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RHYNCHOTEUTHION LARVAE OF OMMASTREPHID SQUIDS OF THE WESTERN NORTH ATLANTIC, WITH THE FIRST DESCRIPTION OF LARVAE AND JUVENILES OF ILLEX ILLECEBROSUS

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Abstract.—The larvae and juveniles of Illex illecebrosus (Ommastrephidae) are described for the first time based on specimens from the western North Atlantic off Cape Hatteras northward to Georges Bank, New England. Two other larval forms of ommastrephid squids, Rhynchoteuthion larvae, are recognized and tentatively identified with Ommastrephes and Ornithoteuthis. Larvae and juveniles of Illex were captured during all seasons, indicating that spawning takes place over an extended period, possibly yearround, when the broad geographical range of the species is considered. Localities of capture of smallest larvae (1.5 mm mantle length) indicate that the spawning site of Illex illecebrosus lies along the outer edge of the continental shelf.

Introduction

Four species of squids of the genus Illex (family Ommastrephidae) occur in the Atlantic Ocean, some distributed over a broad geographical range. Illex illecebrosus (Lesueur, 1821) occurs in the western North Atlantic from Labrador and Newfoundland to central Florida. Single records from Greenland and Iceland, and those from northern European waters as far south as the Bristol Channel are in doubt (Lu, 1973). Illex coindetii (Verany, 1837) occurs in the eastern Atlantic from the North Sea to 14°S in Africa (Angola), in the Mediterranean and Adriatic Seas, as well as in the Caribbean Sea, Gulf of Mexico, and east coast of South Florida. Illex argentinus (Castellanos, 1960) occurs along the coast of Argentina and over the Patagonian Shelf, but the limits of its distribution are unknown because of incomplete sampling. Illex oxygonius Roper, Lu & Mangold, 1969 occurs in the western Atlantic from New Jersey to Florida and in the Gulf of Mexico. Details of the distributions of these four species as well as their systematics are reported in Roper, Lu, and Mangold (1969) and in Lu (1973).

All four species of *Illex* are fished extensively in nearly all sections of their ranges and the combined annual catch is estimated to be around several hundred thousand metric tons, of which 80,000 tons of *I. illecebrosus* are caught in the Canadian Atlantic provinces (Amaratunga, et al., 1978, unpublished MS report) and 55,000 tons are taken off the Middle Atlantic

States of the U.S. (Tibbetts, 1977, unpublished MS report). Catches have risen sharply as the demand for squid has increased markedly during recent years.

In spite of the broad distribution of *Illex* species around nearly the entire continental margins of the Atlantic and of the significant fisheries these species support, very little is known about their biology. Especially lacking is information about the spawning habits and spawning sites, as well as the larvae and juveniles which were unknown until recently (Lu & Roper, in press). Without knowledge of the spawning sites and life histories of each species, it is impossible to make the predictions about the populations (fecundity, recruitment, size, mortality, age, and growth, etc.) that are necessary for the management and utilization of this important resource.

We present data gathered during two U.S. National Marine Fisheries Service programs that indicate the locations of spawning sites of *Illex illecebrosus*. The larvae and juveniles of *I. illecebrosus* (1.5–18 mm mantle length) are characterized for the first time, and they are compared with two other types of sympatric western North Atlantic ommastrephid larvae.

The larvae of ommastrephid squids are characterized by the fusion of the two tentacles, initially for their entire length, into an elongate, often robust, "proboscis" that bears a few minute suckers at the terminal disc, the precursors of the suckers on the clubs when the proboscis separates. Larvae bearing the tentacles fused into a proboscis are termed the Rhynchoteuthion stage, a general designation that carries no nomenclatorial status. Chun (1903) originally recognized the form and described it as *Rhynchoteuthis*, but Pfeffer (1908) pointed out that the name was preoccupied by a fossil form and suggested the non-generic term Rhynchoteuthion, a designation followed by most subsequent workers. Okutani (1965) briefly reviewed the history of the use of the term Rhynchoteuthion.

Materials and Methods

This report is based on the material collected by the MARMAP (Marine Monitoring Assessment and Predicting) Program of the National Marine Fisheries Service (NMFS) and by the biological portion of the NMFS Deepwater Dumpsite 106 Program that was conducted by the Smithsonian Institution.

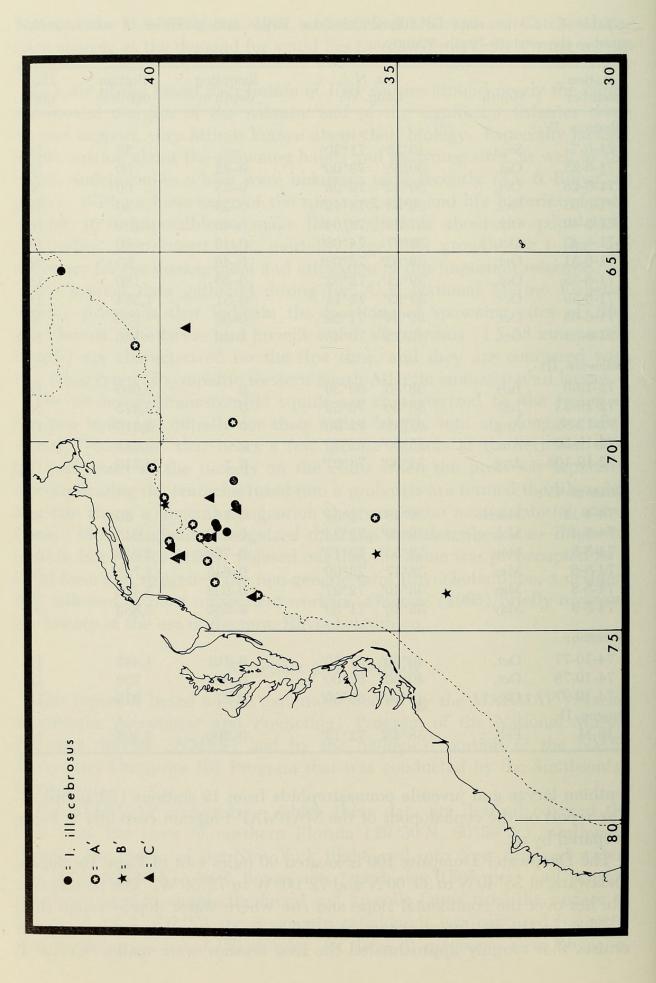
The MARMAP cruises from which these data are derived covered the area from the coast of northern Florida $(29^{\circ}30'N, 80^{\circ}59'W)$, northward through the region of the New York Bight, and into New England waters $(44^{\circ}00'N, 66^{\circ}30'W)$. Both Bongo nets (mesh size 0.505 mm) and neuston nets were used to sample the larval and juvenile fauna from the surface to 115 m. A total of 2,074 specimens of cephalopods was captured from 136 stations that consisted of 150 samples. Of these, 61 specimens were Rhyncho-

