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FIELD AND LABORATORY BEHAVIOR OF "MACROTRITOPUS LARVAE" REARED TO *OCTOPUS DEFILIPPI* VERANY, 1851 (MOLLUSCA : CEPHALOPODA)

*R.T. HANLON, J.W. FORSYTHE and S. von BOLETZKY**

The Marine Biomedical Institute, The University of Texas Medical Branch
200 University Boulevard, Galveston, Texas 77550-2772, USA
** Laboratoire Arago, Université Pierre et Marie Curie,*
U.A. 117, CNRS, 66650 Banyuls-sur-Mer, France

CEPHALOPODA
BEHAVIOR
DISTRIBUTION
OCTOPUS
LARVAE

ABSTRACT. — Seventeen advanced macrotritopus "larvae" from 7 to 15 mm mantle length were attracted to underwater lights in St. Croix, U.S. Virgin Islands. Their behavior was observed *in situ,* then seven were captured alive and one female was reared to an adult *Octopus defilippi.* The characteristic long arms of the planktonic young appear to function in flotation, feeding, crawling and defense. There is evidence that larger macrotritopus may be planktonic by night and benthic by day; thus the transition from a planktonic to benthic life may be controlled to ensure widespread distribution on to a suitable habitat. Morphological examination of 106 specimens from the Atlantic indicate that all macrotritopus "larvae" from this ocean are *O. defilippi.*

CEPHALOPODA
COMPORTEMENT
DISTRIBUTION
OCTOPUS
LARVES

RÉSUMÉ. — Dix-sept individus juvéniles « macrotritopus » ont été observés en mer, sous des projecteurs, et sept ont été capturés vivants. Une femelle a été élevée jusqu'au stade adulte. La troisième paire de bras, très longs, semble jouer un rôle dans la sustentation, la prédation, la locomotion au fond, et pour la défense. Certains indices permettent de conclure que les macrotritopus de taille relativement grande vivent entre deux eaux pendant la nuit et ne descendent au fond que sous l'influence de la lumière. Le changement de mode de vie peut ainsi être repoussé jusqu'à ce qu'un fond approprié soit trouvé, éventuellement loin du lieu d'éclosion. L'examen morphologique de 106 spécimens provenant de l'Atlantique permet de conclure que tous les macrotritopus de cette région appartiennent à l'espèce *Octopus defilippi.*

INTRODUCTION

Macrotritopus "larvae" are young planktonic octopods with the third arms longer than the others. There has been continued confusion over their identity before they were recognized in the Atlantic as the young of a known species, *Octopus defilippi.* We attempt in this report to address the following questions concerning macrotritopus : (1) is there a species complex characterized by a macrotritopus juvenile ? (2) what are the long arms for ? (3) how and why do relatively large macrotritopus stay in the plankton ? and (4) if this is a continental shelf octopod, why are the macrotritopus most often found in the open sea and not on the continental shelf ?

Grimpe (1922) proposed the genus *Macrotritopus* based upon a juvenile (11 mm mantle length, ML) pelagic *Octopus gracilis* Verrill, 1884 that had long third arms. Issel (1925) thought that macrotritopus "larvae" were *Octopus defilippi,* while Degner (1925) thought that they were the young of *Scaeurgus unicirrhus* because of a specimen 6.3 mm ML that had a knob on the left third arm, which he viewed as a rudimentary hectocotylus. In 1929, Joubin and Robson described two species of *Macrotritopus* from the Mediterranean, Atlantic and Caribbean. In 1929, Robson placed *Macrotritopus* back as a subgenus of *Octopus*. Adam (1938) described *Octopus (Macrotritopus) elegans* from the Indo-Pacific and later (Adam, 1954) noted the similarity to *O. defilippi*. In 1954, Rees considered the "macrotritopus problem" and, based upon the radula and distribution, concluded that they were *Scaeurgus unicirrhus* (curiously he did not mention the paper by Issel, 1925 !). In 1964, Voss described *O. defilippi* from the western Atlantic. Meanwhile, oceanographic sampling worldwide produced macrotritopus "larvae" in nearly all tropical and temperate seas (e.g., Rancurel, 1970; Cairns, 1976; Lu and Clarke, 1975). Boletzky (1977a) described the young of *Scaeurgus unicirrhus* and confirmed that macrotritopus were unrelated. Hanlon *et al.* (1980a) and Nesis and Nikitina (1981) independently confirmed that macrotritopus in the Caribbean Sea are *O. defilippi*. The present paper expands and clarifies the latter two reports.

