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Giant eggs in a deep-sea squid

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The deep-sea water column below 200 m is a vast three-dimensional habitat with an enormous but largely unexplored biodiversity (Robison, 2009). Cephalopod mollusks are abundant in the deep sea and are important prey for many kinds of predators. Still, most deep-sea cephalopods have never been observed alive in their natural habitat and their reproductive biology remains poorly documented. In March of 2015, at a depth of 2566 m, we observed a female squid of an undescribed species but likely belonging to the Gonatidae, carrying few but exceptionally large eggs in her arms. This raises questions as to how these and other related animals reproduce in the deep sea, an environment that is generally characterized by darkness, low temperature, reduced oxygen, limited food availability, and low population densities.

The authors were conducting dives with deep-sea robots (remotely operated vehicles or ROVs) equipped with cameras in the deep basins of the Gulf of California, to investigate how deep-sea fauna are distributed in relation to the extensive low-oxygen zones in the region (Gilly et al., 2013). The squid (Individual 1, Table 1) we observed with an ROV at 2566 m in the Gulf of California in 2015 was carrying 30–40 large eggs (average maximum diameter 11.2 mm, $n = 5$; measured eggs were 11.4, 10.4, 11.5, 11.7 and 11 mm maximum diameter) embedded in a small external egg sheet that did not extend beyond the arm tips. The size of the eggs was similar to those of two squid (Individuals 2 and 3, Table 1) that were observed close to the seafloor during earlier expeditions in the same region.

The two squid (Individuals 2 and 3, Table 1) encountered near the bottom at 3148 and 3126 m did not carry eggs in their arms but had seemingly inflated mantles, indicating ripe gonads. Both of these specimens were collected and examined by the authors on board the ROV's support ship, R/V *Western Flyer*. They were identified as belonging to the family Gonatidae based on the morphology of the mantle, fin and the armature of the arms (lateral suckers and two series of hooks) (Young, 1973). None of the three specimens described here aligned with any existing taxonomic species description and they are likely an undescribed species of the family Gonatidae. No tissue was available for genetic analysis. Two collected female specimens (Individuals 2 and 3, Table 1), were deposited in the Santa Barbara Museum of Natural History (only Individual

3 has been accessioned; SBMNH461978). One of these females (Individual 3, Table 1) had only five arms, and it appeared that three arms had been bitten off. Sperm packages (spermatangia) were visible in the buccal area of this individual, giving evidence of mating activity. The morphology of spermatangia was similar to those described for other gonatids (Golikov et al., 2019). In both examined female specimens (Individual 2 and 3, Table 1) oocytes of various sizes were present in the ovaries including large ones up to 15 mm in length. All three observed specimens (Individuals 1–3, Table 1) were of similar size (ML 214–230 mm) and all had scars on the dorsal sides of their bodies, including scratches (Figure 1) that may have been caused during mating by the hooks on the males' arms.

Squids have a semelparous life history strategy, where reproduction includes a single reproductive cycle, which ultimately results in death (Boyle & Rodhouse, 2007). The exact spawning strategies vary among species and differ in the number and size of eggs produced, as well as the number of spawning events (Hoving et al., 2014). Although spawned eggs remain undocumented for most

TABLE 1 Information on size (mantle length; ML), location, environmental data and observation details of giant-egg gonatid specimens encountered in the deep basins of the Gulf of California by remotely operated vehicles.

Individual (museum no. if available) and reproductive state	Date	ML (mm)	Latitude, longitude	Depth (m)	*T* (°)	$[O_2]$ (mL/L)	ROV	Dive no.	Video
Individual 1									
Brooding	8 March 2015	214	25°26′ 52.7994″ N, 109°50′ 42.0″ W	2566.3	2.2	1.52	Doc Ricketts	722	D0722-08HD
Individual 2									
Mature, nonbrooding	28 March 2003	230	25°27′ 39.6″ N, 109°50′ 45.6″ W	3148 (nb)	2.3	1.47	Tiburon	545	Tape 6: 7:03; J-day 087
Individual 3 (Museum no. SBMNH461978)									
Mature, nonbrooding	23 February 2012	216	25°27′ 0″ N, 109°50′ 56.4″	3126.3 (nb)	2.4	1.33	Doc Ricketts	341	D0341-03HD

Note: The sizes of the squid were measured in situ with lasers on the ROV (Individual 1) or in the lab after collection (Individuals 2 and 3).