| Station | | Lat | . N./ | Sampling | Bottom | Day/ |
|----------------------------------|--------------|------------------|----------------------------|--------------|-----------|--------|
| umber | Month | Long. W. | | depth m | depth m | night |
| patross IV: | | | | | | |
| 71-6-7 | Sept. | 40°58′ | 71°30′ | _ | 55 | D |
| 71-6-25 | Oct. | 39°38′ | 73°00′ | 0-42 | 60 | N |
| 71-6-26 | Oct. | 39°42′ | 73°06′ | 0-25 | 60 | Ν |
| 71-6-33 | Oct. | 38°53′ | 73°42′ | 0-25 | 40 | D |
| 71-6-40 | Oct. | 37°59′ | 74°04′ | 0-46 | 130 | Ν |
| 71-6-43 | Oct. | 38°07′ | 74°06' | 0-46 | 80 | D |
| 71-6-51 | Oct. | 39°02′ | 73°09′ | 0-46 | 75 | Ν |
| 71-6-55 | Oct. | 39°11′ | 72°32′ | 0-56 | 180 | D |
| 71-6-59 | Oct. | 39°22′ | 72°14′ | 0-51 | 1,555 | D |
| 71-6-63 | Oct. | 39°54′ | 71°32′ | 0-53 | 230 | Ν |
| 71-6-68 | Oct. | 40°13′ | 70° 43′ | 0–46 | 130 | Ν |
| elaware II: | | | | | | |
| 72-19-9 | July | 38°30′ | 69°30′ | 0 | 3,660 | Ν |
| 72-19-25 | July | 38°30′ | 70°59′ | 0 | 3,475 | Ν |
| 72-19-88 | Aug. | 35°31′ | 72°00′ | 0 | 4,210 | D |
| 72-19-89 | Aug. | 35°30′ | 72°59′ | 0 | 3,845 | D |
| 72-19-106 | Aug. | 34°00′ | 74°01′ | 0 | 4,210 | D |
| batross IV: | | | | | | |
| 74-4-11 | March | 39°48′ | 72°51′ | 0-76 | 80 | Ν |
| 74-5-4 | May | 39°00′ | 72°34′ | 0-620 | 915 | N |
| 74-5-5 | May | 38°53′ | 72°17′ | 0-720 | 2,015 | N |
| 74-5-6 | May | 38°47′ | 72°00′ | 0-615 | 2,745 | Ν |
| 74-5-8 | May | 38°40′ | 72°27′ | 0-630 | 2,470 | Ν |
| 74-5-9 | May | 38°26′ | 71°50′ | 0–550 | 2,855 | Ν |
| ieczno: | | | | | | |
| 74-10-77 | Oct. | 40°30′ | 67°30′ | 0-101 | 1,465 | D |
| | | | | | 730 | D |
| | | | | | 915 | D |
| | | | | | | |
| 16-M | Feb. | 38°49′ | 72°13′ | 0-200 | 2,195 | Ν |
| 74-10-78 74-10-97 egon II: | Oct. Oct. | 40°30′ 42°00′ | 67°00′ 65°30′ 72°13′ | 0–85 0–87 | 730 91 | 0 5 |

Table 1. Station data for Rhynchoteuthion larvae and juveniles of ommastrephid squid in the western North Atlantic.

teuthion larvae and juvenile ommastrephids from 19 stations (22 samples). The report on the cephalopods of the MARMAP Program currently is being prepared by us.

The Deepwater Dumpsite 106 is located 90 miles east of Cape Henlopen, Delaware, at 38°40'N to 39°00'N and 72°00' W to 72°30'W. The rectangular site lies over the continental slope and rise where water depths range from 1,550 m in the northwest corner to 2,750 m in the southeast corner. Four cruises that roughly approximated the four seasons were made: Cruise 1,



1042

4

May, 1974 (Spring); Cruise 2, July-August, 1975 (Summer); Cruise 3, February, 1976 (Winter); Cruise 4, August-September, 1976 (Fall). Cruises 1 and 4 employed a non-closing net, a 10-foot Isaccs-Kidd midwater trawl (IKMT). All tows were made at night, and sampling depths ranged from 550-0 m to 790-0 m during Cruise 1 and from 675-0 m to 950-0 m during Cruise 4. Cruises 2 and 3 employed the closing-net technique with a discrete depth sampler on a 10-foot IKMT. A total of 111 stations, consisting of 390 samples, captured 342 specimens of cephalopods. Of these 12 were ommastrephid Rhynchoteuthion larvae and juveniles taken in six stations (six samples). Details of the sampling program and its results are presented in Lu & Roper (in press).

The station data for the Rhynchoteuthion larvae and the juveniles of ommastrephid squids reported here are presented in Table 1, and the distribution of specimens is plotted in Figure 1.

