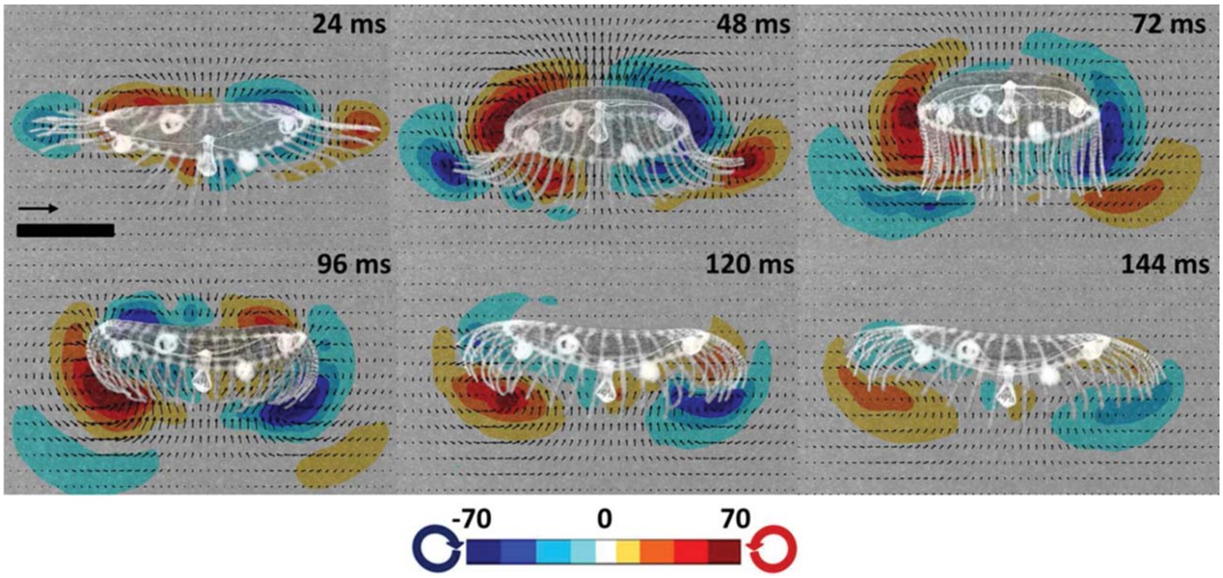

Fig. 4. Flow field (black vector arrows) and vorticity (s^{-1}, colored contours) around swimming *Obelia* over one full pulsation cycle. Bell is relaxed at 24 ms and fully contracted at 72 ms. The recovery stroke begins at 96 ms and ends at 144 ms. Velocity through the tentacles is at a maximum midway through the contraction (48 ms). Vector scale arrow in the first panel represents 20 mm s^{-1}; size scale bar is 1 mm.

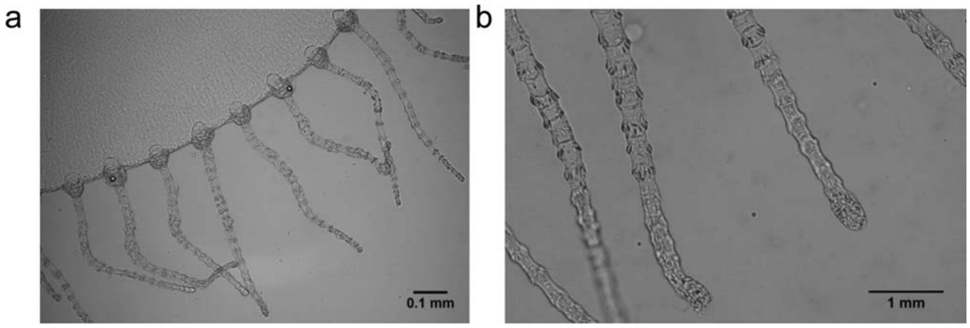

Fig. 5. Images showing tentacles and nematocyst arrangement in annulae (**a**) with higher densities at the tentacle tips (**b**).

