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CONTENTS

Introduction 1

Materials and methods 2

Species accounts 4
- Family Sepiolidae 5
  - *Semirossia tenera* 5
  - *Stoloteuthis leucoptera* 7
- Family Loliginidae 7
  - *Loligo pealeii* 7
  - *Lolliguncula brevis* 9
- Family Lycoteuthidae 10
  - *Selenoteuthis scintillans* 10
- Family Enoploteuthidae 10
  - *Abralia cf. veranyi* 10
  - *Abraliopsis cf. pfefferi* 12
- Family Ancistrocheiridae 14
  - *Ancistrocheirus lesueurii* 14
- Family Pyroteuthidae 15
  - *Pyroteuthis margaritifera* 15
  - *Pterygioteuthis* sp. 17
- Family Octopoteuthidae 19
  - *Octopoteuthis* sp. 19
- Family Onychoteuthidae 22
  - *Onychoteuthis cf. banksii* 22
  - *Onykia carriboea* 25
- Family Gonatidae 25
  - *Gonatus fabricii* 25
- Family Histioteuthidae 26
  - *Histioteuthis* spp. 26
- Family Bathyteuthidae 29
  - *Bathyteuthis abyssicola* 29
- Family Chtenopterygidae 30
  - *Chtenopteryx sicula* 30
- Family Brachioteuthidae 30
  - *Brachioteuthis* sp. 30
- Family Ommastrephidae 30
  - *Illex* sp. 30
  - Rhynchoteuthion Type A′ 33
  - Rhynchoteuthion Type B′ (revised) 33
- Family Chiroteuthidae 34
  - *Chiroteuthis* sp. 34
- Family Mastigoteuthidae 34
  - *Mastigoteuthis hjorti* 34
- Family Cranchiidae 36
  - *Leachia lemur* 36
  - *Teuthowenia megalops* 37
  - *Heliococranchia* cf. *papillata* 39
  - Other Cranchiidae 39

CONTENTS (continued)

Family Octopodidae 39
Octopodid spp. 39
Family Tremoctopodidae 40
Tremoctopus violaceus 40
Family Argonautidae 40
Argonauta argo/Argonauta hians 40

Distributional patterns 43

Acknowledgments 50

Literature cited 51

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Abstract—Paralarval and juvenile cephalopods collected in plankton samples on 21 western North Atlantic cruises were identified and enumerated. The 3731 specimens were assigned to 44 generic and specific taxa. This paper describes their spatial and temporal distributions and their developmental morphology. The smallest paralarvae recognized for a number of species are identified and illustrated. The two most abundant and most frequently collected taxa were identifiable to species based on known systematic characters of young, as well as on distribution of the adults. These were the neritic squids *Loligo pealeii* and *Illex illecebrosus* collected north of Cape Hatteras, both valuable fishery resources. Other abundant taxa included two morphotypes of ommastrephids, at least five species of enoploteuthids, two species of onychoteuthids, and unidentified octopods. Most taxa were distributed widely both in time and in space, although some seasonal and mesoscale-spatial patterns were indicated. The taxa that appeared to have distinct seasonal distribution included most of the neritic species and, surprisingly, the young of the bathypelagic cranchiids. In eight seasonal cruises over the continental shelf of the middle U.S. Atlantic states, neritic taxa demonstrated approximately the same seasonal patterns during two consecutive years. Interannual differences in the oceanic taxa collected on the shelf were extreme. The highest abundance and diversity of planktonic cephalopods in the oceanic samples were consistently found in the vicinity of the Gulf Stream. Only eight of the oceanic taxa appeared to have limited areal distributions, compared with twelve taxa that were found throughout the western North Atlantic regions sampled in this study. Many taxa, however, were not collected frequently enough to describe seasonal or spatial patterns. Comparisons with published accounts of other cephalopod surveys indicate both strengths and weaknesses in various sampling techniques for capturing the young of oceanic cephalopods. Enoploteuthids were abundant both in our study and in other studies using midwater trawls in several areas of the North Atlantic. Thus, this family probably is adequately sampled over its developmental range. In contrast, octopoteuthids and chtenopterygiids are rare in collections made by small to medium-sized midwater trawls but are comparatively common in plankton samples. For families that are relatively common in plankton samples, paralarval abundance, derived similarly to the familiar ichthyoplankton surveys of fisheries science, may be the most reliable method of gathering data on distribution and abundance.

Introduction

The value of life-history studies exceeds the knowledge gained on the individual species studied. While primary goals may include answering limited questions about the reproduction or population dynamics of a particular species, ultimately such studies should be directed toward distinguishing general patterns with which we can understand the organisms in their ecosystems. Vecchione (1986) and Sweeney et al. (1992) reviewed studies on the early life histories of cephalopods. Although these authors could draw some generalizations from the diverse literature on the subject, some major deficiencies were observed. Important among the deficiencies pointed out were taxonomic problems and contradictory statements on seasonal and geographical distributional patterns.

We have examined cephalopods collected during several major zooplankton and ichthyoplankton projects in the western North Atlantic Ocean. This study is not an analysis of detailed distribution of individual species, but rather it presents large-scale distribution patterns made possible by the broad diversity of projects and cruises. Additional, specific details are provided in the references cited. Our objectives in this study were as follows:

1) To assign each morphological type to the lowest possible taxonomic category.
2) To determine the spatial and temporal patterns of distribution and relative abundance of these taxa. Seasonal distributions need to be determined so that inferences can be made about spawning seasonality. Determination of large-scale and meso-scale geographical distributions enables us to discuss possible causes for the observed patterns.
3) To address several species-specific hypotheses that have been pro-

posed in the literature, as presented in the individual species accounts.
4) To describe developmental morphology and provide illustrations of taxonomic voucher specimens for poorly known or previously undescribed paralarvae.

Materials and methods

This study includes cephalopods and associated data collected during several projects with diverse goals:

1) The National Marine Fisheries Service's (NMFS) Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, a fisheries study of the Northwest Atlantic Fisheries Management Zone of the United States;
2) A multidisciplinary baseline study of the continental shelf in the middle U.S. Atlantic states, funded by the Bureau of Land Management (BLM) and conducted by the Virginia Institute of Marine Science (VIMS);
3) A study of the continental slope and rise in the vicinity of Norfolk Canyon by VIMS, funded by the National Science Foundation (NSF);
4) A VIMS study of the zooplankton of the lower Chesapeake Bay, funded by the Commonwealth of Virginia to determine long-term changes in the zooplankton of the Bay; and
5) Several oceanic cruises to the tropical western North Atlantic, the area between the middle U.S. Atlantic states and Bermuda, and to the area from Delaware Bay to the Scotian Shelf.

Areas covered

The areas covered by all sampling programs are shown in Fig. 1.

The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program The zooplankton and ichthyoplankton of the Gulf of Maine, Georges Bank, southern New England, and the middle U.S. Atlantic states were surveyed by the National Marine Fisheries Service Northeast Fisheries Science Center (NEFSC) periodically from 1961–1993 (Sherman et al., 1998). The primary sampling gear was 61-cm bongo frames rigged with 505-µm and 333-µm mesh nets. This gear was used for oblique subsurface sampling of the entire water column. A neuston sampler with 947-µm mesh netting was used at selected stations to sample the surface layer, as well.

We have obtained 2087 cephalopod specimens from four MARMAP cruises over the continental shelf of the area described above: R/V *Albatross* cruise 7106, R/V *Albatross* cruise 7308, R/V *Delaware* cruise 7219, R/V *Wieczno* cruise 7410. One of these cruises, R/V *Delaware* cruise 7219 (DEL7219), also sampled the continental shelf of the southern U.S. Atlantic states. We understand that some of the MARMAP material was sent to the Polish Oceanographic Sorting Center and a portion might not have been returned for all cruises. Therefore, in the absence of precise records, it is not clear for which of the cruises the data might be incomplete. This wealth of specimens has been relied upon primarily for the systematic descriptions of life history stages and the illustrations that we present here. The data on presence of taxa, in spite of any gaps, also have been used in the distributional and seasonal analyses.