Results

A. *Rhynchoteuthion larvae.*—This study of cephalopods from the Deepwater Dumpsite and the MARMAP Program reveals that three types of Rhynchoteuthion larvae of the Ommastrephidae occur in the western North Atlantic. The larvae are categorized in the manner used by Sato (1973), Sato & Sawada (1974) and Yamamoto and Okutani (1975). Our designations of larval types are A', B', and C' to indicate the similarity between the Rhynchoteuthion stages in the western North Atlantic and in the western North Pacific, while at the same time they show that the species or species groups from the two areas are not identical.

The Rhynchoteuthion larvae that we found to occur in the northern waters of the western North Atlantic are listed in Table 2 and are characterized below.

1. Rhynchoteuthion Type A' (Figs. 2, 3): Rhynchoteuthion Type A' is characterized by having the 2 lateral suckers in the ring of 8 suckers on the tip of the proboscis greatly enlarged (Fig. 2b). The enlarged suckers are 2 to 3 times the diameter of the remaining 6 suckers. The length of the proboscis in relation to the length of the mantle (dorsal), called the tentacular index (Sato, 1973; Yamamoto and Okutani, 1975), is short to moderate (TI = 3.0–7.0, mean 4.51 ± 1.60 S.D., n = 10). A single, small reflective patch, possibly the anlage of a photophore, occurs on the ventral surface of each eye. A small, round, well-defined light organ is located near the anterior end of the intestine between the intestine and the ventral

Fig. 1. Locations of capture of Rhynchoteuthion larvae and juvenile Illex illecebrosus.

| Station number | Mantle length (ML) mm | $\begin{array}{c} \text{Tentacle Index} \\ \frac{\text{TL}}{\text{ML}} \times 10 \end{array}$ | |
|---------------------------|----------------------------|---|--|
| Туре С': | en galacio del Escolgan El | and it restored a state of the | |
| 74-4-11 | 1.50 | 2.5 | |
| 71-6-26 | 1.56 | 3.6 | |
| 74-4-11 | 1.67 | 4.0 | |
| 71-6-26 | 2.13 | 4.7 | |
| 71-6-43 | 2.19 | 6.3 | |
| 71-6-43 | 2.19 | 7.1 | |
| 71-6-25 | 2.63 | 3.6 | |
| 71-6-26 | 2.63 | 4.0 | |
| 71-6-43 | 2.69 | 3.3 | |
| 71-6-7 | 3.13 | 3.6 | |
| 74-5-9 | 3.13 | 5.2 | |
| 71-6-26 | 3.50 | 3.0 | |
| 74-5-4 | | 3.1 | |
| 74-10-78 | 4.69 | 3.3 | |
| | 4.69 | 0.0 | |
| Illex—Type C' Transition: | | | |
| 74-6-6 | 6.87 | 4.4 | |
| Illex illecebrosus: | | | |
| 74-10-97 | 6.87 | 2.5 | |
| 74-5-9 | 7.13 | 3.2 | |
| 0-II-16 | 7.75 | hough L'acific while a | |
| 72-19-25 | 8.25 | 4.8 | |
| 74-5-4 | 8.75 | 3.4 | |
| 74-6-6 | 10.63 | 4.0 | |
| 74-5-4 | 11.25 | 3.8 | |
| 74-5-8 | 12.13 | 2.3 | |
| 74-5-4 | 15.63 | 4.6 | |
| 74-5-4 | 17.50 | 3.9 | |
| Type A': | | | |
| 71-6-68 | 1.00 | 6.2 | |
| 71-6-59 | 1.04 | 3.6 | |
| 71-6-40 | 1.25 | 3.0 | |
| 71-6-33 | 1.46 | 3.4 | |
| 71-6-55 | 1.67 | 3.5 | |
| 71-6-63 | 1.67 | 3.8 | |
| 71-6-51 | 1.67 | 4.5 | |
| 74-4-11 | 2.04 | 3.1 | |
| 72-19-88 | 3.13 | 7.0 | |
| 72-19-9 | 3.13 | 7.0 | |
| 72-19-9 | 4.75 | - | |
| 72-19-9 | 7.25 | | |
| 74-10-77 | | _ | |
| | | | |

Table 2. Specimen data for Rhynchoteuthion larvae and juveniles of ommastrephid squid in the western North Atlantic.

| Station number | Mantle length (ML) mm | $\begin{array}{l} \text{Tentacle Index} \\ \frac{\text{TL}}{\text{ML}} \times 10 \end{array}$ | |
|-------------------|--------------------------|---|--|
| Type B': | | and the second se | |
| 72-19-89 | 2.06 | 10.3 | |
| 71-6-63 | 2.09 | 5.4 | |
| 72-19-89 | 2.19 | 7.7 | |
| 72-19-106 | 2.19 | 13.7 | |
| 72-19-106 | 2.81 | 9.6 | |
| 72-19-106 | 3.75 | 7.0 | |
| 72-19-106 | - | _ | |
| 72-19-106 | | | |

| Tab | le s | 2. (| Continued. | |
|-----|------|------|------------|--|
| | | | | |

surface of the liver (Fig. 3). The liver is short, transversely oblong, spherical in cross-section, and covered with reflective tissue.

The smaller specimens available (1.00-1.46 mm ML) (Fig. 2a) have the distinctive arrangement of suckers on the tip of the robust proboscis. The arms are very small; arms I & II are of equal length with fine, tendrilous tips and a single, mid-arm sucker each. Arms III are precursory buds only, while precursors of arms IV are not present. A few chromatophores occur on the mantle, fins, and head. The slightly stalked eyes are directed anterolaterally. Specimens of 1.67 mm ML have added 1-2 minute suckers to arms I & II; arms III have lengthened and developed 1-2 small suckers; the minute buds of arms IV are present. By the time specimens have reached 3 mm ML, arms IV are developing well, and a small, triangular slit has formed at the base of the proboscis, the beginning of the separation of the tentacles (Fig. 2c, d). The liver is spherical and is covered with reflective tissue. A single, small, round light organ occurs on the ventral surface of each eye. None of the smaller specimens show the emergence of the light organs on the liver/intestine, because both the photophores and the structures on which they lie are very easily damaged during capture. However, both types of photophores are distinctive and well-developed at 4.75 mm ML (Figs. 2e, 3).

