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Elevating the predatory effect: Sensory-scanning foraging strategy by the lobate ctenophore *Mnemiopsis leidyi*

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Abstract

The influential predatory role of the lobate comb jellyfish *Mnemiopsis leidyi* has largely been attributed to the generation of a hydrodynamically silent feeding current to entrain and initiate high encounter rates with prey. However, for high encounter rates to translate to high ingestion rates, *M. leidyi* must effectively capture the entrained prey. To investigate the capture mechanisms, we recorded and quantified, using three-dimensional videography, the outcome of encounter events with slow swimming *Artemia* prey. The auricles, which produce the feeding current of *M. leidyi*, were the primary encounter structures, first contacting 59% of the prey in the feeding current. Upon detection, the auricles manipulated the *Artemia* to initiate captures on the tentillae, which are coated with sticky cells (colloblasts). Using this mechanism of sensory-scanning to capture prey entrained in the feeding current, *M. leidyi* uses a similar foraging strategy to that of feeding-current foraging copepods. As such, *M. leidyi* has a higher capture efficiency than do medusae, contributing to the greater predatory effect of *M. leidyi* in both its endemic and invasive ecosystems.

Jellyfish, including both medusae and comb jellies (i.e., ctenophores), are widely recognized as important predators capable of substantially affecting the trophic structure of pelagic ecosystems (Matsakis and Conover 1991; Brodeur et al. 2002). Their predatory success has been largely attributed to both their inflated gelatinous bodies and to their effective foraging strategies (Acuna et al. 2011; Pitt et al. 2013). Understanding the mechanics of foraging by predators is essential for prediction of predatory ingestion rates and prey selection patterns (Kiørboe 2011) as well at the effect of environmental variations on trophic exchange (Kiørboe and Saiz 1995).

Jellyfish taxa which exert the greatest trophic effect forage as feeding-current suspension feeders (Costello et al. 2008; Regula et al. 2009; Colin et al. 2010). Medusan taxa which generate feeding currents do this by pulsing their bell to entrain and transport fluid through their trailing tentacles and oral arms (Costello et al. 2008). The ctenophore taxa which use feeding currents are generally lobate ctenophores and they use cilia to transport fluid between their lobes and past capture surfaces (Waggett and Costello 1999; Colin et al. 2010). Both of these strategies are highly effective at transporting large volumes of fluid and result in high encounter rates with prey. The fluid-processing capabilities of feeding-current foraging jellyfish have been quantified and used to estimate maximum clearance rates (f_{max}). However, maximum clearance rates based on fluid interactions are often much greater than observed clearance rates of prey, particularly for medusae (Katija et al. 2011). This is because feeding depends not only on encounter processes but also on postencounter capture processes.

For most jellyfish taxa, the transport of prey to capture surfaces (such as tentacles) is a passive process that relies on fluid transport to initiate contacts between prey and capture surfaces. This is especially true for medusae that have trailing tentacles and oral arms positioned in the circulating wake generated by bell pulsations (Ford et al. 1997). Predation by lobate ctenophores on passive and weakly swimming prey has also been described as a passive process where feeding currents transport prey and initiate contacts with tentillae

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(Larson 1988; Waggett and Costello 1999; Colin et al. 2010). However, some lobate ctenophores, such as *Mnemiopsis leidyi*, are capable of detecting actively swimming prey, such as copepods, once they are entrained in their feeding current. Prey detection triggers a reaction from the predator that assists prey capture (Costello et al. 1999). Such behaviorally mediated foraging responses greatly increase the capture efficiency of *M. leidyi* on prey such as copepods (Waggett and Costello 1999). The combination of a feeding-current with sensory capabilities for prey detection and manipulation is a common foraging strategy of copepods but has never been described for other pelagic suspension feeders (Kiørboe 2011).

The mechanism used to initiate contacts with prey (passive particle interception vs. active particle trajectory manipulation) has important implications for predator capabilities in different fluid environments. For example, it is known that contact rates with prey for passive feeding-current foragers using direct interception are determined by the feeding current velocity and the radius of the prey (Humphries 2009). Sensory capabilities can greatly enhance contact rates by increasing the encounter radius depending on their detection capabilities (Kiørboe 2011). Furthermore, feeding-current foraging medusae, which rely on passive mechanisms, have been found to have relatively low capture efficiencies that are often much less than 50% (Colin et al. 2006; Katija et al. 2011). In contrast, copepods are generally found to have capture efficiencies greater than 70% (Jonsson and Tiselius 1990; Doall et al. 2002) and *M. leidyi* had efficiencies of 74% on copepod prey (Costello et al. 1999). These enhanced rates and efficiencies also have the potential to be accentuated in turbulent environments where turbulence has been predicted to enhance feeding rates of feeding current copepods with sensory capabilities by >30% (compared to only 10% for predators without sensory capabilities; Kiørboe and Saiz 1995).

