Brooding in a Bathypelagic Octopus[1]

RICHARD EDWARD YOUNG[2]

ABSTRACT: A mature female and 12 larvae of the octopus *Bolitaena microcotyla* were captured at bathypelagic depths off Hawaii. The female appears to have been brooding the larvae in a large chamber formed by the oral arms and web. This finding supports the likelihood that the brooding habit is universal in pelagic incirrate octopods.

VERY LITTLE IS KNOWN about the reproductive habits of oceanic cephalopods, particularly those inhabiting the deep sea. Recently a specimen of the poorly known octopus *Bolitaena microcotyla* Hoyle, 1886, was captured off Oahu, Hawaii. The specimen was taken at depths between 830 and 975 m in an opening-closing mid-water trawl (modified Tucker Trawl). Off Hawaii these depths lie within the bathypelagic zone. Examination of the specimen revealed that it was a brooding female.

DESCRIPTION

In formalin, the small female specimen has a lateral mantle length of 30 to 35 mm and a total of about 75 mm. Although fragile—it has the consistency of a jellyfish—it was only slightly damaged in the trawl. A number of larval octopods were fortuitously attached to the head and body of the adult by radiolarian skeletons. Nearly all of the fragile deep-living octopods that have come to my attention have had radiolarians stuck to their bodies as a result of contact within the trawl. The larval octopods are equally susceptible to empalement by radiolarians, and it was by this means that they were attached to the surface of the adult specimen. A total of 12 larvae were recovered, including a few that were found in the bottom of the specimen jar; all were at the same stage of development.

The arms of the female are in a rather unusual position. They arch forward and converge near their tips. All of the arms except the two ventral ones are connected by a deep web which is characteristic of this species. The web is longest between the dorsal arms where it reaches about 60 percent of the arm length, becomes progressively shorter between arms I and II, arms II and III, and arms III and IV although still extending to about 40 percent of the arm length in the latter. The web is almost completely lacking between the ventral arms. The arms and web, therefore, form a capacious pouch which, very likely, held the larvae (Fig. 1*A*). Unfortunately all of the young had been dislodged by the time the specimen was examined and no remnants of egg capsules, stalks, or any special modifications for egg attachment were found.

The buccal mass, which lies at the posterior end of this pouch is entirely sealed except for a minute central pore. This closure is not formed by the fusion of the lips that surround the buccal mass; rather, it is the integument of the oral surface of the buccal crown that extends over the lips and buccal mass. Careful examination initially failed to reveal the presence of any opening. Only when the overlying integument was being dissected, did pressure by the scissors force a small amount of white flocculent material through the integument, indicating the presence of a minute pore. Although it was still impossible to see the pore, a short canal was detected leading from a cavity around the lips and beaks to the area where the pore was presumed to be. The presence of this canal suggests that a pore and not a rupture allowed the material to escape. The flocculent material consisted of a cellular debris heavily infested with several

[1] This work was supported by National Science Foundation Grant GB 20993. Manuscript received 10 May 1972.

[2] Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822.