The Rhynchoteuthion Type A' larva becomes a juvenile when the proboscis splits along the longitudinal axis and the tentacles separate. This occurs at about 4–5 mm ML.

Eleven specimens of Rhynchoteuthion Type A' (1.0-3.1 mm ML; one with head only) and 2 juveniles (4.8 and 7.3 mm ML) in which the tentacles have just separated were captured from the New York Bight south to the latitude of Cape Hatteras over bottom depths of 50–4,100 m. Eight specimens were captured in October in separate stations in the upper 101 m, 4 during the day and 3 at night. Four specimens, including the 2 juveniles,

1046

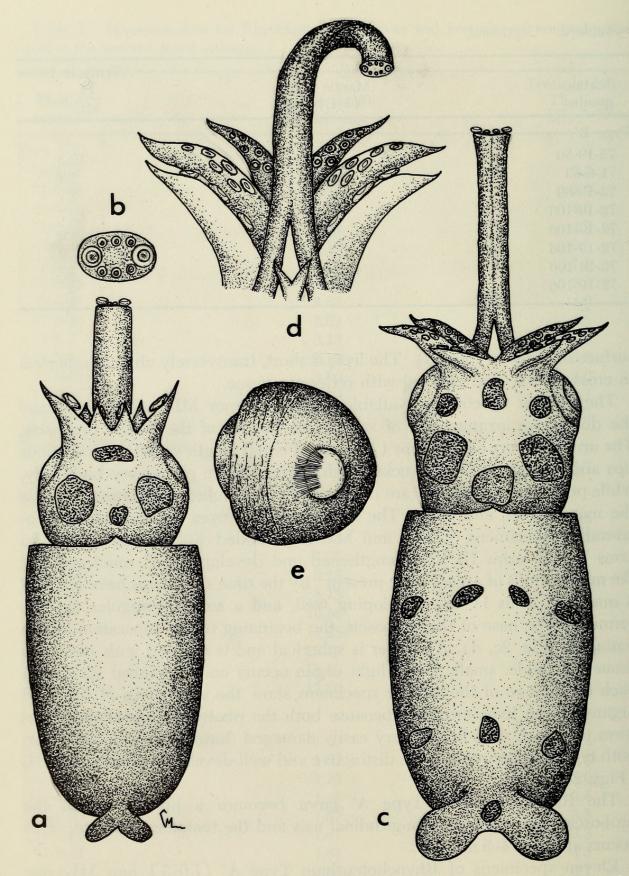


Fig. 2. Rhynchoteuthion Type A'. a, Dorsal view, 1.25 mm ML (Sta. 71-6-40); b, Suckers on tip of proboscis of a; c, Dorsal view, 3.13 mm ML (Sta. 72-19-88); d, Arm crown of c, ventral view; e, Photophore on eye, ventral view, 4.75 mm ML (Sta. 72-19-9).

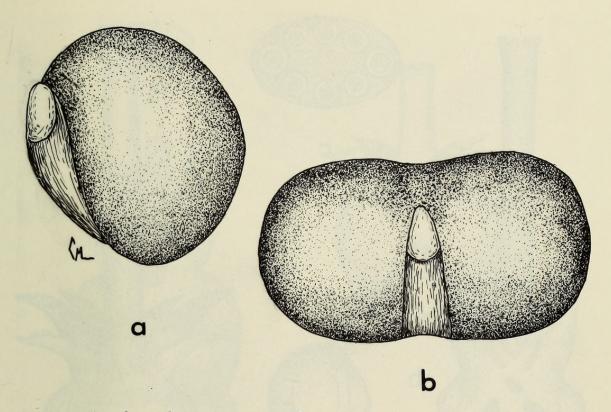


Fig. 3. Rhynchoteuthion Type A'. a, Photophore on liver, lateral view, 4.75 mm ML (Sta. 72-19-9); b, Ventral view of photophore, ink sac and liver of a.

were caught in July/August at the surface during both day and night. A single specimen was taken in March at night at 0–76 m.

2. Rhynchoteuthion Type B' (Fig. 4): Rhynchoteuthion Type B' is characterized by having the two lateral suckers on the tip of the proboscis slightly larger than the remaining six suckers, and in no case do they reach twice the diameter of the small suckers (Fig. 4c). The proboscis is very thin and narrow and it is moderately long to very long (Fig. 4a, b). The tentacular index ranges from 5.4–13.7 (mean 8.95 ± 2.92 S.D., n = 6). A single, relatively large, round, raised photophore occurs on the ventral surface of each eye (Fig. 4d). This photophore is easily dislodged and often is missing, but a circular bare patch of tissue, surrounded by reflective epithelium, may remain on the eye. A distinct, round photophore is present between the intestine and the liver on specimens from a MARMAP series well south of the Deepwater Dumpsite and northern MARMAP area (Fig. 4e). The liver appears to be quite delicate in larvae, and it and the photophore are damaged or missing in all specimens from the area of the present study. As only Rhynchoteuthion stage specimens are present in the collections (2.1-3.8 mm ML), the size at separation of tentacles is unknown.

