

## DEVELOPMENTAL FEATURES OF *OCTOPUS MACROPUS* RISSO, 1826 (MOLLUSCA, CEPHALOPODA)

S.v. BOLETZKY, M. FUENTÈS, N. OFFNER

Observatoire Océanologique de Banyuls, UMR 7628, 66651 Banyuls-sur-Mer, France  
boletzky@obs-banyuls.fr

CEPHALOPODA  
OCTOPODA  
DEVELOPMENT  
LIFE-STYLE

**SUMMARY** – *Octopus macropus* Risso, 1826 is known from the Mediterranean Sea and may occur also in the Atlantic. Embryonic development is briefly described, the emphasis being on features related to the existence of a planktonic/micro-nektonic post-hatching phase. At the end of this phase, juveniles switch to the adult mode of bottom life, but the actual conditions of this change of life-style are not yet known for this species. The observations are discussed in relation to the difference, which is known only in the Octopodidae, between merobenthic species (characterized by a planktonic/micro-nektonic post-hatching phase) and holobenthic species (characterized by a benthic post-hatching phase).

CÉPHALOPODES  
OCTOPODES  
DÉVELOPPEMENT  
MODE DE VIE

**RÉSUMÉ** – *Octopus macropus* Risso, 1826 est connu de la Méditerranée; l'espèce est également signalée dans l'Atlantique. Son développement embryonnaire est décrit brièvement, mettant en relief les caractères liés à l'existence d'une phase post-embryonnaire de type planctonique ou micronectonique. Celle-ci aboutit à l'adoption du mode de vie benthique, mais les conditions exactes de ce passage au mode adulte sont encore inconnues chez cette espèce. La discussion replace les observations dans le contexte d'une différence, connue uniquement chez les Octopodidae, entre espèces mérobenthiques (caractérisées par une phase post-embryonnaire planctonique) et espèces holobenthiques (caractérisées par une phase post-embryonnaire benthique).

### INTRODUCTION

The white-spotted octopus, *Octopus macropus*, is a rather common species on both near-shore and deeper bottoms of the Mediterranean Sea. Originally described by Risso (1826) from the area of Nice, it was listed and figured by Férussac & d'Orbigny (1835-1848), Delle Chiaje (1841), Vérany (1851), Jatta (1896) and Naef (1923). Its occurrence outside the Mediterranean was stated by Férussac & d'Orbigny (1835-1848) who examined specimens from the eastern Atlantic, the Red Sea and the Indo-Pacific and considered them all as members of the same species as the specimens collected in the Mediterranean. [These authors claimed priority for the name *Octopus cuvierii* d'Orbigny, since an illustration of the animal under that designation was made available to the public as early as 1825; see Norman (1992) on synonymy with *O. lechenaultii* d'Orbigny]. *O. macropus* was considered a cosmopolitan species until recent decades (Voss & Williamson 1971). It now appears, however, that several species similar to the original *O. macropus* live in shallow tropical and temperate waters throughout the world (Norman 1992, Mangold 1998). Whether the Mediterranean species is

the same as the one observed in the Atlantic Ocean remains to be established (Rees & Maul 1956, Norman 2000, Wirtz 2001). All these species are characterized by very long arms, those of the first arm pair being longer than others, a very shallow web, and an adult life-style marked by predominant or exclusive night activity (Norman 2000). When observed under day light in an aquarium, the bright red color and the brilliant white spots may convey the false impression of poor camouflage. In contrast, when animals active at night are observed in the field (Fuentès & Offner pers. obs.), the skin patterns of *O. macropus* offer particularly eloquent examples of cephalopodan background mimicry (Tardent 1993, Messenger 2001).

The biological cycle of *O. macropus* is poorly known, and until recently there were no reliable data on spawning, embryonic development, and post-hatching life-style (Hochberg *et al.* 1992). Although Naef (1923) identified very early juvenile stages of *O. macropus* from plankton samples obtained in the Bay of Naples and in the Straits of Messina, it was long before evidence was obtained that the smallest specimens described by Naef (1923: 705, Figs 417, 418) indeed represent an immediate post-hatching stage (Boletzky *et al.* 2001). In the Caribbean Sea, a closely related species was



observed to lay very similar eggs producing also similar hatchlings (see photographs by RT Hanlon & M Wolterding in CephBase, <http://www.cephbase.utmb.edu/imgdb/imgsrch2.cfm>).