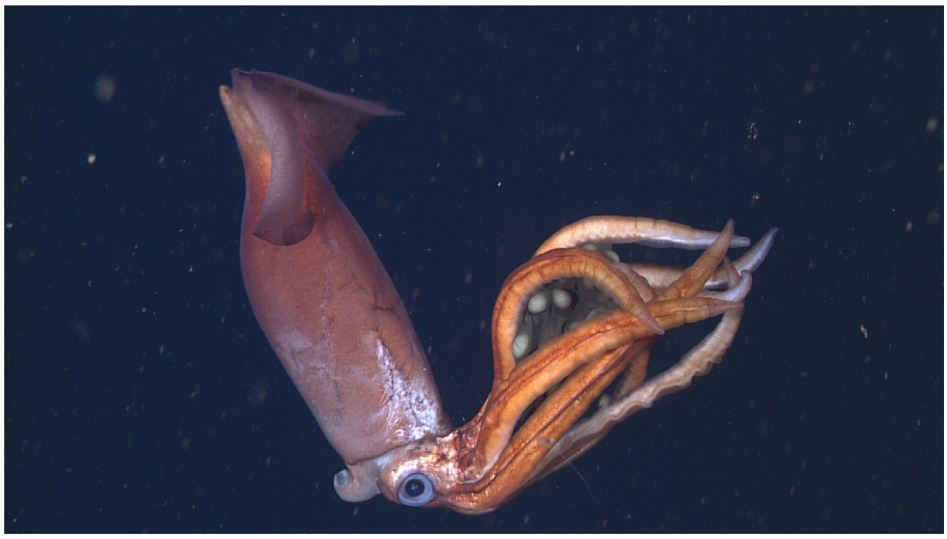

FIGURE 1 The gonatid squid (possibly sp. nov.) holding on to a mass of 30–40 large eggs, at 2566 m of depth in the Gulf of California as observed by remotely operated vehicle *Doc Ricketts* of the Monterey Bay Aquarium Research Institute on March 8, 2015. Estimated mantle length 214 mm. Average maximum egg diameter is 11.2 mm. © Copyright MBARI, 2015. Published with permission.

squid species, thysanoteuthid and ommastrephid squid produce neutrally buoyant cylindrical or spherical egg masses, respectively, that float independently in the water column (Birk et al., 2017; Guerra et al., 2002). The squid species that hold an egg mass externally, as we observed here for the squid (Individual 1, Table 1) we encountered up in the water column at 2566 m, presumably do so until hatching of the eggs. This "brooding" or "post spawning egg care" is only known for a few other bathypelagic squid including the genera *Bathyteuthis* and *Gonatus* (Arkhipkin & Bjørke, 1999; Bush et al., 2012; Seibel et al., 2005) and observations are extremely rare.

The giant size of the eggs that were held for brooding by the gonatid female in the Gulf of California is unprecedented for squids. Eggs previously documented for other gonatid squids typically do not exceed 6 mm (Table 2). It is expected that juveniles of cephalopods that produce few but large eggs have increased survival rates compared to cephalopods that produce many small eggs. The spawning of many small eggs, over multiple events, is beneficial in environments with high variation in food availability or predation for hatchlings. Via bet-hedging, many offspring that hatch over extended periods, have a higher chance of encountering beneficial circumstances for growth (Rocha et al., 2001). Squids that spawn in the epipelagic zone (the upper 200 m of the water column), where egg development times are relatively short due to higher temperatures, typically employ this strategy. In contrast, the stable and predictable environmental conditions of the deep water column (1000–4000 m) allow high relative investment in fewer offspring and may select for fewer, larger eggs and advanced hatchlings. In the cold waters of the deep sea this comes at the cost of long development times (Laptikhovsky, 2006; Robison et al., 2014; Seibel et al., 2005).

