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# Ink Release and Swimming Behavior in the Oceanic Ctenophore *Eurhamphaea vexilligera*

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**Abstract.** Of the more than 150 ctenophore species, the oceanic ctenophore *Eurhamphaea vexilligera* is notable for its bright orange-yellow ink, secreted from numerous small vesicles that line its substomodeal comb rows. To date, *in situ* observations by scuba divers have proved the most fruitful method of observing these animals' natural behavior. We present the results of one such contemporary scuba-based observation of *E. vexilligera*, conducted in the Gulf Stream waters off the coast of Florida, using high-resolution photography and video. Utilizing underwater camera systems purpose built for filming gelatinous zooplankton, we observed *E. vexilligera* ink release and swimming behavior *in situ*. From these data, we describe the timeline and mechanics of *E. vexilligera* ink release in detail, as well as the animal's different swimming behaviors and resulting ink dispersal patterns. We also describe a rolling swimming behavior, accompanied and possibly facilitated by a characteristic change in overall body shape. These observations provide further insight into the behavioral ecology of this distinctive ctenophore and may serve as the foundation for future kinematic studies.

## Introduction

Even among the morphologically diverse ctenophores, the lobate *Eurhamphaea vexilligera* Gegenbaur, 1856 is distinct. Dozens of bright-red vesicles line the comb rows on either side of its body, following the path of the substomodeal meridional canals (see Fig. 1A for anatomical overview). These vesicles contain a bright orange-yellow ink (Gegenbaur, 1856; Chun, 1880; Jonescu, 1908; Mayer, 1912) that *E. vexilligera* releases as an apparent stress response or defense mechanism (Mayer, 1912; Hamner *et al.*, 1975; Harbison *et al.*, 1978; Harbison and Madin, 1982). *Eurhamphaea vexilligera* also releases a substance that produces blue-green luminescent sparkles (Hamner *et al.*, 1975; Harbison *et al.*, 1978; Harbison and Madin, 1982). Harbison and Madin (1982, p. 714) state simply that "the ink is bioluminescent and produces blue-green sparks." However, it is not clear whether the bioluminescence is a separate component of the ink released from the same vesicle structures or whether it is formed and exuded from elsewhere and is released under the same stimuli as the ink. It has been suggested that the ink might serve as a distraction for visual predators (Hamner *et al.*, 1975) or that it is noxious to nearby animals (Taniguchi, 1975), but these intriguing ideas have never been experimentally assessed. Likewise, the mechanical details of how *E. vexilligera* releases its ink and any behaviors it uses to disperse it have remained murky.

Though originally described more than a century ago from scattered samples collected in the shallow coastal waters of the Mediterranean (Gegenbaur, 1856; Chun, 1880; Jonescu, 1908) and the Tortugas (Mayer, 1912), *E. vexilligera* is primarily found in the currents of the open ocean, with most modern observations coming from the Gulf Stream in the Atlantic Ocean (Harbison *et al.*, 1978; Harbison and Madin, 1982). It is unsurprising then that *E. vexilligera* kept in an aquarium will rapidly discharge all its ink (Mayer, 1912) and that the species is generally not amenable to being kept in culture (Taniguchi,

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*Online enhancements*: videos.

