Reproduction in the Giant Octopus of the North Pacific, *Octopus dofleini martini*

BY

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(1 Plate)

INTRODUCTION

THERE HAVE BEEN several laboratory studies of reproduction in octopods. *Octopus joubini,* for example, has been reared through four consecutive generations (THOMAS & OPRESKO, 1973), and the eggs of *Hapalochlaena maculosa* have been raised through to the subsequent generation (TRANTER & AUGUSTINE, 1973). The young also have been described of *Octopus ocellatus* (YAMAMOTO, 1941), *Paraledone nigra* (REES, 1954), *Eledone cirrhosa* and *Eledone moschata* (REES, 1956), *Octopus vulgaris* (see for example VEVERS, 1961 and ITAMI *et al.,* 1963), *Octopus briareus* (MESSENGER, 1963 and WOLTERDING, 1971) and *Robsonella australis* (BROUGH, 1965), to cite some examples.

Octopus dofleini (Wulker, 1910) is the large octopod inhabiting the waters of the North Pacific. According to Pickford (1964), there are at least three subspecies: *O. dofleini apollyon* (Berry 1912) from the Pacific far North, *O. dofleini dofleini* (Wulker 1910, emend. Sasaki, 1929) from the temperate western North Pacific, and *O. dofleini martini,* Pickford, 1964, which inhabits temperate waters of the eastern North Pacific. In Japan, OKUBO (1973) made a detailed study of the eggs and juveniles of the Western Pacific subspecies, *O. dofleini dofleini.* The only previous report on the behaviour of young of *O. dofleini martini* was a recent description in "Oceans" of the emergence from the egg of juveniles (RUGGIERI & ROSENBERG, 1974). The opportunity to further study life history and behaviour arose in March, 1973, when the Vancouver Public Aquarium acquired a mature female *O. dofleini martini,* a mature male already being in their possession at that time.

MATERIALS AND METHODS

The adult octopuses were mated in a 2782-liter fiberglass tank on March 15, 1973. The female was placed in the tank on March 14, and the male on the following morning. After mating, they were separated and the female was transferred to a 265-liter fiberglass brooding tank. Tanks were supplied with running sea water pumped directly from nearby Burrard Inlet and passed through a series of sand filters. For the duration of the study, the female was offered frozen herring (*Clupea* sp.) and large, live cancer crabs *(Cancer magister* Dana, 1852) as food, both of which were generally accepted.

Temperature, salinity and pH of the water were measured throughout the spawning, brooding and hatching periods. Table 1 shows the range of each during the three periods.

Beginning on July 26 and every few days thereafter, a small quantity of eggs was removed and preserved in buffered formosaline. The figures in Table 2 are averages based on the measurements of a sample of 20 animals.

After hatching, the young were transferred into tanks ranging from 38 to 114 liters. The mouth of the outflow tube was expanded by attaching a styrofoam cup with a 70 mm diameter. Plankton netting (mesh size approximately ¾ mm) was stretched across the mouth of the cup thereby preventing the juveniles (and their food) from being swept through the outflow. The inflow tube directed water past the mouth of the cup to prevent animals from becoming entangled in the netting. The water flow in the tanks was approximately one liter per minute. Juveniles were offered a variety of foods including crushed egg yolk,

Table 1

	Spawning period	Brooding period	Hatching period
Duration	April 27 - May 11	April 27 - October 5	October 3 - December 20
Temperature	9.2° - 10.3° C	9.2° - 13.9° C	12.8° - 10.0° C
Salinity	28.1 - 28.8 ‰	27.3 - 29.4 ‰	27.6 - 28.9 ‰
pH	7.9 - 8.0	7.9 - 8.1	7.7 - 7.9

ground shrimp and mussel, live brine shrimp (both young and adult stages) and the fry of the red Irish lord sculpin *(Hemilepidotus hemilepidotus)*.

