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Association of deep-sea incirrate octopods with manganese crusts and nodule fields in the Pacific Ocean

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Incirrate octopods (those without fins) are among the larger megafauna inhabiting the benthic environments of all oceans, commonly in water depths down to about 3,000 m. They are known to protect and brood their eggs until the juveniles hatch, but to date there is little published information on octopod deep-sea life cycles and distribution. For this study, three manganese-crust and nodule-abundant regions of the deep Pacific were examined by remote operated-vehicle and towed camera surveys carried out between 2011 and 2016. Here, we report that the depth range of incirrate octopods can

now be extended to at least 4,290 m. Octopods (twenty-nine individuals from two distinct species) were observed on the deep Ka'ena and Necker Ridges of the Hawaiian Archipelago, and in a nodule-abundant region of the Peru Basin. Two octopods were observed to be brooding clutches of eggs that were laid on stalks of dead sponges attached to nodules at depths exceeding 4,000 m. This is the first time such a specific mineral-biota association has been observed for incirrate octopods. Both broods consisted of approximately 30 large (2.0-2.7 cm) eggs. Given the low annual water temperature of 1.5°C, it is likely that egg development, and hence brooding, takes years [1]. Stalkedsponge fauna in the Peru Basin require the presence of manganese nodules as a substrate, and near total collapse of such sponge populations was observed following the experimental removal of nodules within the DISCOL (DISturbance and COLonisation) area of the Peru Basin [2]. Stalked fauna are also abundant on the hard substrates of the Hawaiian archipelago. The brooding behavior of the octopods we observed suggests that, like the sponges, they may also be susceptible to habitat loss following the removal of nodule fields and crusts by commercial exploitation.

During the dives, four octopod morphotypes were observed, likely representatives of two incirrate species (Figure 1). The majority of individuals we observed were of the 'Casper' morphotype (Figures 1A, 1C-1E, S1A-S1E), so named after the Necker Ridge individual observed during the Okeanos Explorer Hawaiian campaign during March of 2016. The lack of chromatophores in this morphotype gives individuals a partially translucent appearance, reminiscent of the cartoon ghost, with reports from the cruise generating much press interest (for example, see http://insider.si.edu/2016/03/ghostoctopod-shows-little-know-deepsea-life/). Several other individuals we observed were less translucent, with biserial suckers (dissimilar to the single series of suckers exhibited by the 'Casper' morphotype), and appeared to be Vulcanoctopus sp. (Figure 1B). Details of the locations, morphotypes, sizes and behaviors of all reported individuals are given in Table S1 in the Supplemental Information.

The benthic octopods reported herein are the deepest individuals of the suborder Incirrata observed to date [3], with the majority observed at depths of 4,120-4,197 m. Prior to the current study, deep-sea octopods of the genus Graneledone have been observed in the northeastern Pacific at depths of 1,500-1,600 m on submarine

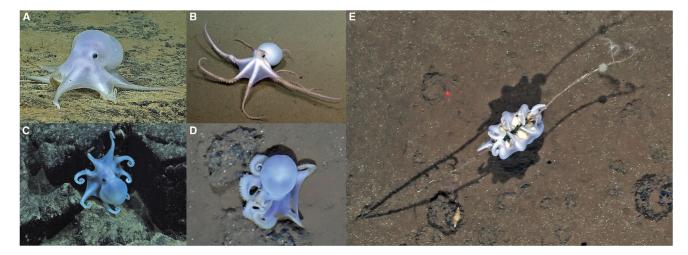


Figure 1. The morphotypes of deep-sea incirrate octopods observed in the current study.

(A) The Necker Ridge 'Casper' octopod (4,290 m), 6.4 cm mantle length, slowly crawling across a basalt outcrop. Image: Deep Discoverer ROV team. (B) Octopod observed in the deep Peru Basin nodule rich DISCOL experimental area (4,099 m), mantle length ~9 cm, potentially Vulcanoctopus sp. Image: KIEL 6000 ROV team (GEOMAR). (C) The Ka'ena Ridge 'Casper' octopod (3,116 m), mantle length 6.5 cm, utilizing a nook in a pillow basalt. Image: Jason 2 ROV team. (D) A 'Casper' octopod observed in the DISCOL area (4,151 m), mantle length 5 cm, the most abundant morphotype observed in the region. Image: AWI-OFOS Launcher team. (E) One of two brooding octopods observed in the Peru Basin (4,150 m). The octopod was observed hanging underneath the brood of ~30 2.0-2.7 cm-long eggs, each individually attached to the sponge stalk. Image: AWI-OFOS Launcher team. See also Table S1.



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plateaus [4], within canyon systems at 1,397 m [1] and at 2,600 m on a basaltic outcrop [5]. On the East Pacific Rise, *Vulcanoctopus hydrothermalis* have been observed at 2,647 m [6], which is 1,500 m shallower than the deepest *Vulcanoctopus* sp. individual observed in the current study (Table S1).