Egg development in deep-sea cephalopods has only been quantified for the octopod *Graneledone boreopacifica*. The eggs (15–33 mm) of this species needed 53 months to hatch at 2.8–3.4°C (Robison et al., 2014). Without direct observations of squid egg incubation times, we can only speculate about the development time of the giant gonatid squid eggs reported here. Considering the environmental temperature of just over 2°C, we expect these eggs to require more than 1.4 years to develop, while some estimates suggest longer than 4 years (Robison et al., 2014). However, development data for large cephalopod eggs at low temperatures are extremely limited, and are absent for squids. If the brooding time is indeed longer than 1 year, it lasts longer than the complete life cycle of most shallow water and coastal cephalopods.

The extensive multiyear brooding of giant eggs seems only possible when predation pressure is very low. To avoid predation in the final reproductive phase, many cephalopods perform ontogenetic migrations where larger, and reproducing individuals occur deeper

TABLE 2 Maximum egg sizes (length × width) in mature, gravid or spent female gonatid squids of mature eggs located in the ovary or oviducts (unless otherwise indicated) as well as squid size (dorsal mantle length unless otherwise indicated).

Gonatid taxa	Egg size (mm)	Female size (mm)	Capture depth (m)	Geographic locality	Reference
Berryteuthis magister	4.1 × 3.7		400–600	Bering Sea, Russia	Nigmatullin et al., 1996
	5.9		500–1000	Japan Sea, Japan	Yuuki & Kitazawa, 1986
Gonatus berryi	3.5	185p	na	NE Pacific, USA, California	Young, 1972
Gonatus fabricii	5.2 × 4.2	na	na	Central Polar Basin	Nesis, 1999
Gonatus fabricii	5.5	215	1229	North East Greenland Sea	Golikov et al., 2019
	5.24 × 4.17	na	na	Northern Norway	Bjørke et al., 1997
Gonatus madokai	2.5 × 1.5+	360	na	Okhotsk Sea, Russia	Nesis, 1989
Gonatus onyx	3.0 × 2.1*	132	1250–1755	NE Pacific, USA, California	Seibel et al., 2000
Gonatus onyx[a]	4.7	na	na	NE Pacific, USA, California	Nesis, 1999
Gonatus pyros	3.0 × 1.7	130/135p	na	NE Pacific, USA, California	Young, 1972
Gonatopsis octopedatus[a]	4.3 × 2.5	390	0–50	Okhotsk Sea, Russia	Nesis, 1993
	2.0+	135	0–50	Japan Sea, Russia	Nesis, 1993
Possibly new species reported here	11.5	221	2566	Gulf of California	This manuscript

Abbreviations: *, Spawned eggs brooded by female; +, Maturing ovarian eggs; na, Information not available; p, Pen length.
[a]Identification doubtful.

(Boyle & Rodhouse, 2007) and beyond the reach of deep-diving air breathers and bottom-dwelling predators (Seibel et al., 2005). The migration into low-oxygen parts of the water column may also contribute to predator avoidance. The downward ontogenetic migration suggests that the deep pelagic is an important habitat for reproducing midwater cephalopods but observations are extremely rare. Future exploration of the deep water column will contribute to resolving this hypothesis, and provide valuable new insights into the biology of enigmatic oceanic fauna.

AUTHOR CONTRIBUTIONS

Henk-Jan Hoving and Brad Seibel conceived the study. Henk-Jan Hoving, Steven Haddock, Brad Seibel, and Bruce Robison collected data. Henk-Jan Hoving, Brad Seibel, and Bruce Robison provided expert insight into data interpretation. Henk-Jan Hoving composed the manuscript and all coauthors contributed to the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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