Therefore, accurate evaluation of the underlying mechanisms used to capture prey substantially influences predictions of foraging capabilities of predators in the variable fluid flows characterizing natural environments. The active prey capture mechanisms used by *M. leidyi* feeding on copepods have been well described and quantified (Costello et al. 1999; Waggett and Costello 1999). However, *M. leidyi* also captures a variety of weakly swimming prey and, in contrast to the active detection of larger, rapidly swimming copepods, the capture of smaller, weakly swimming prey has been thought to be a passive capture process involving tentillae that line the oral groove (Waggett and Costello 1999). However, this process has not been rigorously examined and little is known about the details of this process or how it is affected by changes in flow. Our goal was to use three-dimensional videography to evaluate the postencounter prey capture mechanisms used by the lobate ctenophore *M. leidyi* when feeding on weak swimming prey. Specifically, we measured: (1) capture probabilities on the different feeding structures of *M. leidyi*; (2) the role of ciliary kinematics and fluid manipulation in determining capture probabilities; (3) the effects of postencounter handling on capture efficiency; and (4) the relationship between swimming speed and capture efficiency.

Methods

To quantify the transport of prey by the feeding current of *M. leidyi* and the postencounter interactions between *M. leidyi* and its prey, individual free swimming ctenophores were video recorded while being incubated in filtered seawater containing *Artemia salina* nauplii (swimming speed = 1–3 mm s^{-1}) as prey. All experiments were conducted at the Marine Biological Laboratory in Woods Hole, MA. Ctenophores were hand-collected from surrounding waters, immediately transported to the laboratory and used in incubation studies. Laboratory and field water temperatures were the same at 22°C. Prior to videoing, *Mnemiopsis* were placed in a filming vessel and acclimated until they opened their lobes and began exhibiting normal foraging behavior (about 10–20 min). The total length of *M. leidyi* used in the incubations ranged from 1.7 cm to 3.0 cm [mean = 2.3 cm ± 0.38 standard deviation (SD)]. A total of 31 ctenophores were observed and we quantified 304 interactions with prey.

The kinematics of the auricular cilia of *M. leidyi* were video recorded in two dimensions (2D) using similar methods as described above except that the ctenophores were placed into regular glass rectangular vessels with the collimated light directed straight into the camera. Auricular motions were recorded at 1000 frames per second using a Photron Fastcam SA2 video camera.

We used methods following Colin et al. (2010) to quantify the motion of the feeding current of *M. leidyi*. Accordingly, the feeding current was measured using 2D particle image velocimetry (PIV) by placing individuals into glass filming vessels in filtered seawater seeded with 10 μm hollow glass beads. *M. leidyi* were illuminated using a red laser sheet (680 nm wavelength) and recorded at 200 frames per second using a Photron Fastcam 1024 PCI video camera that was placed perpendicular to the laser sheet. The velocity vectors of particles illuminated in the laser sheet were quantified from sequential images that were analyzed using a cross-correlation algorithm (LaVsion Software). Image pairs were analyzed with shifting overlapping interrogation windows of decreasing size (64 × 64 pixels, then 32 × 32 pixels).

For incubations with prey, individual *M. leidyi* were placed into right-triangular filming vessels (height of vessel = 7 cm, width of the three sides: 6 × 6 × 8.75 cm). We used three-dimensional (3D) video to enable us to accurately identify encounters and encounter locations. To get a 3D view of the interactions, the hypotenuse side of the right triangular filming vessel (8.75 cm wide) was a mirror (Kiørboe 2007). The

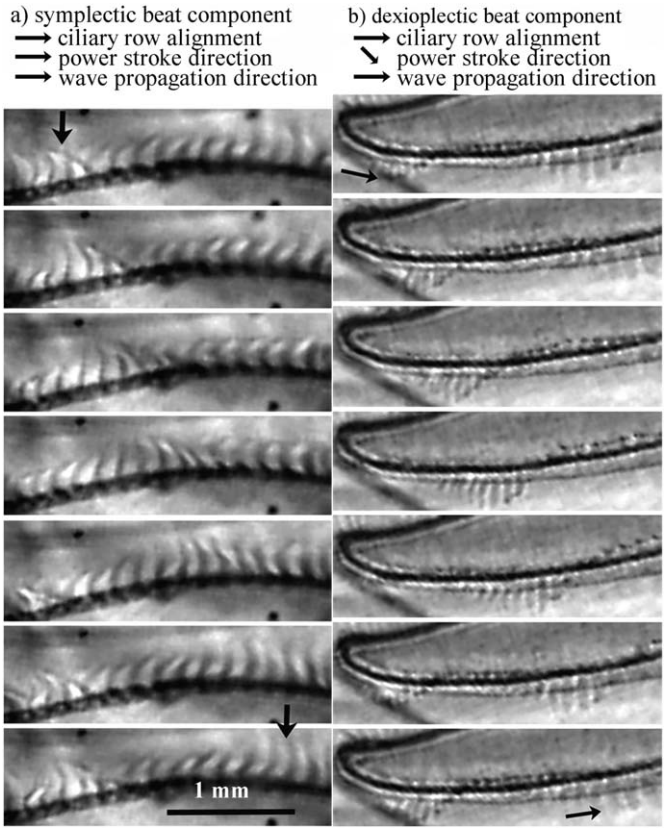

Fig. 1. Sequential images (moving from top to bottom) of the kinematics of auricular cilia. The different view enable us to observe both (a) symplectic and (b) dexioplectic metachronism in the auricular cilia. The arrows locate the beginning (top) and end (bottom) location of the cilia in the effective (or power) stroke.

