

## In situ Observations of the Meso-Bathypelagic Scyphozoan, *Deepstaria enigmatica* (Semaeostomeae: Ulmaridae)

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### ABSTRACT

*Deepstaria enigmatica* (Semaeostomeae: Ulmaridae) is one of the largest and most mysterious invertebrate predators of the deep sea. Humans have encountered this jellyfish on only a few occasions and many questions related to its biology, distribution, diet, environmental tolerances, and behavior remain unanswered. In the 45 years since its formal description, there have been few recorded observations of *D. enigmatica*, due to the challenging nature of encountering these delicate soft-bodied organisms. Members of *Deepstaria*, which comprises two described species, *D. enigmatica* and *D. reticulum*, reside in the meso-bathypelagic region of the world's oceans, at depths ranging from ~600 to 1750 m. Here we report observations of a large *D. enigmatica* (68.3 cm length × 55.7 cm diameter) using a custom color high-definition low-light imaging system mounted on a scientific remotely operated vehicle (ROV). Observations were made of a specimen capturing or “bagging” prey, and we report on the kinetics of the closing motion of its membranelike umbrella. In the same area, we also noted a *Deepstaria* “jelly-fall” carcass with a high density of crustaceans feeding on its tissue and surrounding the carcass. These observations provide direct evidence of singular *Deepstaria* carcasses acting as jelly falls, which only recently have been reported to be a significant food source in the deep sea.

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## INTRODUCTION

*Deepstaria enigmatica* was first described as a “remarkable new scyphomedusan” and its species name “*enigmatica*” was based on its puzzling systematic position between Semaestomeae and Rhizostomeae (Russell, 1967). The genus *Deepstaria* currently comprises two species, *D. enigmatica* (Russell, 1967) and *D. reticulum* (Larson et al., 1988). Members of *Deepstaria* are characterized by a lack of tentacles, an extensive, thin membranelike umbrella, and long oral arms. *Deepstaria enigmatica* was described by Russell (1967) from a 50 cm diameter male specimen (gonads located at the proximal ends of fan-shaped mesenteries, which continue distally into the oral arms) collected at 723 m in the San Diego Trough. This partial specimen, of what first appeared as “a large collapsed and puckered, gelatinous bag with a few tentacles streaming from it,” was collected by Eric C. Barham, George Pickwell, and Ronald Church on October 21, 1966 using the U.S. Navy deep submersible *DEEPSTAR 4000* (Barham, 1969). *DEEPSTAR 4000* was a three-person submarine in service from 1965–1972 with an operational depth of 4000 feet and designed by the Westinghouse Corporation in collaboration with Jacques Cousteau and based on the *DIVING SAUCER* (Merrifield, 1969). A suction sampler was used to obtain the incomplete specimen, as the individual *D. enigmatica* was so large it needed to be taken to the surface with part of it still extending from the suction funnel. Much of the existing information about *D. enigmatica* is from this specimen (now in the British Museum of Natural History, BMNH 1967.5.24.1).

Members of *Deepstaria* display unique behaviors compared to other scyphozoan species, such as peristaltic locomotion and pursing of the bell margin. Larson et al. (1988) hypothesized that the peristaltic locomotion was necessary because the umbrella is too thin and the subumbrella musculature too diffuse to support more rapid pulsation (Larson et al., 1988). Lacking tentacles, *D. enigmatica* feeds in a novel fashion by encapsulating its prey within its entire gelatinous umbrella. *D. enigmatica*’s bell is remarkably thin, broad, and delicate, and is easily deformed by the flow of water created by the thrusters of submersibles and ROVs. This trait has contributed to the rarity of observations and collections, as midwater trawls easily shred them.

Gelatinous macroplankton including cnidarian medusae, ctenophores, and pelagic tunicates are becoming increasingly recognized as key ecosystem consumers of energy and nutrients (Doyle et al., 2014; Graham et al., 2014). For many years this field was neglected with gelatinous zooplankton often referred to as “forgotten fauna” (Pugh, 1989). Globally, gelatinous zooplankton are now estimated to constitute a carbon biomass of 38.3 Tg C (Lucas et al., 2014) and are receiving increasing attention. Nevertheless, species of *Deepstaria* and other large deep-sea semaestome scyphomedusae (30–70 cm) are still rarely observed.

