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Dumbo octopod hatchling provides insight into early cirrate life cycle

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Cirrate octopods (Cephalopoda: Cirrata) are among the largest invertebrates of the deep sea. These organisms have long been known to lay single, large egg capsules on hard substrates on the ocean bottom [1], including cold-water octocorals (Anthozoa: Octocorallia). The egg capsule is comprised of an external egg case as well as the chorion and developing embryo. Development in cirrates proceeds for an extended time without parental care [2]. Although juveniles have previously been collected in the midwater [3], cirrate hatchlings have so far never been observed. Here, we provide the first video of a living hatchling and use magnetic resonance imaging (MRI) to analyze its anatomy and assign the specimen to the genus *Grimpoteuthis,* the so-called dumbo octopods. The specimen's behavior and advanced state of organ development show that cirrate hatchlings possess all morphological features required for movement via fin-swimming, for visually and chemically sensing their environment, and for prey capture. In addition, the presence of a large internal yolk sac reduces the risk of failure at first feeding. These data provide evidence that dumbo octopods hatch as competent juveniles.

Cirrate egg capsules are rarely reported in the literature and, although morphological variation between egg cases has been documented [4], confident identification past the ordinal level has never been achieved [2]. Until recently, all egg capsule collections have come from benthic trawling activities, and identifications were based on egg capsules and adults being sampled together [1]. Consequently, the early life cycle of deep-sea cirrates is virtually unknown, with most information indirectly obtained from mid- to shallow-water species [2].

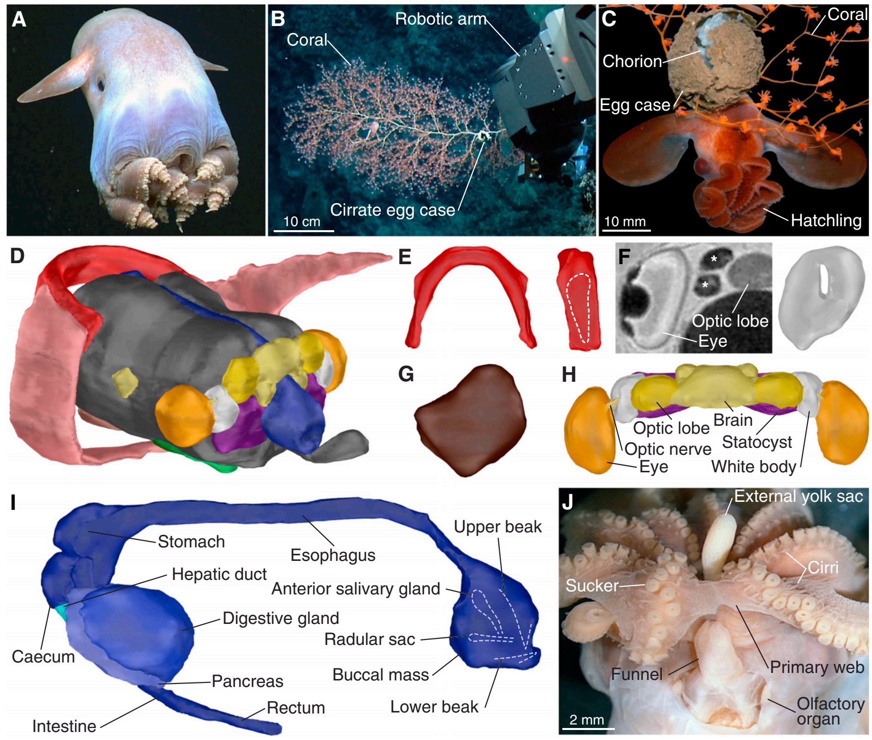

Figure 1. Evidence that dumbo octopods hatch as competent juveniles.
(A) Adult *Grimpoteuthis* sp. photographed at about 2,000 m depth on the West Florida Escarpment during the 2014 Exploration of the Gulf of Mexico cruise. Image courtesy of NOAA-OER, modified. (B) Deep-sea octocoral *Chrysogorgia tricaulis* with empty cirrate egg case being collected at 2,379 m depth on Yakutat Seamount during the 2005 Deep Atlantic Stepping Stones cruise. Image courtesy of NOAA-OER, modified. (C) Cirrate hatchling with opened egg case attached to octocoral *Chrysogorgia artospira* collected at 1,965 m depth on Kelvin Seamount during the 2005 Deep Atlantic Stepping Stones cruise. (D) Anterolateral view of an MRI-based 3D reconstruction of selected internal organs of the hatchling. (E) Dorsal and lateral views of the shell. Stippled line indicates attachment area of the fin cartilage. (F) Left: MRI-based virtual horizontal section through a white body (asterisks); right: lateral view of a white body with opening for the single optic nerve. (G) Posterior view of the systemic heart. (H) Dorsal view of central nervous system and selected sensory organs. (I) Right lateral view of the digestive tract. (J) Ventral view of the arm crown. Branchial glands = dark green, fin cartilages = pink, gills = light green, nervous system = yellow, shell = red, yolk = grey.

