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Observations on the Embryonic Development of *Octopus mimus* (Mollusca: Cephalopoda) from Northern Chile

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Abstract. The embryonic development of *Octopus mimus* Gould, 1852, was studied under normal upwelling temperature conditions (16°C) and under conditions of medium and strong El Niño Southern Oscillation (ENSO) events (20°C and 24°C, respectively). The embryonic development under high temperature conditions is faster than at lower temperature. Embryonic development of *Octopus mimus* under normal upwelling temperature conditions (represented by a constant temperature of 16°C) takes about 35% more time than under conditions of medium ENSO events (at a constant temperature of 20°C), and 62% more on average than under conditions of strong ENSO events (at a constant temperature of 24°C). There were no abnormalities visible on the embryos developed at 24°C. The hatching rate was high (estimated at about 95%). The higher temperature had no adverse effect on the viability of the hatchlings. This suggests genetic fixation of a wide temperature tolerance.

The embryonic development of *Octopus mimus* is very similar to that of *O. vulgaris* Cuvier, 1797. However, egg and hatchling size, number of gill lamellae per demibranch, and heartbeat frequencies differ between the two species.

INTRODUCTION

Octopus mimus Gould, 1852, is common along the Chilean coast from 18°S to 37°S (Osorio et al., 1979). This octopus is an important resource for artisanal fisheries in the northern part of Chile. From 1978 to 1994 the total catch increased from 4 tons to 3732 tons (Servicio Nacional de Pesca, 1994).

During El Niño Southern Oscillation (ENSO) conditions in 1982/1983, the population size of *Octopus mimus* increased significantly, in contrast to most other invertebrates of this region which died out or were significantly reduced (Arntz & Fahrbach, 1991). Near Antofagasta (northern Chile) the population of *O. mimus* increased by a factor of 100 (Tomicic, 1985).

Little is known about the life cycle of *Octopus mimus*. Size at maturity and the reproductive cycle were studied by Arancibia (1984) and Cortez et al. (1995b). Wolff & Perez (1992) investigated aspects of population dynamics, food consumption, and conversion efficiency, and Cortez et al. (1995a) observed feeding dynamics. *Octopus mimus* was long synonymized with *O. vulgaris* Cuvier, 1797, and has only recently been recognized again as a separate species (Guerra et al., personal communication). Apart from a few pictures of an egg mass given by Cortez (1995), nothing has been published on the embryonic development of *O. mimus*. The present study provides details of the embryonic development, under normal upwelling conditions (16°C) and under conditions of medium and strong ENSO influence (temperature 20°C and 24°C, respectively). The aims of this study are (1) the assessment of the influence of ENSO type temperature changes on embryonic development, and (2) to define the differences in embryonic development between *O. mimus* and *O. vulgaris*.

METHODS

Adult *Octopus mimus* were collected off the coast of northern Chile in the region of Iquique, by SCUBA diving at depths of 5–10 m. Dorsal mantle length (measured from the midpoint between the eyes to the apex of the mantle tip), head width, and weight were determined in all adult females. In the field, the main spawning season of *O. mimus* is between November and March, although egg laying is observed throughout the year. Animals were maintained in 500 L tanks at the Departamento Ciencias del Mar (Universidad Arturo Prat). All octopuses were kept in the laboratory under constant temperature conditions of 16°C, 16.5°C, 20°C, and 24°C (±1°C) with a slow continuous flow of clean seawater resulting in a daily renewal of the whole water volume.

The nitrate content of the aquarium water was monitored following the recommendation of Boletzky & Hanlon (1983). When a high nitrate concentration was observed, the aquarium water was partly changed until nitrate could no longer be detected.

Females were kept isolated in covered tanks. Each tank contained a clay flower pot as a hiding place for the female, providing her with a substrate on which she could attach her eggs and brood them as she would do in a den under natural conditions.

Brooding females of *Octopus mimus* were fed daily at least one item from a variety of clams (*Venus antiqua,*

Protothaca thaca, Gari solida, and *Tagelus dombii*), and crabs (*Leptograpsus variegatus* and *Cancer setosus*). *Venus antiqua* was the dominant food item.

