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ITEROPARITY IN THE LESSER PACIFIC STRIPED OCTOPUS *OCTOPUS CHIERCHIAE* (JATTA, 1889)

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Cephalopods are generally thought to be semelparous. Females are supposed to spawn once in their lifetime and then die, either promptly or after a brief delay during which the eggs are brooded (Wells, 1962; Packard, 1972). This strategy is characteristic of many species. It is not, however, universal within the class. Iteroparity has also been observed in other species of octopods that occur in the same area as *O. chierchiae.* One of these is the larger Pacific striped octopus (Moynihan and Rodaniche, 1982; Rodaniche, in prep.) and the third is a single female from an unidentified species.

O. chierchiae is common along the Pacific coast of Panama. Field observations there suggest that adult individuals usually inhabit rocky pools at the extreme low intertidal zone.

MATERIALS AND METHODS

The scientific nomenclature of octopods is often difficult and confusing. The species discussed in this paper is called *O. chierchiae* following the recommendation of Dr. Gilbert L. Voss of The University of Miami. The same species was called *Octopus oculifer* in an earlier publication (Moynihan and Rodaniche, 1977). It was given the vernacular name Lesser Pacific striped octopus by Moynihan and Rodaniche (1982).

Seven sexually mature *O. chierchiae* were captured in February 1975, after being anesthetized in a tidepool with a mixture of one part quinaldine and seven parts ethanol. They were immediately taken to the laboratory and each individual was placed in a separate aquarium.

At the beginning of the project, rocks, small gastropod shells and empty transparent bottles were placed in each aquarium for use as shelters or nests. However, when it became evident that the bottles were readily accepted as lairs, the rocks and shells were removed to facilitate observation.

Water temperature in the aquaria was 27°C ± 2°C. pH was occasionally monitored and found to be within natural limits. The captured animals were fed with small live shrimps and crabs *ad. lib.* Feeding of the hatchlings was more complicated. They required smaller prey that was not always readily available. An effort was made to feed them live newly-hatched brine shrimp but the hatchlings did not accept them. The lack of a constant supply of food may have inhibited the hatchlings' growth.

To minimize inhibiting their behavior while captive, a special effort was made to keep handling and disturbances to a minimum. For this reason the animals were only measured upon capture, and later through the aquarium glass after each spawning, and also after death. Newly captured individuals ranged from 8 mm to 18 mm in dorsal mantle length (DML). They continued growing in captivity. One female grew to a maximum DML of 25 mm.

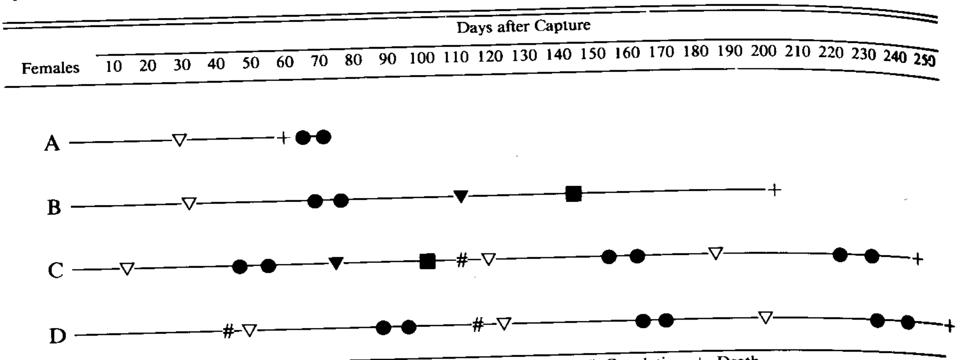
The third right (hectocotylized) arm of the male of *O. chierchiae* is modified. However, since this species is so small, this feature is only apparent when viewed under a microscope. Females were identified as such only by finding eggs in their lairs. Individuals that did not spawn were, when deemed necessary, placed in an aquarium with known females and observed for copulation. These experiments revealed that four of the captives were females and three males (Table 1).

RESULTS

In the laboratory, males always attempted direct copulation as soon as they encountered a mature female. No color changes or other signs of preliminary courtship were noted. To copulate, a male mounted a female dorsally, enveloping her body with his arms and web, and then inserted his hectocotylus into the female's mantle opening. Copulations were brief, lasting for approximately 1 min.

