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Reproductive biology and embryonic development of *Eledone cirrosa* (Cephalopoda : Octopoda)

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Abstract

Analyses of bottom trawl samples and feeding experiments in the laboratory revealed a reproduction period ranging from late March to early August in *Eledone cirrosa* of the Catalonian Sea (Western Mediterranean). The embryonic development, studied for the first time on eggs laid in the laboratory, shows no basic difference from that of other Octopodidae. The newly hatched animals are planktonic; morphologically, this feature is expressed by a relatively small arm-length.

Introduction

The lesser octopus *Eledone cirrosa* is probably the most abundant cephalopod of the Northwestern Mediterranean Sea. It is a truly benthic species but, unlike *Octopus vulgaris*, it lives the whole year in large schools and females only retire for spawning. We shall ignore, however, the place and extent of the actual spawning area. Observations on spawning and breeding behaviour in the laboratory strongly suggest that *E. cirrosa* deposits its eggs on rocky substrate in a similar way to *O. vulgaris*, and certainly not on open smooth muddy or sandy bottom (as e.g. *Loligo vulgaris*). There is little chance of collecting egg clusters by means of conventional fishing gear. To this day, we are aware of only 1 egg mass found in the sea, near the Shetland Islands (Stephen, 1944). The little information we have on breeding spots is based on recordings of the presence of fully mature females in some places and their absence in others.

Egg laying in the laboratory has been observed several times in the past (Joubin, 1888; Gravely, 1908; Isgrove, 1909; Hertling, 1936; Moore, 1937; Mangold-Wirz, 1963). But all eggs failed to develop normally.

In the present paper, new data on reproductive biology are given, and the embryonic development is described for the first time.

Material and methods

In winter and spring of the years 1965 to 1968, a total of more than 100 bottom trawl samples taken in the area of Banyuls-sur-Mer, France revealed a particular concentration of *Eledone cirrosa* in 3 distinct areas. Accordingly, animals were captured between late February and early June 1969 at the following 3 stations: 2, 9.5, and 20 miles off Banyuls, at depths of 60 m, 90 to 100 m, and 250 to 400 m, respectively. Some females were immediately isolated in 100 l plastic tanks, others were left together with males in a big tank and isolated after copulation.

Embryonic development was studied on eggs deposited on 26 March and during the subsequent days. Temperature of the running sea water in the laboratory was 14 °C at the time of spawning. Illumination was provided by natural daylight in these experiments.

Results

Sexual maturation

In winter and spring, 3 distinct groups of *Eledone cirrosa* are recognisable in the region of Banyuls-sur-mer. The first group lives at 50 to 60 m depth, 2 miles off the coast. This large group contains very few males (Wirz, 1958). Average weight of the females in March is 350 g, when their eggs are still immature. The second group, found 9 to 10 miles off the coast, at a depth of 90 to 100 m, is composed of an equal number of males and females; the latter are distinctly smaller than the females living in more coastal waters (60 m); their eggs are slightly less developed. Finally, a few animals of small size are captured in deeper waters, between 250 and 400 m. Among these, we found some individuals of distinctly larger size, which were fully mature as early as March, when they contained smooth, fertilized eggs. Females of all 3 groups and males of the second group were brought into the laboratory where they lived for several months.

The females brought to the laboratory in March from 60 and 100 m depth, respectively, were fed regularly on crabs. The growth rate was slightly higher in those specimens from 100 m (Mangold-Wirz, in preparation). Those collected from 60 m stopped eating in early May and spawned in late May and

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Table 1. *Eledone cirrosa. Growth and sexual maturation during spring 1969. Data from females analysed after capture (*Sea*) and from those kept in the laboratory (Lab.)*

Material	March	April		May		June	
	Sea	Sea	Lab.	Sea	Lab.	Sea	Lab.
Females captured between 50 and 60 m depth							
Total weight (g)	350	425	430	480	495	485	500
Ovary weight (g)	9.5	20.2	21.1	32.0	31.2	38.0	40.0
Diameter of oviducal gland (mm)	8.1	10.5	10.5	13.8	13.9	16.3	16.6
Females captured between 95 and 100 m depth							
Total weight (g)	200	300	310	350	365	380	370
Ovary weight (g)	5.5	16.3	17.2	28.8	29.0	34.3	35.6
Diameter of oviducal gland (mm)	7.1	9.0	9.0	13.0	13.1	15.0	15.3

June, females from 100 m laid their eggs 2 to 4 weeks later.