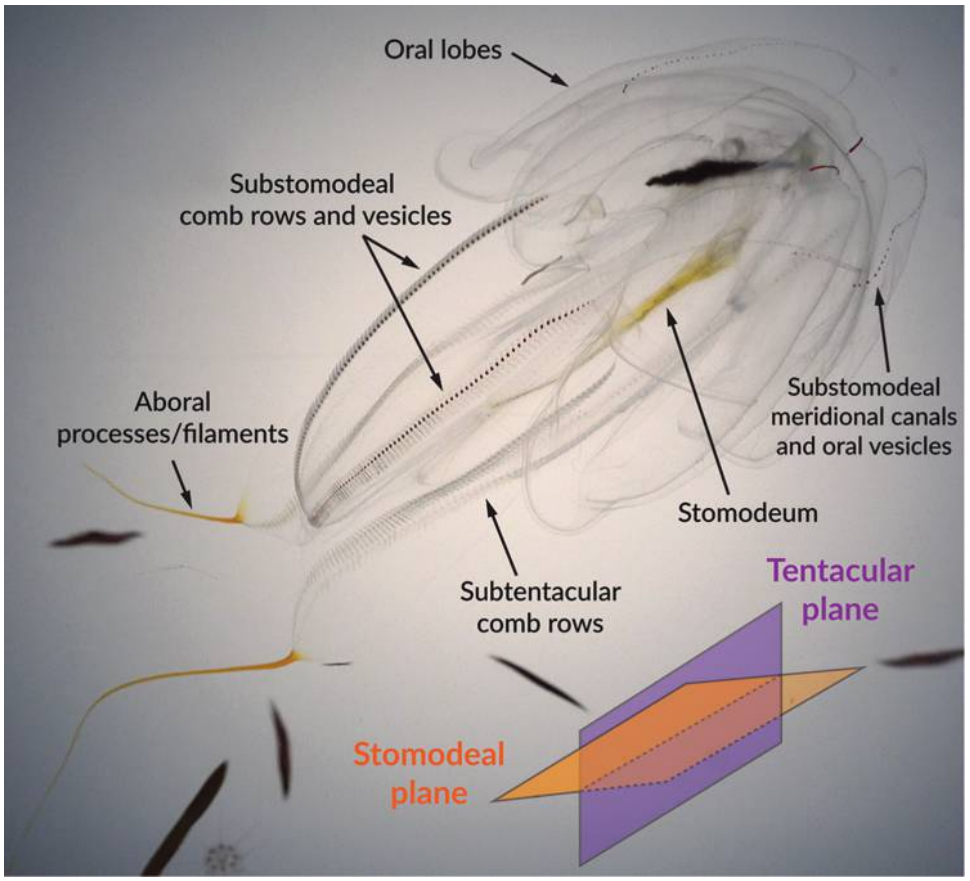


**Figure 1.** Adult *Eurhamphaea vexilligera* showing major organs and body axes. The anatomy of *E. vexilligera* is similar overall to most other lobate ctenophores, with the addition of its namesake flag-like aboral processes and its rows of ink-secreting vesicles extending along the substomodeal meridional canals. Image collected *in situ* from brightfield video system.

1975). As a result, many aspects of the behavior and ecology of *E. vexilligera* remained unknown until the advent of blue-water scuba diving in the late twentieth century made *in situ* observations of this species—and other fragile oceanic plankton—possible (Hamner *et al.*, 1975). Such dives have permitted direct observation of *E. vexilligera* swimming and feeding in greater detail, but these observations have been limited. Complex systems of behavior, like the release and dispersal of *E. vexilligera* ink and the effects of this ink on nearby organisms, require detailed review of as much naturalistic footage as possible.

To that end, we have observed *E. vexilligera* ink release during blue-water scuba dives by using high-definition camera equipment and lighting rigs purpose built for the filming of transparent, gelatinous animals. These data reveal new details of the morphology of *E. vexilligera* ink vesicles and the mechanics of ink release. Over numerous observations, we also saw several distinct patterns of swimming and ink dispersal behavior, as well as signs of the ink's possible effects on nearby organisms. Though many questions remain about *E. vexilligera* and its ink, the present study demonstrates the continued necessity and utility of direct observation for uncovering new levels of detail in studies of fragile and difficult-to-access marine organisms.

## Methods

Individuals of *Eurhamphaea vexilligera* Gegenbaur, 1856 (Fig. 1) were observed and collected *in situ* by blackwater scuba diving (*i.e.*, nighttime blue-water scuba) off the coast of West Palm Beach, Florida (26°43′93″ N, 79°59′15″ W), at depths between 3 and 15 m. Collected animals were placed into 1-L jars and transported at ambient temperature back to the lab for laboratory observations. Brightfield video was captured *in situ* on a custom rail-mounted camera rig consisting of a Sony AX100 camcorder recording at 4K resolution and 30 frames per second (fps), illuminated by a LED light tablet with an in-line diffuser. A total of 11 individual *E. vexilligera* were filmed with this apparatus and subsequently analyzed for their *in situ* behavior. Additional *in situ* wide-angle video was captured on a GoPro HERO4 Black Edition (San Mateo, CA) recording at 1080p and 60 fps. Still photos were captured

using a Nikon D750 digital single-lens reflex (DSLR) camera with a 24.3-megapixel full-frame complementary metal oxide semiconductor (CMOS) sensor. *In situ* DSLR stills were captured by using a 60-mm prime lens in an underwater housing, while micrographs were captured in the lab by fitting the D750 to a Motic SMZ-168 stereo microscope (Kowloon, Hong Kong), using an F-mount adapter. Length and angle measurements from still images and frames from video data were analyzed in ImageJ (Rueden *et al.*, 2017). Frame-by-frame reviews of *in situ* videos for behavioral and morphological details were conducted in Adobe Premiere. Throughout the text, counted or measured values are reported in the form of mean ± standard deviation.

## Results

### *Anatomy of* Eurhamphaea vexilligera *comb row- and oral lobe-associated ink vesicles*

We observed two broad classes of ink vesicles in *Eurhamphaea vexilligera*: those associated with the four substomodeal comb rows (Figs. 1–3) and those associated with the oral lobes (Fig. 1, 4). Both types of ink vesicle were red in color and appeared directly adjacent to the substomodeal meridional canals, but they differed in overall size, shape, and number.

The ink vesicles associated with the substomodeal comb rows were covered by the ctenes of the comb rows when the ctenes were not active. Ostensibly full ink vesicles appeared deep red-orange in color in transmitted light under a stereo microscope (Fig. 2A); but after repeated ink release events, the color faded to yellow, with the center of the discharged vesicle appearing almost transparent (Fig. 2B). Comb row-associated ink vesicles were semi-ellipsoidal (Fig. 2A, B) and slightly elevated in profile relative to the surrounding tissue (Fig. 2C). Ink vesicles were consistently offset from the center line of the comb row (dashed line in Fig. 2A) by about 0.5 mm, lying on the side of the meridional canal, facing toward the major axis defined by the center of the stomodeal plane (Fig. 2D; see Fig. 1 for symmetry plane reference).