The majority of the octopods described here were utilizing seafloor structures such as cracks, joints and fissures in the basaltic crust, or manganese nodules. In many cases octopods seem to have 'cleaned' the surface sediments around the nodules with which they were associated (Figure 1D). This is possibly a result of foraging in surface sediments, a behavior previously reported in deep-sea octopods [7]. This hypothesis is further supported by the fact that octopods actively penetrated, and in some cases undulated, their arms within the sediment (Figure S1C).

Both brooding octopods were observed encircling their eggs on the dead sponge stalks (Figures 1E, S1E). Sponges are also used for egg deposition by deep-sea sepiolids (Rossia mollicella [8]), but to date, rocky overhangs and cliffs have been the primary substrates observed for incirrate-octopod brooding [1]. The batch sizes observed within the Peru Basin (~30 eggs) are lower than those reported for other deep-sea octopod species, such as Graneledone sp. (150-165 eggs, observed in the Pacific Ocean [1]). For Graneledone sp., egg lengths at the time of hatching have been reported to be ~3.5 cm, under temperatures of 2.8-3.4°C, with a developmental time of more than 4 years [1]. At the survey site in the Peru Basin, the colder average temperature of ~1.5°C (data not published) is possibly indicative of a long brooding period, which in combination with the low fecundity and probable low natural mortality rates, renders these octopods highly susceptible to disturbance.

Nodule fields are known to provide a hard substrate for various epifauna such as sponges [9]. In the late 1980s, the DISCOL experiment was instigated in the Peru Basin to assess the potential impacts of commercial removal of surface nodules on the seafloor communities by experimentally ploughing them into the sediments.

Nodules from 10-15% of an 11 square km area were so removed and community change monitored over time [10]. Though impacts on mobile-fauna abundances were only observable for a few years following ploughing [2], the removal resulted in the near total collapse of sessile fauna (including the stalked sponge fauna) with little recovery evident after seven years [2]. Removal of manganese-rich crusts from the deep seafloor may expose a hard surface suitable for recolonization by sessile organisms, but community recovery will still take decades given the slow growth rates of many deep-sea fauna [9]. The potential reproductive impacts of such resource removal on charismatic large, mobile octopod megafauna will now have to be considered when developing management plans for these commercially attractive, yet biodiverse and poorly-understood deep-sea ecosystems.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure, one table, experimental procedures, and author contributions, and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.10.052.

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REFERENCES

- Robison, B., Seibel, B., and Drazen, J. (2014). Deep-sea octopus (*Graneledone boreopacifica*) conducts the longest-known egg-brooding period of any animal. PLoS One 9, e103437.
- Bluhm, H. (2001). Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor. Deep Sea. Res. II 48, 3841–3868
- Voss, G.L. (1988). Evolution and phylogenetic relationship of deep-sea octopods (*Cirrata* and *Incirrata*). In The Mollusca. Vol. 12. Palaeontology and neontology of Cephalopods, M.R. Clarke and E.R. Trueman, eds. (London: Academic Press), pp. 253–276.
- Drazen, J.C., Goffredi, S.K., Schlining, B., and Stakes, D.S. (2003). Aggregations of eggbrooding deep-sea fish and cephalopods on the Gorda Escarpment: a reproductive hot spot. Biol. Bull. 205, 1–7.
- Voight, J.R., and Grehan, A.J. (2000). Egg brooding by deep-sea octopuses in the north Pacific ocean. Biol. Bull. 198, 94–100.
- Gonzalez, A.F., Guerra, A., Pascual, S., and Briand, P. (1998). Vulcanoctopus hydrothermalis gen. et sp. nov. (Mollusca, Cephalopoda): an octopod from a deep-sea hydrothermal vent site. Cah. Biol. Mar. 39, 169–184.
- Quetglas, A., Ordines, F., Gonzalez, M., and Franco, I. (2009). Life history of the bathyal octopus *Pteroctopus tetracirrus* (Mollusca, Cephalopoda) in the Mediterranean Sea. Deep Sea Res. I. 56, 1379–1390.
- Okutani, T., and Sasaki, T. (2007). Eggs of Rossia mollicella (Cephalopoda: Sepiolidae) deposited in a deep-sea sponge. J. Moll. Stud. 73, 287–289.
- Vanreusel, A., Hilario, A., Ribeiro, P.A., Menot, L., and Arbizu, P.M. (2016). Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna. Nature Sci. Comm. 6, 26908.
- Foell, E.J., Thiel, H., and Schriever, G. (1990). DISCOL: a long-term, large-scale, disturbancerecolonization experiment in the abyssal eastern tropical south Pacific ocean. Offshore Technology Conference, 7–10 May. Houston, Texas. http://dx.doi.org/10.4043/6328-MS.

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