## MATERIALS AND METHODS

The observations we report on took place aboard the exploration vessel (E/V) *Nautilus* (leg NA092) and the *Deepstaria enigmatica* specimen was encountered on November 15, 2017, off San Benedicto Island, Mexico (19.2° N, 110.77° W) via the remotely operated vehicle (ROV) *Hercules*.

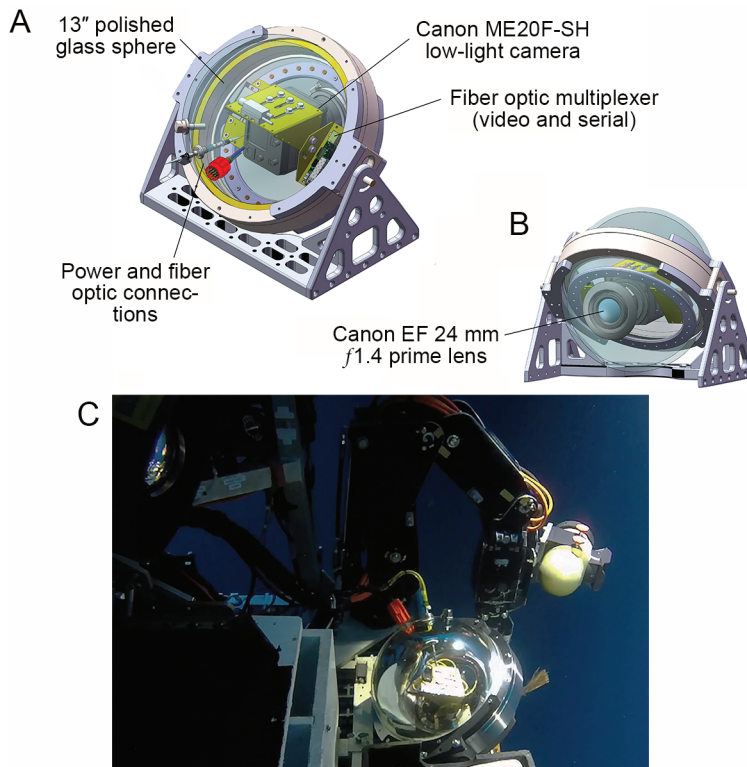


FIGURE 1. Canon ME20F-SH configuration showing A, backside, B, frontside, and C, mounted to the front of ROV *Hercules*.

For deep-sea imaging, we configured a polished VITROVEX 13" Deep Sea Sphere (Nautilus Marine Service) to house a high-definition/low-light camera with an ISO of 4,560,000 (Canon ME20F-SH) (fig. 1). The camera was equipped with a Canon EF 24 mm f/1.4L II USM lens. The camera and lens settings were controlled live from the ship via a remote controller (Canon RC-V100). All video and control signals were transmitted using a fiber optic multiplexer (Moog Focal 914 HDE).

The midwater *Deepstaria enigmatica* was filmed on dive no. H1666 at 974 m for 9 min 49 sec using the Canon ME20F-SH camera system described above. Scaling lasers (DeepSea Power & Light) placed 10 cm apart were used to obtain information on the size of the individual (fig. 2). The *Deepstaria* (jelly fall, either *D. enigmatica* or *D. reticulum*) was filmed on dive H1664 at 899 m among a dense assemblage of sponges and corals on a pillow basalt outcrop just below the oxygen minimum zone east of Socorro Island. Videos from Dive H1664 were obtained using an Insite Pacific Zeus Plus HD video camera outfitted with an Ikegami HDL-45A head and Fujinon HA 10 × 5.2 lens.

## RESULTS

The encounter with *D. enigmatica* lasted 9 minutes and 49 seconds (see Video 1, available at <https://doi.org/10.5531/sd.sp.32>). The specimen was observed while testing a new color