Females captured at both 60 and 100 m in May had approximately the same total and ovary weight as those from the same depth which had been kept in the laboratory since March (Table 1). Growth and maturation of gonads proceeded at the same rate in those females still in the sea and those maintained under laboratory conditions during the same period.

Males had some ripe spermatophores in February (some even in late January). In March and April, the Needham sac is tightly packed with fully ripe spermatophores, the number of which decreases at the end of the reproduction period.

Mating

In contrast to *Octopus salutii*, which begins or continues copulation immediately after capture (MANGOLD-WIRZ, unpublished), *Eledone cirrosa* does not mate for several days after they have been collected from the sea. Mating behaviour in *E. cirrosa* was described by VON ORELLI (1962). The male approaches and grasps the female from behind similar to *Octopus dofleini* (MANN, 1969), unlike *Octopus vulgaris* (RACOVITZA, 1894; VON ORELLI, 1962).

Similar to most cephalopods (MANGOLD-WIRZ, in press), females of *Eledone cirrosa* may copulate several weeks before egg laying begins. Specimens have been observed with ovaries full of spermatophores but with still unripe (reticulated) eggs. Sperm can be preserved for at least 6 weeks (period between capture or observed copulation, and egg deposit). As many as 400 spermatophores were found in ovaries of both females collected from the sea and those maintained several weeks in the laboratory. In general, however, the number of spermatophores varies from 20 to 50.

Spawning

In the laboratory, egg clusters, composed of varying numbers of eggs (up to 36) are attached to the wall of the tank, rather closer to the water surface than the tank bottom. Whereas *Octopus vulgaris* deposits all its clusters close together, *Eledone cirrosa* attaches them in various places (bunches or single clusters), including the plexi glass cover of the tanks, which is normally several cm above water level. Females may proceed with spawning for 10 to 15 days, exceptionally for 3 to 4 weeks. The total number of eggs deposited by 1 female varies from 800 to 1500. The female *E. cirrosa* broods on the eggs in exactly the same manner as the female *O. vulgaris*. Some females release eggs separately and do not attach them to a substratum. This behaviour is aberrant. Attached and unattached eggs are sometimes eaten by the female.

Females stop feeding regularly about 3 weeks before spawning. While some eat a few crabs during the brooding period, others refuse to eat; the latter generally die within a few weeks.

The general structure of an egg cluster of *Eledone cirrosa* (Fig. 1) is similar to that of *Octopus* sp. (excluding *Octopus joubini*, which deposits single eggs) and of *Eledone moschata*. The major portion of the egg stalks are glued together in a cluster axis by a greenish matrix, which also forms the basis of the cluster in the form of a thin sheet covering the substratum. In this basal sheet, one to several single eggs may be included with their stalks. All transition stages, from single eggs to eggs united in a bunch with a common axis, are found in small clusters.

The chorion of newly laid eggs is about 7.5 mm long and about 2.6 mm in diameter, with a stalk about 2 cm in length. For increase in size during development consult Table 2). The earlier literature provides some information about these details. A fine

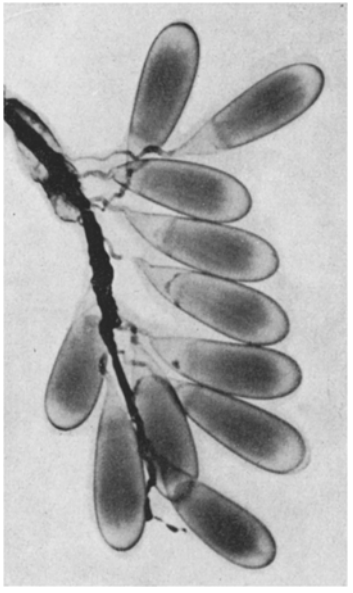

Fig. 1. *Eledone cirrosa*. Egg cluster

illustration of part of an egg cluster was given by REES (1956) in his plate 10. It should be noted, however, that the egg mass figured in his plate 9 shows the contents of an ovary, with the ova at different stages of ovogenesis; small whitish tips, which are sperm, are visible at the side of the micropyle.

Length of embryonic development

Embryonic development within the range given by the egg size, depends upon water temperature. Taking this into account, we supposed that eggs more than 7 mm in length, at a temperature of 13° to 14 °C, would have an embryonic development period of about 2 months (MANGOLD-WIRZ, 1963). Laboratory rearing shows, however, that development takes a considerably longer time: more than 100 days at a total mean temperature of about 16 °C (Fig. 2).

