THE EMBRYONIC DEVELOPMENT OF THE OCTOPUS SCAEURGUS UNICIRRHUS (MOLLUSCA, CEPHALOPODA) Additional data and discussion

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OCTOPODA — INCIRRATA
OCTOPODIDAE
DÉVELOPPEMENT
ECLOSION
PROPORTIONS DU CORPS
COMPORTEMENT JUVÉNILE

RÉSUMÉ. — Complétant les données rapportées dans une note préliminaire, l'auteur décrit le développement embryonnaire de *Scaeurgus unicirrhus* (Orbigny, 1840), octopodidé de la sous-famille des Octopodinae. Ce développement se calque pratiquement sur celui d'*Octopus vulgaris*, à l'exception de la livrée chromatique réalisée avant l'éclosion (chromatophores plus nombreux) et de la couronne brachiale (4 ventouses par bras au lieu de 3). L'action des bras pendant l'éclosion ainsi que le comportement des très jeunes animaux planctoniques sont discutés sous l'aspect évolutif du développement des octopodidés.

OCTOPODA — INCIRRATA
OCTOPODIDAE
DEVELOPMENT
HATCHING
BODY PROPORTIONS
JUVENILE BEHAVIOUR

ABSTRACT. — As a complement to data reported in an earlier note, the embryonic development of *Scaeurgus unicirrhus* (Orbigny, 1840) is described and discussed with special reference to features different from the otherwise very similar development of *Octopus vulgaris* (chromatophore pattern, sucker complement). Use of the arms during hatching, and early juvenile behaviour of the essentially planktonic young animals are viewed from the angle of evolutionary biology of octopodid development.

INTRODUCTION

Scaeurgus unicirrhus (Orbigny, 1840) is a medium-sized octopus easily recognizable by its markedly granular skin structure. In the male, the third *left* arm is hectocotylized (for discussion of the systematic significance of sinistral hectocotylization see Naef, 1923, p. 691; Voss, 1975). The living animal is capable of a wide variety of colour patterns, skin textures and body postures (pers. observations). This is noteworthy in an animal that lives at low light levels, at depths always greater than 50 m, mostly beyond 100 m and sometimes beyond 500 m in the western Mediterranean (Mangold-Wirz, 1963).

The species is now generally considered to have a worldwide distribution. Indeed Robson (1929) placed the Hawaiian species *S. patagiatus* Berry, 1914 in the synonymy of *S. unicirrhus*. Voss (1951) discussed the systematic relationships and also concluded that these species are identical. The distribution of the supposedly cosmopolitan *S. unicirrhus* has been summarized by Cairns (1976).

In an earlier report (Boletzky, 1977 a), the embryonic and early post-hatching features of *S. unirirrhus* from the Mediterranean were briefly described with reference to the « Macrotritopus problem » (Rees, 1954). Behavioural features of the hatchling were also discussed by Boletzky (1977 b).

The present article provides additional data and the first photographs of embryonic stages of *S. unicirrhus*. The embryological data relevant to an understanding of the developmental and evolutio-

nary processes characterizing the benthic family Octopodidae within the incirrate octopods are discussed at the end of this paper.

MATERIAL AND METHODS

Although a few adult *S. unicirrhus* have been captured in the Banyuls area (Catalan Sea, western Mediterranean) at irregular intervals since 1974, no more egg masses have been obtained since then. The present description is entirely based on the first egg mass obtained in the aquarium.

Animals were captured in March and April 1974 by bottom trawl at depths varying from 250 to 300 m on the slope of the canyons (« rechs ») SE of Banyuls. Two to three individuals were placed together in rectangular 50 l tanks supplied with running sea water at environmental temperatures (13 to 15°C before the onset of spawning). The tanks were constantly lit from above by fluorescent tubes (the absence of a dark phase has proved useful in the maintenance of octopods as it prevents « nocturnal » roaming).