This note considers some developmental features of *O. macropus*, with special emphasis on aspects relating to life-style switching during juvenile development. Although the eggs of this species are much larger than those observed for instance in *O. vulgaris*, they are still small relative to the adult body size. As in other octopus species producing such relatively small eggs, the short-armed hatchlings of *O. macropus* start out as active swimmers feeding on planktonic organisms (Boletzky 1974). These hatchlings are indeed planktonic as far as their limited mobility in greater water masses is concerned, but they are micro-nektonic in terms of their swimming and hunting behavior (Boletzky 1977). Their behavioral characteristics will be viewed here in relation to morphological features resulting from embryonic development, with special attention to the question whether arm development reflects specific size relationships between egg (or hatchling) and adult.

## OBSERVATIONS

All observations reported here were made in autumn 2000 on eggs spawned in the aquarium by a female *O. macropus* that had been captured during early summer of the same year in Banyuls-sur-Mer, north-western Mediterranean (Boletzky *et al.* 2001).

### Eggs and embryos

Eggs measured  $4.0 \times 1.2$  mm at laying, not including the chorion stalk that measured 4 mm in length (Boletzky *et al.* 2001). The female attached the chorion stalks individually or in small clusters to a hard surface, thus forming a sheet of eggs that covered the walls of the artificial den inhabited throughout brooding. Eggs were flask-shaped when freshly laid, the chorion membrane tapered into a poorly defined chorion stalk. The overall aspect of the eggs changed slowly during early embryonic development as a constriction formed at the stalk base (Fig. 1), but the lumen of the hollow stalk remained in open connection with the main chorion space (Fig. 8).

Embryonic development closely resembled the developmental patterns described in other octopodid species (Boletzky 1978-79). Similarities included the occurrence of a first reversal of the embryo, which results in the position shown in Figure 1 (Boletzky & Fioroni 1990). As in other octopus species, reversal can fail so the embryo continues to develop in the initial position (Fig. 2). Under

normal conditions, an embryo having undergone the first reversal returns to the initial orientation at a later stage (Fig. 8).

The portion of the yolk remaining in the visceral complex of the embryo during organogenetic stages is strongly compacted (Boletzky 2002). It forms a distinct inner yolk sac, which decreases in size due to an overall contraction of the embryonic body (Fig. 3). The minimum size of the inner yolk sac is attained by stage XV of Naef (1928), i. e. at a time when the mantle begins to grow in length (Fig. 4). During the subsequent stages of embryonic development, yolk transfer from the outer yolk sac results in a strong size increase of the inner yolk sac (Fig. 5). During these stages, the arms grow in length, each developing a set of 7 suckers that are arranged in a zigzag pattern on the oral arm surface (Figs 6, 7). The rounded ends of the arms (Fig. 6) become more pointed, each forming a terminal bud (Fig. 7), which is the rudiment of a prospective whip-like arm end (cf. Fig. 9). The arms remain sub-equal in length till hatching. The surface structure is marked by the formation of a dense set of Kölliker's organs in the skin (Fig. 9).

During these advanced stages, the first chromatophores appear on the head surface (Fig. 5). At the final embryonic stages the integument shows about 145 red chromatophores (Boletzky *et al.* 2001). The arrangement of 22 chromatophores in a double row behind the mantle edge (Fig. 8) could be a species-specific feature. The single file of chromatophores on the aboral surface of each arm pleads against the tentative identification of post-hatching stages by Rees (1955).

From stage XIX of Naef (1928) to hatching, the outer yolk sac becomes very small due to the combined effects of yolk absorption in the outer sac and yolk transfer to the inner sac (Fig. 8). The young hatched (at 16°C), about 2 months after the onset of embryonic development (at 22°C). If the temperature had remained above 20°C, embryonic development would have been shorter.