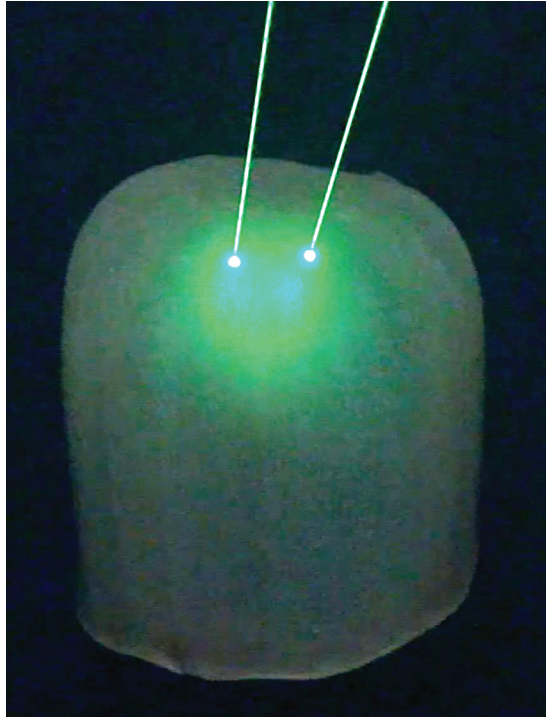


FIGURE 2. Screenshot taken from video of *Deepstaria enigmatica* recorded at 974 m, showing the 10 cm spacing of lasers.

low-light camera system (Canon ME20F-SH) with dimmable LED lighting (SeaLite 2000, DeepSea Power & Light) mounted on the ROV *Hercules*. The lights were set at their lowest setting (~274 lumens), a lighting regime <0.04% of the high-power setting (~76,000 lumens) often used on ROV *Hercules*. The combined sensitivity of the camera sensor (ISO 4,560,000) and the minimized light disturbance enabled the visualization of bioluminescence from *Tomopteris* sp. swimming alongside *D. enigmatica* (fig. 3; see also Video 2, available at <https://doi.org/10.5531/sd.sp.32>). While bioluminescence is a common feature in the deep sea, this feature is not captured using standard ROV lighting and HD cameras.

In *D. enigmatica*, we observed that the peristaltic wave is related to the closing of the mouth of the bell, which takes place in <3 sec. The wave begins at the bottom of the organism at a rate of approximately 1.5 cm/sec and then forms a bulge in the center (fig. 4). This bulge persists for the duration of the time that the bell margin is closed (fig. 5A). As *D. enigmatica* lacks tentacles, this process could be used as a mode of upward propulsion, as well as the mechanism by which it entraps prey. However, it was necessary to move the ROV only ~1 m upward in the water column directly following the closing sequence. Once the umbrella is closed, there remains only a small circular opening (~10 cm) that does not open upon disturbance (fig. 6). The specimen of *D. enigmatica* filmed bumped into the dome of our camera and afforded the opportunity of a close-up of its anastomosing canals (fig. 5B).

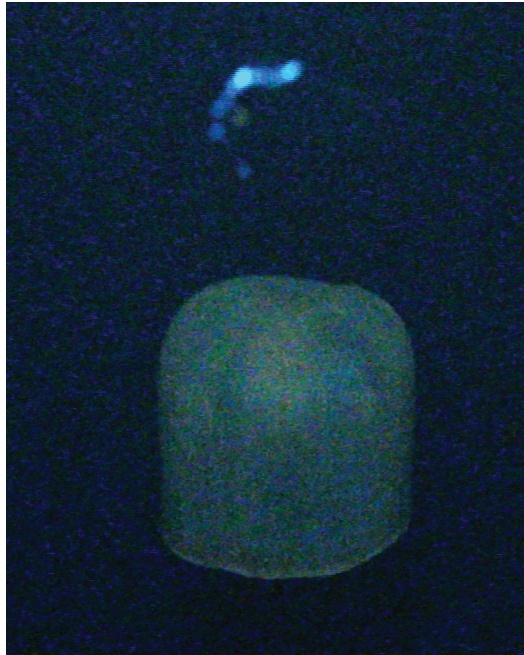


FIGURE 3. *Deepstaria enigmatica* (below) with a blue-emitting bioluminescent *Tomopteris* sp. (above).

In a nearby benthic area at a depth of 899 m, we came across a *Deepstaria* sp. (*D. enigmatica* or *D. reticulum*, specific ID not possible from video) carcass (fig. 7). This was among a dense assemblage of sponges and corals on a pillow basalt outcrop just below the oxygen minimum zone east of Socorro Island. The carcass (“jelly fall”) was being consumed by several larger lithodid crabs (*Paralomis* sp.) (fig. 7) and caridean shrimp (density of  $>80$  individuals/m<sup>2</sup>).