RESULTS

a) **Mating:** It has generally been reported that, during mating, the male octopod remains at a distance from the female and reaches out to insert the tip of its hectocotyl into the mantle cavity of the female. This has been observed, for example, with *Polypus bimaculatus* (Fox, 1938), *Octopus horridus* (Young, 1962) and *O. vulgaris* (Wells & Wells, 1972). In this case, the male *O. dofleini* mounted the female from above, enveloping her body with his arms and web, a position also reported for the blue-ringed octopus, *Hapalochlaena maculosa* (Tranter & Augustine, 1973). The female remained positioned beneath his body for the entire four-hour duration of the mating (see Figure *1*). Two long and narrow spermatophores, both empty, were recovered from the tank the following morning. According to Mann *et al.* (1970), the spermatophores of *O. dofleini* average a meter in length. Those removed from the tank averaged 0.9 meters.

A variety of courtship routines have been described for octopods including sucker display (Packard, 1961) and colour changes (see for example Wells & Wells, 1972). In the present study, the male displayed a variety of colour changes during the mating, the most conspicuous of which were alternating light and dark bars. Wells & Wells (1972) described this pattern in reference to the sexual display behaviour of *Octopus cyanea*. Changes in patterns and colours were most rapid in the periods immediately prior to mating and following disengagement. Changes during the four-hour mating were generally slow and gradual.

b) **Spawning:** Spawning began on April 27, 42 days after mating, and appeared to take place only at night. On the morning of April 27, 4 clusters of smooth, rice-sized eggs were discovered "glued" to the back wall of the tank. The egg capsules were chitinous and translucent. A single cluster contained several hundred elongate-ovoid eggs, each attached by a fine thread-like stalk (1.6 mm in diameter) to a central cord. The female continued to deposit eggs for 15 days until approximately 35 000 eggs covered more than 60 cm^2 of space on the tank wall. Water temperatures during the spawning period ranged from 9.2° to 10.3° C.

c) **Brooding behaviour:** As is typical of all brooding octopods, the female continuously agitated the eggs with the tips of her arms. She generally maintained the characteristic brooding position below the eggs with her arms curled upwards to comb through the clusters. Such behaviour has been described for a number of octopus species (see for example Le Souef & Allen, 1933; Fox, 1938; Batham, 1957; Vevers, 1961; Brough, 1965). Occasionally, the female ventured a short distance from the egg masses, but always maintained arm contact with them. The careful attention of the mother is essential to the survival of the eggs. Her constant brushing sweeps away any debris that may chance to settle on the eggs and cause decay. Figure *2* illustrates the brooding position normally maintained by the female.

The female occasionally siphoned streams of water onto the eggs, although with considerably less frequency than has been reported for species such as *Polypus bimaculatus* (Fox, 1938), *Octopus vulgaris* (Vevers, 1961) and *Robsonella australis* (Brough, 1965). In fact, during brooding, her rate of exhalation remained the same as before that period.

Contrary to what has usually been observed, both in nature and in the laboratory, the female octopus never ceased to feed. She accepted both crabs and herring, care-

fully siphoning away resulting bits of detritus from the eggs. The usual inhibition of the feeding response (see for example FISHER, 1923; VEVERS, 1961; ARAKAWA, 1962) may be a behavioural adaptation aimed at protecting the eggs from potential damaging debris, or from predatory attack in the absence of the female.

Brooding continued over 5 months. During the night of October 5, only 2 days after hatching had begun, the female pulled out the plug of her tank. The next morning she was found with one arm deep in the drain. Half of her arm was torn off and what remained was badly infected and had to be amputated. The next day, she was dead. An autopsy confirmed that her digestive system was healthy, unlike the condition found in most brooding octopuses. The male had also died, on May 8, only 54 days after mating. After the female's death, the rate of water flow in the brood tank was greatly increased to compensate for the change.

d) **Development and hatching:** No changes in the external appearance of embryos in the egg capsules were detected until July 26, on which day the eyes became apparent. The eggs averaged 6.28 mm in length and 2.86 mm in width on that date. Observations of the embryos began on August 2, 98 days after initial spawning.

On August 2, the embryos were very small and still unpigmented. The dorsal mantle length (DML)—the length from mid-eye to the posterior tip of the mantle—measured 1.06 mm about ¼ the length of the yolk which averaged 4.28 mm in length on that date. The head width, at 1.68 mm, was considerably greater than the mantle width which was 0.91 mm. The eye diameter measured 0.32 mm, and the arms averaged 0.41 mm in length. In the August 7 sample, there were 3-4 suckers per arm.