In 2005, the *Deep Atlantic Stepping Stones* cruise explored the New England and Corner Rise Seamount chains in the Northwest Atlantic (Figure 1). Using a remotely operated vehicle, a sample of the octocoral *Chrysogorgia artospira* was collected on Kelvin Seamount at 1,965 m depth with associated epifauna, including multiple feather stars (Crinoidea: Comatulida) and a putative cirrate egg capsule. The egg capsule was 19 x 14 mm in size, chocolate brown, rugose, with no linear patterning and no regular sculpturing, and was partially wrapped around the coral's branches (Figure 1C). On deck, the egg capsule ruptured and a hatchling slowly emerged, starting with its posterior end, followed by fins and ultimately arms. The specimen that emerged was fully developed, but the hatching event was probably premature due to the stress of being collected. After observing and filming the living hatchling for about two hours (Movie S1), the egg case, chorion, and hatchling were fixed for long-term storage. After fixation, the specimen was measured at 13 mm mantle length and high-field MRI scans were performed that served as the basis for an interactive three-dimensional reconstruction of the hatchling's internal anatomy (Figure 1D and supplemental information).

Although there is considerable uncertainty in cirrate systematics due to a lack of specimens, four families may be recognized based on morphological and molecular evidence: Cirroteuthidae, Cirroctopodidae, Opisthoteuthidae, and Grimpoteuthidae [2]. The presence of a lateral pair of fins, a single series of arm suckers bordered on both sides by cirri, and an internal cartilaginous shell are the main characters of cirrates and are all present in the hatchling. The specimen has a U-shaped shell with well-developed shoulders and parallel wings with blunt tips (Figure 1E) as well as two white bodies, each penetrated by a single optic nerve (Figure 1F). These characters are consistent with *Grimpoteuthis* and *Cryptoteuthis*. However, the shell wings in *Cryptoteuthis* widen slightly and distally have a sharp point. The hatchling's fin cartilages attach along a large part of the shell wings (Figure 1E) and extend out to 80% of the fins' length, a feature compatible with adult individuals of *Grimpoteuthis* [5], but not *Cryptoteuthis*, which has short, stubby fins [2]. Therefore, we identify the hatchling as belonging to the genus *Grimpoteuthis*. However, species identification is impossible due to incomplete type material for North Atlantic species and a paucity of sequence data for *Grimpoteuthis* specimens [2].

The dominant embryonic character is the presence of a large, single-lobed internal yolk sac (Figure 1D); no hatching gland was found. The internal anatomy is similar to *Grimpoteuthis* adults [5]. The systemic heart is rhombic-shaped (Figure 1G), not S-shaped as in *Opisthoteuthis* [6]. The statocysts are large (Figure 1D), with statoliths present. The optic lobes are approximately half of the brain by volume (Figure 1H), and stellate ganglia as well as a gastric ganglion are present (Supplemental information). The digestive tract does not differ significantly from that of the adult [5], although the digestive gland is reduced in size (Figure 1I). A posterior salivary gland is absent, but branchial hearts, renal appendages, and branchial glands are well-developed. The gills appear to be of half-orange shape, but are partially distorted by the large internal yolk sac. Externally, the olfactory organs, suckers, arms, cirri, funnel, and primary web (Figure 1J) resemble the respective structures in the adult [5]; web nodules are absent.

In cirrate reproduction, males presumably use their penis-like terminal organ for copulation. The fertilized egg is covered by an egg case in the female oviducal gland and subsequently kept in the distal oviduct, presumably until a suitable substrate is found [4]. Egg-laying in cirrates is continuous, with no evidence of parental care [2]. In contrast, the deep-sea incirrate *Graneledone boreopacifica* has a single reproductive episode, broods its eggs, and dies after its offspring hatches [7]. However, deep-sea cirrates and incirrates have large eggs and long development times in common [7,8].

Cephalopods may either hatch as competent juveniles, immediately adopting the adult niche, or may hatch as paralarvae that occupy a separate ecological niche from the adult [9]. Adult grimpoteuthids are benthopelagic and move primarily by fin-swimming. As shown in the video accompanying this article (Movie S1), the hatchling's robust shell with extensive fin cartilages and musculature permits synchronous fin-flapping immediately post-hatching. Furthermore, the hatchling's arms have numerous well-developed suckers similar to *G. boreopacifica* [10], but in contrast to most planktonic incirrate octopod paralarvae. While early cirrate embryos were shown to lack cirri [4], this hatchling has robust cirri that can presumably be used to sense the environment. Combined with the extensive development of its eyes and brain, the morphological features suggest that the hatchling can coordinate seeing, pursuing, and seizing prey after emerging from the egg case. We therefore conclude that *Grimpoteuthis* cirrates hatch as competent juveniles.

Our MRI- and video-based functional inferences not only help to provide essential data on the early life cycle of deep-sea cirrates, but also highlight the importance of conserving their natal habitat. Cold-water octocorals appear to be critical in this respect and their destruction by bottom trawling or mining will impact populations of mobile animals like the charismatic dumbo octopods.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures, one interactive figure and one video can be found with this article online at https://doi.org/10.1016/j.cub.2018.01.032.

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AUTHOR CONTRIBUTIONS

E.K.S and A.Z. conceived and performed experiments, analyzed the data, and wrote the manuscript. C.F. performed experiments and provided expertise and feedback, and T.M.S. led the field program, collected the specimen and provided ecological expertise and feedback.

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