The females laid their eggs in long strings or festoons. The number of strings was counted and the string length was measured. The number of eggs in 1 cm of string was determined, providing an estimation of total egg number per egg mass. At 3-day intervals, 3–10 eggs were removed from each egg mass and examined under a dissecting microscope. Drawings were made, and photographs of the eggs were taken with a camera (Nikon System of Microflex HFM-35A-35 mm camera box M35FA) connected to the dissecting microscope (Nikon SMZ-10). A video camera (Sony video color 1 CCD model DXC107A) attached to the microscope was used occasionally to monitor embryos.

Eggs were fixed in Bouin's fixative (15 vols. picric acid, 5 vols. formalin, 1 vol. acetic acid) and preserved in 70% ethanol for later examination. Developmental stages of the embryos were identified according to Naef (1928). The rate of embryonic growth was determined by regular control measurements of egg size, yolk volume, and size of the embryo body. The standard deviation (SD) of size was calculated for each sample size (n). The time required for embryonic development was determined for the different temperatures, along with the frequency of heartbeat at advanced stages. Embryonic mortality within an egg mass was estimated based on the daily observation records. In addition, embryonic development was described and compared to the observations reported for other species of *Octopus* (Boletzky, 1967, 1969, 1971a, b, 1987, 1989; Fioroni, 1978; Hochberg et al., 1992; Joll, 1978; Mangold-Wirz, 1983).

The size of hatchlings, total length, dorsal mantle length, and head width were measured following Hochberg et al. (1992) and standard deviations were calculated. For close observation of behavior, groups of 100 hatchlings each were maintained in six small glass aquaria equipped with air bubblers surrounded by fine mesh to avoid damage to the hatchlings. Each aquarium contained 55 L of still seawater, which was changed once a day. The hatchlings were fed various planktonic organisms (mainly larvae of *Pagurus* sp. and of *Cancer setosus*). First feeding was observed through the transparent aquarium wall and was subsequently validated by close inspection of the digestive tract of the observed individuals under the dissecting microscope.

RESULTS

The smallest mature female *Octopus mimus* found during this study in the field had a mantle length (ML) of 120 mm and a head width of 45 mm, with a total wet weight of 868 g. The ovary weighed 165 g; the capsule length of the mature ovarian eggs measured 1.95 mm. The largest female *Octopus mimus* observed weighed 2818 g with a mantle length of 230 mm, and a head width of 50 mm.

Brooding females were fed daily. All females survived for at least 2 weeks after hatching of the last young.

Egg and string size. Egg laying was observed nearly throughout the year (see Table 1). From the egg string counts and subsamples of eggs, the average fecundity of a female *Octopus mimus* was estimated at between 60,000 and 200,000 eggs. Indeed each female laid about 200 strings of eggs ranging from 3–10 cm in length and containing an average of 100 eggs in 1 cm.

The eggs of *Octopus mimus* are small in terms of both absolute and relative size. The chorion capsule of freshly laid eggs measured on average 2.03 mm in length (n = 50; SD = 0.25) and 0.9 mm in width (n = 30; SD = 0.08); the stalk measured 5.7 mm (mean of five measurements) in length (cf. Mangold-Wirz 1983: fig. 21.2 for *O. vulgaris*). The yolk mass on average was 1.7 mm long (n = 27; SD = 0.17) and 0.8 mm wide (n = 27; SD = 0.09). The increase of chorion length through embryonic development was similar in all egg masses except "C" and "F" (Table 1). The value for egg mass "C" is not significant, however, given the small sample size (see Table 1). In this case, the initial chorion length was relatively small compared to the other egg masses. Thus the average increase of chorion length of all egg masses, excluding egg mass "C", was about 11%. There was no correlation between magnitude of size increase and temperature. The hatchlings measured on average 2.34 mm (n = 60 individuals; SD = 0.19) in total length. The range of variation in the hatching size was 2.1–2.6 mm total length. Hatchlings had an average mantle length of 1.85 mm (n = 30; SD = 0.08) and a head width of about 0.84 mm (n = 30; SD = 0.09).