At a size of 2.1–2.3 mm ML the proboscis is long and slender, and arms I, II, and III are well-developed; arms I are the shortest, while arms II and III are equal in length. Arms IV are precursory buds only. The round, raised

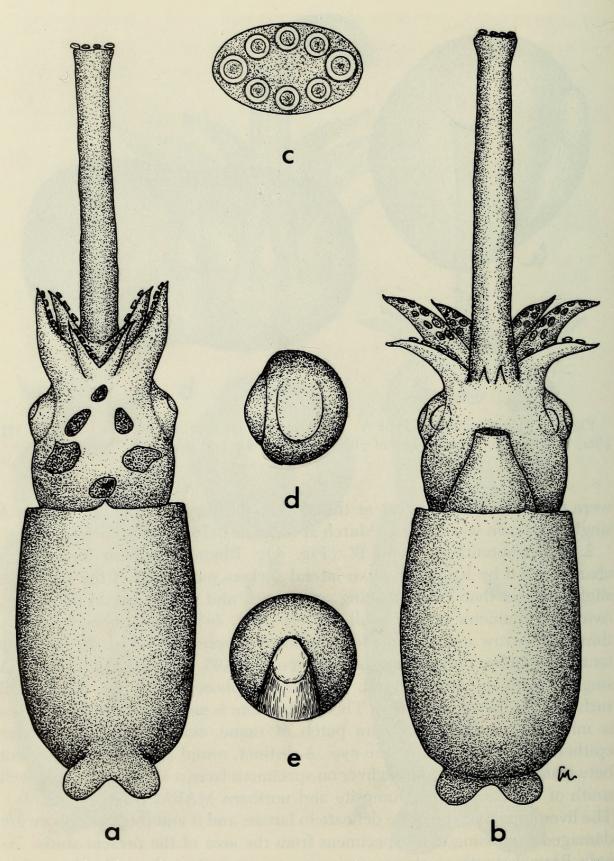


Fig. 4. Rhynchoteuthion Type B'. Composite of 2.09–2.29 mm ML (Sta. 72-6-55). a, Dorsal view; b, Ventral view; c, Suckers on tip of proboscis; d, Eye with ventral photophore; e, Photophore on ventral surface of liver.

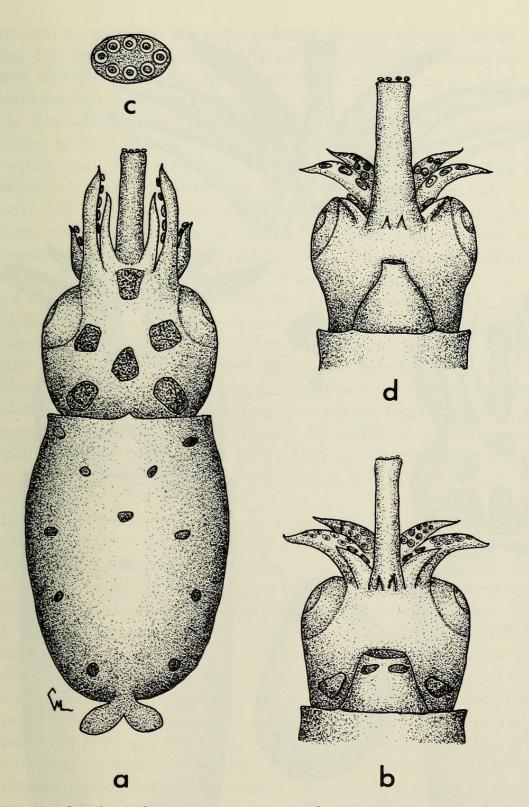
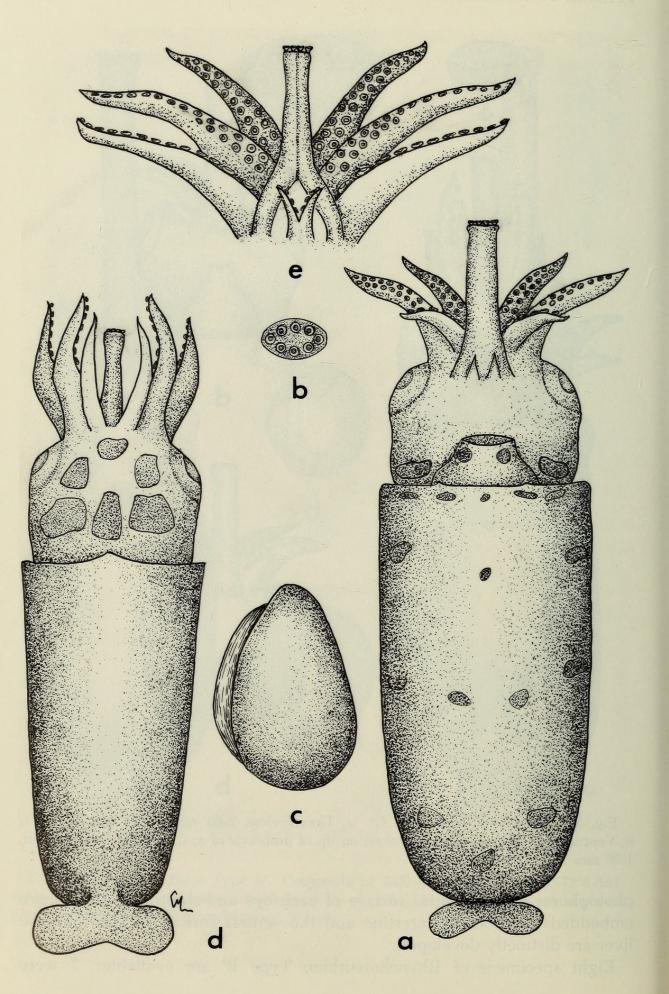


Fig. 5. Rhynchoteuthion Type C'. a, Dorsal view, 2.63 mm ML (Sta. 71-6-26); b, Ventral view of head of a; c, Suckers on tip of proboscis of a; d, Ventral view of head, 1.56 mm ML (Sta. 71-6-26).

photophores on the ventral surface of each eye and the round photophore embedded between the intestine and the ventral surface of the spherical liver are distinctly developed.