Embryonic development

Other than the notes published by KORSCHELT (1893), PORTMANN (1937) and SACARRÃO (1943), very little is known about the embryonic development of *Eledone moschata*, still less about that of *Eledone cirrosa*. A brief description of the embryogenesis of *E. cirrosa* is, therefore, given in this section, emphasis being placed on some typical phenomena known for *Octopus vulgaris*, and recently reported from two large egg forms, *Octopus joubini* and *O. briareus* (BOLETZKY, 1969).

Two peculiarities of the embryogenesis of large egg forms were noted by NAEF (1928) in his brief discussion of the then known developmental aspects of *Eledone moschata*. The first is the structure of the blastodisc, which remains rather flat due to its comparatively small size in relation to the large amount of yolk. The second is the suppression of the "larval" stage at which the young animals of *Octopus vulgaris* hatch. While the first characteristic is also true for *Eledone cirrosa* (as for *O. briareus* and for *O. joubini*, whose egg size is similar to that of *E. cirrosa*), the second statement can only partly be applied to *E. cirrosa*, since the young animals of this species are planctonic in contrast to *E. moschata*, *O. joubini* and *O. briareus*.

Table 2. *Measurements of newly hatched Eledone cirrosa, compared to data from 3 species of Octopus (after* BOLETZKY, *1969). Note the basic difference in morphometry of planktonic larvae and benthonic juveniles as expressed by relative arm length (arm mantle index) and relation between the relative arm length and presence of anteriorly oriented "Kölliker bundles" which is important for hatching mechanism. ML: Mantle length*

State after hatching	*E. cirrosa*	*O. vulgaris*	*O. joubini*	*O. briareus*
	Planktonic		Benthonic	
Dorsal ML (mm)	4.5	2	4.5	7.5
Arm length (mm)	2.2	0.7	5	12
Mantle arm index	205	285	90	65
Number of suckers/arm	8	3	26	35
Gill lamellae/demibranch	9 (adult 10—12)	5 (adult 8—10)	5 (= adult)	8 (= adult)
"Köllikers bundles" present	+	+	+	–
Oriented anteriorly	+	+	–	
Length and width of chorion				
stage I	7.5 2.6	2.2 0.95	6 2.1	12 3.6
stage XX	8.5 3.9	2.75 1.1	8 2.9	14 5

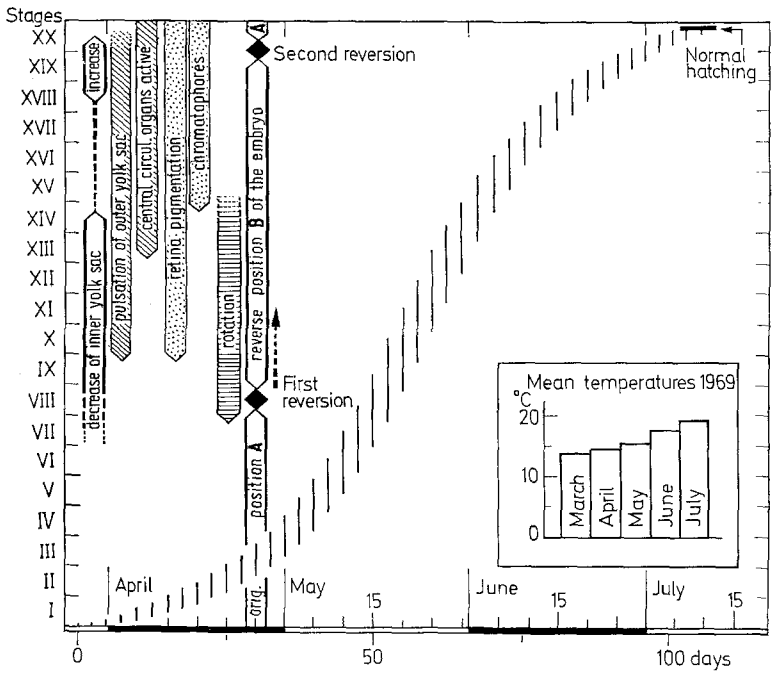

Fig. 2. *Eledone cirrosa*. Course of embryonic development in an egg mass, with approximate range of stages at a given time, and (left) some important states and processes plotted for the stages at which they take place

In the present paper, we pass over the early stages of cleavage and blastodisc formation, which need a particularly thorough analysis taking into account the results of recent studies on cleavage and cellulation.