### Post-hatching mode of life

The newly hatched animals measured 4 mm in dorsal mantle length (ML) and were planktonic/micro-nektonic, in other words they actively swam or hovered in the water column. During hovering the body was in an oblique position, the funnel tube and the short arms pointing downward (Fig. 10). When placed in a very small volume of water, the young animals spread out their arms and attached the suckers to the substrate (Fig. 9). Unconstrained, swimming individuals occasionally approached a vertical hard surface (e. g. the window of the aquarium), spread their arms (Fig. 11), and pounced at the hard surface to attach their arms



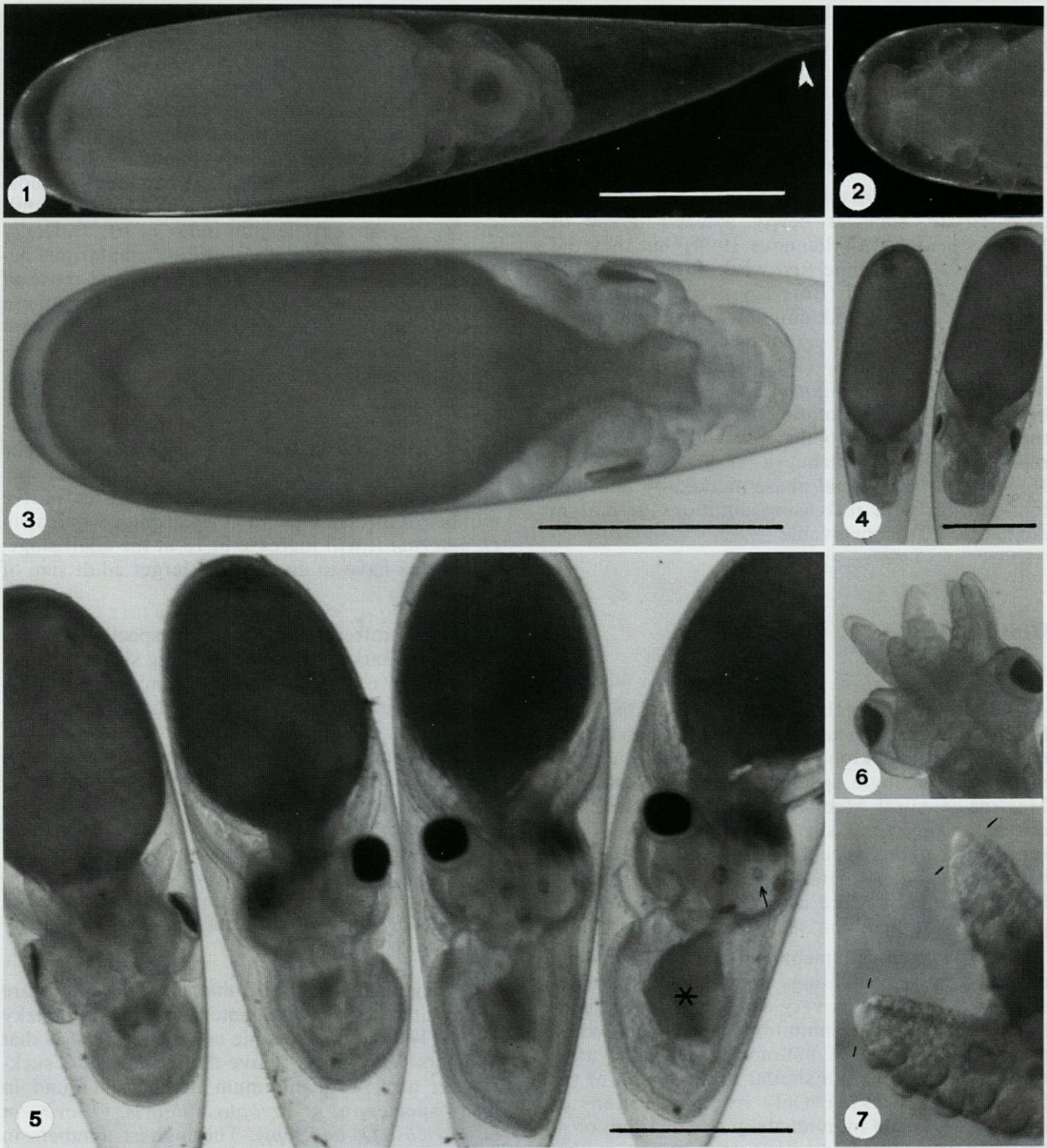


Plate I. — Fig. 1. Early organogenetic stage of *O. macropus* in lateral view (stage XI-XII of Naef); the orientation of the embryo in the chorion results from the first reversal. Note faint pigmentation of the retina. The arrow head points at the base of the chorion stalk. Scale bar = 1 mm. Fig. 2. Similar stage as in Fig. 1, but having missed the first reversal, so the embryo proper (seen from the oral side) lies close to the thick micropyle zone of the chorion. Fig. 3. Advanced organogenetic stage (stage XIII) in normal orientation, seen from the oral side. Scale bar = 1 mm. Fig. 4. Stages XIII (left) and XIV (right). Note size increase of head and mantle, and darkening of retinal pigmentation. Scale bar = 1 mm. Fig. 5. Stages XV (left) to XVI-XVII (right). Note the small size of the inner yolk sac (left) and its increase (at right\*), and the differentiation of chromatophores (arrow). Scale bar = 1 mm. Fig. 6. Detail of head and arms at stage XIV after removal of the outer yolk sac. Note the rounded arm tips. Fig. 7. Some arms at stage XVI after removal of the outer yolk sac. Note the bare knobs (to the left of the bars) that are the rudiments of the future whip-like arm tips.



with the suckers (Fig. 12). It is significant that the mantle end was always slightly pointed (Figs 9, 10). This foreshadowed the tendency of benthic juveniles to stretch the mantle end into a conical shape (Naef 1923, p 707) and of benthic adults to give the whole mantle a slender cyrtoconic shape (Bergbauer & Humberg 1999).

Hatchlings readily attacked and seized crustacean larvae, such as newly hatched larvae of *Pagurus prideaux* (Villanueva 1994), but they did not survive beyond the first week of post-hatching life in the aquarium (Boletzky *et al.* 2001). Thus the length of the planktonic/micro-nektonic phase of *O. macropus* is not yet known. Given the larger size of the hatchling (ML 4 mm) compared to newly hatched *O. vulgaris* (ML 2 mm), the time before switching to bottom life is possibly shorter than the nearly two months observed in *O. vulgaris* reared at 21°C (Villanueva *et al.* 1995, 1996). However, a transitional phase marked by intermittent settling with increasing durations of bottom contact is also conceivable.