MATERIALS AND METHODS

Seventeen live macrotritopus were attracted to an underwater 1 500 watt mercury vapor light at depths of 15 to 40 m over both coral reef and sand plain bottoms in Salt River Canyon on the north shore of St. Croix, U.S. Virgin Islands (17°45' N, 64°45' W) between 1 and 7 September 1978. Deep water was immediately adjacent to the island. The octopods were observed and photographed *in situ* for several hours during saturation diving mission 78-5 in NULS-1 (NOAA's first Undersea Laboratory System; Hanlon *et al.*, 1980b). Seven animals were collected, two were transported live to the Marine Biomedical Institute (MBI) at Galveston and one survived to sexual maturity in a small closed seawater system (see system details in Forsythe and Hanlon, 1980).

Eighteen preserved specimens collected from four extensive MBI research cruises in the western Gulf of Mexico (November 1975, April 1976, March 1977 and August 1977) were examined. In addition, the 77 specimens of Nesis and Nikitina (1981) were examined as well as two specimens from the Discovery investigations (Station 7824) and two from the Albatross IV (73-2; Station 109). Seven very young individuals from South Africa were also studied. Geographically this material covers all the Caribbean Sea and Gulf of Mexico as well as the central and south Atlantic. Specimen sizes ranged from 1.3 to 15.0 mm ML. In addition, 20 specimens from the Indo-Pacific (Hawaii, Australia, Indian Ocean) were examined for general comparison with the Atlantic material. Nearly all of these specimens were collected with standard Bongo nets or 1 m and 2 m plankton nets with mesh sizes of 0.50 to 0.65 mm.

RESULTS

Behavioral observations underwater

During one night-lighting station (Station 10 in Hanlon *et al.*, 1980b), twelve macrotritopus were observed at 21 m in the lighted area within one hour. The water was clear, and large quantities of plankton were attracted to the light. Feeding by the macrotritopus was not observed. The octopods drifted in from offshore towards the light in midwater in a distinct posture (Fig. 1 A) in which all the arms were spread out radially; we term this the Spread-arm drift posture. In this position the octopods seemed almost neutrally buoyant; they would occasionally jet slowly backwards. They were observed in this position for at least 15 minutes at a time. Five other macrotritopus were observed at 18 other night-lighting stations ranging from 15 to 40 m.

Two other forms of swimming were seen. During slow swimming the octopods jetted backwards with the arms trailing in a V, the tips usually curled; we term this Backward-V swimming (Fig. 1 B). When the animals slowed, they drifted downward only very slowly in this posture. During fast swimming the octopods jetted rapidly backwards with all arms tapered straight behind into a point. When quickly approached by a diver the octopods would go swiftly from the Spread-arm drift posture to fast backward jetting with inking; these small octopods could easily cover 0.5 m per jet and could go at least three consecutive meters outswimming a diver. They usually then went to slow Backward-V swimming towards the bottom.

On two occasions octopuses were followed slowly to the substrate, in which case they spread the arms radially and landed oral surface first (Fig. 1 C). They moved upon the substrate very deftly and were well coordinated to walk or crawl around, over or under the varied objects on the coral reef. Both animals quickly slid into holes and disappeared from view. It was clear that the substrate was not alien to them.

Observations in the laboratory

After removal from the sea the octopods never again spent time in the water column of the small tanks. They became exclusively benthic and their activity pattern was strongly nocturnal. At dusk, they frequently crawled forward across the substrate with all arms spread radially while each searched the bottom (Fig. 1 D). They often climbed vertical objects with the arms drooping downward while they observed the surroundings (Fig. 1 E). They ate small live mussels within two days and then small live crabs throughout laboratory rearing.