At the early stages of organogenesis, we note a phenomenon known from *Octopus briareus*: a great variability in the formation of the yolk envelope (making up the external yolk sac of the embryo), and, apparently related to this, a comparatively wide range of stages at which the so-called first reversion (PORTMANN, 1933) may occur. Whereas, in eggs of *Octopus vulgaris*, the yolk envelope is completed at the end of stage VIII (staging according to NAEF, 1928) and the first reversion ends not later than stage VIII, the yolk sac of *Eledone cirrosa* is often completed at stage IX or even stage X (Fig. 3). In some cases, it never includes the entire yolk mass, part of this being cut off by constriction of the edge of the yolk envelope, a phenomenon noted in *O. briareus* and very rarely occurring in *O. vulgaris*.

Rotation, due to the ciliary activity of the yolk sac surface (BOLETZKY, in press), begins prior to completion of the yolk envelope, but not before stage VII is reached. The first reversion starts at stages VII to VIII or later, and can be completed up to stage XI. We found that the entire reversion takes 3 days at 15 °C. Embryos which have not included the entire yolk mass in their external yolk sac, can undergo a complete first reversion. Rotation ceases in all cases at about stages XIV to XV (Fig. 2). The second reversion, by which the animal actively regains its original position, with the vegetative pole facing the stalk of the chorion, occurs at stages XIX to XX, but larvae are able to hatch on the stalk side when heavily disturbed prior to the second reversion. During hatching, the "Kölliker bundles" of the skin seem to have the same function as in *Octopus vulgaris* (BOLETZKY, 1966).

Circulatory activity begins at stage IX with a slow pulsation of the yolk sac envelope (PORTMANN, 1926;

Fig. 3. *Eledone cirrosa*. Embryos at 4 different developmental stages, drawn after preserved specimens. (A) stage VIII, lateral, dorsal, ventral and caudal view; development of yolk envelope in specimen illustrated is retarded and first reversion has not yet started; (B) stage X, after completion of first reversion; outer yolk sac is closed and eye rudiments are closed chambers; note state of development of stomodaeum corresponding to stage IX in *Octopus*; (C) stage XIV—XV, note length of arms, each showing 5 sucker rudiments; development of primary lid is in progress; mouth is still covered by thin, transparent membrane; dissection of ventral part of mantle shows visceral mass with gills and anal papilla projecting from ventral mantle septum; (D) stage XIX, prior to second reversion; except for its size and presence of a large yolk sac, the animal is already similar to hatching stage; eighth sucker of each arm is being formed, while gills have 6 to 7 lamellae only on each demibranch. *a* arm; *bh* branchial heart; *c* chromatophore; *e* eye; *f* funnel; *fr* funnel retractor; *g* gill; *i* intestine; *k* kidney with vein appendages; *m* mantle; *ms* mantle septum; *mo* mouth; *pl* primary lid; *s* sucker; *sg* salivary gland; *st* stomodaeum; *stg* stellate ganglion; *vc* vena cava; *y* yolk; *ye* yolk envelope