On the opposite side of the meridional canal from each vesicle, there was a small triangular projection of tissue (green arrows in Figs. 2A, 3). In a single *in situ* image of a particular *E. vexilligera* individual, we observed that in the space between two mature ctenes, there was not one but two vesicles present, positioned very close to one another, equidistant around the midpoint between the two nearest ctenes (Fig. 3, inset). Each of these vesicles appeared smaller than vesicles associated with neighboring ctenes, and these smaller twinned vesicles each had its own triangular projection associated with it on the opposite side of the meridional canal (Fig. 3, inset, green arrows).

Filled comb row-associated vesicles were 82 ± 27 $\mu$m tall ($n$ = 8), 196 ± 40 $\mu$m long ($n$ = 13), and 127 ± 35 $\mu$m wide ($n$ = 13) (Fig. 2A–C). Using these values, we estimated the approximate volume of a single comb row-associated vesicle as 1.1 ± 0.51 nL. Each of the 4 substomodeal comb rows displayed 48 ± 15 filled vesicles (average per comb row across

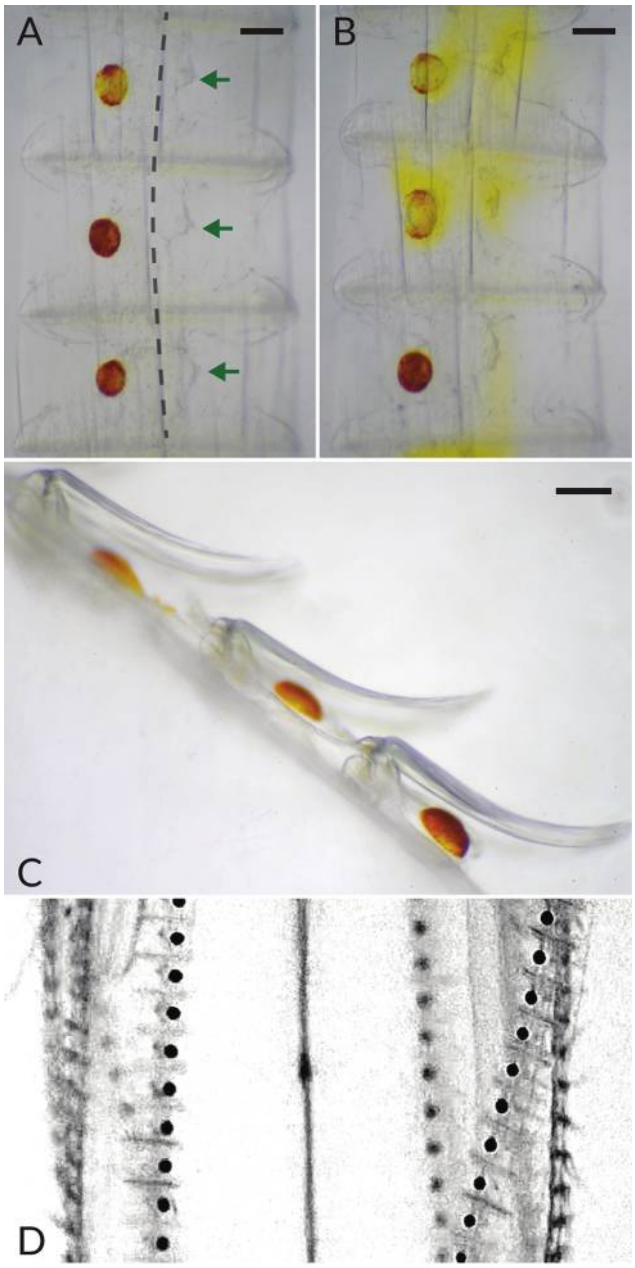


**Figure 2.** Microscopic views of *Eurhamphaea vexilligera* ink vesicles and their position. Top-down view of ink vesicles before (A) and after (B) an ink release event. Arrows indicate triangular structures associated with vesicles. Ink can be released from particular localized vesicles along the same comb row (scale, 200 $\mu$m). Viewed in profile (C), the semi-ellipsoidal shape of the vesicles and their occlusion by each adjacent ctene becomes apparent (scale, 300 $\mu$m). The offset of the vesicles from the center line of the comb row, observable in (A) and (B), is consistent across the comb row, such that the vesicles are offset toward each other in the tentacular plane (D). Micrographs in (A–C) from laboratory observations; photograph in (D) collected *in situ*. Contrast has been enhanced for clarity in (D).