vessel was illuminated using collimated light from a halogen light source that was provided from one side, and feeding *M. leidyi* and their mirror images were video recorded through the perpendicular side of the aquarium, similar to Kiørboe (2007) and Kjellerup and Kiørboe (2012). Video of interactions between *M. leidyi* and prey were recorded at 30 frames per second using a Sony camcorder. Three-dimensional interactions were analyzed using ImageJ software (National Institute of Health [NIH]). As the focus of this study was to quantify postencounter events, we used white light illumination. An encounter was identified when an *Artemia* prey was transported by the feeding current into the region between the lobes of *M. leidyi*. The outcome of each observed encounter was then observed (e.g., transported through the feeding current region without a contact with *M. leidyi*, a contact without capture, or a contact with capture). We identified whether *M. leidyi* reacted to the prey and the morphological location of *M. leidyi* (i.e., body parts) that were involved in both prey contact and capture. We identified a detection when *M. leidyi* reacted to the prey. We also quantified the relationship of capture efficiency with swimming speed to evaluate the influence of swimming-induced alteration of feeding current flow rates on prey capture by *M. leidyi*. This was done by quantifying the swimming speed of *M. leidyi* at the time of each encounter with prey and quantifying the outcome of that encounter.

Statistical analysis of encounter rates among individual ctenophores use the nonparametric Kruskal–Wallis Ranks test because the data were not normally distributed (Shapiro–Wilk test, $p > 0.05$) and, therefore, did not fulfill the assumptions of the parametric analysis of variance (ANOVA) test. Replicates for the statistical analyses were separately videoed individuals.

Results

The auricles of *M. leidyi* are lined by fused cilia which beat nearly continuously. The kinematics of the cilia reveal that their beat pattern differs from that of the ctene rows that are used for propulsion. Ctene rows are known to beat with an antiplectic metachronal wave, while high-speed video demonstrated that the auricular cilia have both symplectic (power stroke of the cilia is in the same direction of the propagated wave; Fig. 1a) and dexioplectic components (power stroke of cilia moves at an angle relative to the propagated wave; Fig. 1b).

These ciliary kinematics result in the transport of fluid along and over the auricles. PIV analysis shows that the auricular cilia (1) entrain fluid from a broad region outside the oral lobes followed by; (2) transport of the fluid between the lobes where it converges toward the auricles (Fig. 2a,b); and is (3) directed over the surface of the auricles (Fig. 2a) then subsequently (4) forced out of the aboral gap between lobes and central body in a flow leading away from the ctenophore (Fig. 2a; please refer to Colin et al. 2010 for a more detailed quantification of the flow field of *M. leidyi*). The fluid was greatly accelerated as it passed the auricles due to conservation of mass when a large volume of fluid was constricted to a much smaller, more rapidly moving volume as it passed over the auricles. Each auricle has two rows of cilia lining opposite sides of the auricle (Fig. 3a), and we observed that the cilia lining both sides beat at the same frequency for the six ctenophores that were examined (average beat frequency among the ctenophores was 11.4 Hz ± 3.0 Hz; $n = 6$). This suggests that roughly the same amount of fluid was transported over both sides of each auricle (i.e., the gap outside the auricles (between the auricle and lobe) and the gap between adjacent auricles; Fig. 3a).

These feeding current characteristics resulted in the most encountered prey (defined as prey entering the space between the lobes) contacting the auricles (Fig. 3b). In fact, 59% of the 304 prey encountered by *M. leidyi* contacted the auricles (contacts identified by the prey bouncing along the auricle or the auricle reacting to the prey). Most of the prey that passed by the auricles without making a contact passed