The first eggs were observed on May 10 with a female that lived in an earthenware pot 20 cm in length, placed horizontally on the tank floor. The inner diameter of this artificial den varied from 7 cm at the open and to 5.5 cm inside. The female, which measured ca 8 cm in dorsal mantle-length (ML), attached a series of egg strings to the inner surface of the pot, in the rear third, and brooded them in the way typical of octopuses (see e.g. Lane, 1960, Plate 28).

Samples of eggs were taken with long forceps at regular intervals for photography and histological preparations allowing the anatomical study of the embryo. The first egg samples recovered were kept for some time in Petri dishes at two different temperatures (15-16 and 20-21°C, respectively). The open circuit water temperatures were slowly rising to 19°C (Fig. 1). After a temporary decrease in late June leading to a temperature of 17.5°C, another female started spawning in a different tank, but these eggs did not develop normally. Newly hatched animals, from the first set of eggs, were placed in circular 50 l tanks and fed half-grown *Artemia* sp.. The animals did not survive beyond 6 days after hatching.

OBSERVATIONS

A. Structure of eggs and egg strings

The individual egg at the time of laying measures ca 2.5 × 1.0 mm, excluding the chorion stalk which is about twice as long. Chorion stalks are interwoven with one another in the central axis that is held together by the « cement » secreted by the oviducal gland at the moment of laying (Frösch and Marthy, 1975). This cement also serves to fix the egg string to the substrate. Each string contains at least one hundred eggs (Fig. 2 A).
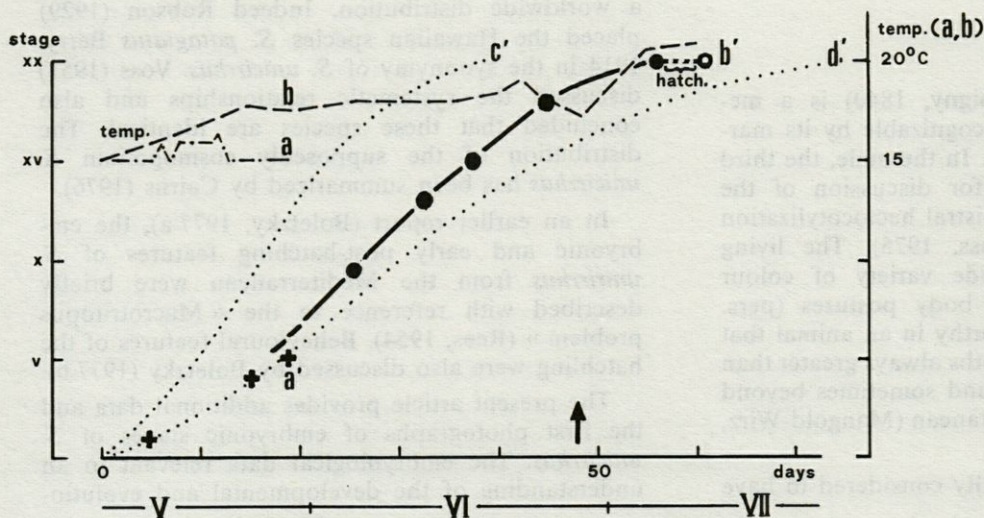
Fig. 1. — The course of embryonic development in *Scaeurgus unicirrhus* in terms of the attainment of developmental stages (according to Naef, 1928) at different temperatures a and b (corresponding stages : a' and b'). The stage-time plots c' and d' are the standard curves of *Octopus vulgaris* at constant temperatures 20 and 15°C, respectively. The arrow in the lower part of the figure indicates the time of the second egg-mass observed (see text).

Apart from the small string length and therefore limited number of eggs per string, these features correspond precisely to the conditions known of many octopus species and are distinct from the situation observed in species laying their eggs one by one (Boletzky, 1981 a). The size of the egg is very similar to that of *Octopus vulgaris* eggs which measure 2.2 × 0.95 mm.

B. Embryonic development

At the earliest stages observed, the animal pole of the egg was already detached from the micropyle area of the chorion (Boletzky, 1974, Plate I), indicating the presence of a fertilization membrane (Fig. 2 B). At 15°C, polar body formation was completed within 36 hours after the beginning of observations (Fig. 2 C). Thereafter, the first four cleavage steps were completed in about 24 hours at the same temperature. The discoblastula stage I (staging according to Naef, 1928) was reached four to five days after spawning (Fig. 1).