The Bureau of Land Management (BLM) study This two-year study began in the autumn of 1975 and was based on four quarterly cruises per year (Vecchione and Grant, 1983). During the first year of the study, six 24-hour stations were occupied on a cross-shelf transect off Atlantic City, New Jersey, that extended from shallow inshore waters to the shelf break at about 200 m depth. Surface collections were made at each of these stations every three hours with a neuston frame rigged with a one meter 505-µm mesh net that sampled approximately the top 12 cm of the sea surface. Double-oblique subsurface tows (from 1 m below the surface to the bottom and back to 1 m to exclude the surface layer) were made at night with 60-cm opening-closing bongo systems rigged with 202-µm and 505-µm mesh nets. During the second year, two stations to the north of Atlantic City and a second transect of four stations off Wachapreague, Virginia, were added. Although sampling intensity varied among stations during the second year (Vecchione and Grant, 1983), nine of the twelve stations were occupied for 24 hours on each cruise, comparable to those of the first year. In addition, four replicate subsurface tows were collected at three stations on each cruise during the second year. Volumes of water filtered for each sample were calculated based on flowmeter readings. Surface temperature and salinity were measured concurrently with all surface samples.

We have examined all 831 cephalopods collected in the 726 samples from the eight cruises of this program. Because we are confident of this data set's completeness, these data are central to our analyses of variability in distribution and abundance. Presence of taxa in the other data sets discussed below, for which we have less complete data, are used to supplement the BLM data to extend seasonal information and geographic ranges.

Continental slope and rise VIMS conducted cruises to the vicinity of Norfolk Canyon in September 1975 and January 1976 to study demersal fish communities in that area (Middleton and Musick, 1986). Zooplankton was collected on these cruises at stations randomly

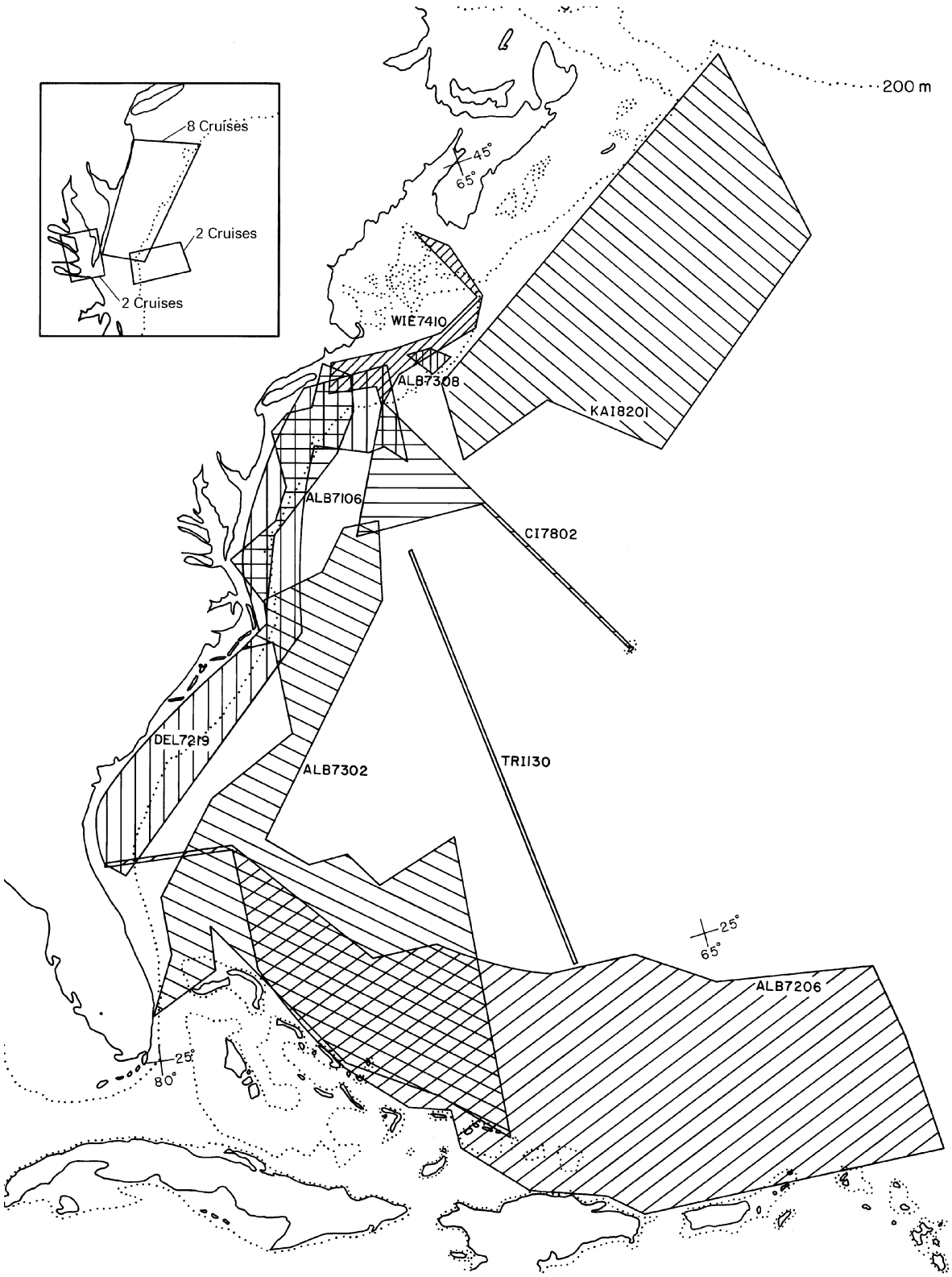

Figure 1

Location of 21 cruises (9 plotted on map, 12 in box) along western North Atlantic Ocean from which paralarval cephalopods were studied.

selected from strata based on bottom depth. Subsurface collections were made at each station by an oblique tow of a 60-cm diameter bongo frame rigged with 202-µm and 333-µm mesh nets, and a surface sample was collected with a 1-m neuston frame rigged with a 202-µm mesh net. Volumes of water filtered for subsurface samples were monitored as described above, as were surface temperature and salinity.

Chesapeake Bay Cruises were conducted by VIMS during March and August 1978 as part of the Lower Bay Zooplankton Monitoring Program (LBZMP). These sampling months were selected based on previous determinations of peaks in zooplankton abundances in the lower Chesapeake Bay, with a winter-spring zooplankton community peak in March and a summer-fall community peak in August (Grant and Olney, 1979). Each cruise sampled ten daytime and ten nighttime stations selected at random from a grid of several hundred possible stations. Each station consisted of a surface tow with a 505-µm mesh neuston net and an oblique subsurface tow with a 61 cm diameter bongo sampler rigged with 333-µm and 202-µm mesh nets. Volumes of water filtered were estimated with flowmeter values for all samples, and surface temperature and salinity were recorded. Sixty-three cephalopods were collected in 80 samples.

Oceanic cruises R/V *Albatross IV* Cruise 7206 (ALB 7206) was a survey of the tropical western North Atlantic between the Lesser Antilles and Cape Canaveral, Florida. Sampling was conducted by NMFS during July and August 1972 with a 60-cm diameter 505-µm mesh bongo net and a neuston net, presumably with 947-µm mesh. We have 458 planktonic cephalopod specimens from this cruise.

R/V *Albatross IV* Cruise 7302 (ALB7302) employed bongo and neuston nets (the same as those described for ALB7206) to survey the southern Sargasso Sea between the Bahamas and Cape Hatteras. Because this cruise was conducted by NMFS during February 1973 and overlapped the area sampled by the summer cruise (ALB7206) described above, seasonal comparisons are possible for the southern Sargasso Sea. We have 164 cephalopods that were collected on ALB7302.

R/V *Trident* Cruise 130 (TRI130) was a transect of six 60-cm diameter bongo net (mesh size=505 µm) stations between the middle U.S. Atlantic states and the southern Sargasso Sea. This cruise, which was conducted in January 1973, collected 29 specimens.

R/V *Columbus Iselin* Cruise 7802 (CI7802) was a deep-sea trawling cruise from Bermuda to Rhode Island to the Caryn Seamount to Norfolk, Virginia. It was conducted by VIMS during February and March 1978. Zooplankton samples collected on this cruise included several subsurface tows with a modified Tucker trawl rigged with a one-meter, 505-µm mesh net, and 19 surface collections made with a one-meter, 505-µm mesh neuston net. Volumes of water filtered were monitored by flowmeter, and surface temperature and salinity were measured concurrently with surface collections. Twenty-nine cephalopod specimens were collected in the plankton samples on this cruise.