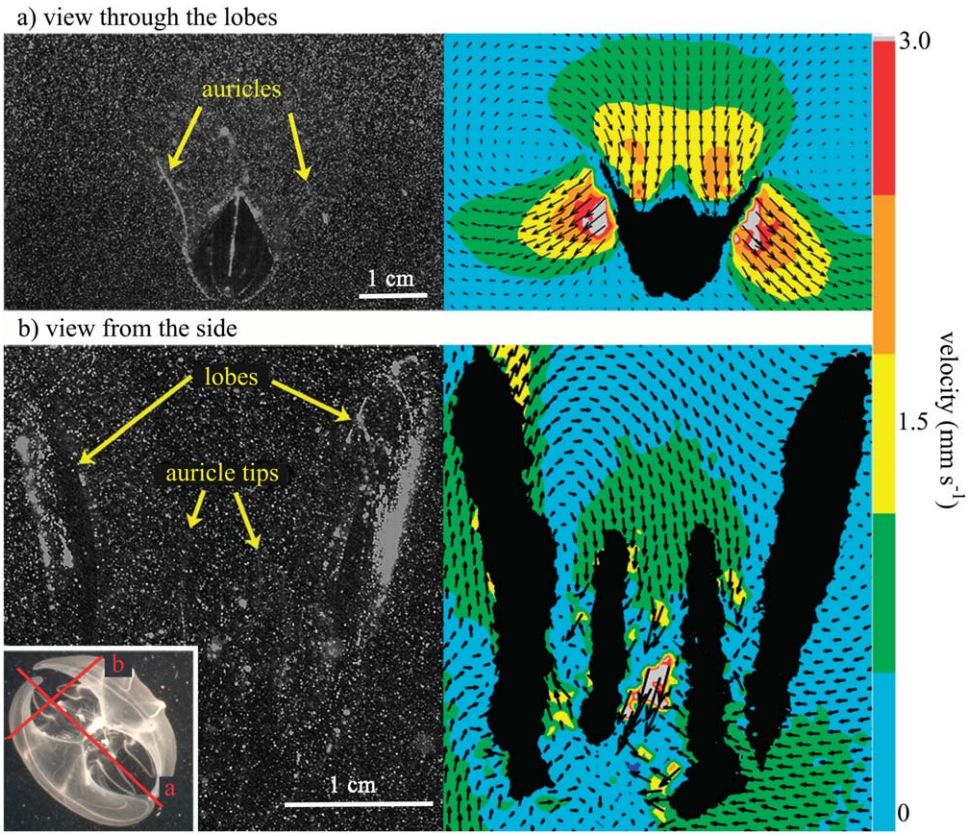

Fig. 2. Two-dimensional PIV of (a) entrained flow passing between the lobes, past auricles and accelerating away from the ctenophore and (b) side view of flow pulled down over auricles. Inset illustrates the location of the laser plane (red line) for both (a) and (b).

by the outside of the auricles (18%) rather than between the two auricles (11%). Very few prey entrained in the feeding current contacted the lobes (6%) and the remaining prey contacted the labial ridge along the mouth. A very small number (5 out of the 304 encounters) of prey encountered *M. leidyi* from the side (not passing between the lobes in the feeding current).

Figures 4 and 5 demonstrate how, upon detection (as evidenced by a reaction by *M. leidyi*), the auricles manipulated prey to redirect them to the tentillae. In both the examples, the *Artemia* prey were transported by the feeding current until they came into close proximity of the auricle. At that moment (time, $t = 7.7$ s in Fig. 4 and $t = 5.3$ in Fig. 5), the auricle reacted and redirected the prey to the tentillae for capture. The low magnification of our video did not enable us to confidently see if the prey needed to contact the auricles to elicit a reaction or if *M. leidyi* reacted precontact. In Fig. 5, it appears that the auricle and the lobe reactions were synchronized to relocate the prey towards the tentillae. Quantification of the effects of prey detection and manipulation on the outcome of encounter events revealed that capture efficiency among the ctenophores increased with the number of detection events. In fact, capture efficiency was increased by $> 50\%$ if prey were detected (Kruskal–Wallis Ranks Test, $p < 0.001$; Fig. 6). Consequently, prey detection greatly enhances the effectiveness of *M. leidyi* prey capture. Another result of this detection behavior is that while most prey first contacted the auricles (Fig. 3b), most prey were captured by the tentillae (61%; Fig. 3c). Over all observed encounters (with and without detection), *M. leidyi* had a relatively high capture efficiency of 65%.

To examine how these mechanics of *M. leidyi* feeding are affected by flow rates or behavior, we quantified how capture efficiency related to swimming speed. The swimming speed of *M. leidyi* is directly related to the volume of fluid passing between the lobes (Colin et al. 2010). Therefore, higher swimming speeds increase not only encounter rates but also the velocity of the flow past capture surfaces. To understand if increased swimming speed can translate into increased feeding rates, we needed to evaluate if behavior affected capture efficiency. We found that capture efficiency did not significantly decrease with speed (Kruskal–Wallis Ranks test, $p > 0.2$; Fig. 7). Although at speeds greater than 6 mm s^{-1} efficiency appeared to decrease. The mean capture efficiency of encounters below 8 mm s^{-1} was 75.0%. However, there were very few events that occurred at swimming velocities