## DISCUSSION

Whereas *Deepstaria enigmatica* has been known for almost half a century and is one of the larger deep-sea predators, it remains largely unstudied. Its biology, behavior, distribution, and abundance remain relatively unknown. There are partial specimens in museum collections, and DNA sequences for three ribosomal RNA genes are deposited in the National Center for Biotechnology Information (<https://www.ncbi.nlm.nih.gov/nuccore/?term=deepstaria>). Scyphomedusae diversity is currently at ~400 described species and it is estimated that at least 400 additional species await description (Gómez Daglio and Dawson, 2017).

Larson (1986) placed *D. enigmatica* in the semaestome family Ulmaridae (Haeckel, 1879) because of the presence of semaestome-like oral arms and a gastrovascular system consisting of canals. Members of *Deepstaria* are unusual among jellyfish in possessing a distinct, highly branched network of anastomosing canal systems distributed uniformly over the bell and resembling wire netting. This network is the animal’s digestive tract and

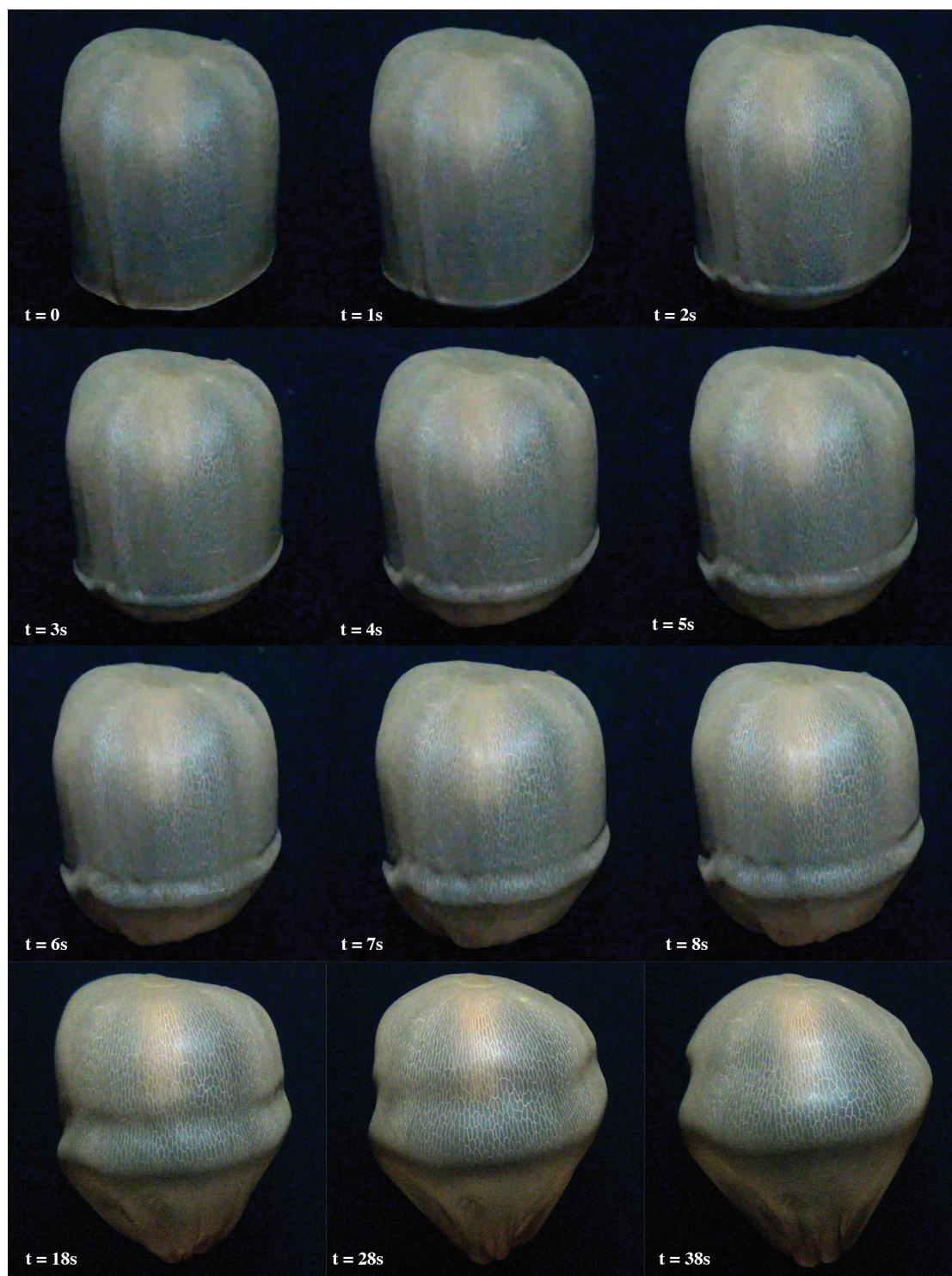


FIGURE 4. Time-lapse series of *Deepstaria enigmatica* closing, illustrating peristaltic motion.

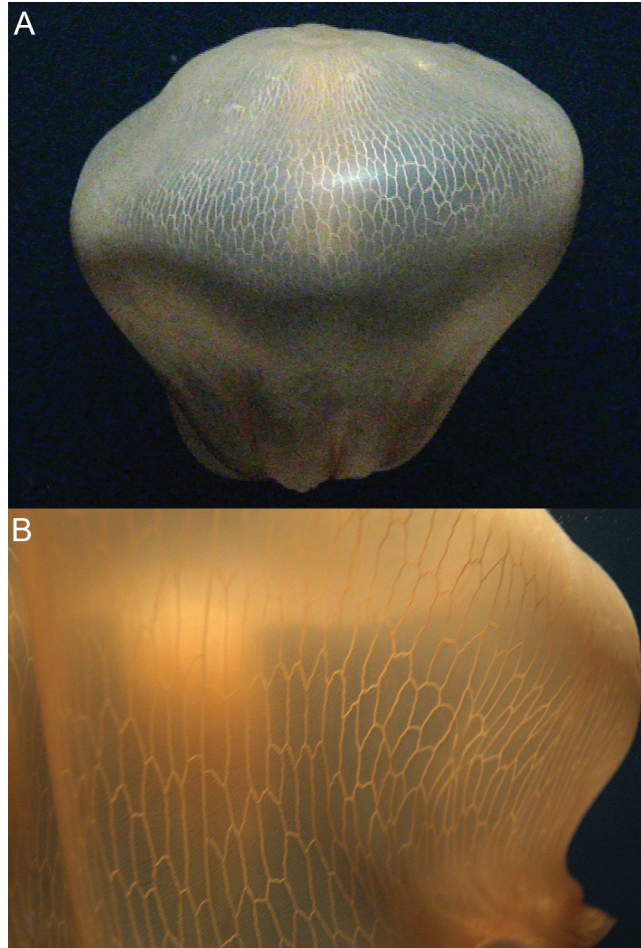


FIGURE 5. **A**, *Deepstaria enigmatica* in a closed/pursed position. **B**, Close-up image of anastomosing canals in of *D. enigmatica*.

is characteristic of several Ulmaridae. Our observations provide unprecedented detail of their anastomosing canal structure and color in situ prior to any damage resulting from physical collection. *Deepstaria enigmatica* and *D. reticulum* (described by Larson, 1986) comprise the subfamily Deepstariinae. Only three Semaestomeae genera are known to be meso-bathypelagic, *Deepstaria*, *Poralia*, and *Stygiomedusa*. Of these, *Deepstaria* is the rarest (Larson et al., 1988). Two recent phylogenetic analyses both confirm *Deepstaria*'s position in the family Ulmaridae. Somewhat surprisingly, both analyses recover the genus *Aurelia*, the moon jellyfish, as closely related to *Deepstaria* (Bayha et al., 2010; Gómez Daglio and Dawson, 2017). *Aurelia*, a widely studied shallow-water jellyfish, has recently been shown to exhibit life cycle reversal (He et al., 2015). It is interesting to hypothesize whether *Deepstaria* might exhibit a similar trait, but the rarity of encounters, compounded by the difficulty in conducting such biological studies in the deep sea, makes testing this hypothesis highly challenging.