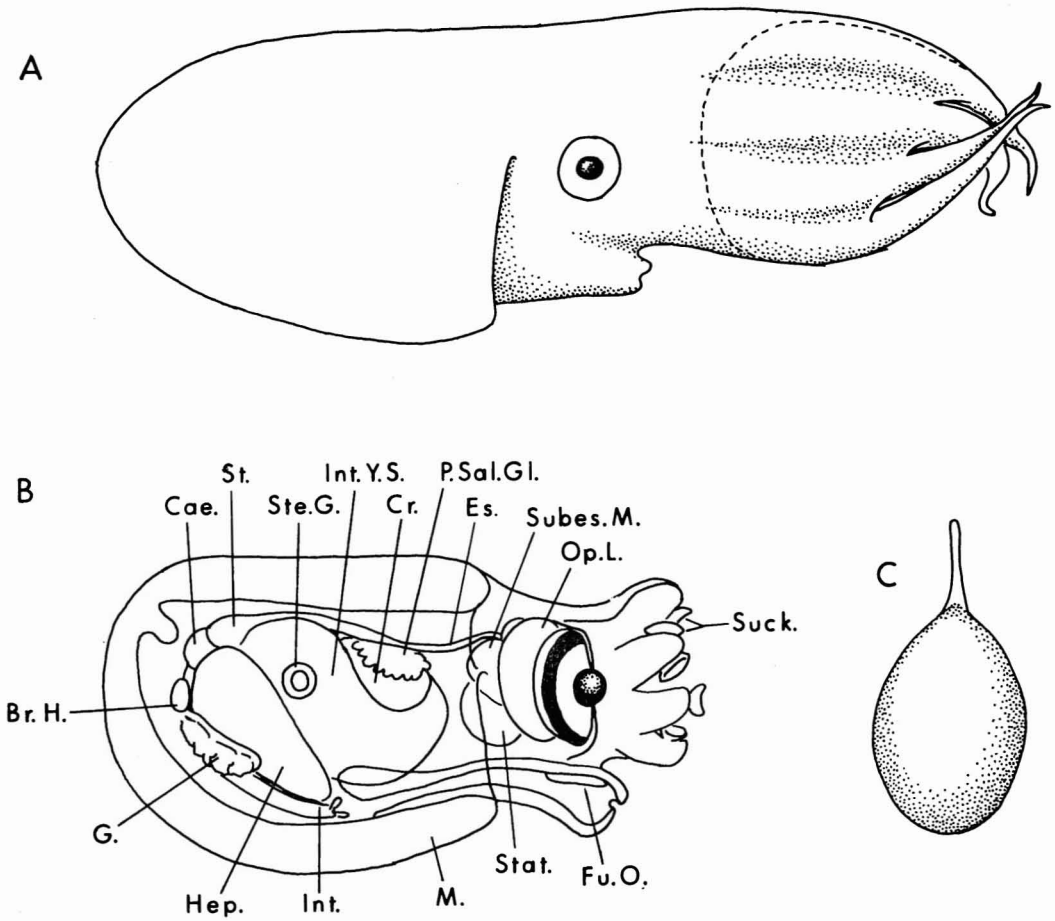

FIG. 1. *A,* lateral view of *Bolitaena microcotyla.* Dashed line indicates extent of brood chamber; *B,* larva of *B. microcotyla; C,* mature egg from ovary.

SYMBOLS: Br. H., branchial heart; Cae., caecum; Cr., crop; Es., esophagus; Fu. O., funnel organ; G., gill; Hep., hepatopancreas; Int., intestine; Int. Y. S., internal yolk sac; M., mantle; Op. L., optic lobe; P. Sal. Gl., posterior salivary gland; St., stomach; Stat., statocyst; Ste. G., stellate ganglion; Subes. M., subesophageal mass of brain; Suc., suckers.

types of ciliate protozoans. This same material could be squeezed from the buccal mass, and similar debris including the ciliates was found in the stomach of the octopus.

The ovary is depleted except for a single large egg and a residue of deteriorating ovarian tissue. The egg is ovate, 2 by 1.5 mm, and possesses a short stalk (Fig. 1*C*). The digestive tract apparently is in a state of degeneration. The crop is collapsed and the stomach is contracted and infested with ciliates. The hepatopancreas is very small and the posterior salivary glands are small and flaccid.