R/V *Kaiyo-Maru* Cruise 8201 (KAI8201) was conducted during January and February 1982 in waters of greater than 1000 m depth offshore between Delaware Bay and the Scotian Shelf. The objective of this cruise, which was a joint operation by the governments of Japan, Canada, and the United States, was to study the ecology of the squid *Illex illecebrosus* (Vecchione and Roper, 1986). Sixty-three oblique tows were made between 0 and 200 m depth with a 61-cm bongo frame rigged with 505-µm mesh nets on both sides. Flowmeters were used to estimate volume of water filtered for each sample. Additional oblique samples between 0 and 1000 m depth were obtained at night with a 3-m rectangular midwater trawl which had dual 5.6 mm mesh cod ends. Physical data collected included vertical profiles of temperature, salinity, and dissolved oxygen. Because the samples were divided arbitrarily among the sponsoring nations, the 70 specimens we have are an unrecorded proportion of the planktonic cephalopods collected.

All samples were fixed in buffered formalin solution, following standard plankton preservation procedures. The cephalopod paralarvae were preserved in 50% isopropyl alcohol following initial sorting from the original plankton samples.

Species accounts

The 3731 specimens collected on the 21 cruises were identified to 44 taxa (Table 1). In the presentation that follows, we describe the distribution of those taxa for which we feel the data are adequate (e.g., a sufficient number of specimens, with a range of sizes, that are in adequate condition to represent a developmental sequence and to enable inferences about distribution). We also present descriptions of taxa for which the early stages are rare in plankton collections or have not been adequately described previously. We describe as many sizes as possible within a given species or taxon, with particular emphasis on the smallest specimens available. Descriptions are presented in ascending-size order. In general, descriptions are most detailed for smaller sizes, with descriptions for larger specimens emphasizing newly developed characteristics, advances in development of earlier-formed characters, or changes in character states.

Table 1

Taxa represented in this study; 44 taxa, 3731 specimens. Classification follows that of Sweeney and Roper (1998).

Class Cephalopoda Cuvier, 1797
- Subclass Coleoidea Bather, 1888
  - Order Spirulida Stolley, 1919
    - Family Spirulidae Owen, 1836
      - ?*Spirula spirula* (Linnaeus, 1758)
  - Order Sepiolida Fioroni, 1981
    - Family Sepiolidae Leach, 1817
      - *Semirossia tenera* (Verrill, 1880)
      - *Stoloteuthis leucoptera* (Verrill, 1878)
  - Order Teuthida Naef, 1916
    - Suborder Myopsina Orbigny, 1841
      - Family Loliginidae Lesueur, 1821
        - *Loligo* sp.
        - *Loligo pealeii Lesueur, 1*821
        - *Lolliguncula brevis* (Blainville, 1823)
        - unidentified loliginids
    - Suborder Oegopsina Orbigny, 1845
        - unidentified oegopsids
      - Family Lycoteuthidae Pfeffer, 1908
        - *Selenoteuthis scintillans* Voss, 1959
        - unidentified lycoteuthids
      - Family Enoploteuthidae Pfeffer, 1900
        - *Abralia cf. veranyi* (Ruppel, 1844)
        - *Abraliopsis cf. pfefferi* Joubin, 1896
        - *Ancistrocheirus lesueurii* (Orbigny, 1842)
        - *Pyroteuthis margaritifera* (Ruppell, 1844)
        - *Pterygioteuthis* sp. Fischer, 1896
        - unidentified enoploteuthids
      - Family Octopoteuthidae Berry, 1912
        - *Octopoteuthis* sp.
      - Family Onychoteuthidae Gray, 1849
        - *Onychoteuthis cf. banksii* (Leach, 1817)
        - *Onykia carriboea* Lesueur, 1821
      - Family Cycloteuthidae Naef, 1923
        - ?*Discoteuthis* sp.
      - Family Gonatidae Hoyle, 1886
        - *Gonatus fabricii* (Lichtenstein, 1818)
      - Family Histioteuthidae Verrill, 1881
        - *Histioteuthis* spp.
      - Family Bathyteuthidae Pfeffer, 1900
        - *Bathyteuthis abyssicola* Hoyle, 1885
      - Family Chtenopterygidae Grimpe, 1922
        - *Chtenopteryx sicula* (Verany, 1851)
      - Family Brachioteuthidae Pfeffer, 1908
        - *Brachioteuthis* sp.
      - Family Ommastrephidae Steenstrup, 1857
        - *Illex* sp.
        - *Illex illecebrosus* (Lesueur, 1821)
        - rhynchoteuthion Type A′
        - rhynchoteuthion Type B′
        - unidentified ommastrephids
      - Family Chiroteuthidae Orbigny, 1841
        - *Chiroteuthis* sp.
      - Family Mastigoteuthidae Verrill, 1881
        - *Mastigoteuthis hjorti* Chun, 1913
      - Family Cranchiidae Prosch, 1847
        - *Leachia lemur* (Berry, 1920)
        - *Teuthowenia megalops* (Prosch, 1847)
        - *Helicocranchia cf. papillata* (Voss, 1960)
        - ?*Bathothauma lyromma* Chun, 1906
        - ?*Taonius/Galiteuthis* sp.
        - unidentified cranchiids
- Order Octopodida Leach, 1818
  - Suborder Incirrina Grimpe, 1916
    - Family Octopodidae Orbigny, 1840
      - *Octopus* spp.-type
      - "*Macrotritopus*"-type
      - unidentified octopodids
    - Family Tremoctopodidae Tryon, 1879
      - *Tremoctopus violaceus* Chiaie, 1830
    - Family Argonautidae Tryon, 1879
      - *Argonauta argo* Linnaeus, 1758/
      - *Argonauta hians* Lightfoot, 1786

The data are presented by families. The format includes the species name, author, and date (or higher taxon name if species identification was not possible) and the figure number(s) associated with that taxon. Each species account begins with a list of the voucher specimens upon which the observations on developmental morphology are based in increasing dorsal mantle length (ML, in mm), the ship acronym, cruise and station number, and the USNM catalog number of the voucher specimen(s). This is followed by a summary of the distributional data, the morphological descriptions of the voucher specimens, the specific figure reference(s), and remarks, principally on growth and development of taxonomic characters.

The abbreviations of anatomical features, primarily measurements and counts, are as defined in Roper and Voss (1983) and Sweeney et al. (1992). Terminology and definitions are as presented in Roper et al. (1984).

Family Sepiolidae

Semirossia tenera (Verrill, 1880)

Voucher specimens 2.3 mm mantle length (ML), WIE7410 sta. 12, USNM 730512; 6.9 mm ML, ALB7208 sta. 13, USNM 816714; 7.5 mm ML, ALB7208 sta. 14, USNM 730513.

Species distribution *Semirossia tenera* was collected throughout the year. Although early juveniles of this species are represented in our samples only from north of Cape Hatteras, breeding probably is not limited to northern latitudes, since the species is common in the Straits of Florida (Cairns, 1976). The 21 specimens of