Embryonic development. The embryonic development of *Octopus mimus* (Figure 1A–F) turned out to be very similar to that of *O. vulgaris* (Boletzky, 1969, 1971a, 1989). Like other cephalopods, *O. mimus* develops a discoblastula at the animal pole of the ovum on the side of the micropyle. Stage I of Naef is defined as the end of cleavage (Figure 1A). Then the prospective yolk sac envelope grows over the yolk surface toward the vegetal pole. At Stage VII the first relief elevation of the embryo in the mantle region is visible at the animal pole (Figure 1B). By this time, aided by the ciliary beat of the yolk sac envelope, the embryos begin to rotate around their longitudinal axis in a clockwise direction (in apical view). Eventually the direction of the ciliary beat changes and the embryos reverse their position in the chorion, as described for *Octopus vulgaris* (Boletzky, 1971a, b). The yolk envelope is completed at about Stage IX and the resulting outer yolk sac begins to pulsate irregularly (about seven beats per minute). At Stage X to XI the arm buds are conspicuous but the mantle rudiment is still flat (Figure 1C). The inner yolk sac shows two posterior lobes at about Stage XII. In the depression between these lobes

Table 1

Duration of embryonic development to the day of hatching and growth of *Octopus mimus* during embryonic development under the influence of different temperatures (n = sample size; SD = standard deviation).

Temperature (°C)	Egg mass (date)	Time to first regular heartbeat (days)	Duration of embryonic development to the day of hatching (days)	Length of egg at beginning of embryonic development (mm; mean value)	Total length of hatchling (mm; mean value)	Increase in chorion length during embryonic development
24	A 5/8/95-6/2/95 autumn	18	25	2.11 n = 10 SD = 0.11	2.23 n = 30 SD = 0.20	5.7%
20	B 9/18/94-10/26/94 spring	23	38	2.28 n = 7 SD = 0.22	2.37 n = 10 SD = 0.44	4.0%
20	C 12/12/94-1/24/95 summer	28	43	1.69 n = 2 SD = 0.58	1.96 n = 1	15.98%
20	D 3/20/95-4/26/95 autumn	22	37	2.27 n = 10 SD = 0.05	2.42 n = 9 SD = 0.09	6.6%
16.5	E 4/28/95-6/30/95 autumn	46	63	2.06 n = 10 SD = 0.10	2.15 n = 10 SD = 0.04	4.3%
16	F 2/2/95-4/10/95 summer/autumn	44	67	1.78 n = 10 SD = 0.16	2.0 n = 10 SD = 0.15	12.3%

the stomach rudiment has been closed (Figure 1D). The coordination and the first regular pulsation of systemic heart and branchial heart occurs at about Stage XV; it was observed after 18 days (d) at a temperature of 24°C, after 24 d at 20°C (average of two egg masses), and after 44 d at 16°C (Table 1). By stage XV the inner yolk sac is very reduced (Figure 1E) as in other octopods (Boletzky, 1975; Joll, 1978); it increases again later (Figure 1F). The outer yolk sac is now clearly demarcated from the body of the embryo. Before hatching, i.e., between Stage XIX and Stage XX when the outer yolk sac has been strongly reduced in size, most of the embryos reverse their position a second time as in *O. vulgaris* (Portmann, 1933).

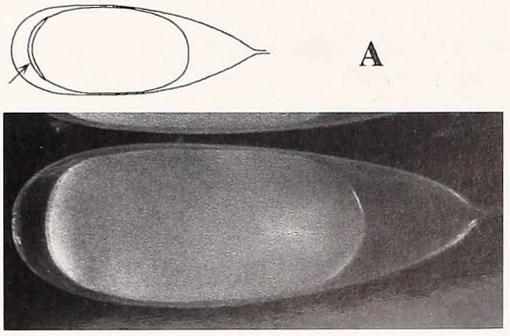
There are only a few notable differences between the embryos and the hatchlings of *Octopus mimus* and *O. vulgaris*. The hatchlings of *O. mimus* have seven (Figure 1G) gill lamellae per demibranch, while those of *O. vulgaris* have only five (Boletzky, 1969). The appearance of pigment in the ink sac is somewhat earlier in *O. mimus* (Stage XVII) than in *O. vulgaris* (Stage XVIII). The chorion stalk length in relation to the chorion capsule length of *O. mimus* (×2.8) is also slightly higher than in *O. vulgaris* (×2.5) (Boletzky, personal communication; cf. Mangold-Wirz, 1983: fig. 21.2 for *O. vulgaris*).