At temperatures varying between 15 and 16°C (exceptionally 16.5°C), the course of early development followed exactly the stage-time plot established for *Octopus vulgaris* at a temperature of 15°C (Mangold and Boletzky, 1973). Starting at 15 °C newly laid eggs transferred to 20-21°C did not develop normally, whereas the eggs undergoing a slow rise of temperature in the spawning tank showed perfectly normal development throughout the embryonic phase. First inversion of the embryo at about stage VIII of Naef occurred in all control eggs taken from the female, whereas many of the eggs kept in Petri dishes at 15-16°C underwent delayed reversal of the beat direction in the yolk sac cilia, as demonstrated by reversed rotation without inversion of the embryo (see Boletzky, 1971 a, b).

Pigmentation of the retina started at about stage X (see Fig. 2 D for a later stage of pigmentation). Chromatophores appeared on the head with light orange pigmentation at stage XV-XVI. Subsequent chromatophore development resulted in a total number of reddish chromatophores about twice as high as in *Octopus vulgaris* by the time of hatching (Fioroni, 1965). However, the distribution of these chromatophores is similar in that the dorsal mantle surface is unpigmented; only the dorsal surface of the visceral mass carries chromatophores which can be seen through the transparent mantle (Fig. 2 H). A schematic presentation compiled from photographs of chromatophores in living hatchlings is given in Fig. 3.

Development of the circulatory organs corresponds exactly to the conditions known for *Octopus vulgaris* and other octopus species (Boletzky, 1968, 1969). The outer yolk sac begins to pulsate as soon as the envelope is completed and the underlying blood lacuna has formed (stage IX). This is the earliest part of the venous system and soon « expands » into the embryo proper. As in *Octopus vulgaris*, the right branch of the original cephalic vein disappears around stage XV and is compensated by the post-intestinal junction that forms a secondary branch leading to the right branchial heart (Fig. 4 C). The central circulatory organs and related arteries form from stage XII onwards, with heart pulsations becoming progressively more regular. Coordination of systemic heart and branchial heart pulsations improves and at stage XV, the pulsation rate is ca 60/min. at 20°C. At this stage the volume of the inner yolk sac reaches its minimum. Subsequent transfer of yolk from the outer sac leads to a substantial size increase of the inner sac as in other species (Fig. 2 E). The embryo goes through the second inversion (Portmann, 1933) between stages XIX and XX when the outer yolk sac is greatly reduced in size. The animals hatch after complete absorption of the outer yolk sac (Fig. 2 F, G).

Differentiation of the arms is also very similar to that of *Octopus vulgaris* embryos, except for the number of sucker rudiments. Instead of three, four sucker rudiments appear nearly simultaneously on each arm around stage XIII (Fig. 2 D). They are all fully differentiated and functional by the time of hatching, each measuring about 0.1 mm in diameter (when measured after fixation, diameters vary from 0.11 mm in proximal to 0.08 mm in distal suckers). In the hatchling, these suckers occupy the proximal 2/3 of the arms, whereas the distal 1/3 is formed by the tapering arm tip which ends in a characteristic « whip-like » process. The latter is slightly more pronounced than in *Octopus vulgaris* hatchlings. The arms are subequal in length and at hatching measure about 1 mm, or 1/2 of ML, in the living animal. After fixation, the length relationships are maintained. Specimens preserved in 70 % ethanol measure ca 1.5 mm ML, with arms ca 0.7 mm in length. The funnel tube, on the other hand, is much larger in the living animal (Fig. 2 H) than after fixation (Fig. 4 A, C).