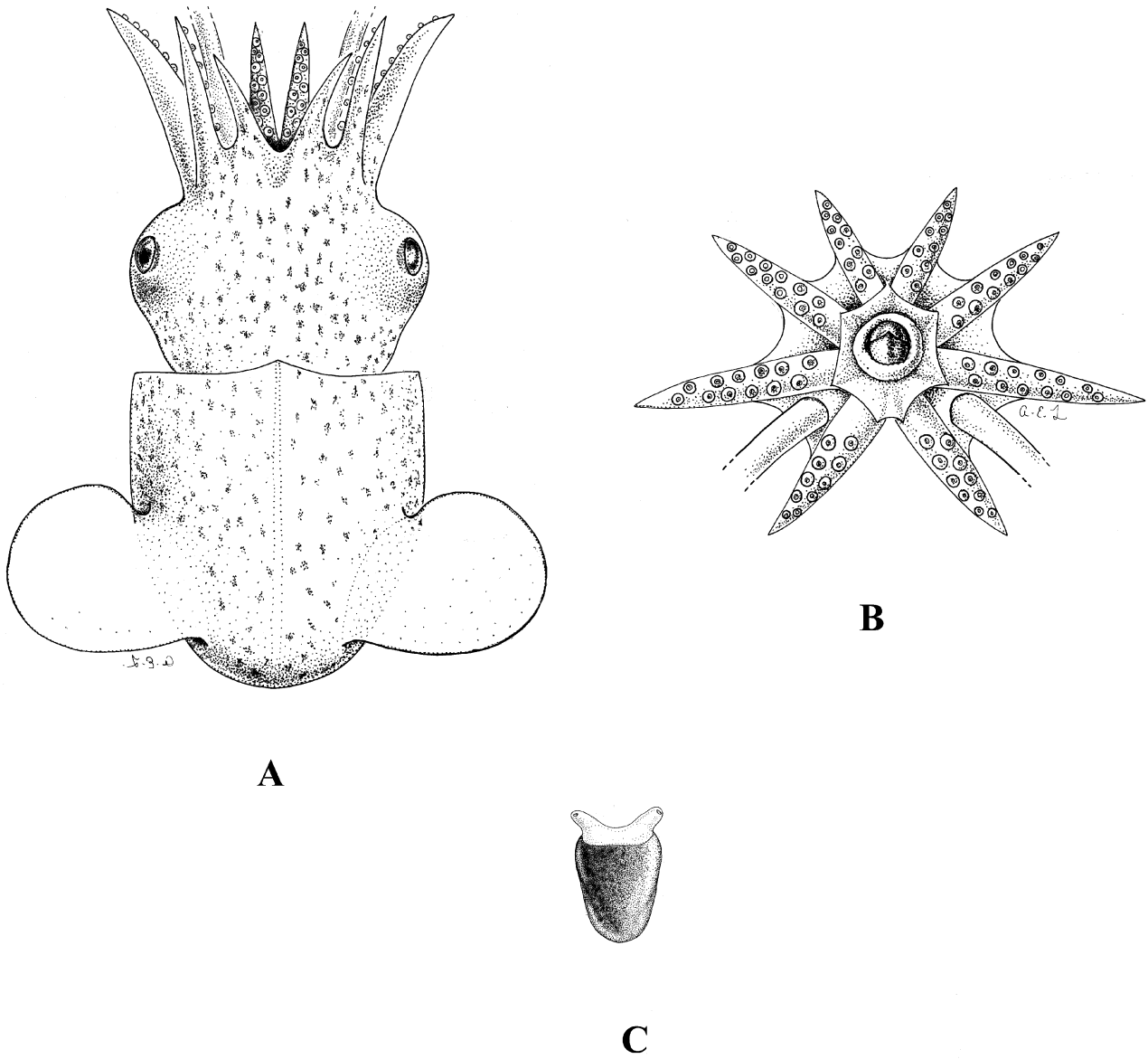

Figure 2

Semirossia tenera (Verrill, 1880). A, dorsal view, 2.25 mm ML, USNM 730512, R/V *Wieczno* sta. 7410-12; B, oral view, same specimen; C, transversely elongate bilobed light organ on anterior surface of ink sac, male 7.5 mm ML, USNM 730513, R/V *Albatross IV* sta. 7208-14.

S. tenera we examined were captured in neritic waters from coastal stations to the outer shelf stations. The range of bottom depths for stations at which specimens were collected was 23–138 m. At shelf-break stations, *S. tenera* appeared to be replaced by *Stoloteuthis leucoptera*, a species found only where depths exceeded 138 m.

Behavioral studies reviewed by Boletzky (1977a) indicate that benthic sepioids, such as *Semirossia,* produce benthic hatchlings. Some of the young specimens of *S. tenera* considered here, however, were collected a considerable distance above the bottom. Time-Depth-Recorder (TDR) records from the subsurface tows of the BLM program indicate that two specimens were captured at least 40–50 m above the bottom (bottom depth minus maximum depth of tow), and eight specimens were collected at least 10–15 m above the bottom. No sepiolids were collected in surface samples.

Morphology of voucher specimens 2.3 mm ML (Fig. 2A,B): Mantle muscular, very plump, rounded posteriorly, MW nearly equals ML. Chromatophores thickly

and evenly distributed over entire mantle, head, and arms. Fins lateral, widely separated, round; FL approximately 50% ML. Funnel long, muscular, tubular, extends to anterior of mid-eye. Head large, HW = MW. Eyes large, round (not ovoid), prominent, covered with very thin transparent membrane. Eyelid not developed. Arms long, robust, II=III>I=IV. Tentacles missing, due to damage. Light organ on anterior ventral surface of ink sac developing as transverse, elongate, translucent, bilobed organ backed with reflective tissue; appears as two nearly separate organs.

6.9 mm ML: Mantle very plump, rounded; MW = ML. Fins lateral, separated, rounded, FL ca. 82% ML. Funnel large, tubular, extends nearly to bases of Arms IV. Eyes covered with thin membrane; eyelid present. Arms elongate, left Arm I hectocotylized with minute suckers. Light organ bilobed, well developed on anterior of ink sac, pores obvious.

7.5 mm ML (Fig. 2C): Mantle short, muscular, broad; MW = 86% ML. Fins separate, very large, FL = 82% ML. Funnel very muscular, tubular, long, extends to bases of Arms IV. Left Arm I hectocotylized with minute suckers, curled. Transversely elongate bilobed light organ on anterior surface of ink sac; reflective tissue golden. Papillose tubes with pores overlie light organ lobes. Ink sac covered with bronze-colored reflective tissue.

Remarks Sepiolid taxonomy currently is in need of extensive revision. As is the general case with sepiolids (Boletzky, 1974; 1977a), all specimens were very similar to adults of the *Rossia/Semirossia* complex in external morphology. Nearly all of the rossiin sepiolids examined in this project had either ink-sac light organs or patches of reflective tissue where such light organs would develop. Because of this primary character, the species is identified as *S. tenera*, which is the only light organ-bearing Rossinae in these waters.

Stoloteuthis leucoptera (Verrill, 1878)

Voucher specimen 9.8 mm ML, Z77.044, USNM 816715.

Species distribution *Stoloteuthis leucoptera* was found only where bottom depths exceeded 138 m in our samples. It occurs in the western North Atlantic Ocean from the straits of Florida to the Gulf of St. Lawrence, in the eastern North Atlantic in the Bay of Biscay, and in the Mediterranean Sea.

Morphology of voucher specimen 9.8 mm ML (Figs. 3–4). Mantle fused dorsally to head; muscular, plump, broad, globular; MW = 110% ML; ventral mantle margin (ventral shield) protrudes anteriorly to level of eye opening; ventral mantle length = 123% dorsal ML. Dark, broad stripe of densely packed chromatophores along dorsal midline, more scattered laterally. Ventral shield covers entire ventral surface of mantle, very darkly pigmented with closely set chromatophores; lateral and posterior surfaces covered with golden reflective tissue. Fins widely separated, broad, elongate-rounded, long, FL = 96% ML. Fin base attached to anterior part of mantle; posterior edges do not extend posterior to mantle. Funnel tip narrow, barely extends anterior to ventral mantle opening; base broad, muscular. Head short, about 50–60% ML, broad, HW = MW; eyes large; eyelids distinct. Arms short, robust, bluntly tipped; deep web connects Arms I–IV, but not between Arms IV; order III=II>IV>I; suckers biserial, globular, reduced in diameter toward tip, closely packed. Tentacles robust, especially on proximal half, clubs short, tip bluntly pointed, suckers very small, closely packed, in 12 to 16 rows. Narrow median adductor muscle connects ventral mantle wall to viscera. Large bilobed photophore covers ventral surface of ink sac.

Remarks The three specimens of *Stoloteuthis leucoptera* were identified based on their distinctive color pattern on the ventral shield, which could be discerned easily even after years of preservation in alcohol.

Family Loliginidae

Loligo pealeii Lesueur, 1821

Species distribution The sympatry of several species of *Loligo* south of Cape Hatteras (Cohen, 1976) prevents absolute identification of specimens from the southern part of our study area. However, the most likely species other than *L. pealeii* that may be present to the south is *L. plei*. Other *Loligo* species, *L. ocula* and *L. roperi*, are restricted to Caribbean islands. *Lolliguncula brevis* and *Sepioteuthis sepioidea* are identifiable at small stages (Hanlon et al., 1992). *Loligo pealeii* is by far the most abundant loliginid species north of Cape Hatteras, thus the many specimens of *Loligo* collected in the middle U.S. Atlantic states and the Gulf of Maine are assumed to be *L. pealeii* (Vecchione, 1981).

The distribution, size, and relative abundance of young stages of this commercially important species have been described previously based on the BLM samples (Vecchione, 1981). Briefly, they were captured throughout the spring, summer, and fall in waters with a salinity range of 31.5–34.0 $\times 10^{-3}$ and were confined to coastal waters except where surface current conditions resulted in strong offshore transport. The higher relative abundances in surface samples and larger specimens in subsurface samples are indicative of an ontogenetic migration, whereby hatchlings leave bottom hatching sites (Griswald and Prezioso, 1981), rise to the surface layer for a short period, and then move deeper into the water column as they grow larger.

Loligo pealeii was the cephalopod species most abundant and most frequently collected in the samples we studied. The maximum abundance recorded from quantitative samples was 71 per 100 m^3 of water filtered.