The surviving octopus grew from 10 to 90 mm ML in 151 days. For the first 4 weeks it buried itself in the oyster shell substrate (particle size approximately 5 × 3 × 2 mm) except during foraging and feeding. Thereafter it hid in small shells. On day 143 this female laid over 10,000 unfertilized eggs, mean length 2.1 mm, which she carried in her arms for 8 days until death. The specimen matched well the characters of *Octopus defilippi* described by Voss (1964) and it is deposited in the National Museum of Natural History, Division of Molluscs (USNM 730019), Washington, D.C. Details of behavior and color change will be the subject of a future publication.

DISCUSSION

The one reared female confirms that macrotritopus near the U.S. Virgin Islands are *Octopus defilippi.*

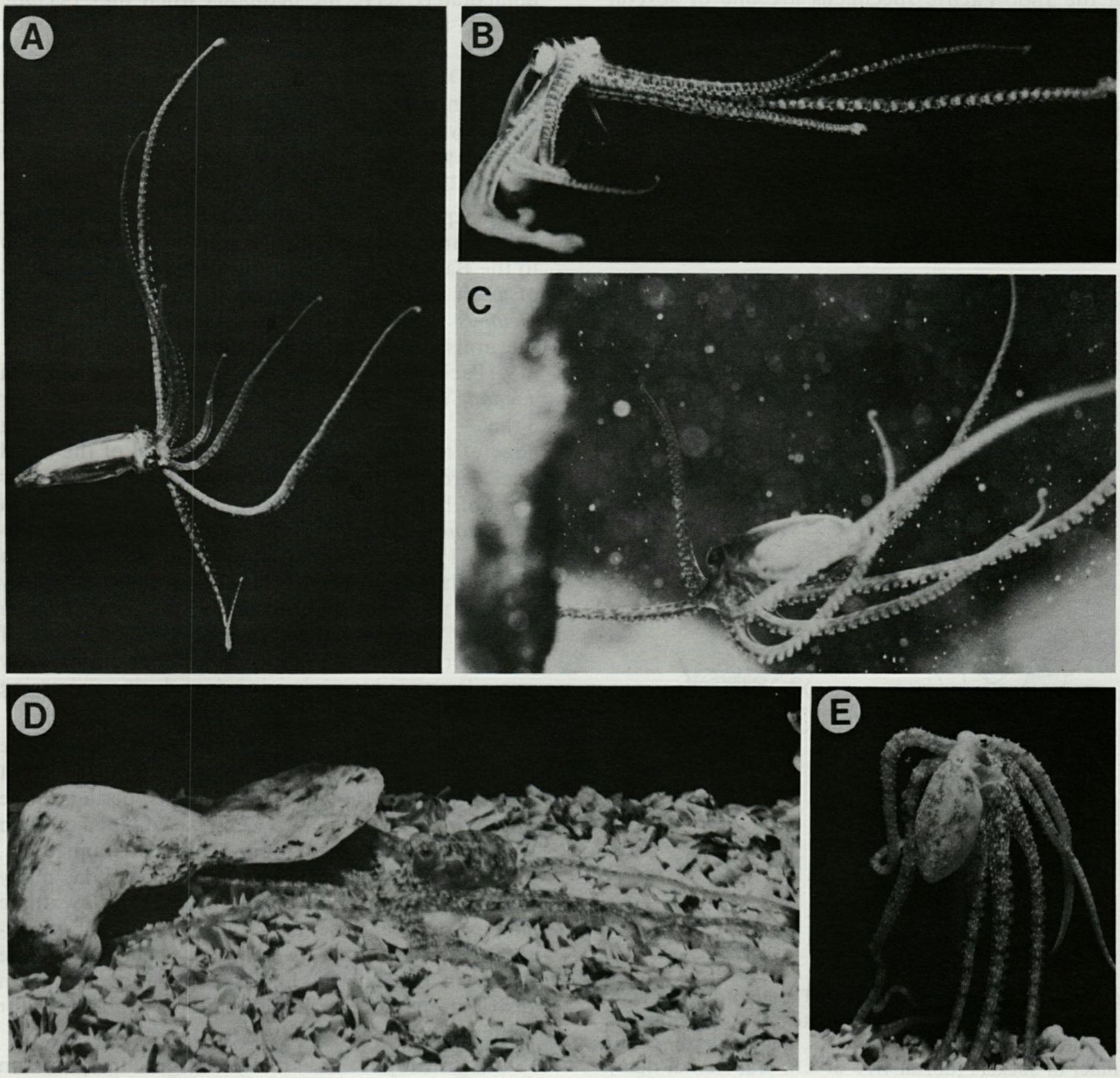

Fig. 1. — Behavior of macrotritopus "larvae" of *Octopus defilippi.* A, Spread-arm drift posture of a 9 mm ML octopod at 16 m underwater at night. B, Same octopod in Backward-V swimming. C, A 12 mm ML octopod about to land on the coral reef substrate at 15 m. D, Small field-caught female, 17 mm ML, after 2 weeks in the laboratory searching the bottom for food. E, Same female as in D at 25 mm ML in typical head-high sitting posture on the glass of the aquarium.

Inspection of 106 other macrotritopus from throughout the Atlantic indicate that all of them represent *O. defilippi.* The same conclusion was reached by Nesis and Nikitina (1981). The known distribution of *O. defilippi* (i.e., Caribbean, central and south Atlantic, Mediterranean) also supports this statement. The egg size, 2.1 mm, in the reared female corresponds to the smallest macrotritopus specimen, 1.3 mm ML after fixation. However, Indo-Pacific