Eight specimens of Rhynchoteuthion Type B' are available: 7 were



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captured in August at the surface during the day in Gulf Stream water off Cape Hatteras over bottom depths of 4,000–4,700 m; 1 specimen was captured in October in the New York Bight at 0–53 m at night over the continental slope in water 500–800 m deep.

3. Rhynchoteuthion Type C' (Figs. 5, 6, 7): The Rhynchoteuthion Type C' larva is characterized by having all 8 suckers on the tip of the proboscis of equal, small, size; the 2 lateral suckers are never enlarged (Fig. 5c). The proboscis is relatively short and robust with a tentacular index of 2.5–7.1 (mean 4.09 ± 1.31 S.D., n = 14). Neither photophores nor anlagen of photophores occur on the eyes or on the liver. The bulbous liver is slightly elongate, pear-shaped, narrower anteriorly (Fig. 6c); it is tilted at an angle with the posterior end dorsal and the anterior end ventral.

In the smaller specimens available (1.5-1.6 mm ML) (Fig. 5d) arms I and II are about equally developed with 4-5 small suckers, but arm I is somewhat shorter. Arms III are very small and bear 2-3 small suckers, while arms IV are represented by minute precursory buds. The stout proboscis is nearly twice as long as arm *II* and bears 8 equally sized small suckers. Six large chromatophores occur on the head, and the mantle has a number of smaller chromatophores. By a ML of 3.1 mm, arms IV are slightly elongate papillae and by 4.7 they are developing rapidly. At this size arms III have caught up with arms I and II, and all are about the same length (Fig. 6d, e).

In Rhynchoteuthion C' of about 4.7 mm ML a small, triangular opening begins to form at the base of the proboscis and a shallow, longitudinal groove, the "splitting groove," forms along the proboscis (Fig. 6e). With growth, the triangular hole enlarges between the bases of the tentacles, the proboscis is distinctly Y-shaped, and the splitting groove deepens. By 6.9 mm ML in some specimens the proboscis has split along the splitting groove nearly to the area of the club, while the tip of the proboscis has bifurcated and the incipient dactyli begin to elongate (Fig. 7b). The circlet of 8 equalsized suckers remains intact, while minute buds of the dactylus suckers appear. The actual changeover from Rhynchoteuthion to juvenile occurs between 6 and 8 mm ML (Fig. 7a, b). All specimens less than 6 mm ML are Rhynchoteuthion and all those greater than 8 mm ML are juveniles.

Fourteen Rhynchoteuthion Type C' larvae were taken in an area that extends from the southern New York Bight $(38^{\circ}N)$ to the southern edge of Georges Bank $(41^{\circ}N)$ in water with bottom depths of 50–2,300 m. All

Fig. 6. Rhynchoteuthion Type C'. a, Ventral view, 3.13 mm ML (Sta. 71-6-7); b, Suckers on tip of proboscis of a; c, Liver and ink sac of a, lateral view; d, Dorsal view, 4.69 mm ML (Sta. 74-10-78); e, Arm crown of d, ventral view.

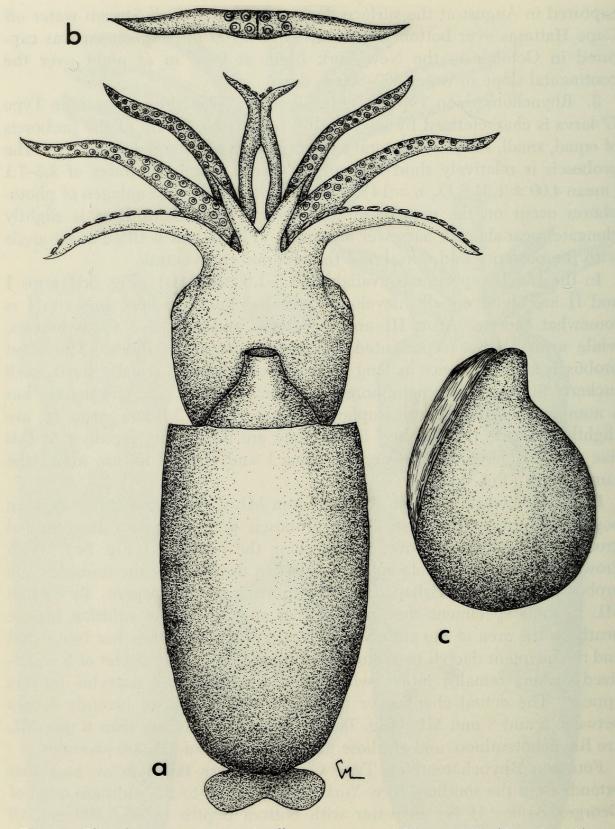


Fig. 7. Rhynchoteuthion Type C'/Illex Transition, 6.87 mm ML (Sta. 74-6-6). a, Ventral view; m, Bifurcated tip of proboscis, anterior view; c, Liver and ink sac, lateral view.

1052

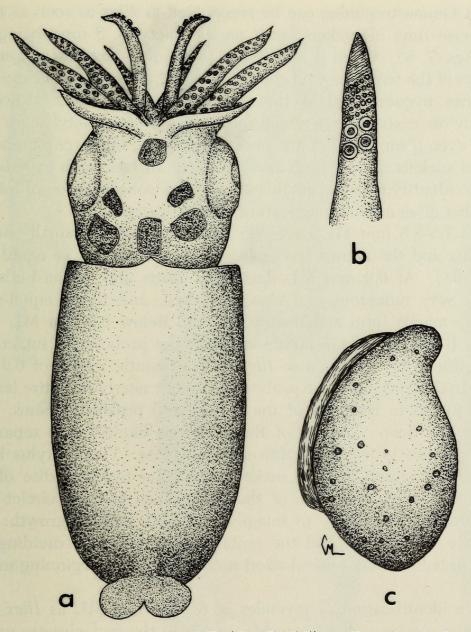


Fig. 8. Illex juvenile, 7.5 mm ML (Sta. 74-5-5). a, Dorsal view; b, Right tentacular club; c, Liver and ink sac, lateral view.

captures were in open nets that fished at the surface and as deep as 720-0 m, but presumably all Rhynchoteuthion Type C' larvae actually were captured close to the surface. Captures were made both day and night and occurred during February, March, May, July, September, and October.