The larvae measured 2 mm in lateral mantle length (Fig. 1 *B*). The eight stubby arms each carry four large suckers. The distal two suckers frequently lie on opposite sides of the arm, apparently due to crowding. The eyes are large, elliptical in outline, and directed forward. A thin layer of iridophores lies on the surface of each eye. The mantle is thick and gelatinous. Large reddish brown chromatophores are scattered over the surfaces of the mantle, head, arms, and dorsal surface of the visceral mass. The larva has the same general appearance as the adult, except that it has relatively shorter

arms and larger eyes that face anteriorly. The largest portion of the viscera consists of the internal yolk sac which suggests that the young octopods had only recently hatched from the egg capsules. In several larvae an elongate pellet was found in the digestive tract at the juncture between the esophagus and crop. The pellet is composed of a mass of droplets of varying sizes, presumably yolk.

CONCLUSIONS

The evidence, summarized below, clearly indicates that this specimen of *Bolitaena microcotyla* was brooding larvae at the time of capture.

1. Twelve recently hatched larvae are associated with a female octopus.
2. The arms and web form a large chamber suitable as a brood pouch.
3. The mouth is almost completely sealed and, apparently, incapable of ingesting food particles.
4. The digestive tract appears degenerate and nonfunctional.
5. The deteriorated and depleted condition of the ovary indicates that the octopus had spawned.

Shallow water octopods feed rarely or not at all while brooding their embryos (Nixon, 1969). Therefore the apparent cessation of feeding in this animal is not unexpected. Feeding, seemingly, would be incompatible with oral brooding. Since the web between the ventral arms is almost totally lacking, the funnel, presumably, could extend into this gape or, at least, reach between the ventral arms when the oral crown is flexed ventrally. In either case insertion of the funnel into the brood chamber would provide a means of depositing eggs and of directing water currents over the embryos.

DISCUSSION

The order Octopoda consists of two suborders: the Cirrata, the finned octopods, whose members are benthic, benthopelagic, or pelagic (Roper and Brundage, in press); and the Incirrata, octopods without fins. Incirrate octopods generally are regarded as benthic animals but six of the nine families are wholly pelagic. (The vast majority of species, however, occurs in the benthic family Octopodidae.) The pelagic incirrate octopods are probably derived from benthic ancestors since their general morphology retains many of the benthic adaptations found in their bottom-living relatives. The pelagic realm has been invaded by octopods on more than one occasion during their history. A great number of species of octopods lay small eggs which produce small larvae that spend considerable periods in the plankton. These larvae generally are similar to juveniles or subadults except for their relative body proportions, and they may reach considerable size while in the plankton. A mantle length of 25 mm and an arm spread of over 100 mm was recorded for a pelagic larva taken off California (Young, in press). This larva is larger than the adults of some benthic octopods (Robson, 1929:1). Seemingly the transition to a wholly pelagic existence by an octopus with an extended larval stage would not be great, although a number of modifications would be required. One of these concerns the reproductive habits.

As far as is known, all shallow water benthic octopods attach their eggs to some solid substrate, usually rocks, coral, or shells. After depositing the eggs, the female broods them until hatching. The brooding process apparently assures (among other things) that the eggs are properly ventilated. Pelagic incirrate octopods, as far as is known, have not adopted what might seem to be the simplest solution to this problem, i.e., abandonment of the brooding habit and the production of free-floating eggs or egg masses. Rather, they have retained the brooding habit, which has necessitated considerable adaptation.

There are three families of octopods which are epipelagic: Argonautidae, Tremoctopodidae, and Ocythoidae. (A fourth family, the Alloposidae, has been reported many times in the near-surface plankton, but species in this family are also found associated with the bottom [Thore, 1949]. Their habits are not clearly understood.) Female members of the monotypic genus *Argonauta* form delicate shells through secretions of the dorsal arms. Egg strings are attached to the inner ends of the shell, where

they are brooded by the female. The shell may also function as a buoyancy device by trapping air at its apical end (J. Z. Young, 1960) and undoubtedly functions as a protective structure. In octopods of the monotypic genus *Tremoctopus,* the eggs are attached to short, rodlike structures formed by interwoven and cemented egg stalks. The rods are held by the suckers of the dorsal arms and the eggs are brooded in this location (Naef, 1923). In female members of the monotypic genus *Ocythoe,* the oviducts are extremely long and convoluted and can hold great quantities of eggs. Embryonic development proceeds as the eggs slowly move down the oviducts (Naef, 1923). This animal is, apparently, ovoviviparous.