As development continued, the DML increased and the size of the yolk gradually decreased. By October 1, 157 days after spawning and less than a week prior to hatching, the DML had increased to 3.51 mm, while the length of the yolk had decreased to 2.35 mm. Furthermore, the mantle width, at 2.89 mm, had not only increased, but had widened beyond the head width, at 2.52 mm. Table 2 shows the growth of the DML and the concomitant decrease in the yolk size, as well as the increases in the head and mantle widths. By October 1, the eye diameter was 0.90 mm and the average arm length was 1.77 mm with 11-14 suckers. The changes in the various dimensions from August 2 to October 1 are given in Table 2. Stretching to accommodate the growing embryo, the length of the egg capsule averaged 6.64 mm and the width averaged 3.41 mm by October 1.

Small faint brown chromatophores first appeared near the eyes in the August 14 sample, 110 days after initial spawning. By August 31, the number of chromatophores had greatly increased, extending to the arms as well as the head and mantle. The ink gland appeared in the September 17 sample.

Until September 13, the embryos were situated proximally within the egg capsule with the yolk sac situated distally. By September 17, 40% of the embryos had rotated so that the mantle came to lie at the wide end of the capsule. By October 1, 78.3% have reversed their position. The actual rotation was not observed. According to OKUBO (1973), the embryos of *Octopus dofleini dofleini* complete reversal in about five minutes. TRANTER & AUGUSTINE (1973) described the 7-minute process as it occurred in *Hapalochlaena maculosa*. The embryo is presumably able to grow more effectively in the broader distal portion of the egg capsule and, in fact, a large increment in DML and mantle width occurred between August 31 and September 17 (see Table 2).

Table 2

Date of Sample	Yolk mm	Dorsal Mantle Length (DML) mm	Yolk/DML	Head Width mm	Mantle Width mm	Head Width/ Mantle Width	Diameter of eye mm	Arm Length mm	No. Suckers per arm
Aug. 2	4.28	1.06	4.04	1.68	.91	1.85	.32	.41	?
Aug. 7	4.34	1.34	3.23	1.96	1.29	1.40	.38	.69	3-4
Aug. 14	4.33	1.73	2.50	1.96	1.40	1.39	.52	1.01	5-7
Aug. 20	4.15	1.59	2.61	2.12	1.48	1.39	.58	1.16	7-8
Aug. 26	3.85	2.22	1.73	2.10	1.69	1.24	.68	1.18	7-9
Aug. 31	3.52	2.61	1.35	2.23	2.08	1.07	.68	1.32	9-11
Sept. 17	2.48	3.18	.78	2.51	2.84	.89	.86	1.39	10-12
Sept. 21	2.53	3.28	.77	2.48	2.83	.88	.88	1.52	10-13
Sept. 27	2.30	3.31	.69	2.50	2.83	.88	.90	1.71	11-13
Oct. 1	2.35	3.51	.67	2.52	2.89	.87	.90	1.77	11-14