This copulatory position has been reported for the blue ringed octopus *Hapalochlaena maculosa* by Tranter and Augustine (1973) and for *Octopus dofleini*

Table 1. A summary, in chronological order from capture to death, of important events in the life cycle of the four females *O. chierchiae* observed in the laboratory



▽, Fertile spawn; ●–●, Hatching period; ▼, Unfertile spawn; ■, Eggs consumed; #, Copulation; +, Death.

by Gabe (1975). Males of *O. chierchiae* were smaller than the females, never exceeding 18 mm in DML, and their lifespans in the laboratory were shorter. None lived more than 150 days after capture.

Of the four females observed, two copulated a total of three times while captive. These animals spawned fertile clutches within 10 days of each copulation. Females that had not recently copulated delayed spawning until 20 to 35 days after the last egg of the previous spawn had hatched. These delayed spawns were not always fertile. Spawning involved the extrusion and placement of eggs (fertilized or unfertilized) onto the walls of the nest. Clutches were deposited inside transparent bottles but the act of spawning was never observed since it always seemed to occur on nights when the observer was absent. Each egg was attached singly by a stalk to the walls of the nest. Clutch size was determined by the size of the spawning female. Each clutch ranged from six eggs by a female with a DML of 8 mm to 35 eggs by the largest female (Fig. 2). Each stalk measured approximately 3 mm in length and the eggs measured 3.8 mm in length by 1.2 mm in width.

When brooding, a female positioned herself in front and below the egg mass, curled her arms over and behind, then "combed" the eggs with the tips of her arms, and occasionally renewed the water around the egg mass by blowing with her funnel or siphon a gentle current of water at the eggs. Similar behavior has been reported for other octopods by Le Soeuf and Allan (1933), Batham (1957), Vevers (1961), Brough (1965) and Gabe (1975).

Associated behavior was less conventional. Post-spawning feeding has been reported for some species of octopods (Gabe, 1975; Wodinsky, 1978). In all cases the brooding females refused or were reluctant to leave the nest completely unattended, venturing a short distance from the egg masses but always maintaining arm contact with them (Borer, 1971; Gabe, 1975; Joll, 1976). Brooding *Octopus cyanea* sometimes captured, killed and dismembered prey, but did not consume it (Van Heukelem, 1973). *O. chierchiae* was repeatedly seen to leave the nest completely unattended for some seconds or minutes in order to hunt for prey in their aquaria.

Hatching began 37 to 44 days after spawning and lasted from 4 to 7 days. The mother did stop feeding during hatching. She resumed feeding as before 2 to 3 days after the last egg hatched. At this stage she ate any newborn young remaining in the nursery aquarium. Cannibalism is well documented in cephalopods (Boy-