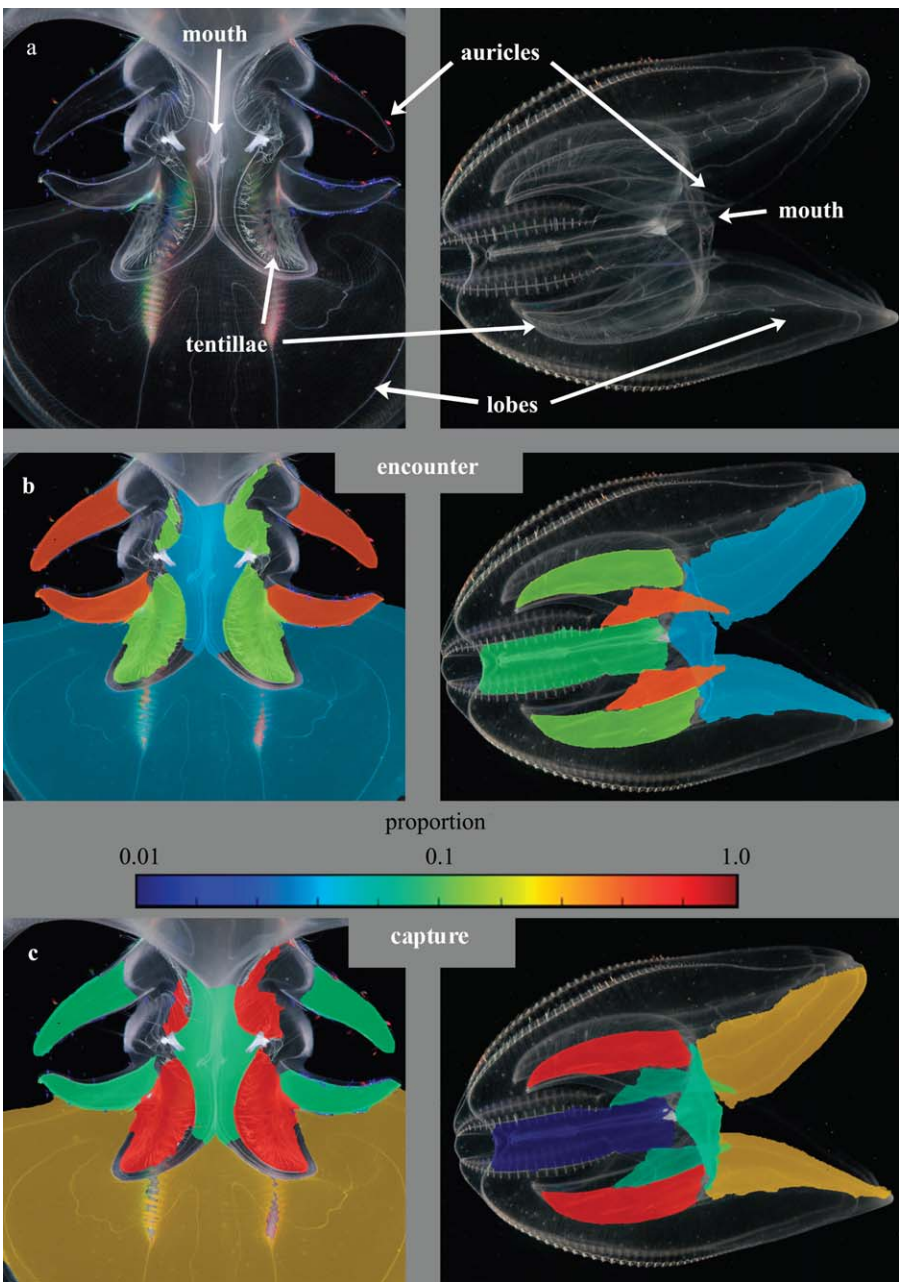

Fig. 3. (a) Feeding structures and proportion of prey, (b) first encountered, and (c) captured on different parts of *M. leidyi*. Most prey first contacted the auricles while most prey were ultimately captured by the tentillae. Two views are provided to better visualize the different locations where prey contacts and captures occur.

above 6 mm s^{-1} because *M. leidyi* generally swims with a mean velocity of 2 mm s^{-1} (Titelman et al. 2012). Although in turbulence, higher swimming speeds are observed (Sutherland et al. 2014)

Discussion

The feeding current generated by *M. leidyi* has been quantified (Waggett and Costello 1999; Colin et al. 2010) and there have been multiple accounts that describe the prey capture mechanisms used by *M. leidyi* for both stronger and weakly swimming prey (Larson 1988; Costello et al. 1999; Waggett and Costello 1999). All of these accounts describe the capture of weakly swimming prey (such as copepod nauplii or invertebrate eggs) as a passive process whereby the auricular feeding current transports prey to capture surfaces via fluid flow past the tentillae. This passive mechanism, analogous to the encounter mechanism used by medusae,

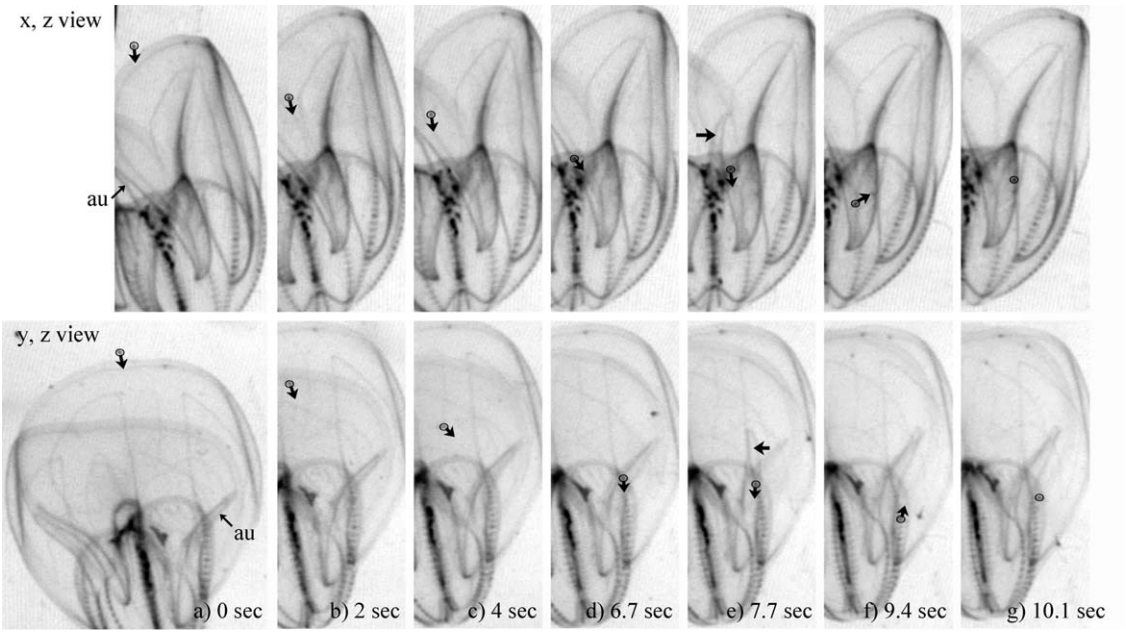

Fig. 4. Sequential images (two views of same event) of (a–d) the entrainment, (e and f) manipulation, and (g) capture of an *Artemia*. The *Artemia* is circled and it trajectory is indicated by the arrow. In (e) (top and bottom), the arrows indicate the reaction by the auricle (au).