## DISCUSSION

Based chiefly on chromatophore patterns, Naef (1923) recognized early juvenile individuals obtained from plankton samples to be young *O. macropus*. A single specimen from the Straits of Messina (Central Mediterranean) had 10 suckers on each arm, i. e. 3 suckers more than the 7 observed in the other specimens. This individual must have been older than the other, likely newly hatched animals. More advanced stages were not present in the plankton samples studied by Naef.

The spontaneous attachment to a hard substrate observed in our hatchlings may suggest that life-style switching occurs very early, but this assumption is unsafe. An inhibitory mechanism could postpone the onset of bottom life until the arms have grown to a length similar to the length of the body (Boletzky 1977). Only live observations of advanced juvenile individuals in an aquarium or in the field can provide a satisfactory answer to this question, as in the case of other octopodid species that have a planktonic/micro-nektonic phase but show very early settling responses (Boletzky 1987).

For all these species, two questions deserve particular attention. How far is life-style switching related to initial body proportions and behavioral maturity? Are such relations linked to a specific magnitude of size difference between the hatchlings and their respective adults? This is of interest in particular with regard to differences in the respective juvenile and adult morphometrics between merobenthic species (undergoing juvenile life-style

switching) and holobenthic species (producing crawl-away young that skip the [supposedly primitive] pelagic phase) (Boletzky 1992).

Considering common features of merobenthic octopodids, the body proportions of the newly hatched animals are virtually identical (arms measuring about 40-50 % of ML at hatching) in most species producing eggs smaller than 10 % of adult ML (i. e., an egg length index < 10; Boletzky 1974). One may note other striking similarities between the hatchlings of *O. macropus* and those of *O. maorum*, a much larger species from southern Australia and New Zealand (Batham 1957) that appears to be a member of the *O. macropus* group (Norman 1992). The hatchlings of *O. macropus* (4.0 mm ML) are only slightly smaller than those of *O. maorum* (4.5 mm ML), and they have 7 suckers on each arm instead of 8 in *O. maorum*. The gills have 10 lamellae per demibranch in both species at hatching. However, this is the definitive number of gill lamellae in *O. macropus*, whereas in *O. maorum* it will increase to 13 at the adult stage. Could this have to do with the larger adult size of *O. maorum*?

Indeed, different merobenthic species can exhibit very marked differences in egg size/adult size relations (i. e. egg length indices may range 2-8), which are reflected by corresponding differences in hatchling size/adult size relations. Thus in terms of the hatchling size *relative* to the adult size (90-100 mm ML in *O. macropus*, 200-300mm ML in *O. maorum*), hatchlings of *O. macropus* are much bigger than those of *O. maorum*. If a definitive number of gill lamellae may suggest something like 'morphological maturity' in *O. macropus* hatchlings, however the sucker numbers cannot be taken to reflect anything of the sort (as once suggested by Boletzky 1977, Table II).