specimens appear to differ somewhat from Atlantic material in arm length ratios, funnel chromatophores and possibly other characters. Further study is required, but it seems likely that macrotritopus "larvae" represent a species complex worldwide and that the Indo-Pacific specimens are one or several species closely similar to *Octopus (Macrotritopus) elegans* (Adam, 1938, 1954) or *Octopus defilippi.*

In newly hatched macrotritopus, the ventrolateral arms (pair 3) are only very slightly longer than the other arms (Fig. 2). Subsequently, they outgrow arms 1, 2 and 4 very largely. The long, slender arms are obvious aids to flotation since they represent a large proportion of the surface area of the animal. The use of extended appendages to retard sinking is a well-documented fact in many pelagic organisms and our behavioral observations verify that macrotritopus can remain nearly stationary with little or no jetting. Long arms may also be useful in feeding upon larger plankton that stray into the extended arms during the Spread-arm drift posture. This type of "passive" and tactile feeding is not uncommon among octopods and is similar to the "speculative attacks" of *Octopus cyanea* (Yarnall, 1969) or *Octopus briareus* (Hanlon, 1975) and the "ambush" strategy of *Octopus burryi* (Hanlon and Hixon, 1980) and *Octopus joubini* (Mather, 1972). The long arms immediately serve the octopods when they become benthic, as we observed in the laboratory when they foraged the bottom with all arms spread radially (Fig. 1 D). The Spread-arm drift posture may also be useful in defense; it is strongly reminiscent of the Flamboyant defense pattern observed in young *Octopus* (e.g., Packard and Sanders, 1971; Hanlon and Hixon, 1980).