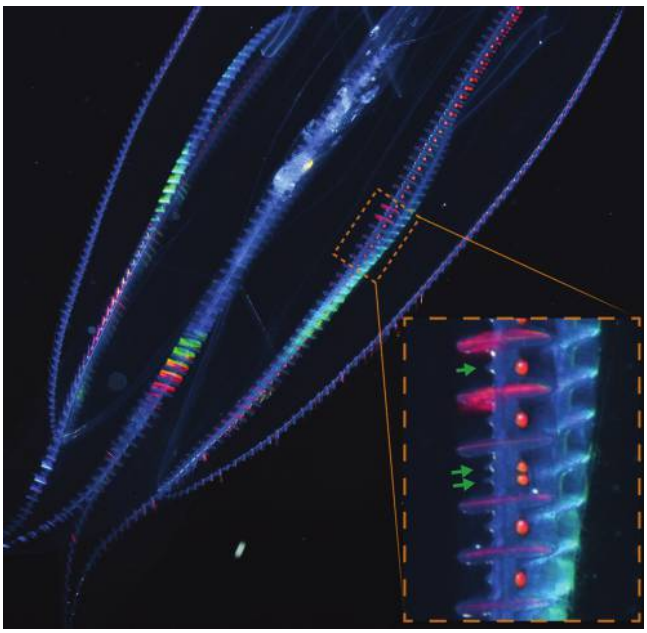

**Figure 3.** "Twinned" ink vesicles. *In situ* photograph of a pair of *Eurhamphaea vexilligera* ink vesicles breaking the regular spacing of their comb row. Each vesicle on the comb row, including this unusual pair, has a triangular projection of tissue associated with it (green arrows).

55 fully in-focus comb rows from 13 *E. vexilligera* individuals), adding up to a total of 51 ± 0.57 nL of ink in the comb row-associated vesicles in an average *E. vexilligera*.

Vesicles associated with the substomodeal canals in the oral lobes (Fig. 4A, black arrows) were much smaller than those associated with the comb rows and were roughly ellipsoidal (Fig. 4B), measuring 55 ± 28 $\mu$m long and 37 ± 6 $\mu$m wide on average ($n = 3$). From this, we estimated that the average volume of each oral lobe vesicle was 0.039 ± 0.021 nL. Each of the 4 portions of the substomodeal meridional canals in the oral lobes displayed around 24 ± 7 vesicles (average across 42 fully in-focus canals from 11 *E. vexilligera* individuals), adding up to a total of 0.93 ± 0.60 nL of ink in the oral lobe vesicles in an average *E. vexilligera*.

The oral lobe vesicles appeared alongside a pair of small red stripes running along the midline of each oral lobe (Fig. 4A, red arrows; also visible in Fig. 1). Each stripe is about 1 mm long and less than 0.1 mm wide. To our knowledge, these stripes have not been described, nor is their purpose known. They were present on all observed *E. vexilligera* individuals.

### *Ink release and concurrent swimming behavior*

As seen in the two ink release sequences annotated for Figure 5, an entire ink release event occurred on the order of seconds. While the exact timing of each step varied, as did the number and position of active vesicles, the release of ink from the vesicles was characterized by the following sequence of events. Starting from a resting position, with the ctenes occluding the vesicles to be activated (Fig. 5A), the ctenes flipped up, uncovering the soon-to-be-active vesicles (Fig. 5B). Then ink began to stream out of the vesicles in thin plumes (Fig. 5C). The release of ink was often slow at first, but eventually the release of ink appeared to peak (Fig. 5D). The release of ink slowed and eventually stopped, accompanied by occasional fluttering of the ctenes around the site of release (Fig. 5E). Then the ctenes returned to the starting position, covering the vesicles again or otherwise resumed active swimming strokes (Fig. 5E).

*In situ* observations of *E. vexilligera* ink release coincided with several distinct swimming behaviors and resultant ink dispersal patterns, resulting in ink clouds of different sizes, shapes, and densities.