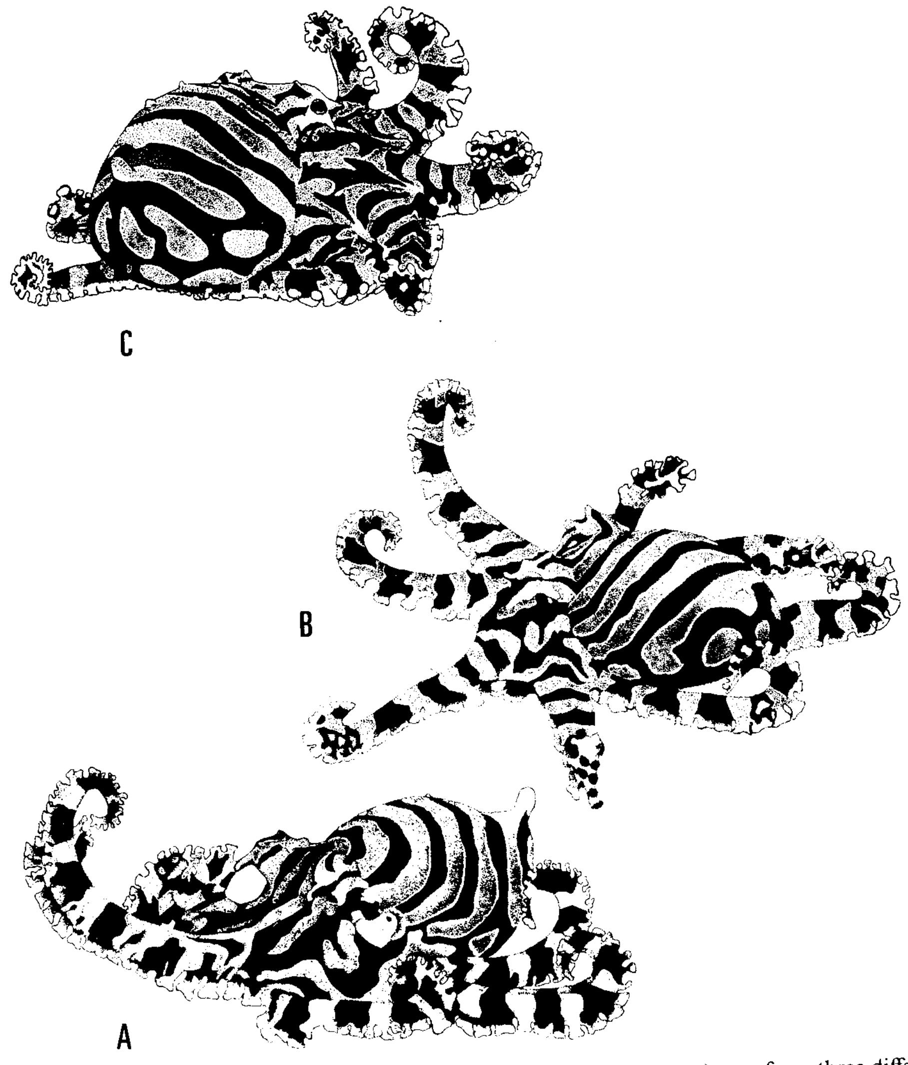
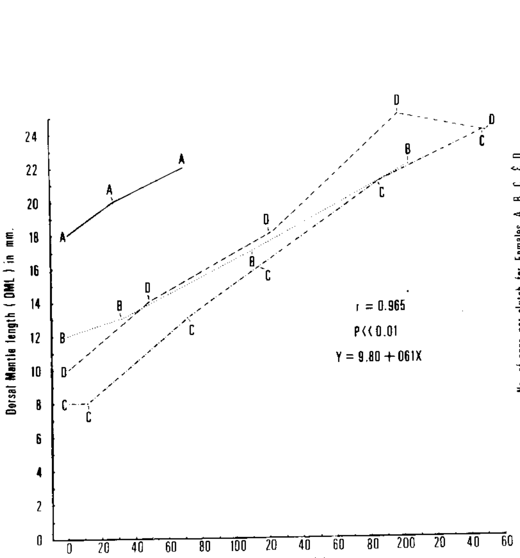


Figure 1. Agonistic displays of a female *Octopus chierchiae* (DML 25 mm) seen from three different angles: A, lateral; B and C, dorsolateral. Note the following patterns which may be performed individually or in combination: rising of cirri over and around the eyes, darkening of permanent striped pattern, and pointing of the cap. Illustration by the author.

cott, 1954). Under natural conditions, the temporary cessation of feeding by the mother probably allows the young to escape from her and move to other areas.

Unlike those octopods whose young go through a planktonic stage, the newborn of *O. chierchiae* are benthic, large when compared to the mother, and fully developed. At hatching they measured 3.5 mm in DML. After 14 days they had grown to 5.5 mm in DML. From then on, probably due to the lack of acceptable food, their growth remained almost static and mortality increased. Only four females from a brood of 26 reached a DML of 8 mm in 67 days, then died shortly afterwards.