C. Hatching

The volume of the chorionic space increases during embryonic development due to water uptake through the chorion. In *S. unicirrhus* this increase is stronger than in *O. vulgaris* and corresponds to the relative increase observed in *O. joubini* (Boletzky, 1969). Volume has been calculated from length and width measurements by Wells and Wells (1977) who showed that *O. joubini* eggs undergo a 159 % volume increase, as compared to 80 % in the egg of *O. vulgaris*. The elasticity of the chorion is limited (i.e. most of the volume increase is achieved by *irrever-*
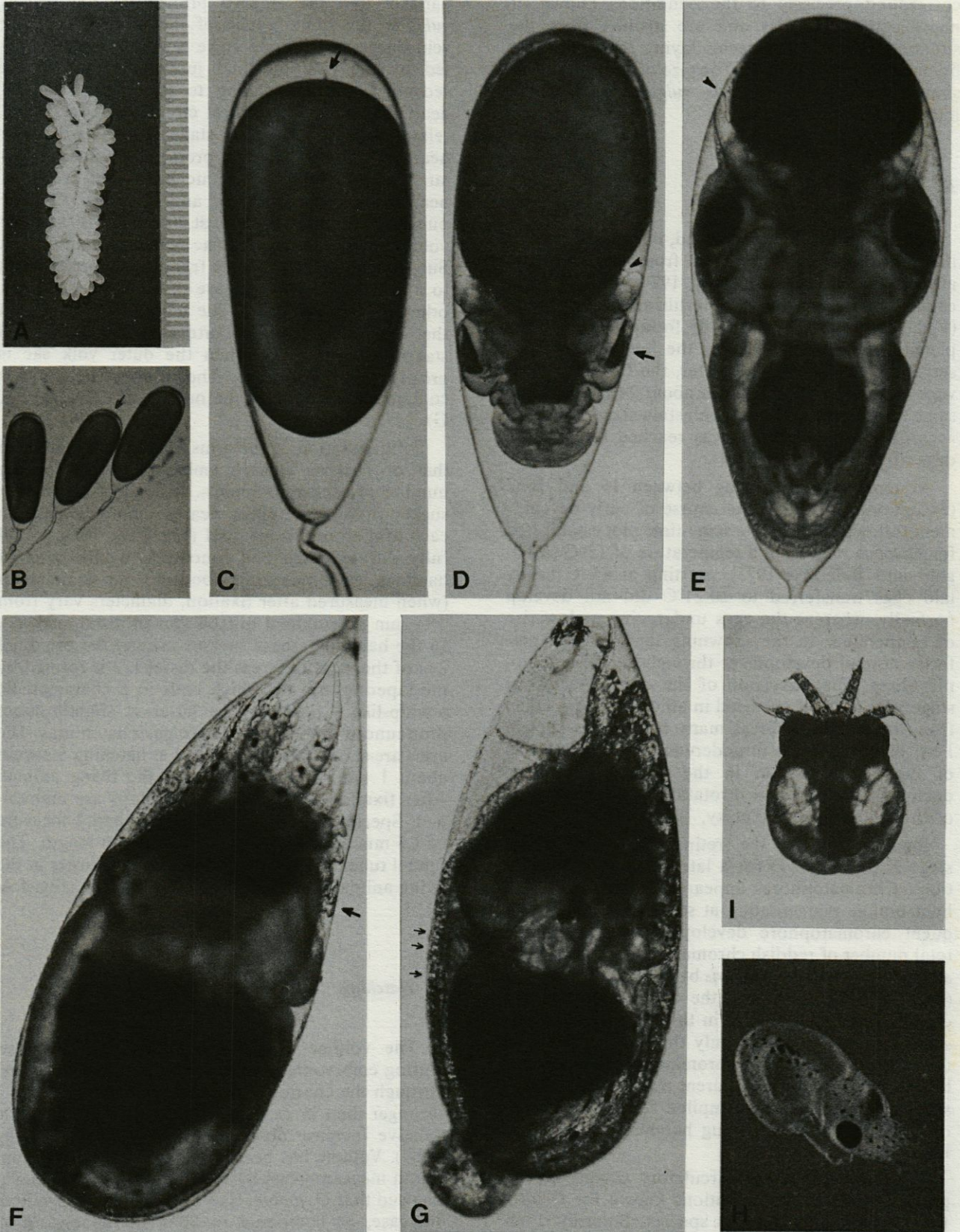
sible stretching of the membrane), but is sufficient to extrude the mantle tip once the hatching gland has opened the chorion by releasing the stored proteolytic enzyme (Wintrebert, 1928). In octopus hatchlings, the actual movement freeing the animal from the chorion is either provided by repeated rapid stretching of the body, resulting in outward movement due to the Kölliker organs (Boletzky, 1966), or by similar stretching movements combined with active use of the arms and their suckers (Boletzky, 1969). In general, the former mode is obser- ved in small hatchlings with short arms, whereas the latter is typical of large hatchlings with long arms. In *S. unicirrhus,* notwithstanding small arm length and full complement of Kölliker organs, the arms actively assist in hatching (Fig. 2 G).
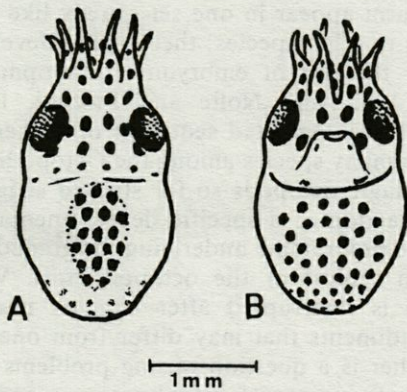