1. While an individual swam with the oral end forward in the direction of travel, ink was released such that it streamed

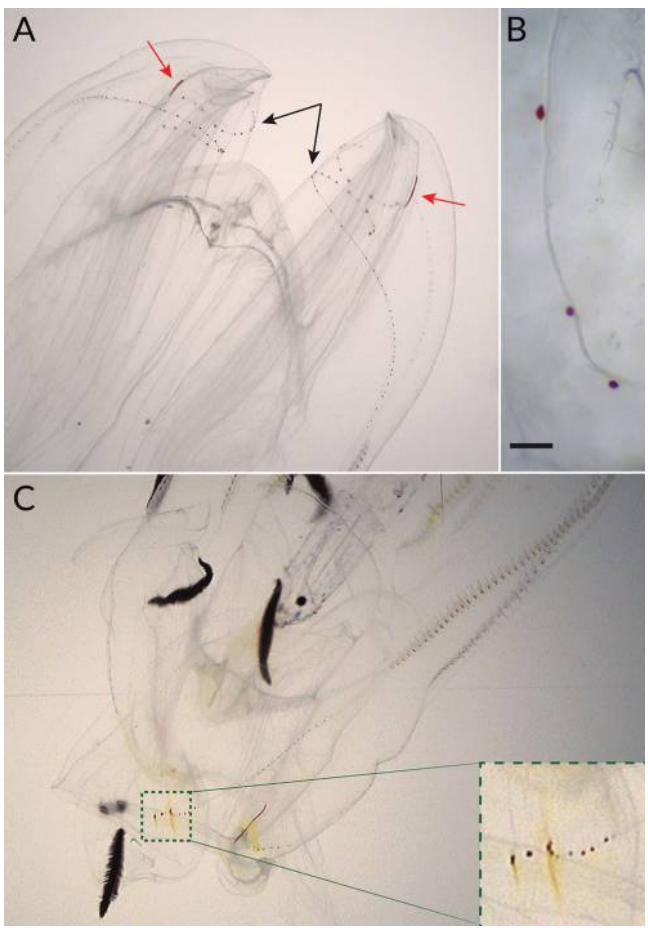


**Figure 4.** Anatomical features of *Eurhamphaea vexilligera* oral lobes. The substomodeal meridional canals extend onto the oral lobes and with them, a series of vesicles similar to those associated with the comb rows (A, black arrows). The oral lobes also possess a pair of red stripes running along the midline of the lobes (A, red arrows). At a microscopic scale, the oral lobe vesicles appear roughly ellipsoidal and are similar in color to the comb row vesicles (B; scale, 200 $\mu$m). We observed the release of ink from the oral lobe vesicles (C). All images collected *in situ* from brightfield video system.

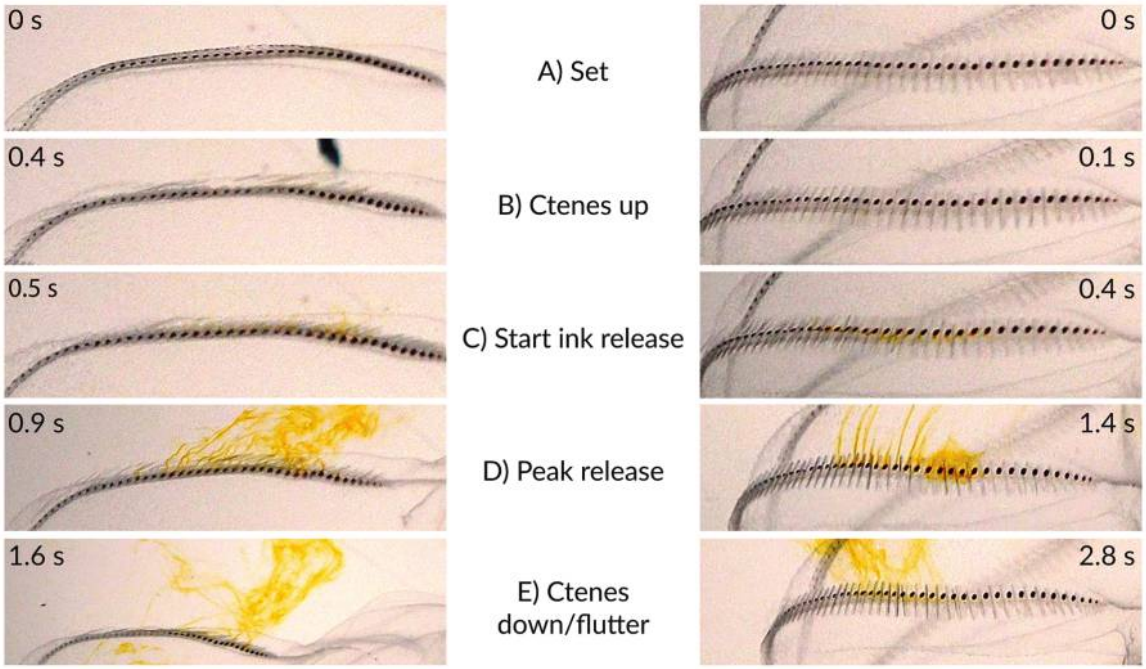


**Figure 5.** Timeline of an ink release event in *Eurhamphaea vexilligera*. Profile (left) and top-down (right) views of two different ink release events, with the times of occurrence of each in the sequence. The sequence starts from a neutral position, with the ctenes all or mostly lying flat against the body. Before ink is released, the ctenes associated with the vesicles that will release ink flip up. Then <0.5 seconds later, ink begins to stream out of the vesicles. This continues for ~1–2 seconds, with the relevant ctenes locked up the entire time. After 1.5–3 seconds from the start of the sequence, the stream of ink cuts off, often accompanied by a fluttering of the ctenes on the row. All images collected *in situ* from brightfield video system. Contrast in all panels has been increased for clarity.

out in trails of variable length extending behind the animal's aboral end (Fig. 6A, B; Video S1, available online).

2. While an individual switched between oral end-first and aboral end-first swimming, ink was released intermittently throughout, producing a dispersed cloud of ink around the animal (Fig. 6C, D; Video S1).

An individual *E. vexilligera* could alternate between these patterns within several minutes of recording. *Eurhamphaea vexilligera* was also observed to swim oral end first without accompanying ink release. Occasionally, all the vesicles on an individual would activate at once. Typically, though, the vesicles on a single comb row, or a subset of vesicles on one or more comb rows, would activate. Hence, ink release was not typically a global event involving all comb rows but rather a restricted event within or between comb rows with apparent local control.