It remains to recall also that sucker numbers are not related to *absolute* hatchling size (Boletzky 1977). The only reasonable conclusion then is that numbers vary widely above a minimum of 3 suckers per arm. This minimum number is found in many species (e. g. *Octopus vulgaris*, *O. cyanea*, *O. tetricus*, *O. defilippi*). The highest numbers in merobenthic species are 14 in *O. dofleini*, the giant octopus of the northeastern Pacific, and 16 in *O. fitchi*, a pygmy octopus of the eastern Pacific (Hochberg *et al.* 1992). These examples again emphasize that there is no positive relation with either absolute or relative hatchling size, as a high number of suckers indeed appears in small hatchlings (2-4 mm ML) that are either very small relative to the adult (< 2 % adult ML in *O. dofleini*) or very large relative to the adult (> 8% adult ML in *O. fitchi*). This large relative size of the hatchling results from an exceptionally high egg length index (ca 20) that would normally predict a holobenthic strategy, with long-armed, crawl-away young hav-



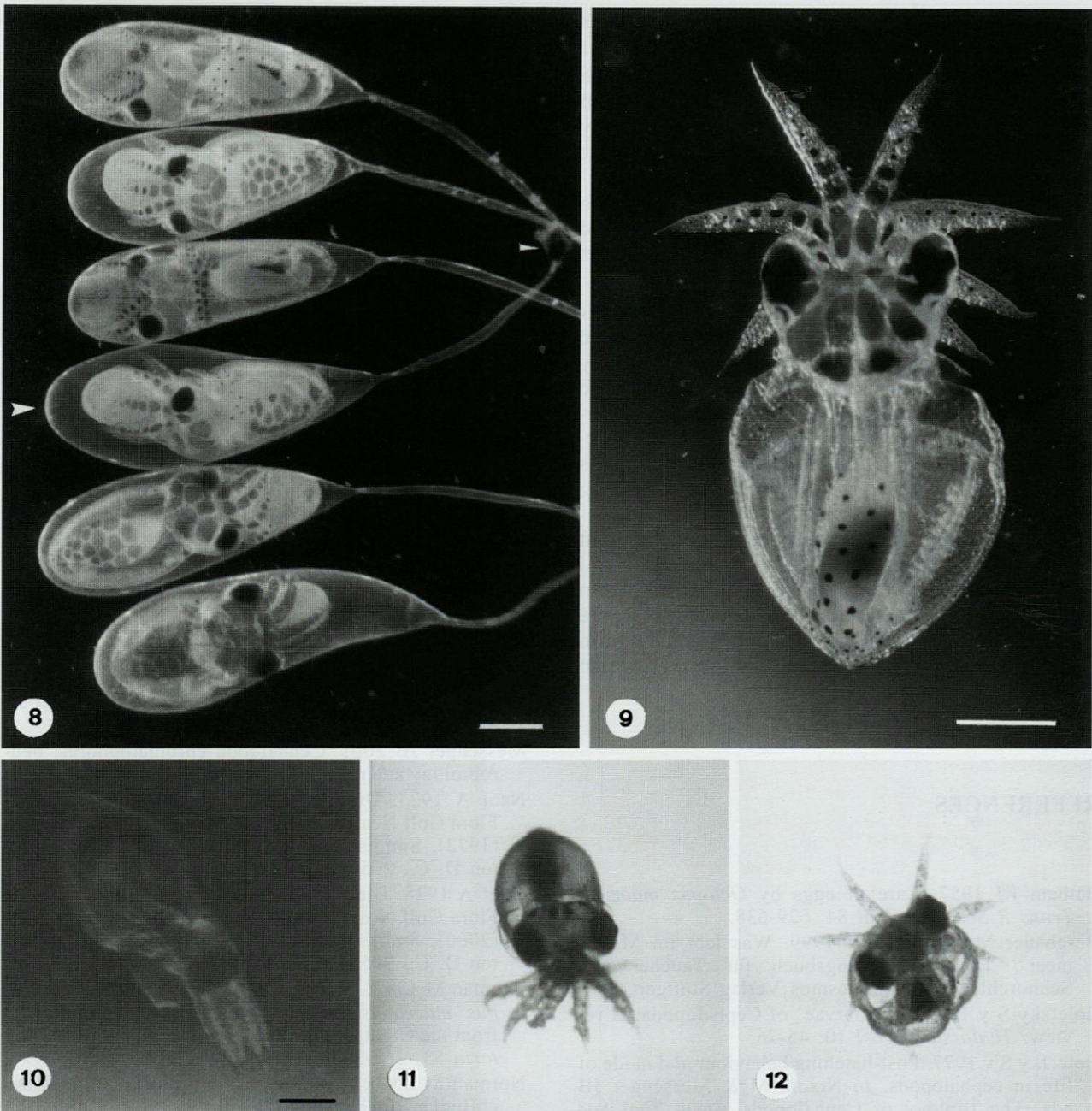


Plate II. — Fig. 8. Late embryonic stages (around stage XIX) before the second reversal (upper four) and after the second reversal (lower two, in normal hatching position). The large arrow head points at a strongly expanded chorion having an intact stalk anchored in a piece of fixation cement (hardened secretion) marked by the small arrow head. The third chorion from top has lost some perivitellin fluid due to rupture of the hollow chorion stalk. Note the dense set of chromatophores, especially the double row of chromatophores behind the mantle edge in the first and third embryo from top, and the very dark pigmentation of the retinae. Scale bar = 1 mm. Fig. 9. Newly hatched animal placed in a drop of sea water on a hollow microscope slide (photo taken through a dissecting microscope). Note the spread arms with their whip-like tips, the