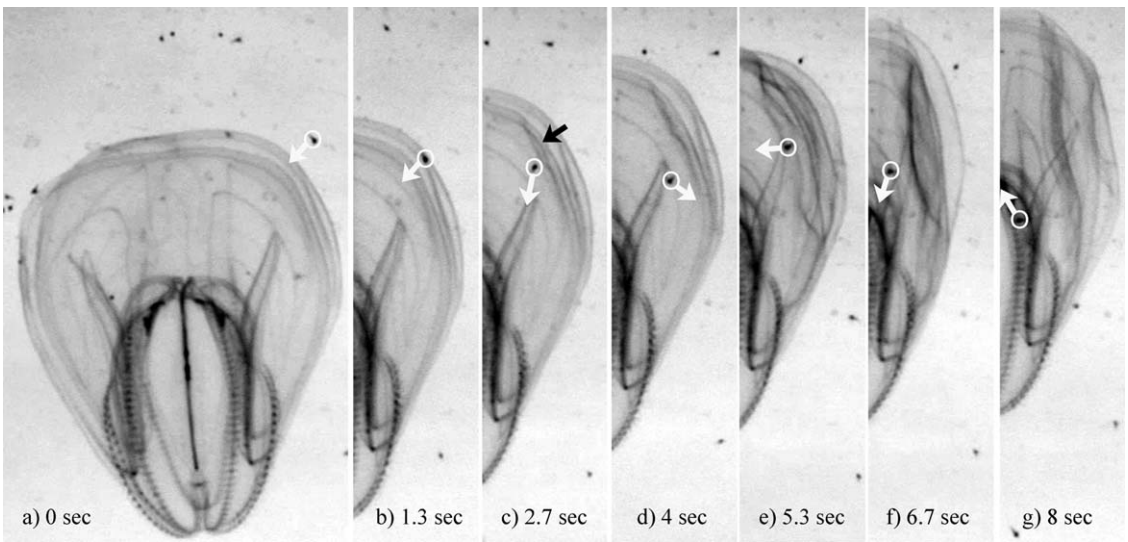

Fig. 5. Sequential images of (a–d) the entrainment, (e and f) manipulation, and (g) capture of an *Artemia*. The *Artemia* is circled and it trajectory is indicated by the arrow. In (c), the arrow indicates the reaction by the lobe.

relies on fluid transport to deliver prey and initiate captures. In fact, the feeding current has been described as spiraling through the tentillae to increase the chance of encounters with tentillae (Larson 1988; Colin et al. 2010). We demonstrate that the capture process is an active process, not passive, during which the auricles detect prey in the feeding current and redirect the prey, hydrodynamically, to initiate captures on the tentillae. Further, we argue that this is the dominant mechanism used to capture weakly swimming or passive prey.

The view that the auricles are actively scanning and relocating the feeding current rather than passively transporting fluid through the tentillae is supported by several lines of evidence. These include kinematic patterns of the auricular cilia, 2D PIV flows past capture surfaces and prey encounter maps. Antiplectic metachronal waves are believed to

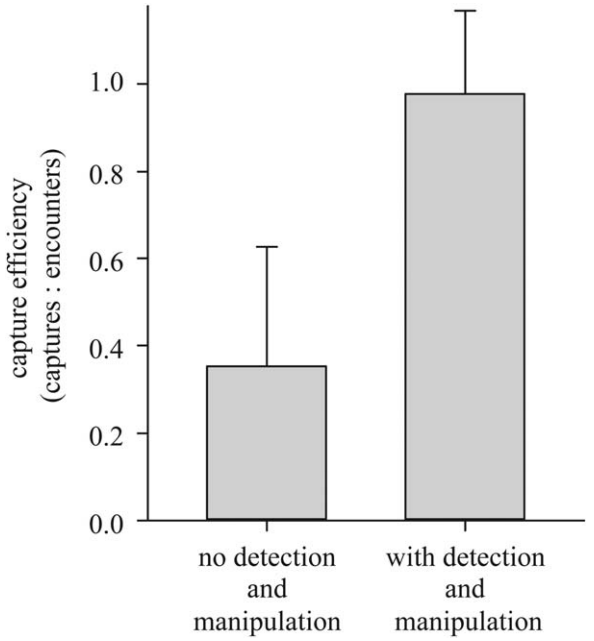

Fig. 6. Effect of prey detection and manipulation on capture efficiency. Mean (± SD) capture efficiency of encounters among ctenophores with and without prey being detected (n = 27 ctenophores). Kruskal–Wallis Ranks test $p < 0.001$.