Embryonic development in *Octopus mimus* takes about 65 d under normal upwelling temperature conditions (represented by a constant temperature of 16°C), about 39 d under conditions of medium ENSO events (at a constant temperature of 20°C), and 25 d on average under conditions of strong ENSO events (at a constant temperature of 24°C) (Table 1 and Figure 2). Thus development duration at 24°C was about 60% of that observed at 20°C, which was about 65% of the development time at 16°C.

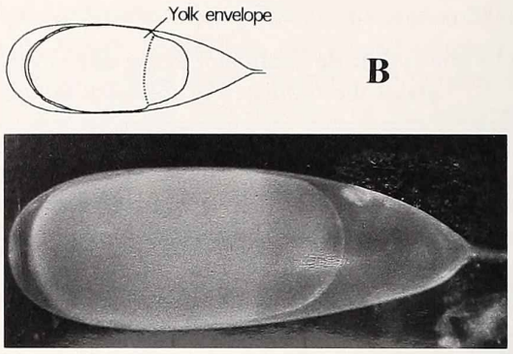
The time lapse between first and last egg laying and between first and last hatching was between 5 and 14 d, respectively, independent of the rearing temperature.

Due to the high room temperature, it was not possible to maintain a constant low water temperature in the Petri dishes used for determination of the heartbeat frequency in embryos when observed under a dissecting microscope. For example, an egg mass kept at an average brooding temperature of 20°C contained embryos showing between 44 and 26 heartbeats/min. Egg mass "E" was kept at a temperature of 16.5°C. At Stage XIX, the heartbeat of an embryo of this egg mass showed a frequency of about 52 pulsations/min. One day later, at a constant temperature of 22°C, the same embryo had a frequency of 94 pulsations/min. This variation is most likely due to the temperature sensitivity of heartbeat rate.

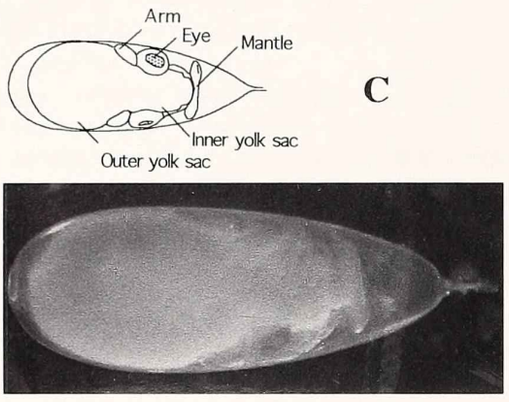
Nevertheless, heartbeat frequency increased with developmental progress in general, until it became relatively