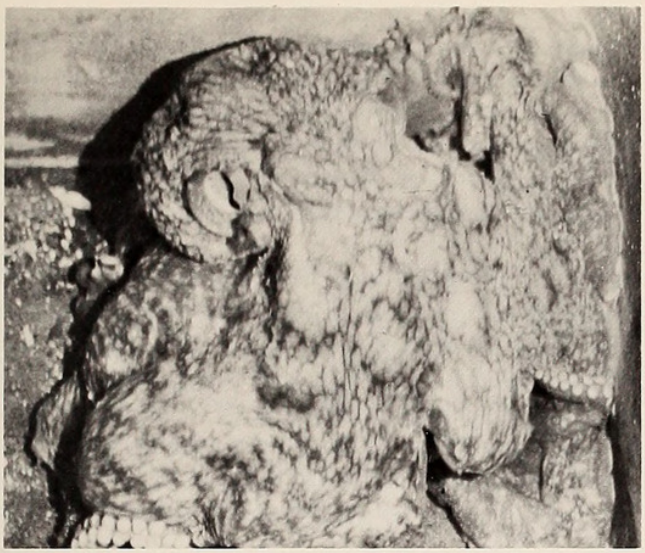

Figure *1*

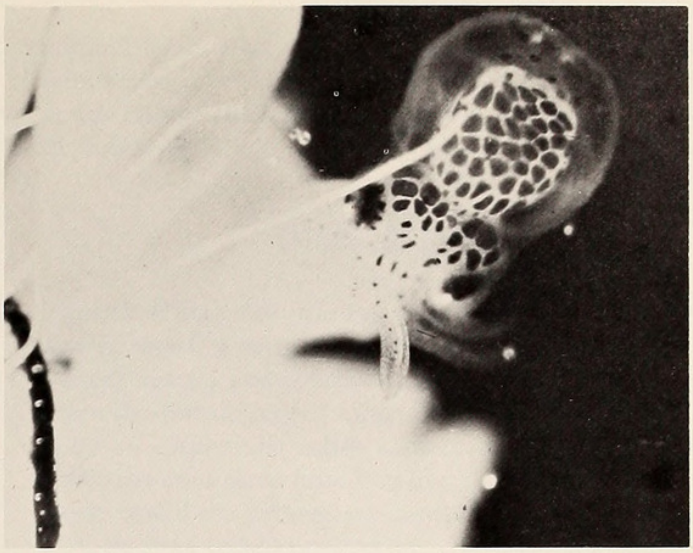

Figure *3*

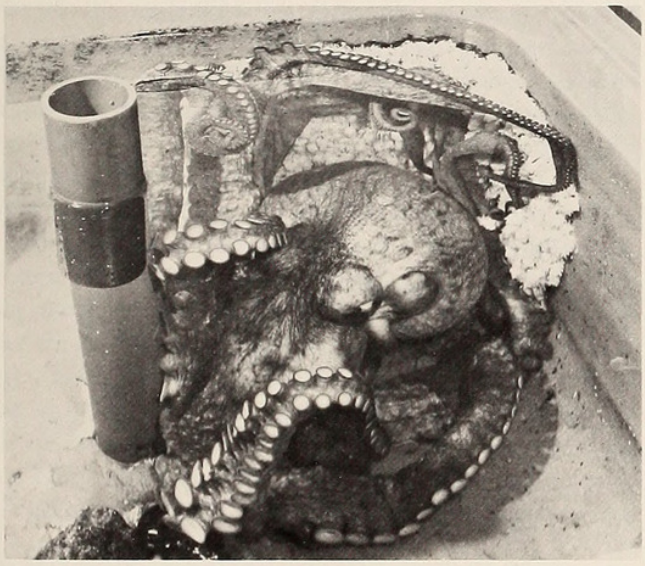

Figure *2*

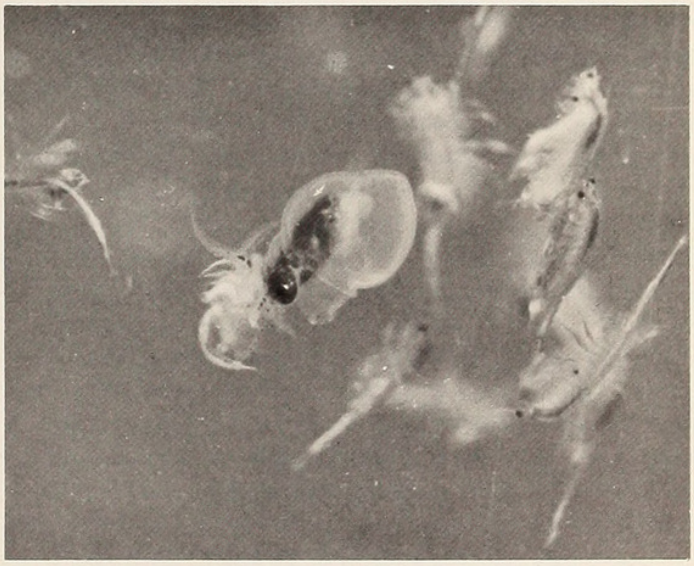

Figure *4*

Figure *1*: During mating, the male remained positioned above the female (photo by S. Gabe)
Figure *2*: Brooding of the eggs by the female (photo by Dr. Pierre Dow)
Figure *3*: A juvenile emerges backward from its egg capsule (photo by Finn Larsen)
Figure *4*: A brine shrimp in the jaws of a juvenile octopus (photo by Dr. Pierre Dow)