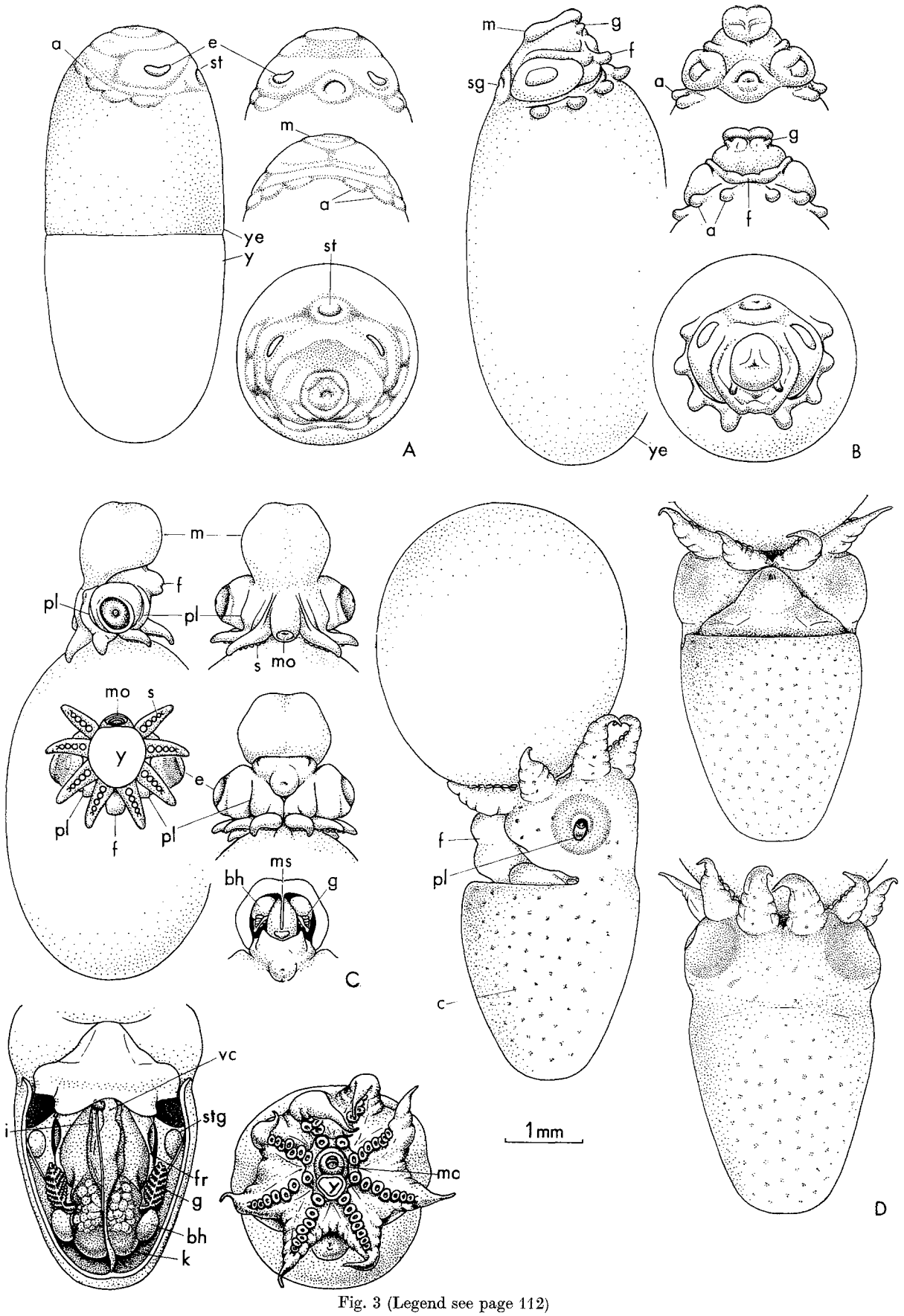

Fig. 3 (Legend see page 112)