A

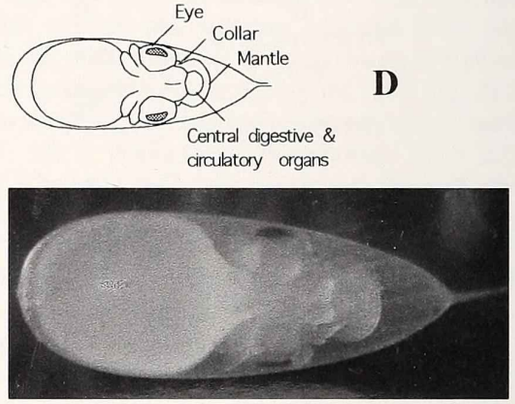

Yolk envelope

B

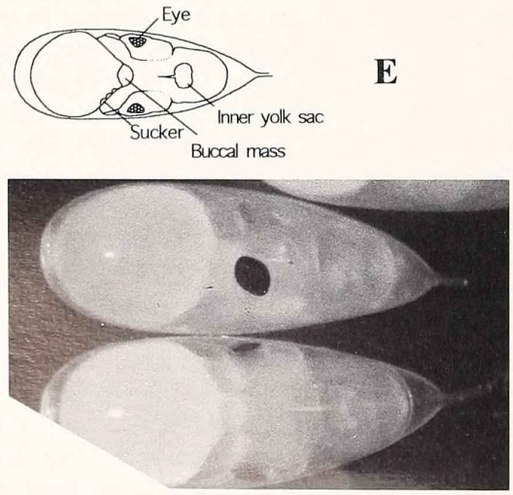


Arm
Eye
Mantle
Inner yolk sac
Outer yolk sac

C

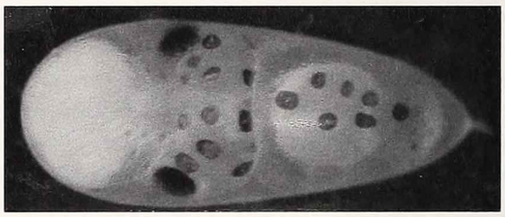

Eye
Collar
Mantle
Central digestive &
circulatory organs

D

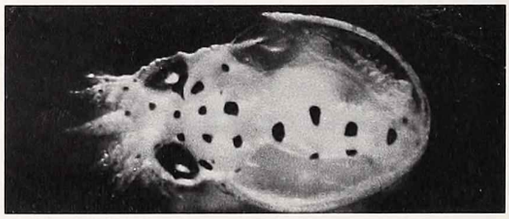

Eye
Inner yolk sac
Sucker
Buccal mass

E

F



G



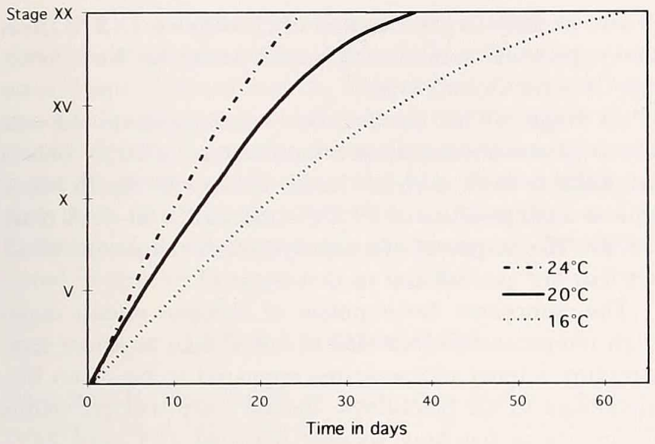


Figure 2

Course of embryonic development in *Octopus mimus* at three different temperatures (stages according to Naef, 1928).

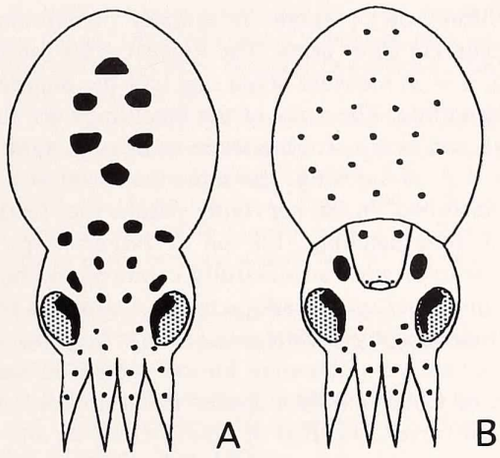


Figure 3

Schematic presentation of chromatophore distribution in *O. mimus* (A = dorsal view, B = ventral view).

stable from Stage XV onward. In autumn (March until May 1995), the environmental temperature of 20°C corresponded to the brooding temperature of the egg mass "I" during the entire time of embryonic development. At Stage XIII, the average heartbeat was 28 pulsations/min. At Stage XVIII, the heartbeat was about 77 pulsations/min.