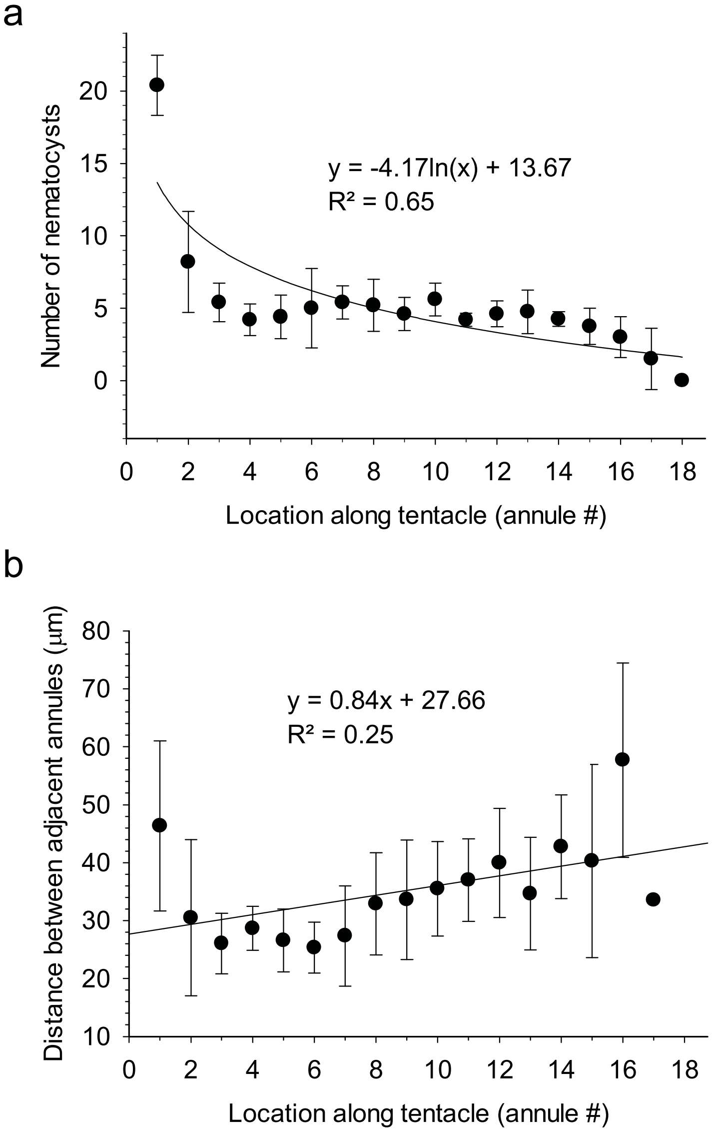

Fig. 6. Number of nematocysts (**a**) and distance between annulae (**b**) along *Obelia* tentacles. Location 1 is the tentacle tip.

boundary layer thickness corresponded closely to the mean size of prey captured (Fig. 2c). The boundary layer thickness determined the lower limit but not upper limit of prey. Instead, behavior appeared to determine the upper limit as larger prey items, including larval forms, rotifers and *Noctiluca* cells, contacted the tentacles but were not actively transferred to the manubrium. Flow visualizations were consistent with kinematic data and showed that tentacle velocity and vorticity were most pronounced at the tentacle tips while flow through the tentacles was more limited proximal to the bell margin (Fig. 4, Supporting Information video 2). Finally, nematocysts were most dense toward the tentacle tips as a result of closer spacing of the annulae and higher numbers of nematocysts per annule (Figs. 5, 6).

Due to the small size of *Obelia*, morphological and fluid mechanical constraints must be overcome in order to encounter prey. Larger medusae that swim in inertial regimes take advantage of passive energy recapture to continually move forward, even when not actively swimming (Gemmell et al. 2013). In contrast, at lower Re the body does not glide in between bell contractions and during the relaxation phase, the body actually moved backwards (Fig. 3). Our observations indicated that as a result of this backward motion, slowly swimming prey that were encountered upstream were only captured after many pulse cycles (Fig. 1, Supporting Information video 1). Instead of achieving forward translation, relatively high instantaneous body and tentacle speeds are necessary to increase the probability of prey capture through entrainment and contact. Peak flow speeds generated by *Obelia* match or exceed the mean escape speeds of even hydrodynamically-sensitive, evasive protists (Gemmell et al. 2015). Therefore, high local fluid velocities and shear around the tentacles likely help entrain prey. Perhaps even more importantly, as evidenced by tentacle speeds $\sim 2\times$ higher than flow speeds (Figs. 2b, 4), capture surfaces are brought into close contact with prey.