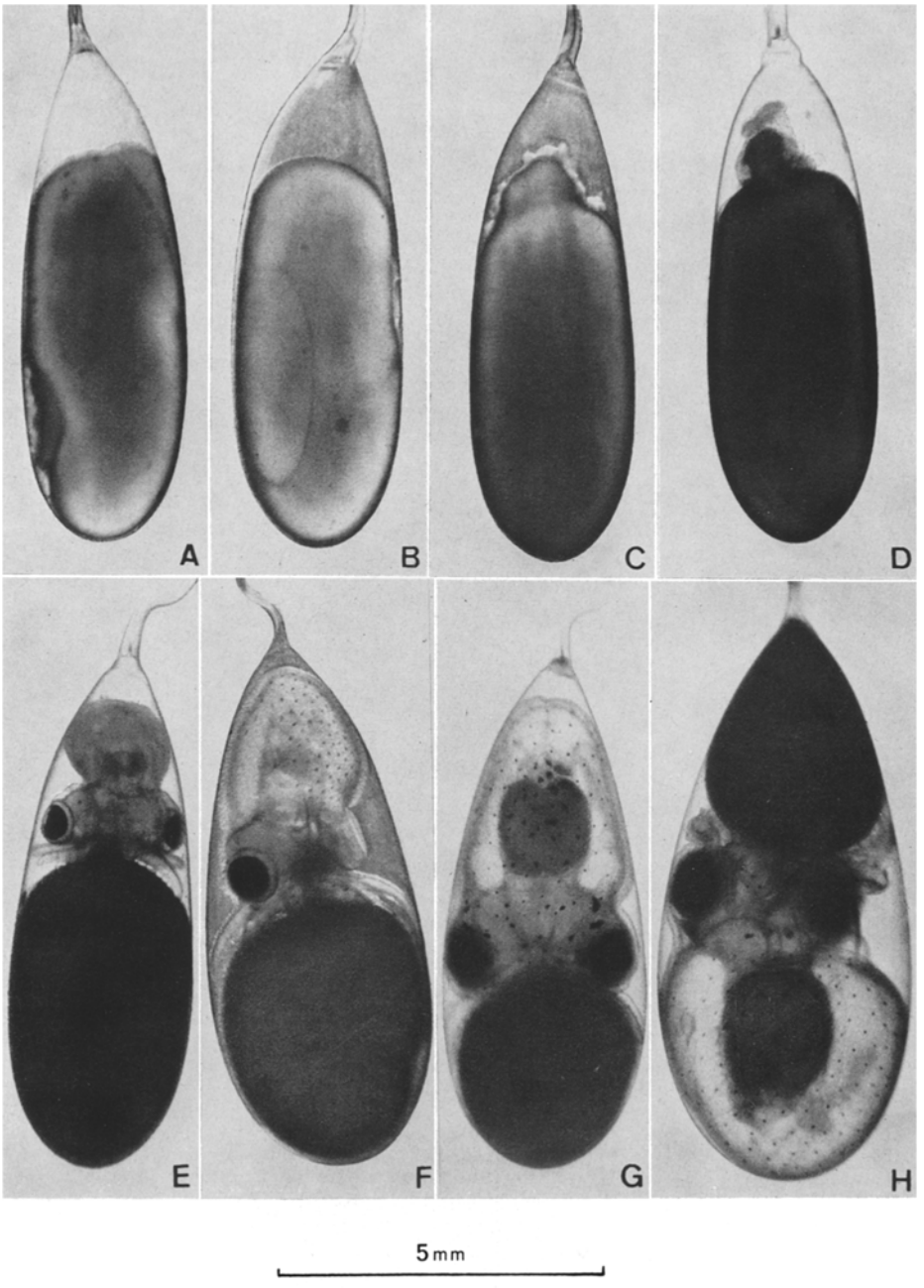

Fig. 4. *Eledone cirrosa.* Living embryos at different stages of embryonic development. (A) stage IX, after beginning of first reversion; (B) similar stage, reversion further advanced, note border of yolk envelope in A and B; (C) stage X, reversion completed; (D) stage XI—XII, constriction of yolk in cephalic region leads to separation of yolk mass into an outer and an inner yolk sac; (E) stage XV, nearly complete resorption of inner yolk sac, first chromatophores on head, long arm rudiments; (F) stage XVII, "absence" of inner yolk sac, large number of chromatophores; contraction of outer yolk sac (circulatory function) is visible on lower right; (G) stage XIX, inner yolk sac refilled; (H) stage XX, after second reversion. Note increase in size of chorion during development

BOLETZKY, 1968), which becomes very distinct at stage X. At room temperature, 5 to 6 contraction waves pass over the yolk sac per min. A maximal rate of 10 waves/min was observed at stage XIII; by stage XV, the rate of pulsation was again 6 waves/min. At stage XIII, the systematic heart and the branchial

hearts begin to pulsate slowly and irregularly. Towards the end of stage XIV pulsation becomes fairly regular and coordination of systematic heart systole and branchial heart diastole (and vice versa) is established during stage XV. At room temperature, the hearts then beat at a rate of 50 to 60 beats/min. The rate is increased to about 80 beats/min by stages XVIII to XIX. The vena cava then contracts rather irregularly at an average rate of about 40 contractions/min.

The arm rudiments begin growing in length at stages X to XI, and a steady formation of suckers from stage XI onward results in a total of 8 suckers on each arm by the time of hatching. The earliest rudiments are already arranged in a single row (NAEF, 1928). There is no hint of a "3 sucker stage", which characterizes the larvae of *Octopus vulgaris* and which is also passed through by embryos of *Octopus salutii*, a form with large eggs (5.5 × 1.9 mm), at stages XIII and XIV before the formation of additional, smaller sucker rudiments (BOLETZKY, unpublished). The development of the arms of *Eledone cirrosa* thus appears very similar to that of *Octopus joubini* and *O. briareus* but, in contrast to these species, the arms of *E. cirrosa* do not reach by far, during embryonic life, a length equal to the mantle length. The arm-mantle-index at time of hatching, places *E. cirrosa* certainly closer to *O. vulgaris* than to *O. joubini*. This morphological feature clearly demonstrates that the young *E. cirrosa* is not an ecologically hindered or ethologically "retarded" settling stage, but a truly planktonic larva. When observed alive, it appears in fact similar to an enlarged duplicate of a newly hatched *O. vulgaris*, but with slower swimming movements, because of its larger size.