suckers being attached to the glass bottom. The granular appearance of the mantle is caused by Kölliker's organs in the skin. Scale bar = 1 mm. Fig. 10. Newly hatched animal hovering (lateral view in aquarium). Note the pointed mantle end at the top and the large funnel tube pointing downwards. Scale bar = 1 mm. Fig. 11. Very young individual (1-2 days after hatching) swimming, arms spread (frontal view in aquarium). Fig. 12. Same individual as in Fig. 11, attached to the aquarium window (oral view). Note the spread arms, the upper two being arm pair I, and the oblique position of the head and body (this twist is due to [perhaps incidental] muscular torsion of the arm crown attachment to the head).



ing at least 20 suckers on each arm (Boletzky 1997).

Among the species in which hatchlings have only 3 suckers per arm, *O. defilippi* differs from others in that the third arm pair is more strongly developed already at hatching, thus emphasizing the 'Macrotritopus' condition that seems to characterize an *O. defilippi* species complex (Hanlon *et al.* 1985). In contrast, the "first arm longest and stoutest" condition of adult *O. macropus* is not yet recognizable at hatching.

If most developmental features of *O. macropus* may appear rather commonplace for a merobenthic octopodid species, several details of morphology and behaviour deserve further attention. Meristic characters of juvenile and adult gills could be of interest. That the gills of the hatchlings have their definitive complement of lamellae in *O. macropus* is remarkable, although probably not unique among merobenthic species. There may be specific combinations of otherwise inconspicuous features that could provide some hints of a common ancestral condition, while some of these features may turn out instructive as discrete character states usable for the distinction of closely related species within the *Octopus macropus* species complex (Norman 2000).