Fig. 3. — Schematic presentation of chromatophore distribution in newly hatched *S. unicirrhus* (compiled from photographs of living animals). Note that the densely set chromatophores in the dorsal view (A) are seen through the transparent, unpigmented dorsal part of the mantle (*cf.* Fig. 2 H).
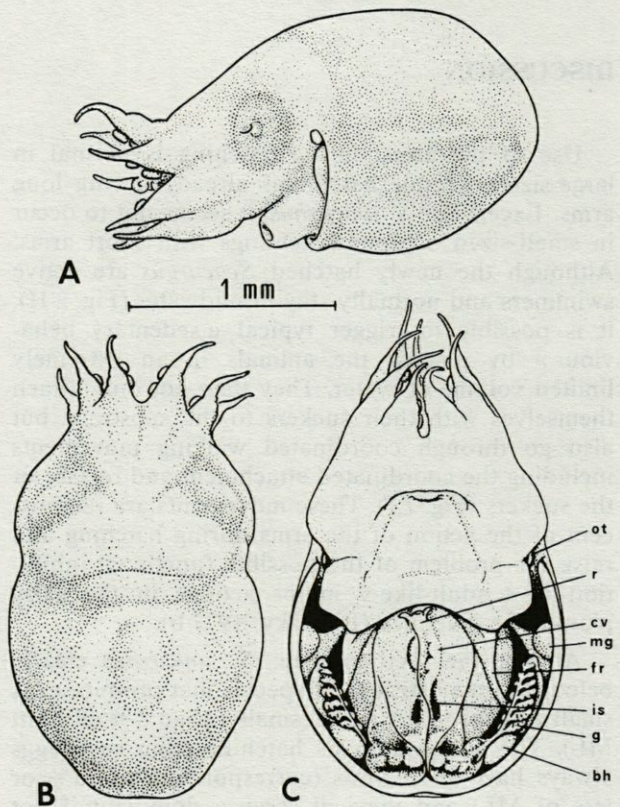

Fig. 4. — Newly hatched *S. unicirrhus* after fixation, preserved in 70 % ethanol. A, lateral view; note shrinkage of funnel tube (cf. Fig. 2 H). B, dorsal view. C, ventral view after removal of the ventral mantle wall. ot = olfactory tubercle, r = rectum with anal opening and anal valves, cv = cephalic vein (secondarily unpaired section) lying beside the intestine, mg = mantle ganglion (stellate g.) fr = funnel retractor, is = ink sac partly covered by intestine, g = gill with 7 leaflets per demi-branch, bh = branchial heart; the nodular structures luing between the branchial hearts are the renal appendages of the cephalic vein branches seen through the will of the kidney sac.