### *Body posture and "rolling"*

We observed that *E. vexilligera* swims with two body postures, which we term "neutral" and "angled." In the neutral posture, the two halves of the body, as divided by the tentacular plane, were aligned with one another such that the substomodeal comb rows lay approximately parallel with the center axis of the body through the stomodeum (Fig. 7A; see Fig. 1 for symmetry plane reference). In the angled posture, individuals tilted the two halves of their bodies in the tentacular plane at opposing angles to one another (Fig. 7B). This is a rough distinction: due to their unique biradial symmetry, all ctenophore bodies have a certain visible "twistedness" to them. Even in an apparently relaxed posture, the body does not show mirror symmetry around the tentacular plane. However, the angled posture we describe in *E. vexilligera* coincided with another distinct behavior—oral-first swimming in which the entire body of the ctenophore rotated around the oral-aboral axis, resulting in corkscrewing forward swimming, reminiscent of an airplane performing an aileron roll. The direction of this roll was consistently clockwise in the direction of travel (from $n = 9$ observed rolling individuals). Swimming rolls were often also accompanied by the release of ink ($n = 7$), leaving semi-coherent trails of ink trailing behind the animal as it moved along (Fig. 6A, B). During a roll, some (Video S2, available online) or all (Video S3, available online) of the comb rows were active, depending on whether ink release was happening at the same time. Rolling maneuvers consisted of between one and five full-body rotations. The maximum angular velocity of observed rolls was ~65° per second (Videos S2, S3) but could be as low as ~33° per second (Video S4, available

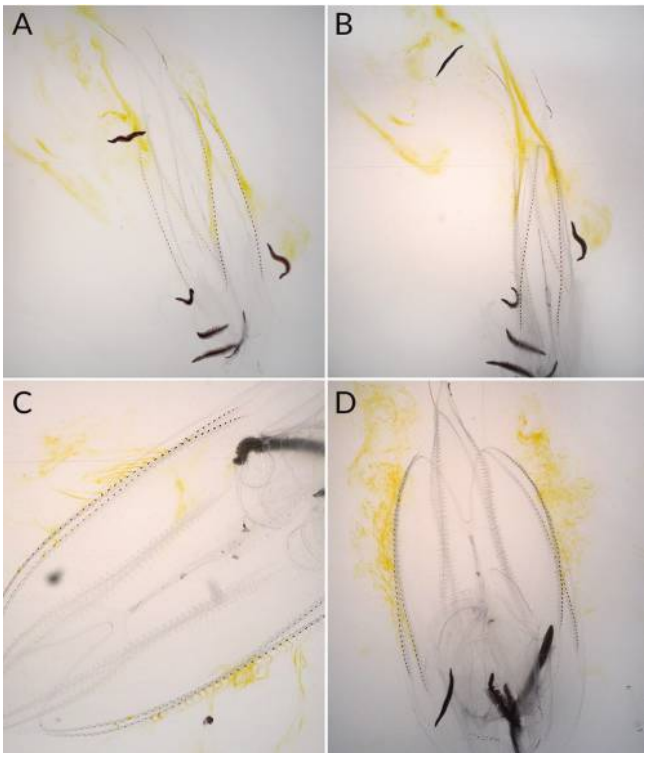


**Figure 6.** Swimming behaviors accompanying ink release. *Eurhamphaea vexilligera* ink release events are accompanied by two distinct swimming behaviors. In the first, the individual swims oral end first (A), releasing ink in streams behind it (B), often accompanied by rolling behavior. In the second pattern, the individual swims forward and backward rapidly (C) to create a cloud of ink around itself (D). All images collected *in situ* from brightfield video system.

online), particularly when accompanied by frequent ink release events. There was no apparent relationship between animal size and rolling rate. The angle of the two halves of the body relative to the midline (as defined by the stomodeum) was consistent: the face of the body half pointing into the direction of the roll was angled out from the midline at $12.9° \pm 2.6°$ ($n = 11$), while the face of the body half pointing away from the direction of the roll was angled out from the midline at $9.3° \pm 2.1°$ ($n = 11$). In other words, in profile, the leading edge of the rolling ctenophore's body tended to be angled more sharply outward than the trailing edge (Fig. 7B).

### *Effects of* Eurhamphaea vexilligera *ink on nereid polychaetes*

Our *in situ* observations of *E. vexilligera* coincided with the swarming of a large number of nereid polychaete worms. These worms can be seen in Video S1 (available online) swimming rapidly in and out of view while making frequent contact with *E. vexilligera*, apparently stimulating ink release events as a response. In several instances, polychaetes swimming through clouds of ink appeared to slow or stop their swimming or swim in a less coordinated fashion briefly, until they exited the ink cloud. Some worms became caught on the oral lobes. After several seconds in this position, sometimes accompanied by rapid back and forth movement and inking (ink dispersal pattern 2 above), the nereid worms appeared to cease movement altogether before eventually being sloughed off (Video S1).