B. Juveniles of Illex illecebrosus (Figs. 7, 8, 9).—During studies on the Deepwater Dumpsite material we identified several juvenile specimens as Illex illecebrosus (Lu & Roper, in press). Additional specimens were discovered in the MARMAP collections. Specimens ranged from 6.9–17.5 mm ML, significantly smaller than the previously known smallest specimen of 68 mm ML (Verrill, 1881).

Juveniles of Ommastrephidae can be recognized as *Illex* as soon as more than 4 transverse rows of suckers occur on the dactylus, 8 rows being the maximum (Figs. 7, 8). Often it is difficult to see the dactylus suckers on the minute tips of the tentacles well enough to count the rows, or, in the case of smallest forms, to count the buds that are precursors to suckers. However, *Illex* is the only ommastrephid in which the suckers on the dactylus are very numerous, so even if an actual count can not be made, the large number of closely-packed suckers and/or buds is diagnostic. In fact, with experience, it is possible to identify the smallest juveniles by the concentration of minute sucker-buds that gives a pebbly appearance to the dactylus.

Juveniles of 7.5-8.8 mm ML have 5-8 transverse rows of small suckers on the dactylus and the manus has at least 4 larger suckers of equal size (Figs. 8a, b, 9a). At 6.9 mm ML dactylus suckers and sucker-buds are recognized as very numerous and closely packed, and the 4 equal-sized suckers on the manus form a diamond pattern. Below 6.9 mm ML most specimens are Rhynchoteuthion larvae in which the proboscis is intact, but we have identified one specimen as Illex with a mantle length of 6.9 mm (Fig. 7a, b). In this specimen, the proboscis has split nearly its entire length, but it is still joined in the area of the carpus and proximal manus. The splitting groove is deep. The tip of the proboscis likewise has separated and the dactyli have grown long, thin and attenuate. The dactylus bears numerous, minute, closely-packed sucker-buds. The terminal disc of the proboscis joins together the bases of the dactyli and bears a circlet of 8 equal-sized suckers. It is easy to imagine the next step in growth: the splitting groove will deepen and the tentacles will separate, dividing the terminal disc in half so that 4 equal-sized suckers form the beginning manus of the club.

The positive identification of juveniles of 6.9-8.8 mm ML as *Illex*, and especially of the specimen of 6.9 mm ML in which the tentacles are undergoing their final separation from the Rhynchoteuthion proboscis, has made it possible to connect juvenile *Illex* with the Rhynchoteuthion Type C' larval stage.

Juveniles of 17.5 mm ML (Fig. 9b) have well developed tentacular clubs with several transverse rows of 4 suckers on the manus; transverse rows of 8 suckers occur on the proximal end of the dactylus, while the distal end is covered with papilla-like precursors to suckers (Fig. 9c).

Twelve specimens of juvenile *Illex* were caught in the same region as Rhynchoteuthion Type C', that is, from the southern New York Bight to the southern Georges Bank. Specimens were caught day and night at or (presumably) near the surface in waters where the depth ranged from 1,500–3,000 m. No juveniles were captured in water with bottom depths shallower than 1,500 m, while Rhynchoteuthion Type C' larvae were caught in water where bottom depths are as shallow as 55 m.

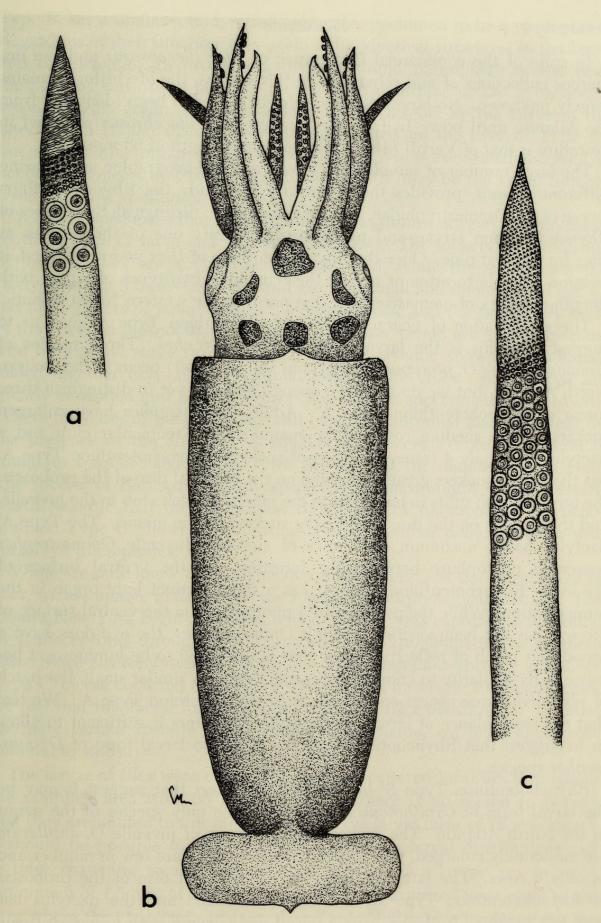


Fig. 9. Illex juvenile. a, Left tentacular club, 8.75 mm ML (Sta. 74-5-4); b, Dorsal view, 17.5 mm ML (Sta. 74-5-4); c, Right tentacular club of b.

Discussion

In spite of the commercial importance of *Illex illecebrosus* and the numerous collections of and references to this species, the life history remains largely unknown. No larva of any species of *Illex* had been identified from the Atlantic until now. In fact, the smallest *Illex illecebrosus* recorded in literature is that of Verrill (1881) with a mantle length of 68 mm.