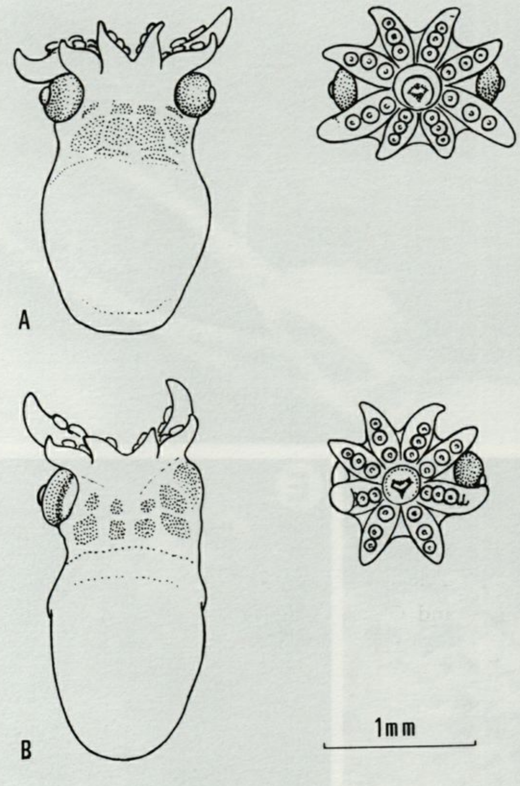

Fig. 2. — Preserved specimens of macrotritopus from South Africa. A, Very young post-hatching stage with third arms distinctly larger than others, but with the same number of suckers (dorsal view at left, oral view at right). B, Slightly more advanced stage, showing beginning formation of additional suckers only on arm pair 3 (dorsal view at left, oral view at right). NB : The extrusion of the eyeball is an artifact due to capture and fixation procedures.

The question why the third rather than another pair of arms is accelerated in growth draws attention to the Backward-V swimming attitude that is typical of adult octopodids when swimming. For example, *Octopus vulgaris* in slow backward swimming trails the arms in two distinct bunches forming together a V (Packard, 1972), the outermost being arms 3. In *Eledone cirrhosa* it is the proximal half of arm pair 3 that — by its strong curvature — forms the leading edge of the "wings" that are so typical of the rapid backward swimming in this species. A very similar form of horizontal "stabilizer" has been observed in *Pteroctopus tetracirrhus* swimming backwards (Boletzky, 1976). The rapid growth of arm pair 3 in macrotritopus suggests an adaptation to rapidly achieve the adult hydrodynamic profile of the arm crown. Conversely, the slower allometric growth of the other arms may present advantages during early juvenile stages by minimizing drag during swimming (Boletzky, 1977 b).

Macrotritopus are capable of remaining in the plankton over a wide size range — from 1.3 to at least 15 mm ML. We estimate this period to be approximately 10 to 20 weeks based upon growth studies of young planktonic octopods (Itami *et al.*, 1963) and squids (Yang *et al.*, 1983). Like many young octopodids, the macrotritopus follow three phases in development — solely planktonic, planktonic/benthic and truly benthic — but the middle phase is particularly long, presumably to aid in distribution and reaching suitable substrate for settlement.

Macrotritopus are rarely caught in plankton samples over continental shelf areas (Rees, 1954; Clarke, 1969; Lu and Clarke, 1975; Nesis and Nikitina, 1981). This could be partially explained by the ability of larger macrotritopus to control their planktonic/benthic phase and thus settle as soon as they reach shelf areas, but it may be due also to the preferred habitat of *O. defilippi*. Takeda and Okutani (1983) recently found *O. defilippi* from 328 to 600 m off Suriname and it is possible that this species is more common on the continental slope than on the shelf. Their ability to bury in the substrate (in the laboratory) indicates that they would be able to inhabit open sand and mud areas of the deep shelf and still find protection by burying.

Thus one might expect small macrotritopus to be carried to open ocean waters after hatching but to settle quickly when they reach the edge of a continental shelf. Rees (1954) described one specimen, 3.45 mm ventral mantle length, from the Discovery Expedition that was captured between 1 500 and 800 m and he suggested that it was seeking bottom to settle.

In summary, the "macrotritopus problem" (Rees, 1954) has been clarified substantially for the Atlantic Ocean. However, the presence of two variations of *O. defilippi* (Robson, 1929) remains a problem. In contrast to the "typical form" with a radula characterized by unicuspidate rhachidian teeth, the variation *dama* described by Robson based upon a specimen from the Mediterranean "has well-developed ectocones with a symmetrical seriation (A 3-4)". The same is noted by Adam (1938) for *O. elegans*, but later (Adam, 1954) the radula of *O. elegans* is described as "caractérisée par l'absence d'ectocones sur les dents médianes" ! Further clarification should result from analyzing the Indo-Pacific macrotritopus to uncover their similarities or differences with *O. defilippi*.

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