The estimated mortality rate of egg masses reported in this paper was low (about 5-20%). The hatching rate of egg masses "B" (20°C) and "A" (24°C) was nearly 100%. Egg mass "E" had fungi on the chorion surfaces, and the mortality rate was more than 50%. After Stage XV, some abnormal stages were visible within this egg mass. The inner yolk sac increased to an abnormally large size. Therefore the data from these embryos are not included in this paper.

Pigmentation. The retina became light orange at Stage X, turned bright red at Stage XIII–XIV (Figure 1E), and finally became dark brown at Stage XVII/XVIII (Figure 1F).

Chromatophores appeared at Stage XV on the head, arms, ventral mantle surface, and on the dorsal surface of the visceral mass (bottom of dorsal mantle cavity). The hatchling chromatophore pattern was nearly complete at Stage XIX (Figure 1F). Hatchlings (Figure 3) have a total of 75–89 chromatophores. Every arm has two to four chromatophores on the outside in a simple row. The dorsal surface of the digestive complex has six to eight large visceral chromatophores. The dorsal head surface has 9–10 chromatophores in a 2 + 4 + 4 pattern and one large chromatophore per eye. The ventral head surface has two large chromatophores. The funnel shows five (six) chromatophores in a 3 (4) + 2 pattern. The ventral mantle is evenly covered with 21–24 chromatophores.

Hatchlings. The hatchling size (ML 1.85 mm) is less than 2% (1.15%) of the size of the adult animals (ML 175 mm). Like the hatchlings of other octopodid species producing relatively small eggs (hatchling ML smaller than 8% of adult ML; Boletzky, 1984), the mode of life

←

Figure 1

Living embryos of *Octopus mimus* (egg size 2 × 1 mm) at different stages of development according to Naef (1928). A. Stage I at the animal pole of the chorion: the end of blastulation is visible (arrow). B. Stage VII: yolk envelope is growing (4/5) over the yolk toward the vegetal pole. At the animal pole the first relief in the mantle region is visible. C. Stage X to XI: dorso-ventral view: after first reversion of the embryo, midgut gland region with huge yolk papilla: clasp of midgut is still open, arm buds conspicuous, mantle rudiment still flat, beginning of retina pigmentation. D. Around Stage XII: arm buds are still rounded, not pointed, inner yolk sac still with two lobes, in the indentation between the lobes the stomach has been closed; the retina is well pigmented, behind the cheek hump the funnel pouches are visible. E. Both animals at Stage XV: lateral view: oval rhomboid retina (red retinal pigment); dorsal view of buccal complex between arms, right dorsal arm with sucker rudiments, inner yolk sac reduced, at this stage regular heartbeats. F. Stage XVIII/XIX: dorsal view: shortly before the second reversion, six to eight chromatophores on dorsal surface located on visceral mass (bottom of dorsal mantle cavity), dorsal head with 10 chromatophores in a 2 + 4 + 4 pattern, each arm with a single row of two to four chromatophores. G. Hatchling of *Octopus mimus* (2.2 × 0.84 mm), note gill with seven lamellae per outer demibranch.

of hatchlings of *O. mimus* is initially planktonic. They have relatively short arms. The longest arms (about 0.9–1.0 mm, n = 3) measure about one half the mantle length of the hatchling. The arms of the hatchlings are subequal in length and every arm has three suckers of similar size.

After 4 d of hatching, the inner yolk sac was almost totally absorbed. In the surviving paralarvae, feeding began 5 d after hatching. Larvae of *Pagurus* sp. and of *Cancer setosus* were successfully captured by the hatchlings. *Cancer setosus* clearly acted as a stimulus for feeding as indicated by Villanueva (1994). *Pagurus* sp. and *C. setosus* are very abundant littoral species in the northern part of Chile and thus appear as an appropriate food source. However, survival of young *Octopus mimus* was very limited under aquarium conditions. The last paralarva died 12 d after hatching.