Fig. 2. — A, newly laid string of eggs (scale with millimeter divisions). B, eggs taken from the cluster immediately after collection; the animal pole is detached from the micropyle area (arrow) of the chorion, but lies still close to it. C, precleavage stage with 2 polar bodies (arrow) at higher magnification; longitudinal contraction of the egg results in enlarged perivitelline space at both ends. D, advanced organogenetic stage (XIII), at same magnification, showing intensive pigmentation of the retina (arrow), and distinct sucker rudiments (arrow head) on the short, rounded arms; note the reduced size of the inner yolk sac which is compressed by the surrounding organs. E, post-organogenetic stage (XIX), at same magnification, prior to second inversion; note enlarged inner yolk sac and pointed arm tip (arrow head). F, stage XX, after second inversion (mantle end at the side opposite to the chorion stalk); note absence of outer yolk sac, slender form of the arm tips and position of the ventral arms with suckers becoming attached to the chorion (arrow). G, beginning of hatching, the mantle end protruding through the newly formed hatch opening (which will become larger during hatching); note position of the arms pressed against the chorion; arrows indicate Kölliker organs appearing as light dots in the skin. H, newly hatched animal swimming in typical oblique position (hovering). I, young animal a few days after hatching, placed in a drop of water, seen from the dorsal side, with arms attached to the substrate (see text).

DISCUSSION

Use of the arms during hatching is normal in large-sized octopus hatchlings already having long arms. Except for *S. unicirrhus,* it seems not to occur in small-sized octopus hatchlings with short arms. Although the newly hatched *Scaeurgus* are active swimmers and normally stay in midwater (Fig. 2 H), it is possible to trigger typical « sedentary behaviour » by placing the animals in an extremely limited volume of water. They then not only attach themselves with their suckers to the substrate, but also go through coordinated walking movements including the coordinated attachment and release of the suckers (Fig. 2 I). These movements are reminiscent of the action of the arms during hatching and raise the problem of the possible functional inhibition of « adult-like » motor actions in the early planktonic juveniles (Boletzky, 1977 b).

Among the Octopodidae, *S. unicirrhus* clearly belongs to the category of species that produce eggs small relative to the adult (smaller than 8 % of adult ML). The young animals hatching from such eggs always have short arms (corresponding to 50 % or less of ML) and they all show a dominant if not exclusive swimming behaviour (Boletzky, 1974, 1978-79). How long this « planktonic » mode of life lasts can not be directly deduced from the behavioural characteristics of the newly hatched animal, or from its body proportions including the number of suckers per arm. In the absence of genetic evidence (that, for example, the Hawaiian *Scaeurgus* represents the same population), hypotheses on long-distance dispersal of early juveniles of *S. unicirrhus* remain guess-work. Opposite evidence may be available in the form of the distinctive spawning and brooding behaviour as observed in the Hawaiian form (W.F. Van Heukelem, pers. communication).

The development of *S. unicirrhus* is nevertheless interesting in several other respects related to developmental mechanisms and the evolutionary changes that they undergo. In the subfamilies Octopodinae and Eledoninae, the embryonic development of each species produces one of two distinct morphometric types : the hatchling either has short arms with a limited number of suckers (less than 15), or has long arms with at least 20 suckers. The third subfamily of the Octopodidae, the Bathypolypodinae, probably shows only the second mode (O'Dor and Macalaster, 1983). It has been shown that each of these two types is related to the magnitude of the size difference between the hatchling (or the egg) and the adult, and it has been suggested that the « short arm » (or « small egg ») mode represents the common ancestral (plesiomorphic) condition of the Octopodidae (Boletzky, 1974, 1977 b, 1978-79). Within this category of species, one finds considera-