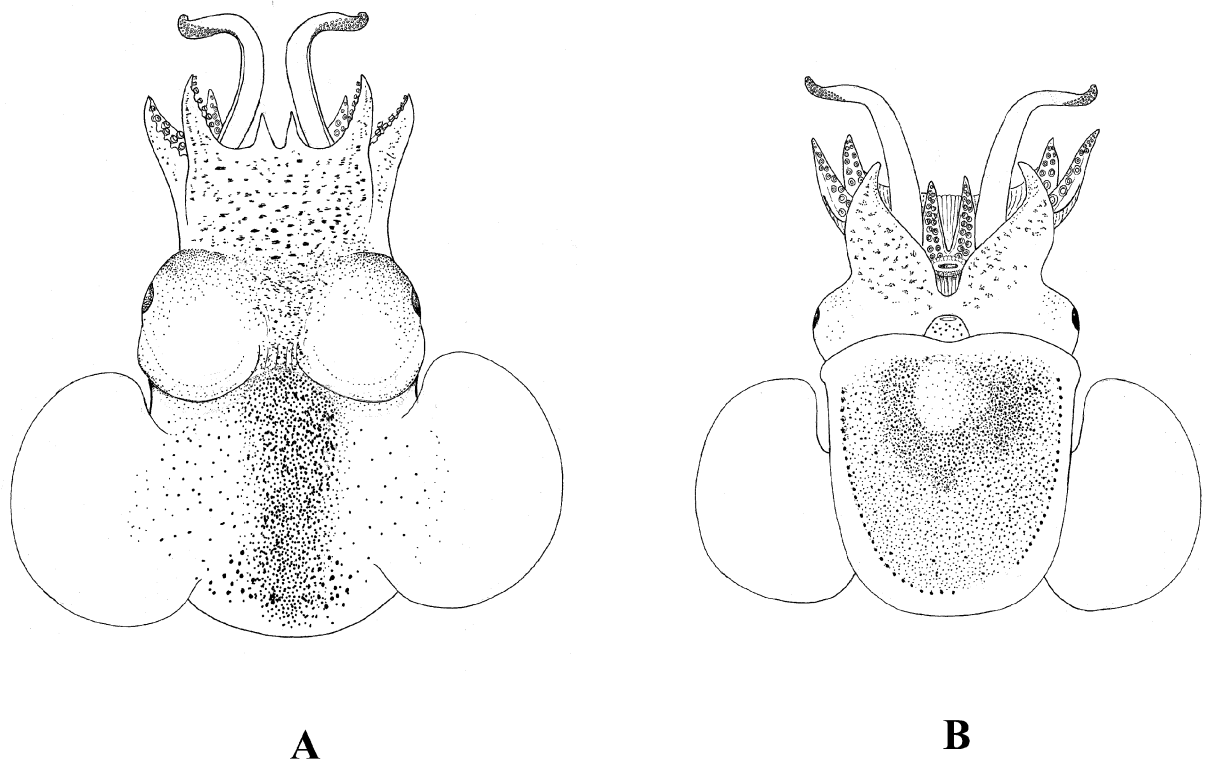

Figure 3

Stoloteuthis leucoptera (Verrill, 1878). A, dorsal view, 9.8 mm ML, USNM 816715, sta. Z77.044; B, ventral view, same specimen.

Peak abundance, however, may be even higher; a single surface tow off Georgia in August 1972 collected 967 loliginid specimens that likely were this species.

The MARMAP samples from north of Cape Hatteras allow us to expand these observations on the early life history of *L. pealeii*. Because of the limited area sampled by the BLM program, large-scale geographic patterns could not be addressed by Vecchione (1981). However, in the MARMAP samples six specimens were captured on Georges Bank in October 1973, and 51 specimens came from the area of Georges Bank in September–October 1974. Four specimens were collected in the Gulf of Maine in October 1974. These captures indicate spawning to the northern limits of the species' range, as far north as Nova Scotia (Roper et al., 1984). No published data were available on details of spawning areas or on water masses present or moving through the sampling area at that time. Transport of paralarvae from southern spawning areas is an alternative hypothesis to explain the presence of these specimens in the Gulf of Maine and Georges Bank, but such transport seems unlikely, as it is contrary to the normal drift of water masses on the continental shelf from northeast to southwest (Bishop and Overland, 1977).

Vecchione (1981) proposed that diel variability in abundance observed in surface samples probably was a result of changes in the ability of young squids to avoid the sampler in different light conditions. Two sets of MARMAP diel subsurface tows do not contradict this hypothesis (Fig. 5). If daytime decreases in surface abundance were a result of diel vertical migration instead of net avoidance, subsurface abundance should increase during the day and decrease at night. Similarly, if the clear temporal patterns seen in the surface collections resulted only from diel periodicity in hatching, abundance in subsurface samples should increase at night and decrease during the day, concurrent with the pattern of the surface samples. Although variability among samples is evident in the time-series of MARMAP subsurface samples (Fig. 5), no consistent diel pattern is apparent. Sampling variability, however, is quite high for young squids. In three sets of closely spaced samples that approximate replication, the median coefficient of variability (standard deviation divided by mean) in abundance for *L. pealeii* was 1.83, indicating a patchy distribution on our sampling scale.

Although *L. pealeii* was not collected in winter north of Cape Hatteras, young *Loligo* were collected throughout

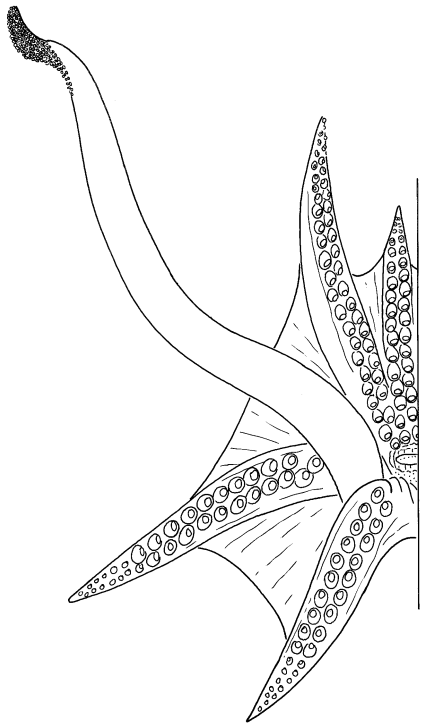

Figure 4

Stoloteuthis leucoptera (Verrill, 1878). Right half of oral view, 9.8 mm ML, USNM 816715, sta. Z77.044.

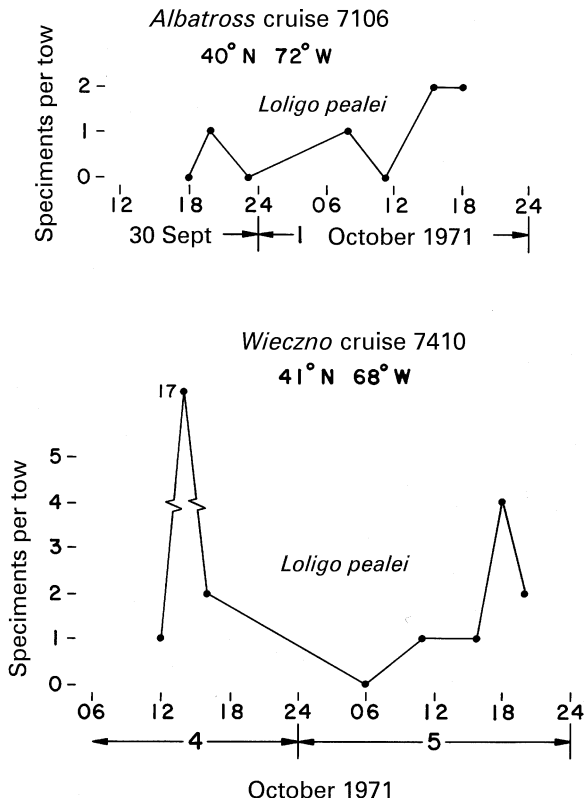

Figure 5

Time series of oblique subsurface tows in two October cruises for captures of *Loligo pealei*. Note absence of consistent diel patterns.

the year in the southern part of our study area. Again, in spite of minor differences in chromatophore patterns among hatchling loliginids (McConnathy et al., 1980), taxonomic problems (Vecchione, 1988) preclude determination of whether the southern specimens represent year-round spawning by *L. pealeii* in warm waters or spawning by more than one species.