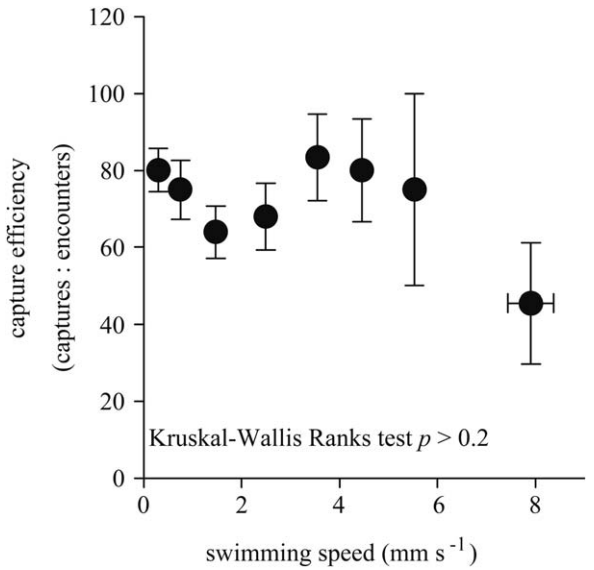

Fig. 7. Mean (± SD) capture efficiencies vs. swimming speed. The symbols represent the mean swimming speed and capture efficiency of individuals grouped into 0.5 mm s^{-1} intervals.

function for propulsion while symplectic metachronal waves, as observed for the auricular cilia, are more effective for processing particles (Knight-Jones 1954). Correspondingly, the ctene rows used for propulsion by *M. leidyi* are characterized by antiplectic metachronal waves (Tamm 2014). However, the specialized kinematic patterns of the auricular cilia are consistent with their role of prey processing rather than solely moving fluid. In addition, the 2D PIV reveals that a bulk of the feeding current drawn between the lobes passes over the auricles and immediately moves away from the ctenophore—not over the tentillae. Although it was not possible using solely 2D PIV to quantify the proportion of fluid passing over the auricles and then away from the ctenophore's body relative to the amount circulating over the tentillae, the fluid acceleration observed past the auricles suggests that the bulk of the feeding current is accelerated past the auricles and away from the body. In contrast, the velocity of the flow circulating through the tentillae is much lower, suggesting that little fluid is diverted over the tentillae during normal ciliary beating. Consequently, 60% of the entrained prey first encountered the auricles while only 18% directly encountered the tentillae (Fig. 3b).

Table 1. Estimated difference in encounter rates (E) with prey based on whether the predator relies on passive (E_p) or active sensory (E_a) foraging mechanism. Enhanced encounter rates are calculated as the ratio $E_a : E_p$. Where $E_a = \pi R^2 v$ and $E_p = \frac{3}{2}\pi a_{prey}^2 v$ and where a_{prey} is the radius of the prey, R is the reactive distance of the predator, and v is the feeding current velocity. $R : a$ ratio represents the number of times greater the reactive distance is than the prey radius and increases with greater sensory capabilities

$R : a$	Enhanced encounter rates
2	3.0
3	6.0
4	11.0
5	17.0
6	24.0
10	67.0

It has already been demonstrated that *M. leidyi* scan their feeding currents for actively swimming copepods (Costello et al. 1999; Waggett and Costello 1999). We expand the role of sensory scanning to being the primary encounter mechanism used for feeding by *M. leidyi* on small and weakly swimming prey as well as larger, stronger swimmers such as late stage copepods. Consequently, *M. leidyi* feeding is not analogous to passive prey capture by medusae, but rather, it is more analogous to feeding-current foraging copepods (Kiørboe 2011; Kjellerup and Kiørboe 2012). One advantage of using sensory scanning rather than relying solely on passive hydrodynamic mechanisms, such as direct interception, is that encounter rates with prey can be greatly increased by the sensory capabilities of the predator (Kjellerup and Kiørboe 2012). *M. leidyi* is known to have numerous sensory structures (Horridge 1965) and to be highly mechanosensitive to copepod prey and other hydrodynamic disturbances (Costello et al. 1999). These behavioral capabilities enable *M.*

leidyi to sense the presence of copepods in the fluid between the lobes and close the lobes before contact is made, greatly enhancing retention efficiencies (Costello et al. 1999). *M. leidyi* is also known to use chemosensory capabilities to avoid predators (Titelman et al. 2012). Therefore, while more research needs to quantitatively evaluate the sensory capabilities of *M. leidyi*, present knowledge indicates that they are likely capable of detecting even passive prey before the prey contact the auricles. Based on encounter probabilities, encounter rates with prey using direct interception and sensory scanning can be estimated as $\frac{3}{2}\pi a_{\text{prey}}^2 v$ and $\pi R^2 v$, respectively, where a_{prey} is the radius of the prey, R is the reactive distance of the predator, and v is the feeding current velocity. Accordingly, even small increases in reactive distance can greatly enhance encounter rates with prey (Table 1). In fact, the sensory capabilities of some copepods enable them to increase their encounter rates by three orders of magnitude (Kjellerup and Kiørboe 2012).