Obelia may be able to take advantage of intermediate Re—between 0.1 and 50—to increase prey encounter on the cylindrical tentacles. At intermediate Re, inertial and viscous forces are both important and numerical simulations show that streamlines compress around a cylinder, allowing for increased encounter with particles traveling along streamlines (Humphries 2009). In fact, a number of aquatic filter-feeders are tuned to operate at intermediate Re based on filter element size and realistic flow velocities (Humphries 2009). Increased encounter rates due to the intermediate Re might help explain how *Obelia* and other small hydromedusae are able to acquire sufficient nutrition by specializing on microplanktonic prey.

Obelia are important members of coastal marine ecosystems and have been reported to reach seasonal abundances of 1856 per m^3 (Yahia et al. 2003) but until now, their trophic role has not been well understood. *Obelia* hydroids are common on both natural and man-made substrates and periodically bud juvenile medusae that eventually reach maximum sizes of several mm. Broadly speaking, the majority of hydrozoans have a two part life history alternating between an asexual polyp stage and a sexual medusa stage though the length of each generation varies considerably and some species lack the medusa stage or the polyp stage (Bouillon and Boero 2000). Because the medusa stage is ephemeral, small and transparent, these cosmopolitan predators are often overlooked. The majority of hydromedusae are smaller than 1 cm with tentacle widths in the sub-millimeter range and are therefore predicted to feed at intermediate Re (Humphries 2009) and may feed omnivorously (Colin et al. 2005; Boero et al. 2007).

Smaller medusae (< 5 cm) comprise a mix of morphologies and, presumably, predation strategies, including filter-feeding and ambush predation (Costello et al. 2008). How do physical constraints play out in small hydromedusae with different predation strategies? Filter-feeding medusae, like *Obelia*, spend the majority of the time swimming with tentacles extended (Colin et al. 2003) in order to maximize encounters with slow or non-swimming prey. Ambush predators, on the other hand, spend the majority of the time motionless with tentacles extended; prey are primarily motile crustaceans—including copepods and barnacle nauplii (Larson 1987; Purcell and Mills 1988; Costello and Colin 2002)—that bump into tentacles and are immobilized upon contact. Though there are few other studies of the feeding ecology of hydromedusae in the mm size range, observations of *Aglaura hemistoma* (< 4 mm) show that it feeds on a combination of crustacean prey and protists using two distinct feeding strategies (Colin et al. 2005). *A. hemistoma* behaves as a classic ambush predator by hanging motionless in the water to encounter motile copepods and nauplii. However, these motile prey frequently escape. A second mode of feeding is through feeding currents of up to 2 mm s^{-1} that are produced by ciliated tentacles; this mode of feeding is effective for capturing and retaining protistan prey. Our historical understanding has been that Cnidarian predators feed on