Remarks The early stages of this species have been described elsewhere (Verrill, 1882; McConnathy et al., 1980; Vecchione, 1981). They have been compared with *Lolliguncula brevis* (McConnathy et al., 1980; Vecchione, 1982; Hanlon et al., 1992) and with *Sepioteuthis sepioidea* (Hanlon et al., 1992), which are the other genera of Loliginidae in our study area. Early stages of loliginids can be identified based on morphometry and the presence of a protective membrane over the eyes (Naef, 1923). Young *Loligo* are distinguishable in the western North Atlantic Ocean based on chromatophore patterns, especially the presence of a trapezoidal arrangement of four chromatophores posterior to each eye on the ventral surface of the head. Morphometric changes during growth, though nonlinear (Vecchione, 1981), are gradual and not adequate for specific or generic identification. Vecchione (1988) presented evidence that chromatophore patterns cannot be used confidently to distinguish paralarval *L. pealeii* from its occasionally sympatric congenor *L. plei*.

Lolliguncula brevis (Blainville, 1823)

Species distribution Planktonic specimens of *L. brevis* were collected only during August–October in the middle U.S. Atlantic states, the period of maximum water temperatures. Because 40°N is the northern limit for this euryhaline species (Haefner, 1964), low temperatures probably limit this seasonal distribution. Near the center of its range, in the northern Gulf of Mexico, planktonic specimens are collected from early spring through late fall (Vecchione, 1982; 1991).

In spite of extensive surface sampling throughout the lower Chesapeake Bay, all specimens collected inside the bay were in subsurface samples from the eastern side of the bay. Such a distribution is characteristic of coastal plankton intruded into the bay (Grant, 1977). Conversely, specimens from over the continental shelf, collected only at the station closest to shore off Virginia,

were taken only in surface samples. Based on what is known of the two-layer circulation in the bay and nearshore areas (Pritchard, 1952; Beardsley and Hart, 1978; Boicourt, 1982), these distributions probably indicate coastal spawning near the mouth of the bay.

Remarks Chromatophore patterns of hatchling *L. brevis* have been described by McConnathy et al. (1980), and development of the species has been described in detail by Vecchione (1982), based in part on the specimens considered here. The most useful character for identification is the triangular arrangement of chromatophores posterior to the eyes on the ventral surface of the head.

The enoploteuthid group of families

The families Enoploteuthidae, Ancistrocheiridae, and Pyroteuthidae were long considered to be subfamilies of Enoploteuthidae. We follow Young and Harman (1998) in treating them as separate families which, together with Lycoteuthidae, comprise the enoploteuthid group of families. This group of families often comprises the most abundant cephalopod paralarvae in oceanic zooplankton samples (e.g., Piatkowski et al., 1993).

Family Lycoteuthidae

Selenoteuthis scintillans Voss, 1958

Voucher specimens 3.8 mm ML, ALB7206 sta. 56, (no longer extant); 6.3 mm ML, ALB7206 sta. 71, USNM 730510; 9.4 mm ML, ALB7206 sta. 71, USNM 730510.

Species distribution Because only four specimens were collected in this program, all on a single cruise, little can be inferred about the early life history of this species.

Morphology of voucher specimens 3.8 mm ML (Fig. 6E): Tentacles and Arms I–III long and attenuate, Arms IV shorter. Eye light organ 3 (counting from anterior to posterior) large and brownish-golden with clear center. Eye light organs 2 and 4 about one half or less diameter of 3, very pale color (Fig. 6E). No trace of precursor to eye light organs 1 and 5. No trace of light organs on viscera.

6.3 mm ML: Tentacles and all arms long. Eye light organ 3 large and purplish-brown with central bright spot, 2 and 4 about one half diameter of 3 and slightly pigmented, 5 visible only as a greyish bump of tissue, 1 barely visible. Medial visceral light organs present as minute anlagen only. Posterior visceral and gill light organs completely undeveloped.

9.4 mm ML (Fig. 6A–D): Arms and tentacles long. Five well-developed eye light organs: number 3 largest, very dark with blue-green bright spot in center, 1, 2, 4, and 5 round to oval and bronze-colored. Pair of relatively large, oval, pearly white light organs medial to bases of gills just anterior to branchial hearts. Small brownish light organs lateral to base of each gill, connected to medial light organs with dark brown strands. One conical median light organ in posterior mantle cavity very near tip and ventral to gonad anlagen. Pair of triangular light organs anteriorly, one on each side of anus.

Remarks The early development of a dark photophore on the ventral surface of the eye at position 3, followed by 2 and 4, is useful to separate lycoteuthids from enoploteuthids. The planktonic forms that we have here seem conspecific in view of Toll's (1983) synonymy of *Oregoniateuthis* with *Lycoteuthis*. Villanueva and Sanchez (1993) synonymized *Lycoteuthis diadema* (Chun, 1900) with *Lycoteuthis lorigera* (Steenstrup, 1875). Furthermore, females of *Selenoteuthis scintillans* seem indistinguishable from *Lycoteuthis springeri* (Voss, 1956).

Family Enoploteuthidae

Abralia cf. veranyi (Ruppell, 1844)

Voucher specimens 3.1 mm ML, ALB7302 sta. 79, USNM 730511; 4.5 mm ML, ALB7302 sta. 79, USNM 730511.

Species distribution In our samples, *Abralia cf. veranyi* was collected year-round and throughout the study area. It was found in the continental shelf waters to bottom depths as shallow as 85 m, but it was not identified from any surface samples. *Abralia veranyi* is distributed in the tropical and subtropical eastern and western North Atlantic Ocean and the Mediterranean Sea; it is associated with continental shelf and slope waters and does not occur in open ocean. Two other species, *A. redfieldi* and *A. grimpei*, occur in the western Atlantic but their systematics and distribution are not well understood. Some of the specimens we refer to as *Abralia cf. veranyi* might include the other *Abralia* species whose paralarvae currently are not distinguishable.

Morphology of voucher specimens 3.1 mm ML (Fig. 7A): Arms I–III long and attenuate with about 14 suckers but no hooks; four chromatophores on aboral surface of each arm. Arms IV much less developed with six to eight suckers, no hooks. Arm order II>I=III>IV. Tentacular stalks very long and robust with row of large aboral chromatophores. Club region undifferentiated, minute suckers along distal one fourth of tentacle. A few small, integumentary photophores, evenly distributed over ventral and ventro-lateral surfaces of head, mantle, and funnel, most in association with small chromatophores. Three round, moderately well differentiated light organs (Fig. 7A) on ventral surface of eyes, anterior (#1) largest, posterior (#5) intermediate, central (#3) smallest; no trace of light organs in positions 2 or 4. Fins are very small, terminal flaps; meet posteriorly.