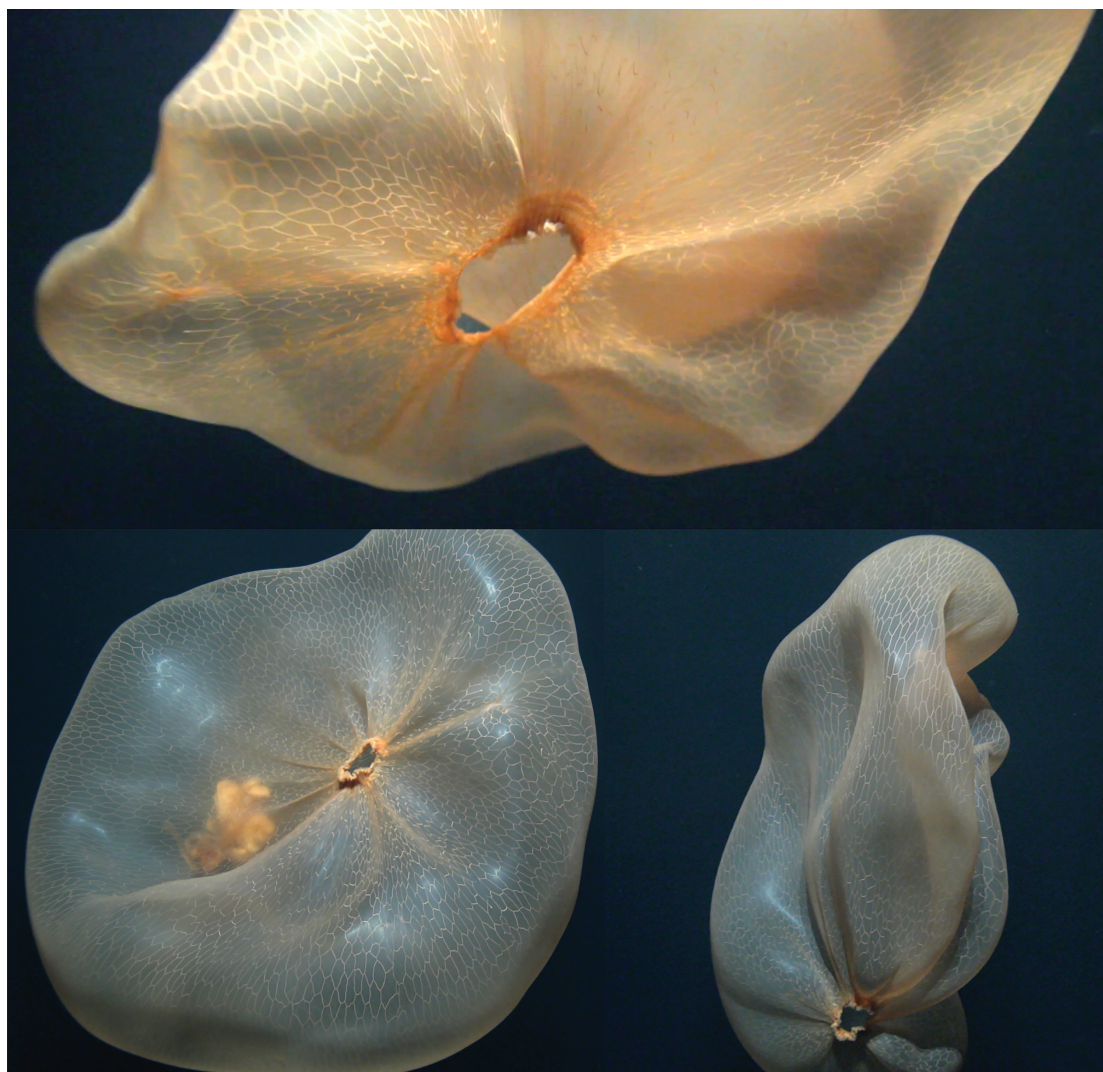


FIGURE 6. Various ventral views of *Deepstaria enigmatica*.

#### OBSERVED JELLY FALL

The sinking of detritus from surface waters is the primary food source in the deep ocean and supports many heterotrophic benthic ecosystems. While this is mainly composed of millimeter-sized particles of “marine snow” (particles of dead plankton and fecal pellets), there are instances where large food falls such as wood (Turner, 1973), fish (Higgs et al., 2014; Soltwedel et al., 2003), and whale carcasses (Smith and Baco, 2003) occur in the deep ocean and create an intense area of organic enrichment.

A dead jelly or “jelly fall” can also be defined as a carcass that sinks through the water column, eventually causing a point-source of organic enrichment on the seafloor. Observa-

TABLE 1. Reports of *Deepstaria* encounters (updated from Larson et al., 1988).