## Discussion

*Eurhamphaea vexilligera* ink and the vesicles that release it have been a subject of fascination since the species' initial description (Gegenbaur, 1856; Chun, 1880; Jonescu, 1908; Mayer, 1912; Harbison *et al.*, 1978; Harbison and Madin, 1982). Referring to the substance as an "ink" evokes an immediate comparison to cephalopod ink—though, anatomically, the distributed system of numerous small ink vesicles in *Eurhamphaea* (Fig. 1) seems to be a sharp departure from the centralized glandular ink sacs of squid and octopuses. Likewise, the small, thin, coherent streams of ink that *Eurhamphaea* leaves behind as potential decoys are much smaller than cephalopod pseudomorphs—defined for cephalopods as clouds of ink and mucous roughly the same size and shape as the animal that produces them. Other useful analogs exist within Ctenophora. For example, the bioluminescent sparkles produced by *E. vexilligera* ink appear similar to the secretions of *Euplokamis stationis* and *Bathyctena chuni* (Haddock and Case, 1999; Widder, 2002). However, these species' bioluminescent secretions have been observed only at significantly greater depths (>300 m) than *E. vexilligera*, which has almost exclusively been observed and collected at the surface or within the operational range of scuba divers (<30 m). A bright orange ink is reportedly released by *Leucothea japonica* (Kubota, 1996), another lobate ctenophore known primarily from surface waters; but no further investigations have been undertaken in that species.

In general, visible secretions from marine animals are hypothesized to be used for intraspecific communication, predator deterrence, or luring prey. Ctenophores' ability to sense light for hunting or communication is limited (Haddock and Case, 1999; Schnitzler *et al.*, 2012), suggesting that the ink trails and bioluminescent sparks of *E. vexilligera* are a signal intended for more visually inclined predators or prey. Unfortunately, little is known about the feeding ecology of *E. vexilligera*; in the field, various copepods, ostracods, pteropods, and siphonophores can be seen in their guts (Harbison *et al.*, 1978), but the role of the ink in capturing any of these prey is unknown. In our *in situ* videos, *E. vexilligera* is seen interacting with numerous nereid polychaetes. These worms were significantly larger than prey previously observed in *E. vexilligera* guts (Harbison *et al.*, 1978) and appeared as a nuisance to *E. vexilligera*, attracted to the dive area by the numerous bright lights from our filming equipment; so what, if any, aspects of their interactions with *E. vexilligera* are natural under the

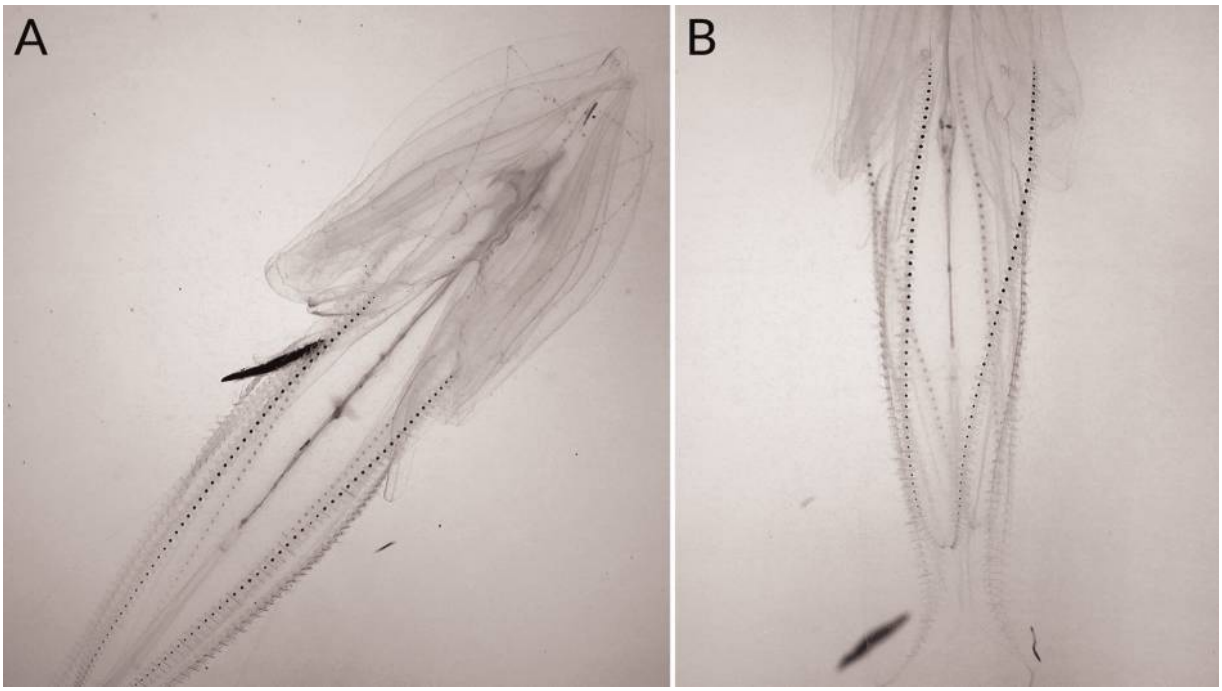


**Figure 7.** Two body postures. While swimming, *Eurhamphaea vexilligera* adopts one of two body postures. In the "neutral" posture (A), the two halves of the animal, as divided through the tentacular plane, are even with one another; and the substomodeal comb rows appear parallel with the center axis of the animal (as defined by the stomodeum). In the "angled" posture (B), those same halves of the animal are positioned at angles opposite to one another. As a result, the substomodeal comb rows are positioned at an acute angle relative to the animal's center axis. All images collected *in situ* from brightfield video system.