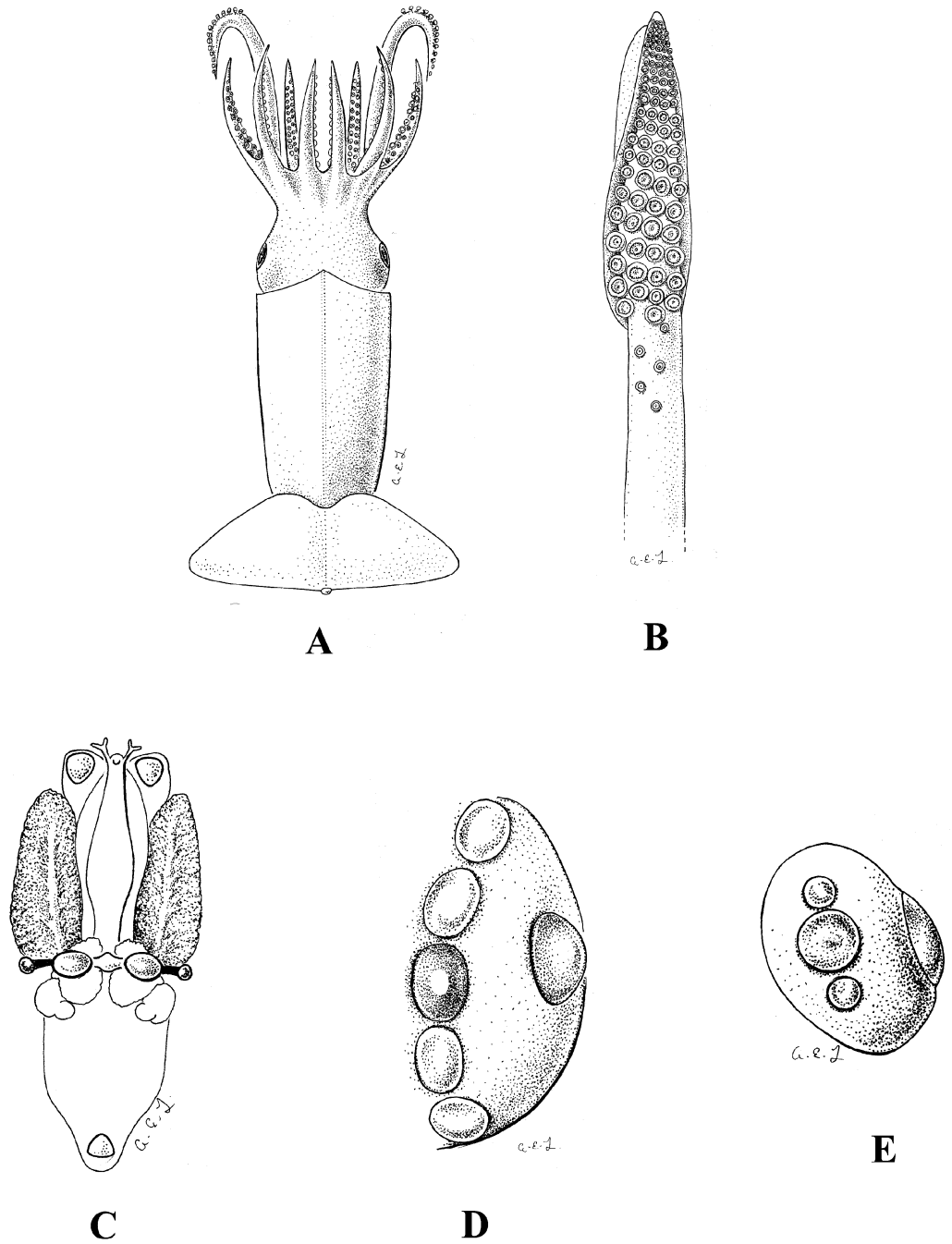

Figure 6

Selenoteuthis scintillans Voss, 1958. A, dorsal view, 9.4 mm ML, USNM 730510, R/V *Albatross IV* sta. 7206-71; B, tentacular club, same specimen; C, internal light organs, same specimen; D, light organs on ventral surface of eye (numbered 1–5 from top to bottom), same specimen; E, eye light organs, 3.8 mm ML, R/V *Albatross IV* sta. 7206-56.

4.5 mm ML (Figs. 7B, 8A–C): Arms II>I=III>IV, long, attenuate. Relatively few suckers on arms, about 20 on I–III, 16 on IV; no hook development. Large chromatophores on Arms I–III and tentacular stalks. Tentacular stalks long and robust. Carpus with four to five suckers, four rows of suckers on manus with six to eight median

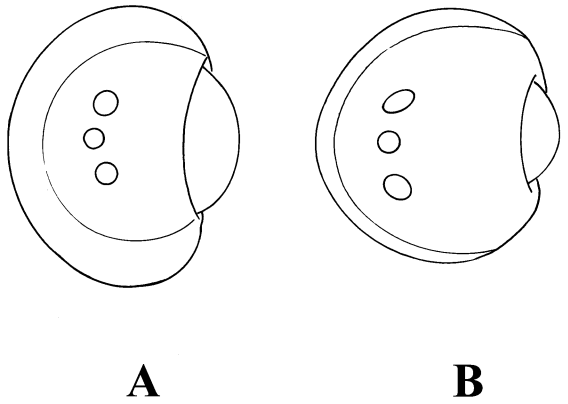

Figure 7

Abralia cf. veranyi (Ruppell, 1844). A, light organs on ventral surface of eye, 3.1 mm ML, USNM 730511, R/V *Albatross IV* sta. 7302-79; B, light organs on ventral surface of eye, 4.5 mm ML, USNM 730511, R/V *Albatross IV* sta. 7302-79.

suckers enlarged; no hook development. Head narrower than mantle opening. Seven large dark chromatophores on dorsal and lateral surface of head. Small photophores in longitudinal rows on ventral and lateral surface of head; one row extends onto Arms IV. Three well-defined light organs on ventral surface of eyes (Fig. 7B); those in positions 1 and 5 largest and oblong, 3 about one third smaller than 1 and 5 and round, no trace of organs in positions 2 and 4. Funnel strongly developed, extends to level of posterior edge of eye. Six small photophores on ventral surface of funnel. Mantle elongate and muscular, with broad opening that tapers to blunt posterior end. Many small chromatophores evenly distributed over ventral and ventro-lateral surface of mantle. Large chromatophores in bands around mantle, corresponding to photophores on ventral and lateral surfaces. Very large chromatophore on each postero-lateral end of mantle ventral to posterior part of fins. Fins terminal, muscular, short, triangular with rounded angles; meet at posterior end of mantle.

Remarks Unlike some species of enoploteuthids, *Abralia* is comparatively rare in midwater-trawl collections in the Atlantic (Roper and Young, 1975). However, the abundance of this genus among the identified enoploteuthids from these plankton samples is comparable to that of the other members of the group of families (except lycoteuthids). There were 16 *Abralia cf. veranyi* vs. 17 *Pterygioteuthis* sp., 21 *Abraliopsis pfefferi*, 26 *Ancistrocheirus lesueurii*, and 30 *Pyroteuthis margaritifera*. If these proportions hold fairly constant among the 128 unidentified enoploteuthids from this study (another genus, *Enoploteuthis*, probably occurs among these specimens as well), then *Abralia* probably is more abundant in the western North Atlantic than is indicated by trawl studies, even though its distribution is restricted in comparison to other species. *Abralia andamanica* commonly is collected in plankton samples from the Indian and Pacific oceans (Silas, 1968; Yamamoto and Okutani, 1975). *Abralia* spp. also are common in the plankton off Hawaii, where Young and Harman (1985) described the paralarval development of *A. trigonura* and *A. astrosticta*.

Abraliopsis cf. pfefferi Joubin, 1896

Voucher specimens 3.0 mm ML, Z76-247 sta. E3, USNM 816946; 5.0 mm ML, ALB7308 sta. 135, USNM 816691; 13.0 mm ML, ALB7302 sta. 41, USNM 730509.

Species distribution Specimens were distributed widely in both time and space. *Abraliopsis pfefferi* also was one of the few oceanic taxa collected during both years of the BLM program. However, it was not collected in any of the surface samples. Thus, the absence of this taxon from cruises for which all or most samples were collected with a neuston net (e.g. CI7802) may be a sampling artifact. In addition to oceanic areas, *Abraliopsis pfefferi* was found on the continental shelf over bottom depths as shallow as 66 m.

Morphology of voucher specimens 3.0 mm ML: Mantle muscular, tapers posteriorly to blunt tip with minute terminal papilla. Fins very small, round. Funnel large, extends to posterior level of eyes. Arms extremely long, well developed. Arms IV with slight swelling near tip, the precursor of the light organ. Suckers only (9–16), no hooks, on Arms I–IV. Arm order III>II>I>IV. Integumentary photophores originally present, but deteriorated during preservation. Tentacles very long, stalks robust. Club with 10 biserial suckers proximally, then three hooks developing in next three pairs of suckers (two ventral, one dorsal), followed by about 20 suckers diminishing in diameter distally, some in three rows, with sucker anlagen at the tip. Eye light organs #1 (anterior), 3, 5 developing as dark bronze reflective swellings.

5.0 mm ML: Arms very long and well-developed. Arms IV with two small terminal light organs and median row of photophores on proximal half. Hooks absent on Arms IV. Four hooks present on Arms I, seven hooks on Arms II, nine hooks on Arms III. Photophores absent on Arms I–III. Three rows of photophores on head, row on ventral midline most conspicuous. Eye photophores 1 (anterior), 3, and 5 developed, 2 and 4 anlagen present.