Pigmentation in *Eledone cirrosa* first appears at stage IX; the retina shows a light orange coloration that becomes slightly darker during subsequent stages, and turns red at stage XIII. The first chromatophores appear at stages XIV to XV in the ventral integument of the head, 1 on each side of the funnel, and 1 or 2 on each side dorsally in the "neck" region. The chromatophores are first yellowish, then orange about one stage later, and finally become red. There are no actual yellow and brown chromatophores present as in *Octopus*. The pigmentation gradients of the head and the body (FIORONI, 1965) are more distinct than in *Octopus vulgaris*, on the dorsal as well as on the ventral side. A marked increase in pigmentation occurs at stage XVII, when chromatophores appear on the arms and the dorsal mantle integument (the earlier dorsal chromatophores of the body are situated on the "inner" body wall surrounding the visceral mass); on the ventral mantle surface about 100 more chromatophores appear. During the subsequent stages, the dorsal and ventral head pattern is completed to about 35 and 20 chromatophores, respectively, and several very small chromatophores appear on the funnel and on the arm web. The first iridocytes were (macroscopically) observed at stage XVII. In general terms, the appearance of early pigmentation is similar to that of *O. vulgaris* but is followed, however, by a very marked increase in the number of chromatophores from stage XVII onward, a process which also occurs in the benthic *Octopus joubini* and *O. briareus* (BOLETZKY, 1969, Fig. 6). It would be erroneous, however, to consider the large number of chromatophores present in *E. cirrosa* at hatching as a "benthic" feature. Their density, due to the evidently limited size of each chromatophore, gives the animal, as far as its colour pattern is concerned, a more "adultlike" appearance; but this is due to the large size of the young animal, not to the way of life of the adult. This fact is (in a reverse sense) demonstrated by the newly hatched individuals of the Sepiolinae, which have, according to their small size, a small number of chromatophores, but are truly benthic.

Yolk resorption in *Eledone cirrosa* is basically identical to the process reported in other Cephalopoda (PORTMANN and BIDDER, 1928). We would particularly emphasize that *E. cirrosa* has a large internal yolk sac during the last embryonic stages; however, in contrast to *Octopus vulgaris*, for example, the inner yolk sac does not increase in size before or immediately after its complete reduction at stages XIV or XV, but only increases at about stage XVIII (staging based on primary lid). From stage XV to stage XVII, no actual internal yolk sac can be recognized. It is as yet uncertain whether there is a transfer of yolk from the outer to the inner yolk sac during these stages, which is completely compensated by resorption by the hepatopancreas, or whether the actual transfer starts at stage XVIII only;[1] the latter is not very likely, however. The external yolk sac is at any rate reduced, prior to normal hatching, to a small bulb about 1 mm in length. Accordingly, the internal yolk sac strongly increases in size in *E. cirrosa* (Fig. 4) but, the rate of resorption evidently being very high, it never becomes as large in relation to the body as in *O. vulgaris*. It is not entirely resorbed by the time of hatching (under laboratory conditions).

Discussion

In his study of the later embryonic stages of *Eledone moschata*, SACARRÃO (1943) stated that the embryos of this species are devoid of an internal yolk sac from about stage XV on. When making his observations on preserved embryos at different stages from XIV to XIX, he assumed that the large external yolk sac present in the most developed specimens of his collection would not have been further reduced, the embryos at that stage being "at the end of embry-

[1] An investigation dealing with the problem of yolk resorption in *Eledone cirrosa* is now in progress at the Zoological Laboratory of the University of Basel, Switzerland.

onic development". For lack of observations on *E. moschata* on our own part, we cannot decide whether or not these statements are correct. But we strongly feel that they are not, since almost complete reduction of the outer yolk sac by means of yolk transfer, which leads to the formation of a more or less bulky internal yolk sac at late embryonic stages, is a process common to all of the species so far investigated, which are members of 3 different orders and exhibit (within each order) very different sizes of their eggs and embryos. The peculiarity of *E. moschata* as suggested by SACARRÃO thus appears doubtful. We suppose that the embryos studied by him were still at the stage prior to increase in size of the inner yolk sac, which increase may begin still later than in *Eledone cirrosa*.