Location	Depth (m)	Reference
1. California	723	Russell, 1967
2. Caribbean	Open Trawl	Phillips, 1973
3. Central Atlantic	510–1090	Van Soest and Winkler, 1981
4. Oregon	1500–1750	Pearcy and Stuiver, 1983
5. Southern Ocean	Open Trawl	Larson, 1986
6. California	600	Larson et al., 1988
7. Bermuda	915	Larson et al., 1988
8. Monterey Bay	not reported	Bayha et al., 2010
9. San Benedicto Island, Mexico	974	This report
10. Monterey Bay	not reported	MBARI, <sup>1</sup> 2011

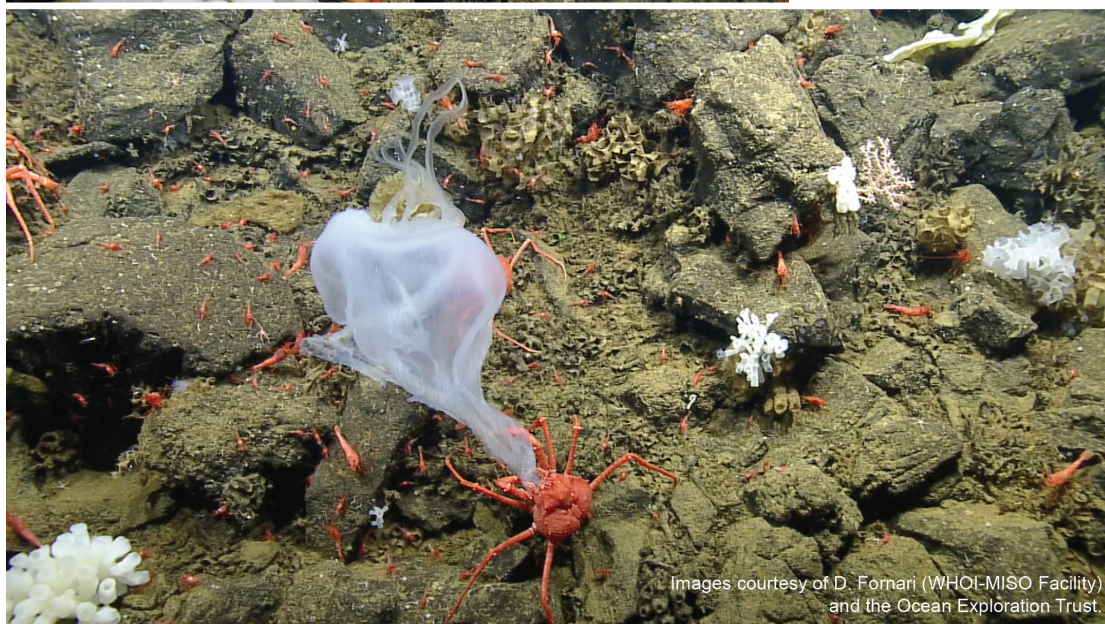
<sup>1</sup> Monterey Bay Aquarium Research Institute.

tions of gelatinous-bodied falls, including both tunicates (families Salpidae and Pyrosomatiidae) and cnidarians (class Scyphozoa), are known from a global review of observations (Lebrato et al., 2012). However, owing to remineralization in the water column (Titelman et al., 2006) and rapid scavenging of a gelatinous body on the seafloor, (Sweetman et al., 2014), it is likely that the contribution of gelatinous material to organic fluxes are underestimated (Dunlop et al., 2017; Sweetman and Chapman, 2011, 2015). For example, it has been shown that dense aggregations of deep-sea scavengers (more than 1000 animals at peak densities) can rapidly assemble at jellyfish baits and consume entire jellyfish carcasses in 2.5 h (Sweetman et al., 2014).