None of these four females ever spawned, perhaps because there were no males



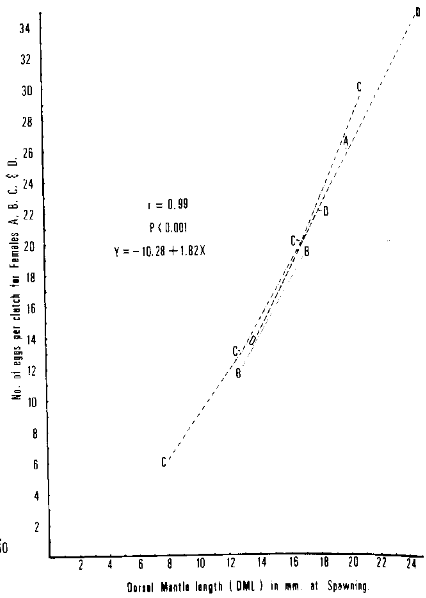


Figure 2. (Left) The first and last datum points on the growth curves are measurements made upon capture and after death of each female. The others are measurements made after each spawning. Note: Since octopus A was larger at capture than octopuses B, C and D, the datum points in curve A were not included when computing R.

Figure 3. (Right) Number of eggs for each clutch is determined by size of female at spawning.

available at this stage. Of the 26 individuals, 23 were dissected shortly after death. No eggs were found in any except the four females that had lived the longest.

The reproductive histories of the four captive females are outlined in Table 1. They may also be summarized as follows:

Female A spawned only once, and while brooding this fertile clutch was killed by a larger octopus of another species that crawled into her tank. Female B spawned twice, the second clutch being infertile. These eggs were brooded but gradually disappeared over a period of 27 to 33 days. Presumably they were eaten by the mother. She never spawned again, stopped eating and died. Female C spawned four times, the second spawn being infertile. When this clutch disappeared, she was provided with a male, they copulated and she spawned two fertile egg clutches. This female died accidentally when she crawled from her aquarium. Female D copulated twice and spawned three fertile clutches. Of her three fertile spawns, two occurred after her last copulation and her last spawn occurred 83 days after copulating. After this clutch hatched she did not resume eating and died 10 days later. The repeated spawning by three of the four females probably was not simply an artifact of captivity. Several lines of evidence support this contention: (1) The females continued to feed during the brooding period, fasting only briefly during the hatching process. They also continued to feed and to grow after copulating or spawning (Fig. 3). (2) The general sequence of events was the same in three individuals, in spite of differences in timing. (3) In the wild, encounters between the two sexes may be more frequent than were allowed in the laboratory. Because males readily copulated with any mature non-brooding female, and since females always spawned shortly after copulating but delayed spawning when they had not, it can be assumed that the number of clutches and frequency of fertile spawns is higher in the wild than was observed in the laboratory. (4) Females of five other unidentified species of octopods, kept in similar conditions at the same times, spawned only once. They stopped feeding while brooding their clutches, and died shortly after the eggs hatched. Females of "the larger Pacific striped octopus" (Moynihan and Rodaniche, 1982), a species known to science but still nameless, laid several clutches; only one clutch of each female was fertile (A. Rodaniche, in prep.). A third unidentified species represented by one female was captured along with a large clutch of about 700 eggs. She brooded these until hatching. Fifty-seven days later she spawned a similar fertile clutch, and brooded them until they hatched. She too continued to feed throughout the 111 days of captivity, fasting only during the hatching period. After her second spawn hatched, she did not resume eating and died 15 or 16 days later. The eggs of both these species were smaller than those of *O. chierchiae* and the newborn were pelagic. It is interesting to note that the female of this third iteroparous species did not exhibit any permanent markings or stripes, so typical of the first two. It is possible that this female did not spawn the egg mass she was captured with but found this particular egg mass abandoned, or evicted its natural mother, and then assumed her brooding duties. But this is unlikely. Three surrogate mothers of the larger Pacific striped octopus could not be induced to brood three different egg masses for longer than 2 h in the laboratory. In one instance one of them, after brooding an egg mass for about 45 min, partially destroyed and then abandoned the nest. (5) Wodinsky, working with *O. hummelincki,* was able to induce brooding females "to cease their broodiness, resume feeding, increase their growth and greatly extend their lifespan" by removing their optic glands (Wodinsky, 1977). These females did not, however, spawn again. It seems very unlikely that the conditions of captivity in *O. chierchiae* females could have interfered with their hormonal systems in the same manner as Wodinsky's operation.

Points 3 and 4 above would seem to indicate that iteroparity is not unusual in *O. chierchiae* nor an isolated case in the Neotropics where warm temperatures, food and space are more or less stable especially when compared to temperate areas where seasonality may restrict spawning to very short periods.

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