circumstances are unclear. *Eurhamphaea vexilligera* secretions do not seem to affect other ctenophores, such as the chemosensing *Beroe cucumis*, which has been observed to eat *E. vexilligera* (Swanberg, 1974). There are also data suggesting that ctenophores make up a large proportion of the diet of visually sensing predators, such as spiny dogfish (Link and Ford, 2006); but to our knowledge there are no extant studies of the interactions specifically between *E. vexilligera* and large, non-gelatinous potential predators.

Though previous authors have also speculated that *E. vexilligera* ink may serve a defensive role against visual predators (Hamner *et al.*, 1975; Harbison *et al.*, 1978; Harbison and Madin, 1982), our observations provide new insights into how the specific behavior and morphology of *E. vexilligera* might facilitate a defensive use for the ink, indicating more than one potential role for this substance.

The two swimming behaviors (Fig. 6) we observed during comb row-associated vesicle ink release suggest two distinct uses for this ink. First, when ink comes out in trails behind the animal as it rapidly moves away, the ink may serve as a decoy left behind to confuse or distract visual predators—either during the day through its yellow-orange pigmentation or at night by its sparkling bioluminescence, which can last for several minutes (Harbison *et al.*, 1978). In this dispersal mode, the animal is able to leave behind semi-coherent streams of ink of variable lengths (Fig. 6A, B). As the ink lingers and slowly disperses, these trails may become a field of decoy targets across a potentially large volume of water. Second, rapid back and forth swimming produces a cloud of ink around the ctenophore (Fig. 6C, D). This, combined with its apparent narcotizing effects on polychaetes' swimming behavior and overall activity (Video S1, available online), suggests that the ink may be acting as a kind of fumigant, similar to the toxic effects of the ink in an aquarium setting observed by Taniguchi (1975)—allowing *Eurhamphaea* to slow or incapacitate swarming pests before an escape or even to produce a field where potential prey animals are narcotized and thus easier to capture. This activity may be similar to the release of ink from the vesicles on the oral lobes (Fig. 4C). If the ink is in some way noxious to prey animals, releasing a small field of ink specifically near the oral lobes and the mouth may serve to stun or slow prey, making them easier to catch. The smaller size of these vesicles may be indicative of the need for less ink to fumigate the relatively small volume between the lobes.

In all these behaviors, the fact that ink may be released locally from a small number of vesicles on a particular part of the meridional canal or globally across an entire comb row or an entire animal appears key. Ink in *E. vexilligera* is a limited resource that can be exhausted, so having local control of when, where, and how much ink is released may help the animal to

conserve this resource. Furthermore, because sections of comb rows frequently become damaged, independent control of vesicles would provide redundancy, allowing this critical system to be resilient in the face of extensive injuries.

To our knowledge, neither the rolling swimming behavior nor the positioning of the body halves in either a neutral or angled posture (Fig. 7), as observed in *E. vexilligera*, has been reported in other ctenophores. Although all ctenophore bodies possess a certain degree of "twistedness" due to their biradial symmetry, the angled posture of *E. vexilligera* during a roll is particularly exaggerated. The lack of consistent differences in comb row beat frequency during rolling suggests that the angle of the body facilitates the roll; and the characteristic angle adopted by the animal may present some favorable properties for executing the maneuver, while comb row beat frequency affects the rate of the roll.

One potential reason for rolling, particularly during an escape response accompanied by ink release, may be to maintain the coherence of the ink trails. Because rolling is consistently clockwise in the direction of travel and because ink vesicles are on the side of the meridional canal facing the center of the major axis, comb row vesicles on the leading and trailing sides of the roll experience consistently different hydrodynamic conditions: ink from the leading edge row's vesicles streams out toward the smooth part of the body wall, while ink from the trailing edge row's vesicles must move past the other half of the comb row, where it meets the sharp angle where the stomodeal and tentacular plane faces of the body wall meet. The effects of these different hydrodynamic environments on ink release and dispersal, and ultimately on the ecology of *E. vexilligera*, are unclear but are worthy of further consideration.

Oceanic ctenophores such as *E. vexilligera* present many challenges to their study: less numerous and amenable to captivity than their inshore relatives such as *Mnemiopsis leidyi*, *Eurhamphaea* practically demands that interested researchers meet it in the open ocean. Once there, we are offered only brief glances into its world, limited by logistics. However, many aspects of these animals can be understood only through the careful review of their behavior in their natural habitats. Our *in situ* data suggest that the ink vesicles of *E. vexilligera* may be just one part of a complex system of anatomical features and swimming behaviors that facilitate the ink's potentially varied uses. Further study and more detailed observations of these organisms are necessary to unravel the significance of these adaptations to life in the open ocean.

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