ble variation in the relative numbers of suckers formed on each arm of the hatchling. Naef (1928) has clearly shown the similarity between arm development leading to a complement of 3 suckers per arm in *Argonauta argo,* a representative of one of the several pelagic octopod families, and in *Octopus vulgaris,* a representative of the only benthic family within the incirrate octopods, namely the Octopodidae. Except for *Ocythoe,* a pelagic form closely related to *Argonauta,* in which the ventro-lateral arms carry only one sucker (Naef, 1928), the minimum number always seems to be 3. How and when subsequent suckers are formed may vary from one species to the other, however. Thus in *Octopus bimaculatus* « a fourth small sucker develops at the tip of the arms by stage XX » (Ambrose, 1981), whereas in the embryo of *O. dofleini,* there is an apparently continuous formation of suckers from the original 3 or 4 to about 14 by the time of hatching (Gabe, 1975). In *S. unicirrhus,* the 4 suckers formed on each arm appear in one set exactly like the first 3 suckers in other species; then sucker development stops for the rest of embryonic development (see Fioroni, 1982, and Nolte and Fioroni, 1983 for review). The interrupted sequence of sucker formation in so many species among the Octopodidae and in the pelagic octopods so far studied suggests the common action of a specific developmental switch within the programme underlying the graded pattern formation typical of the octopod arms. Why the sequence is interrupted after a given number of sucker rudiments that may differ from one species to the other is a question raising problems of both intrinsic constraints of morphogenesis and limitations related to scaling and morphometrics. Only the latter aspect can be discussed here from an evolutionary viewpoint.

The adaptive value of arrested arm growth is understandable only in the context of adaptation to life in midwater where arms are used mainly for prey-capture. Within this function, short arms are sufficient to seize and handle prey after it has been approached by rapid, jet-propelled forward pouncing. Most of the limited mass of muscle that can be formed during embryonic development is distributed among the propulsive mantle-funnel complex, the prehensile arm complex, the musculature of the buccal mass used in the processing and ingestion of food, and the eye muscles involved in the visually guided attack. Given the limited energy sources available to the embryo, a relative enlargement of one of these muscular components in the course of evolutionary change would inevitably be achieved at the expense of other components. If the energy resources of the embryo increase through enlargement of the eggs, the change is not apparently translated in all cases into enlargement of the arms. Body proportions characterized by short arms exist in the hatchlings of certain species producing eggs (theoretically) large enough for the construction of

a more adult-like juvenile with long arms (e.g. *Octopus salutii, Eledone cirrhosa*). This situation suggests selection favouring the *maintenance* of an actively swimming juvenile adapted to midwater conditions. It is interesting that the species showing this conservative feature are on average larger as adults than those in which selection apparently favours the opposite, i.e. an embryonic development leading to body proportions characterized by long arms, as is typical of bottom-living young octopuses. A good example of such small-sized species is *Octopus joubini* in which the egg size is similar to the egg sizes observed in *O. salutii* and *Eledone cirrhosa* (see Boletzky, 1981 b for other aspects of reproductive strategies in cephalopods).

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REFERENCES

AMBROSE R.F., 1981. Observations on the Embryonic Development and Eearly Post-Embryonic Behavior of *Octopus bimaculatus* (Mollusca : Cephalopoda). *Veliger*, 24 : 139-146.

BOLETZKY S. v., 1966. Zum Schlüpfen von *Octopus vulgaris* Lam.. *Verhandl. Naturf. Ges. Basel*, 77 : 165-170.

BOLETZKY S. v., 1968. Untersuchungen über die Organogenese des Kreislaufsystems von *Octopus vulgaris* Lam.. *Rev. suisse Zool.*, 75 : 765-812.

BOLETZKY S. v., 1969. Zum Vergleich der Ontogenesen von *Octopus vulgaris, O. joubini* und *O. briareus*. *Rev. suisse Zool.*, 76 : 716-726.

BOLETZKY S. v., 1971 a. Rotation and First Reversion in the *Octopus* Embryo — A Case of Gradual Reversal of Ciliary Beat. *Experientia*, 27 : 558-560.

BOLETZKY S. v., 1971 b. Zu den Lageveränderungen von Octopoden-Embryonen (Mollusca : Cephalopoda). *Rev. suisse Zool.*, 78 : 538-548.

BOLETZKY S. v., 1974. The « larvae » of Cephalopoda : A review. *Thalassia Jugosl.*, 10 : 45-76.

BOLETZKY S. v., 1977 a. Le développement embryonnaire de *Scaeurgus unicirrhus* : Contribution à l'étude du « Macrotritopus Problem ». *Rapp. Comm. int. Mer Médit.*, 24 (5) : 53-63.