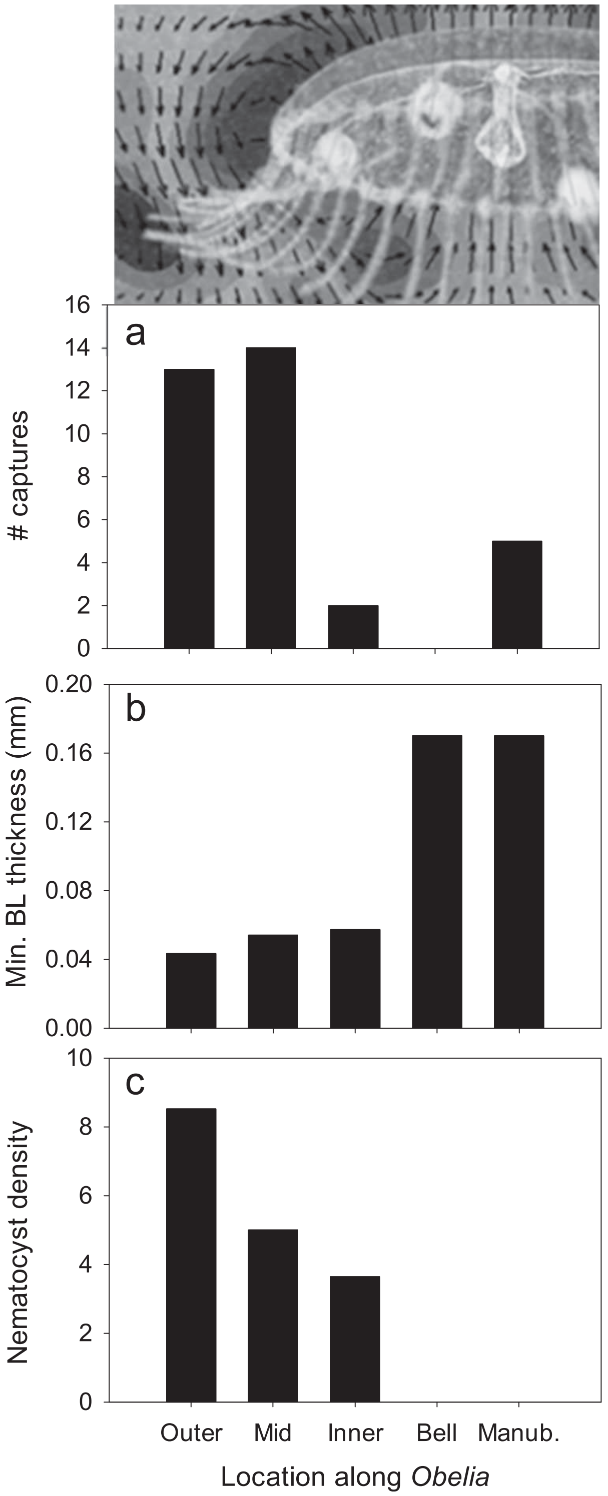

Fig. 7. Summary figure showing the relationship between prey captures (**a**), the minimum boundary layer (BL) thickness around feeding surfaces (**b**), and the number of nematocysts per annule (**c**), along sections of the tentacle, the bell and manubrium of *Obelia*. Upper image of *Obelia* is included to help visualize the different prey capture regions. Note that the BL thickness for the bell and manubrium correspond to the BL along the aboral side of the bell. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

other metazoans but more recent studies of small hydromedusae suggest that predation on protists and even bacteria may be more prevalent than originally thought (this study; Colin et al. 2005; Boero et al. 2007). Conversely, the observation that *Obelia* consumes relatively small prey is consistent with predator-to-prey ratios for other planktonic filter-feeders (Hansen et al. 1994). *Obelia* in this study had a length-based predator to prey size ratio of 24:1-44:1 (depending on whether the tentacles are included in the predator length measurement) and the ratio for cladocerans and meroplanktonic larvae is ∼ 50:1 (Hansen et al. 1994). Consistency among predator-to-prey ratios for a particular feeding strategy points to the value of a trait-based approach for predicting feeding ecology (e.g., Kiørboe 2011; Andersen et al. 2016).

A mechanistic approach to understanding predation provides useful insight for generating hypotheses. The finding that the boundary layer sets the lower limit on prey capture can help with predictions about how predation will shift in response to changes in the underlying variables. For example, an increase in temperature will decrease viscosity, thereby thinning the boundary layer, and decreases the lower limit of possible prey size. Species of *Obelia* are distributed in tropical, temperate and subpolar latitudes (Stepanjants 1998) in temperatures that are expected to range from −2°C to 27°C; this broad temperature range corresponds to a ∼ 50% difference in boundary layer thickness around tentacles and, therefore, putative prey. Though an understanding of the underlying physics helps constrain the possible prey types, direct behavioral observations are also necessary. The observation that *Obelia* did not consume larger prey items is somewhat enigmatic though may be partially explained by challenges with handling certain prey items that have morphological defenses (e.g., spines on trochophore larvae) or behavioral responses (escape jumps of copepods). This study demonstrates the value of combining behavior, morphology, kinematics, and fluid mechanics to understand the mechanisms underlying feeding ecology of an important marine predator.

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Conflict of Interest

None declared.

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