## REFERENCES

- Batham EJ 1957. Care of eggs by *Octopus maorum*. *Trans R Soc New Zeal* 84: 629-638.
- Bergbauer M, Humberg B 1999. Was lebt im Mittelmeer? Ein Bestimmungsbuch für Taucher und Schnorchler. Franckh-Kosmos Verlag Stuttgart.
- Boletzky S v 1974. The 'larvae' of Cephalopoda: A review. *Thalassia Jugosl* 10: 45-76.
- Boletzky S v 1977. Post-hatching behaviour and mode of life in cephalopods. In Nixon, M & Messenger JB eds, *The Biology of 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 (1AB): 85-120.
- Boletzky S v 1987. Embryonic phase. In Boyle PR ed. *Cephalopod Life Cycles* vol. II. Academic Press, London: 5-31.
- Boletzky S v 1992. Evolutionary aspects of development, life style, and reproductive mode in incirrate octopods (Mollusca, Cephalopoda). *Rev suisse Zool* 99: 755-770.
- Boletzky S v 1997. Developmental constraints and heterochrony: a new look at offspring size in cephalopod molluscs. *Geobios Mém Sp* 21: 267-275.
- Boletzky S v 2002. Yolk sac morphology in cephalopod embryos. In Summesberger H, Histon K & Daurer A eds, *Cephalopods – Present and Past*. *Abh Geol B-A* 57: 57-68.
- Boletzky S v, Fioroni P 1990. Embryo inversions in incirrate octopods: the state of an enigma. *J Ceph Biol* 1(2): 37-57.
- Boletzky S v, Fuentes M, Offner N 2001. First record of spawning and embryonic development in *Octopus macropus* (Mollusca: Cephalopoda). *J Mar Biol Ass UK* 81: 703-704.
- Delle Chiaje S 1841. Descrizione e notomia degli animali invertebrati della Sicilia citeriore. I. Molluschi Cephalopodi e Pteropodi. Napoli.
- Férussac AE, d'Orbigny A 1835-48. Histoire naturelle générale et particulière des Céphalopodes acétabulifères vivants et fossiles. Baillière, Paris.
- Hanlon RT, Forsythe JW, Boletzky S v 1985. Field and laboratory behavior of «Macrotritopus larvae» reared to *Octopus defilippi* Verany, 1851 (Mollusca, Cephalopoda). In Mangold K & Boletzky S v eds, *Biology and distribution of early juvenile cephalopods*. *Vie Milieu* 35: 237-242.
- Hochberg FG, Nixon, M, Toll, RB 1992. Order OCTOPODA Leach, 1818. In Sweeney MJ, Roper CFE, Mangold KM, Clarke MR & Boletzky S v, eds, "Larval" and Juvenile Cephalopods: A Manual for Their Identification. *Smiths Contr Zool* 513: 213-280.
- Jatta G 1896. I Cefalopodi viventi nel Golfo di Napoli. *Fauna Flora Golf Neapel* 23: 1-264.
- Mangold K 1998. The Octopodinae from the Eastern Atlantic Ocean and the Mediterranean Sea. In Voss NA, Vecchione M, Toll RB & Sweeney MJ eds, *Systematics and Biogeography of Cephalopods*, vol II. *Smiths Contr Zool* 586: 521-528.
- Messenger JB 2001. Cephalopod chromatophores: neurobiology and natural history. *Biol Rev* 76: 473-528.
- Naef A 1923. Die Cephalopoden (Systematik). *Fauna Flora Golf Neapel* 35(I-1): 1-836. [English translation (1972), Smithsonian Institution Libraries, Washington D. C., 20560, U.S.A.].
- Naef A 1928. Die Cephalopoden (Embryologie). *Fauna Flora Golf Neapel* 35(I-2): 1-357 [English translation (2000), Smithsonian Institution Libraries, Washington D. C., 20560, U.S.A.].
- Norman M 1992. Four new octopus species of the *Octopus macropus* group (Cephalopoda: Octopodidae) from the Great Barrier Reef, Australia. *Mem Mus Victoria* 53: 267-308.
- Norman M 2000. *Cephalopods – A World Guide*. ConchBooks, Hackenheim (D).
- Rees WJ 1955. The larvae and late-larval stages of *Octopus macropus* Risso. *Proc Malac Soc Lond* 31: 185-189.
- Rees WJ, Maul GE 1956. The Cephalopoda of Madeira – records and distribution. *Bull Brit Mus Zool* 3: 259-281.
- Risso A 1826. Aperçu sur l'histoire naturelle des Mollusques. In *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes maritimes*, 4: 1-8.
- Tardent P 1993. *Meeresbiologie – Eine Einführung*. Georg Thieme Verlag Stuttgart.
- Villanueva R 1994. Decapod crab zoeae as food for rearing cephalopod paralarvae. *Aquaculture* 128: 143-152.
- Villanueva R, Nozais C, Boletzky S v 1995. The planktonic life of octopuses. *Nature* 377: 107.



Villanueva R, Nozais C, Boletzky S v 1996. Swimming behaviour and food searching in planktonic *Octopus vulgaris* Cuvier from hatching to settlement. *J Exp Mar Biol Ecol* 208: 169-184.

Vérany JB 1851. Céphalopodes de la Méditerranée. *In* Mollusques Méditerranéens 1: 1-132.

Voss GL, Williamson G 1971. Cephalopods of Hong Kong. Hong Kong Government Press.

Wirtz P 2001. New records of invertebrates from the Cape Verde islands. *Arquipélago* 18A: 81-84.

*Reçu le 29 août 2002; received August 29, 2002*  
*Accepté le 16 octobre 2002; accepted October 16, 2002*