To our knowledge, this is the first known observation of a *Deepstaria* jelly fall (see Video 3, available at <https://doi.org/10.5531/sd.sp.32>). It was located at the lower boundary of the oxygen minimum zone (OMZ) at 899 m ( $O_2 = 2.98 \mu\text{moles/liter}$ ; temperature =  $5.05^\circ\text{C}$ ). ROV observations show a number of species of caridean shrimp and several individual lithodid crabs (*Paralomis* sp.), actively scavenging the recently deposited carcass. We suspect this to be a recent jelly fall as the meshwork of the gastrovascular system (Russell, 1967) was still visible within the thin, translucent bell structure of the individual. Where these OMZs intercept the seafloor, strong gradients in oxygen availability and organic matter flux are observed (Devol and Hartnett, 2001; Wishner et al., 1995). Sudden pulses of organic matter can therefore be important in supporting benthic ecosystems on the seafloor regions of the OMZ. Given that members of *Deepstaria* are physically large animals, their relatively sparse distribution in the deep sea may represent a significant flux of detrital material to benthic scavengers. Studies from ROV videography have recently shown the significance of gelatinous predators to deep pelagic food webs (Choy et al., 2017). These in situ ROV images of a deep-sea jelly fall further highlight the importance of utilizing ROVs to make such observations and the overall role that jellies may play in the export of carbon to the deep ocean.



FIGURE 7. Two lithodid crabs (*Paralomis* sp.) crabs and several caridean shrimp species surrounding carcass of *Deepstaria* sp. (at left and below). At right (opposite page) a close-up of one crab feeding on the carcass shows the meshwork of the jelly's gastrovascular system.



Images courtesy of D. Fornari (WHOI-MISO Facility)  
and the Ocean Exploration Trust.

#### MODE OF PERISTALTIC MOTION AND PREY CAPTURE

By approaching a specimen of *D. enigmatica* with a relatively low light intensity (274 lumens) and utilizing a low-light camera, we were able to film the organism with its umbrella open. It is not clear whether the light or ROV noise/vibrations caused the umbrella margin to purse closed. *Deepstaria* is hypothesized to be an ambush predator that catches upward-swimming prey (Larson et al., 1988). While there are no direct observations of this feeding strategy, subumbrella nematocyst clusters support the hypothesis. Once the prey is enclosed



within the umbrella, we show that *D. enigmatica* can close rapidly ( $<10$  sec) and then open again in  $\sim 1$  min (see Video 1, available at <https://doi.org/10.5531/sd.sp.32>). “Bagging” prey is not known to occur in other medusae, but has been reported in ctenophores (Harbison et al., 1978). Via analysis of videos (from Larson et al., 1988) we estimated that the peristaltic wave contraction moved at 2 cm/sec. Our observations show a similar rate, but we also note that the wave ultimately stops halfway up the organisms and stays in that pursed position until reopening (figs. 4, 5A).

#### OTHER PUBLISHED RECORDINGS OF *DEEPSTARIA*

Two *Deepstaria* individuals were observed off the coast of southern California from the submersible Alvin (Dive 966/November 1979). One of these specimens was collected and described as a new species, *Deepstaria reticulum* (Larson et al., 1988). In the same paper, Larson et al. (1988) noted that on dive 961 they saw, but did not collect, a *D. enigmatica* specimen of at least 30 cm in height. Images of this specimen are also shown in Harbison (1987). *Deepstaria* has also been reported from the Gulf of Mexico, and was collected using an Isaacs-Kidd mid-water trawl (Phillips, 1973). Although this specimen was badly damaged, the researchers were able to identify it as a female *D. enigmatica*. The medusa was described as a deep purple-blue in color and appeared to have had a diameter in excess of 70 cm. The mesoglea was 18 mm thick near the center of the disc. A badly damaged individual (umbrella margin torn, portions of umbrella distorted) was collected via midwater trawl by Van Soest and Winkler (1981). Known scientific observations of *Deepstaria* are summarized in table 1.

Manned submersibles and ROVs from both scientific and industry-led studies have produced many novel observations of scyphozoans since the first pioneering bathysphere dives more than 80

years ago (Beebe, 1934). Even on these initial bathysphere dives, it was noted that the biodiversity the observers witnessed in this noninvasive fashion was quite different from collections made via net sampling projects in the same areas. In recent years, there have been significant advances in both low-light deep-sea imaging technology (Phillips et al., 2016) and soft robotics (Galloway et al., 2016). These advances show promise in both noninvasive in situ deep-sea observations and delicate collecting techniques for gelatinous zooplankton, and will hopefully lead to the discovery and description of more remarkable meso-bathypelagic organisms, such as *Deepstaria*.

#### ACKNOWLEDGMENTS

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