The substantial predatory effects of *M. leidyi* [reviewed in Costello et al. (2012)] are likely due to a synergistic effect of its inflated gelatinous body, its characteristic laminar feeding current and its active sensory scanning (described here). The combination of a gelatinous physiology—which inflates the size of the predator with low carbon requirements (Acuna et al. 2011; Pitt et al. 2013)—and a laminar feeding current—which enables *M. leidyi* to entrain large volumes of fluid (Colin et al. 2010)—results in *M. leidyi* having very high encounter rates with prey. However, cruising foraging medusae have similarly high encounter rates with prey using the same combination of gelatinous physiology and high-flow feeding current (Acuna et al. 2011). Yet, a comparison of clearance rates of *M. leidyi* to several predatory medusae (Fig. 8) demonstrates that *M. leidyi*, for its biomass, has much higher feeding rates than medusan counterparts. We suggest that active sensory scanning by *M. leidyi*, leading to considerably higher capture efficiencies (≈80%), elevates the feeding rates of *M. leidyi* above those of medusae. Higher feeding rates can ultimately result in a greater predatory effect. Several studies have demonstrated that medusan populations alone, including population of *Aurelia aurita* and *Chyrsaora quinquecirrha*, do not effectively suppress zooplankton prey populations, such as copepods (Purcell and Decker 2005). However, in its endemic environments, *M. leidyi* diminishes zooplankton populations, particularly copepods, in seasons when *M. leidyi* is abundant (Purcell and Decker 2005). Likewise, *M. leidyi* greatly diminished zooplankton populations after invasive introductions to novel environments (Shiganova and Bulgakova 2000; Finenko et al. 2006).

Sensory scanning of its feeding current may assist *M. leidyi* to negotiate the wide range of environmental conditions that it experiences in coastal marine ecosystems. Capture efficiencies and ingestion rates of passive suspension feeders are highly sensitive to flow conditions and are frequently

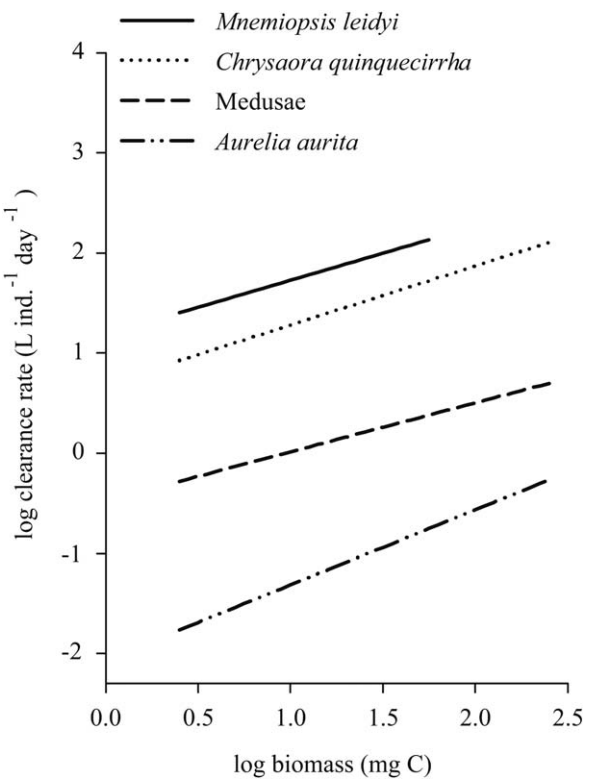

Fig. 8. Comparison of individual (ind.) clearance rates of gelatinous predators vs. biomass. *M. leidyi* and *Chrysaora quinquecirrha* relationship is based on feeding rates on copepods from Purcell and Decker (2005). *Aurelia aurita* relationship is based on feeding rates on copepods from Møller and Riisgård (2007). Medusae relationship is from Titelman and Hansson (2006) and is a regression of multiple medusan species including, *Catablema vesicarium, Chrysaora quinquecirrha, Cyanea capillata, Staurophora mertensi, Pseudorhiza haecklelii,* and *Aurelia aurita*, feeding on fish larvae. Regression equations follow log $F = F_0 + a$ log x, where F = clearance and x = biomass. *M. leidyi:* $F_0 = 1.19$, $a = 0.54$; *C. quinquecirrha:* $F_0 = 0.69$, $a = 0.59$; mixed medusae: $F_0 = -0.48$, $a = 0.49$; *A. aurita:* $F_0 = -2.07$, $a = 0.75$.

reduced at both low and high flow levels (Best 1988; Sebens et al. 1998). Although flow rates through *M. leidyi* are directly related to the swimming rates (Colin et al. 2010), measured capture efficiencies did not decline during more rapid swimming [except at the highest swimming speeds which are not commonly observed (Titelman et al. 2012) except at times in turbulent environments (Sutherland et al. 2014)]. Feeding rates of many aquatic predators, most commonly ambush foragers, are characterized by decreased performance at higher turbulence levels so that feeding rates exhibit a dome-shaped curve in relation to turbulence intensity (Mackenzie et al. 1994; Saiz et al. 2003). In contrast, swimming speed did not reduce efficiencies and did increase encounter rates (Colin et al. 2010) for *M. leidyi*. These traits may allow *M. leidyi* to maintain capture high capture efficiencies during periods of elevated swimming in turbulent regimes (Sutherland et al. 2014). Consequently, moderate

levels of turbulence may even have the potential to enhance predation.

In conclusion, we have demonstrated that the lobate ctenophore, *M. leidyi*, feeds by actively scanning its feeding current for prey using its sensory capabilities. This mechanism places *M. leidyi* (and potentially other lobate ctenophores) in a category of suspension feeders similar to copepods. It also helps us to better understand how *M. leidyi* is capable of foraging effectively as an important predator that is capable of having a greater effect on pelagic ecosystems than medusae. Furthermore, this new appreciation of its feeding mechanics may help explain how such a delicate gelatinous predator which generates a slow laminar feeding current is capable of thriving in unpredictable and highly variable coastal fluid environments.

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