DISCUSSION

Recent morphological investigations (Guerra et al., personal communication; Hochberg & Mangold, personal communication) and DNA-sequencing results (Söller et al., work in progress.) indicate that *Octopus mimus* and *O. vulgaris* are closely related, but distinct species. It appears that their embryonic development is rather similar. Therefore the staging system of Naef (1928) for embryonic development of *O. vulgaris* can be applied to all stages of *O. mimus*. The first and second reversion, the earliest pulsation of the outer yolk sac, and the beginning of the heartbeats occur at the same development stages. Also the stage when pigmentation begins to be visible in *O. mimus* and *O. vulgaris* is the same. In contrast to the chromatophore pattern of *O. mimus* as described by Cortez (1995), I found no clear difference between the chromatophore patterns observed in *O. mimus* and those described by Fioroni (1965) for *O. vulgaris*, since there is always a relatively high natural variability in the respective patterns.

A clear difference was observed in the number of gill lamellae per demibranch at the time of hatching: five for *Octopus vulgaris* (adult: eight to ten [Boletzky, 1969]) and seven for *O. mimus* (adult: seven to eight [Cortez, 1995]). The hatchlings of *Scaeurgus unicirrhus* delle Chiaje, 1830, also have seven lamellae per demibranch of the gill; they are in the same size range, but have four instead of three suckers and more numerous chromatophores than *O. mimus* (Boletzky, 1984). Another distinction between *O. mimus* and *O. vulgaris* is the earlier appearance of the ink in the sac in *O. mimus*. The arm length of *O. mimus* was found to range from 0.9–1.0 mm (measurements from fresh animals), which is somewhat longer than that reported for *O. vulgaris* (0.7 mm; see Hochberg et al., 1992). This slight difference in the arm length is probably insignificant due to the small number of individuals measured (n = 3). The chorion stalk length in relation of chorion capsule length of *O. mimus* (×2.8) is also slightly larger than that of *O. vulgaris* (×2.5) (Boletzky, personal communication; cf. Mangold-Wirz, 1983, fig. 21.2 for *O. vulgaris*).

At Stage XVIII, the heartbeat of *Octopus mimus* was about 77 pulsations/min at a temperature of 20°C. This is comparable to *O. tetricus* Gould, 1852, with 65–75 beats/min at a temperature of 19.5°C at Stage XVIII–XIX (Joll, 1978). The stages of the embryonic development of *O. tetricus* are also similar to *O. vulgaris*.

The embryonic development of *Octopus mimus* under high temperature conditions is faster than at lower temperature. Higher temperatures appeared to be of no disadvantage to the hatchlings. Indeed there was no visible difference in hatching success between 20°C and 24°C, the hatching rate in egg masses "B" (20°C) and "A" (24°C) being nearly 100%.

The low survival rate of the hatchlings could be related to failures in the system used for preparing the seawater for the small culture aquaria, and/or to the limited variety of natural food items available. Whether the rather small average increase of egg size in *Octopus mimus* (chorion capsule length 11% for *O. mimus* in these experiments in contrast to 25% for *O. vulgaris*; Boletzky, 1969) is a normal feature or reflects a less than optimal water quality remains to be seen. In any event, embryonic development appeared perfectly normal (except in egg mass "E"; these abnormal embryos are not considered in the results of this paper).

Compared to the developmental rates in *Octopus vulgaris* at a variety of temperatures (Boletzky, 1987), the speed of embryonic development of *O. mimus* is not significantly different. It is within the normal range determined for other warm water octopods with planktonic young, such as *O. cyanea* Gray, 1849, *O. tetricus* and *O. bimaculatus* Verrill, 1883, (see Boletzky, 1969).

Tomicic (1985) described an increase of the population of *Octopus mimus* by a factor of 100 in northern Chile during the last major ENSO event 1982–1983. Thus, *O. mimus*, which is clearly adaptated to life in the cold upwelling waters off Chile, can also live under warm water conditions. This population increase may be due to several factors—environmental ones such as decrease in numbers of predators or increase of food supply—or to intrinsic ones, i.e., genetic factors making the animals more competitive, perhaps through physiological improvement of food conversion at higher temperatures.

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