The large number of samples taken over a broad geographic area, during different seasons, provides the opportunity to study the Rhynchoteuthion larvae of the Ommastrephidae. We now are able to distinguish three types of Rhynchoteuthion larvae and to positively identify one of these types as *Illex* for the first time. Once the Rhynchoteuthion of *Illex* was recognized, it became possible to attempt to link the remaining two types of larvae with the other genera of ommastrephids that occur in the western North Atlantic.

The combination of characters of Rhynchoteuthion Type A' lead us to suggest that this is the larval form of Ommastrephes. Three species of Ommastrephes (O. pteropus, O. bartrami and O. caroli) occur in the western North Atlantic, but we do not have enough material yet to distinguish three forms of Rhynchoteuthion Type A'. Adult Ommastrephes have enlarged suckers on the median rows of the manus of the tentacular club and a dactylus with only 4 transverse rows of suckers. Rhynchoteuthion Type A' has the lateral suckers greatly enlarged on the terminal disc of the proboscis; the terminal disc splits in half to form the manus of each club in the juvenile, and the suckers on the disc become the suckers on the manus. The Type A' dactylus has a maximum of 4 rows of suckers. Juvenile Ommastrephes possess a photophore between the intestine and the ventral surface of the liver. Rhynchoteuthion Type A' has a small distinct light organ in the same position. While the presence of a photophore on the ventral surface of the eye has not been verified in adult Ommastrephes, the eye does have a broad, flat patch of reflective tissue that is suspected to be luminescent because of its similarity to known photogenic tissue. A similar small, flat patch of reflective tissue occurs on the eye of Rhynchoteuthion Type A'. We feel that the resemblance of larval and juvenile characters is sufficient to allow us to suggest that Rhynchoteuthion Type A' is the larval form of Ommastrephes species.

Rhynchoteuthion Type B' has several characters that suggest it may be the larval form of *Ornithoteuthis antillarum*, the only species of the genus in the North Atlantic. The suckers on the manus of juvenile *O. antillarum* are moderately enlarged, while those on the dactylus are few in number and in only 4 rows. The lateral suckers on the terminal disc of the proboscis of Rhynchoteuthion Type B' are slightly enlarged and the dactylus has very few suckers. Juveniles have a raised pad covered with reflective tissue on the ventral surface of each eye, very reminiscent of a photophore, while Type B' has a similar round, raised organ also presumed to be a photophore. Regardless of their function, they seem to be identical structures in the larva and the juvenile. In juveniles a distinct, round photophore occurs near the anterior end of the intestine on the ventral surface of the liver, and a second smaller organ occurs posteriorly on the ink sac by the curve in the intestine. A similar distinct anterior organ exists on the liver of Type B', but no posterior organ has been found yet. While additional material is needed, it appears that Rhynchoteuthion Type B' may be the larval form of *Ornithoteuthis antillarum*.

We have specimens that show the direct transition between the Rhynchoteuthion Type C' larva and the juvenile of *Illex*. The suckers on the manus of juvenile *Illex* are not appreciably enlarged, while the suckers on the dactylus are in 8 transverse rows and are very small and numerous. Type C' has all 8 suckers of equal size on the terminal disc and the precursory buds of the dactylus suckers that emerge in more than 4 rows are very numerous. The transitional stage from Type C' to *Illex* juvenile shows the tentacles joined together only at the proximal ends of the clubs. The dactyli are greatly elongated and bear 5–8 rows of numerous suckers and sucker-buds. Where the bases of the dactyli are still fused, the terminal disc is evident by the presence of the circlet of 8 equal-sized suckers. When separation is complete 4 equal-sized suckers form the basis of the manus of each club. The species of *Illex* are the only species of ommastrephids in the western North Atlantic that do not possess some type of photophore. Rhynchoteuthion Type C' shows no indication of having either photophores or precursors of photophores.

While we now know that Rhynchoteuthion Type C' is the larval stage of *Illex*, we are unable to determine the species on morphological grounds. The greater New York Bight area from which Type C' was captured is inhabited by *I. illecebrosus* throughout the area and by *I. oxygonius* in the southern part. Since *I. illecebrosus* is by far the more abundant species, and since Type C' larvae occurred throughout the area and into New England waters, we feel that this larval form probably is that of *Illex illecebrosus*. In order for more certain specific identifications to be made, we must have more material to study.

The larvae of *Illex* were captured at widely scattered localities throughout the sampling area from $38^{\circ}N$ to $42^{\circ}N$, but there is no reason to believe that they are limited to this area. Now that the larval form of *Illex* is known it should be possible to more precisely determine larval distributions and to infer spawning areas. Because some of the *Illex* larvae are so small (minimum of 1.5 mm ML) they must have been captured very close to the sites where they hatched. In fact, the samples indicate a tendency for the Rhynchoteuthion Type C' larvae (1.5–3.5 mm ML) to occur in near-shore

waters over the continental shelf (50-80 m bottom depth), while the juveniles (7-17.5 mm ML) tend to occur over the continental slope and rise (1,500-3,000 m bottom depth). A larger sample is required before this observation can be verified, but we suggest that spawning and hatching occur along the outer half and to the edge of the continental shelf (shelf-break) off the mid-Atlantic states and New England, and probably to the north and south of this area, as well. After hatching the larvae ascend to the near-surface shelf waters, are transported seaward, and occur as juveniles in slope water and Gulf Stream water. This pattern is consistent with the general pattern of water circulation, whereby an inshore drift of bottom water occurs across the shelf, while the surface water moves offshore and mixes with slope water (review in Warsh, 1975).

The spawning season apparently extends over much of the year, as the smaller larvae (1.5–3 mm ML) have been taken in March, May, September and October and the smaller juveniles (7–8 mm ML) were taken in February, May and October.

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