BOLETZKY S. v., 1977 b. Post-hatching behaviour and mode of life in cephalopods. *Symp. zool. Soc. Lond.*, 38 : 557-567.

BOLETZKY S. v., 1978-79. Nos connaissances actuelles sur le développement des Octopodes. *Vie Milieu*, 28-29 (1 AB) : 85-120.

BOLETZKY S. v., 1981 a. Morphologie de l'œuf et mode de ponte chez *Pteroctopus tetracirrhus* (Mollusca, Cephalopoda). *Vie Milieu*, 31 : 255-259.

BOLETZKY S. v., 1981 b. Réflexions sur les stratégies de reproduction chez les Céphalopodes. *Bull. Soc. Zool. Fr.*, 106 : 293-304.

CAIRNS S.D., 1976. Cephalopods collected in the Straits of Florida by the R/V Gerda. *Bull. Mar. Sci.*, 26 : 233-272.

FIORONI P., 1965. Die embryonale Musterentwicklung bei einigen mediterranen Tintenfischen. *Vie Milieu*, 16 (2 A) : 655-756.

FIORONI P., 1982. Zur Epidermis- und Saugnapfentwicklung bei Octopoden, ein entwicklungsgeschichtlicher Vergleich. *Rev. suisse Zool.*, 89 : 355-374.

FRÖSCH D., MARTHY H.-J., 1975. The structure and function of the oviducal gland in octopods (Cephalopoda). *Proc. Roy. Soc. B*, 188 : 95-101.

GABE S. h., 1975. Reproduction in the Giant Octopus of the North Pacific, *Octopus dofleini martini*. *Veliger*, 18 : 146-150.

LANE F.W., 1960. Kingdom of the octopus. The life-history of the Cephalopoda. Jarrolds (London), 287 pp.

MANGOLD-WIRZ K., 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu*, 13 (suppl.), 1-285.

MANGOLD K. & BOLETZKY S. v., 1973. New data on reproductive biology and growth of *Octopus vulgaris*. *Mar. Biol.*, 7-12.

NAEF, 1923. Die Cephalopoden. *Fauna Flora Golf. Neapel*, 35-1 : 1-863.

NAEF A., 1928. Die Cephalopoden. *Fauna Flora Golf. Neapel*, 35-11 : 1-357.

NOLTE K. & FIORONI P., 1983. Zur Entwicklung der Saugnäpfe bei coleoiden Tintenfischen. *Zool. Anz.*, 211 : 329-340.

O'DOR R.K. & MACALASTER E.G., 1983. *Bathypolypus arcticus*. In : Cephalopod Life Cycles (P.R. Boyle, ed.), Academic Press (London) : 401-410.

PORTMANN A., 1933. Observations sur la vie embryonnaire de la pieuvre (*Octopus vulgaris* Lam.). *Archs Zool. exp. gén.*, 76 : 24-36.

REES W.J., 1954. The *Macrotritopus* Problem. *Bull. Br. Mus. nat. Hist.*, ser. Zool., 2 : 69-99.

ROBSON G.C., 1929. A monograph of the recent Cephalopoda. Part I : Octopodinae. *Br. Mus. Nat. History* (London), 236 pp.

VOSS G.L., 1951. A First Record of the Cephalopod, *Scaeurgus unicirrhus*, from the Western Atlantic. *Bull. Mar. Sci.*, 1 : 64-71.

VOSS G.L., 1975. *Euaxoctopus pillsburyae*, new species, (Mollusca : Cephalopoda) from the southern Caribbean and Surinam. *Bull. Mar. Sci.*, 25 : 346-352.

WELLS M.J. & WELLS J., 1977. Cephalopoda : Octopoda. In : *Reproduction of marine invertebrates* (A.C. Giese et J.S. Pearse, eds.), 4 : 291-336.

WINTREBERT P., 1928. L'éclosion par digestion de la coque chez les poissons, les amphibiens et les céphalopodes dibranchiaux décapodes. *C.R. Assoc. Anat.*, Prague, 1928 : 501-503.