As to the reproductive period of *Eledone cirrosa*, we claimed in an earlier paper that it begins in May and continues until early August (MANGOLD-WIRZ, 1963). This assumption was based upon the state of ovaries and oviducts as well as upon spawning observed in the laboratory. It appears now that egg laying may begin in late March and certainly in April. In early spring, fully mature *E. cirrosa* females were only found in deeper waters (250 to 400 m), always in small numbers. It could be argued that, in the laboratory, eggs are deposited earlier than they would be in the sea. Nevertheless, females analysed after capture appeared completely mature, with smooth fertilized eggs in the ovary; some of these eggs had already entered the oviducts. However, the bulk of females, captured in more coastal waters, are mature between May and early August. The whole reproductive period in the Catalonian Sea lasts 5 months.

MORALES (1960) claimed that the main spawning area near Blanes (north of Barcelona, Spain) is localized 4 miles off the coast, at a depth of 100 m. Indeed, in this particular area, small *Eledone cirrosa*, 4 to 5 months old (see below) are extremely abundant in late winter and early spring. MORALES found a few small animals only, at the same depth, but 10 miles off the coast. No juvenile *Eledone* were captured at 30 miles, at a depth of 400 m. We found that juvenile *E. cirrosa* are particularly abundant in spring on the vast sandy grounds between 90 and 100 m east of the coast of French Catalonia (MANGOLD-WIRZ, 1963). Further investigations confirmed this finding. The juveniles live in this area during March, April and May (June); in more coastal as well as in deeper waters, they were captured only occasionally. We supposed that the eggs must be deposited on the small isolated rocky isles lying in this area. We assumed that newly hatched *E. cirrosa*, since they emerge from large eggs, have only a very brief planktonic phase (if at all) and adopt, within a few days, the benthonic way of life of the adults. The presence of huge numbers of juveniles, therefore, could be an indication for spawning grounds. However, newly hatched *E. cirrosa* are truly planktonic larvae. The only reliable indication, then, is the presence of completely mature females. The problem demands a different approach; experiments focussing on the factors involved in spawning of *E. cirrosa* are now in progress.

The length of embryonic development depends upon egg size, i.e. yolk quantity. Within the ranges determined by egg size, water temperature exerts a great influence. It would be dangerous, however, to conclude that, at a given temperature, length of embryonic development is equal for eggs of the same size but of different species. Several *Octopus* species have egg sizes that could be compared with that of *Eledone cirrosa*. According to BATHAM (1957), length of embryonic development in *Octopus maorum* (egg size 6 mm) is 80 days at a temperature of 13° to 17 °C, almost the same as in *Robsonella australis* (81 days) the eggs of which have a size of 2.9 mm, at a temperature of 11.5° to 18.6 °C (BROUGHT, 1965). Mr. E. HOCHBERG (University of California) told us that embryonic development requires 2 to 3 months in *Octopus micropyrus* (egg size 8 to 10 mm) and about 2 months in *O. digueti* and *O. dofleini* (egg sizes 6 mm) on the coast of California.

We can admit that the species are adapted to a certain temperature range. A temperature coefficient for embryonic development valid for this range may well change at temperatures below and beyond this range.

It is surprising that the very long embryonic development in *Eledone cirrosa* does not lead to an adult-like newly hatched animal. As a rule, we supposed that larvae emerged from large eggs in Octopodidae soon adopt the benthic way of life. It may be that this statement is only valid for species of the genus *Octopus*. It would be particularly interesting to follow embryonic development in some members of the subfamily Bathypolypodinae.

As to dependence on temperature, we should focus now our interest on the relation between the rate of yolk resorption and temperature.

Allowing a length of embryonic life of about 4 months for *Eledone cirrosa* in the sea, and taking into account that spawning is most intensive in June, hatching should occur in October. The juvenile individuals captured in spring, therefore, are about 6 months old at the most. Since they do not reach sexual maturity before the end of the spawning season, they spawn not before March of the following year.

Summary

1. The reproductive period of *Eledone cirrosa* in the Catalonian Sea ranges from late March to early August.

2. For the first time, eggs laid in the laboratory developed until hatching.

3. Length of embryonic development at a mean temperature of 16 °C was a little over 100 days.

4. The newly hatched animals are planktonic.

5. The embryonic development is similar to that of *Octopus* species with large eggs, but the relative arm length characterizes the newly hatched animals as planktonic larvae.

6. At late embryonic stages, the inner yolk sac increases in size due to transfer of yolk from the outer yolk sac. There is no basic difference between the mechanism of yolk resorption in *Eledone cirrosa* and other cephalopods.

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