There are three families of bathypelagic or mesopelagic incirrate octopods: Bolitaenidae, Amphitretidae, and Vitreledonellidae. Information on spawning habits was previously known for only a single species in these three families. Joubin (1929) found hundreds of larvae within the mantle cavity of a specimen of *Vitreledonella richardi.* (Thore, [1949] considered adults of this species to be bathypelagic.) Some specimens were also found near the bases of the arms around the mouth. Peculiarly, three embryos were found embedded in the skin on the dorsal surface between the first and second arms on the left side. Joubin had no explanation for this occurrence. The relative size of the mantle of this species is rather small. Joubin's specimen had a total length of 330 mm and the dorsal arms had a length of 240 mm. The mantle length, therefore, must be about 80 mm (see Thore, 1949:58). In spite of the small cavity, there can be little doubt that the larvae originated within this cavity. This octopus apparently brooded its embryos somewhere within the mantle cavity or viscera and, therefore, has quite a different method from that described here for *Bolitaena.* It is interesting that, in both of these species, larvae, not embryos, were found with the female, indicating that the brooding period extends past hatching although it is possible that the trauma of capture initiated hatching.

Bolitaena microcotyla is only the second species of bathypelagic incirrate octopod in which the reproductive habits are clearly known. In both of these bathypelagic species the young are brooded. All species of epipelagic octopods are known to have some means of brooding their young. It seems likely that the remaining pelagic incirrate octopods also possess this habit, even though some evidence to the contrary exists. Thore (1949) examined the Dana collections for eggs of bathypelagic octopods. He found eggs in four deep trawls which he attributed to *Eledonnella pygmaea* and *Japetella diaphana* (both family Bolitaenidae). He suggested that mating and oviposition in these species take place at great depths and that the ova float in great clusters at these depths until hatched. Clearly more information is needed before we can be certain that brooding is universal in pelagic incirrate octopods.

ACKNOWLEDGMENTS

I would like to thank the following people for reading and commenting on the manuscript: C. F. E. Roper, Smithsonian Institution; S. v. Boletzky, Laboratoire Arago; J. M. Arnold, Pacific Biomedical Research Center; and J. Walters, University of Hawaii.

LITERATURE CITED

HOYLE, W. E. 1886. Report on the scientific results of the voyage of the H.M.S. Challenger during the years 1873–1876. Vol. 16, pt. 44, Cephalopoda, p. 1–246. Reprinted 1966. Johnson Reprint Corp., New York.

JOUBIN, L. 1929. Notes préliminaires sur les céphalopodes des croisières du "Dana" (1921–1922). Octopodes ze partie. Ann. Inst. océanogr., Paris 7:1–24.

NAEF, A. 1923. Die Cephalopoden. Fauna u. Flora Neapel, monogr. 35, pt. 1 (2):149–863.

NIXON, M. 1969. The lifespan of *Octopus vulgaris* Lamarck. Proc. Malac. Soc. Lond. **38:** 529–540.

ROBSON, G. C. 1929. A monograph of the recent Cephalopoda. Part I. Octopodinae. British Museum. 236 p.

ROPER, C. F. E., and W. L. BRUNDAGE, JR. In press. Cirrate octopods with associated deep-

sea organisms: new biological data based on deep benthic photographs (Cephalopoda). Smithson. Contr. Zool.

THORE, S. 1949. Investigations on the "Dana" Octopoda. Dana Rep. 33:1–85.

YOUNG, J. Z. 1960. Observations on *Argonauta* and especially its method of feeding. Proc. Zool. Soc. Lond. 133 (3):471–479.

YOUNG, R. E. In press. Systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithson. Contr. Zool.