13.0 mm ML (Fig. 9): Arms IV with three terminal light organs, two rows of photophores that extend one half arm length, and 16 hooks. Arms I with 13 hooks, II with 17 hooks; no photophores. Arm order IV>III>II>I. Tentacular club with four large hooks in ventral row and five small hooks in dorsal row, carpus with eight suckers, dactylus with three to four rows of small suckers. Aboral keel of club developing. Two kinds of pho-

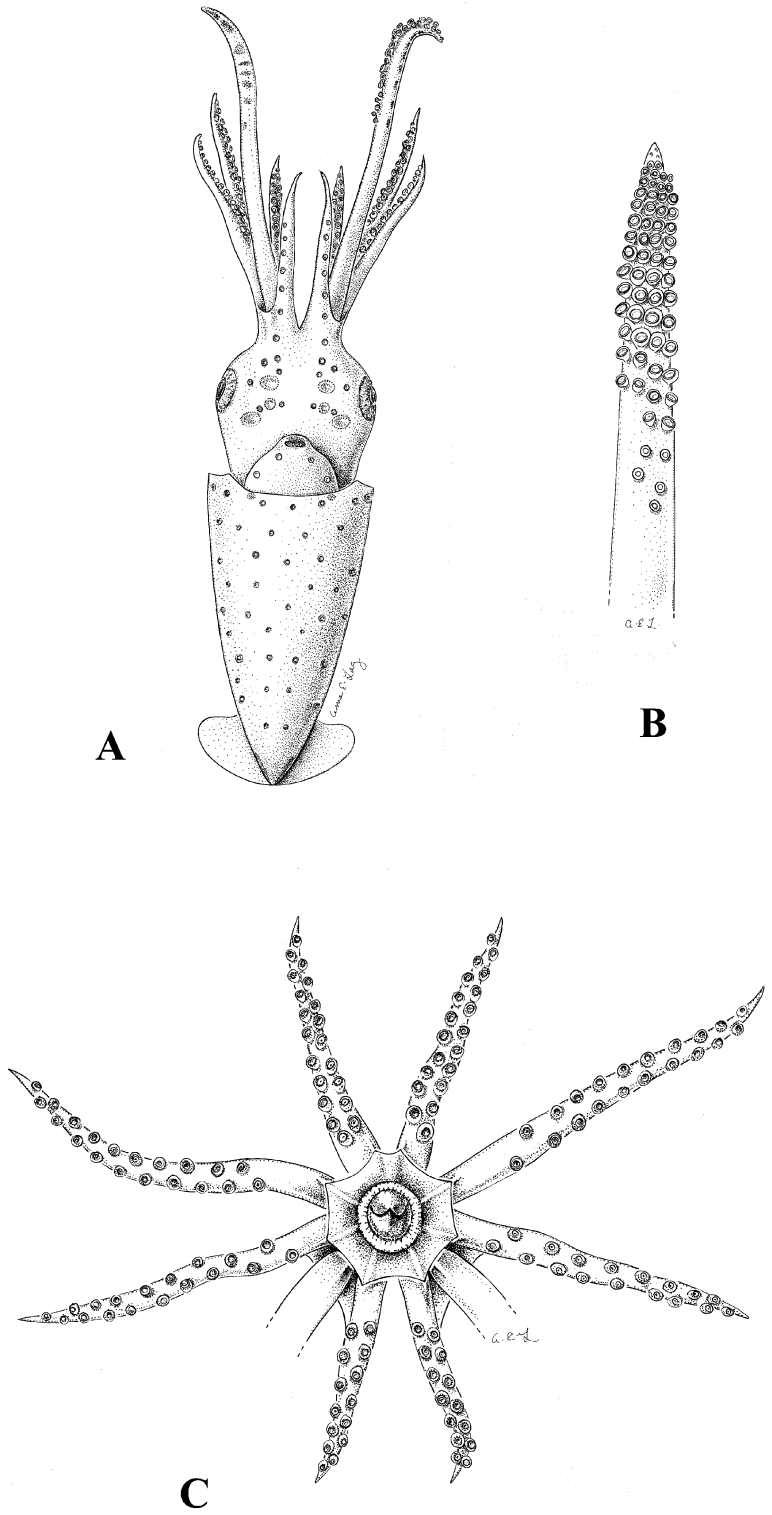

Figure 8

Abralia cf. veranyi (Ruppell, 1844). A, ventral view, 4.5 mm ML, USNM 730511, R/V *Albatross IV* sta. 7302-79; B, tentacular club, same specimen; C, oral view, same specimen.

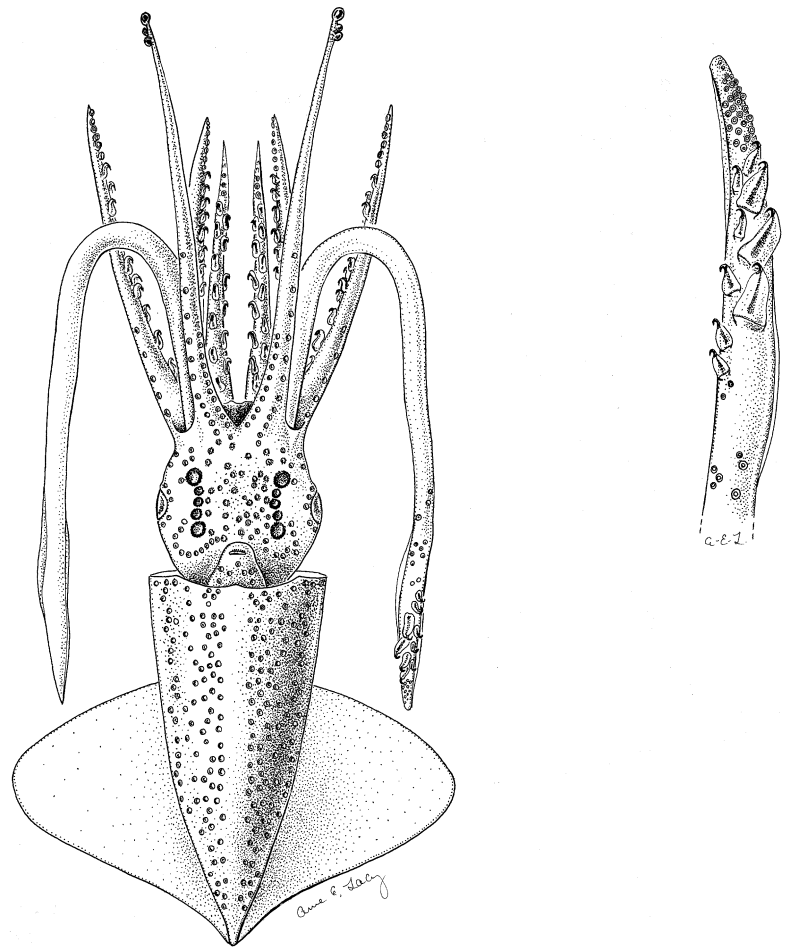

Figure 9

Abraliopsis cf. pfefferi Joubin, 1896. A, ventral view, 13.0 mm ML, USNM 730509, R/V *Albatross IV* sta. 7302-41; B, tentacular club, same specimen.

tophores (large, spherical, dark; and small, spherical, translucent) in about nine indistinct rows on ventral surface of head. Ventral periphery of eyes with five photophores in single row; 1 and 5 largest, 2 and 4 small, 3 intermediate. Thirteen small integumentary photophores around eyelids. Photophores on mantle and funnel similar to those on head, two kinds in indistinct rows; dense ventrally, sparse dorsally on mantle. Ventral midline devoid of photophores.

Remarks In this study, all *Abraliopsis* paralarvae have been placed in *A. pfefferi* by default. Nesis (1987) considered *pfefferi* to be a subspecies of *A. hoylei* Pfeffer, 1884. *Abraliopsis pfefferi* is the most common species of this genus in the western North Atlantic (Roper, 1977; Lu and Roper, 1979) and our specimens probably belong to this species. In all, 21 paralarvae were identified as *A. pfefferi*. Nesis (1987) described *A. atlantica* from the tropical western Atlantic, Caribbean Sea, and Gulf of Mexico. Some of our southernmost material might belong to this species, but its paralarvae and juveniles are unknown. This genus also is common in plankton samples from the California Current (Okutani and McGowan, 1969) and the Indian Ocean (Silas, 1968). The paralarval development of two species of *Abraliopsis* from Hawaiian waters has been described by Young and Harman (1985).

Family Ancistrocheiridae

Ancistrocheirus lesueurii (d'Orbigny, 1842 in Ferussac & d'Orbigny 1834–1848)

Voucher specimens 2.8 mm ML, BLM08W sta. L6, USNM 884242; 3.8 mm ML, GI7508 sta. 7, USNM 884243; 5.6 mm ML, ALB7106 sta. 26, USNM 730528; 8.2 mm ML, ALB7308 sta. 126, USNM 730529.

Species distribution Whereas this species is not very abundant in midwater-trawl samples (Roper and Young, 1975), the 26 specimens reported here rank eleventh in abundance of planktonic cephalopods from the western North Atlantic Ocean, and eighth if only oceanic taxa are considered. This is one of the few species we examined that had a paralarval distribution that was limited in time and space. Although *A. lesueurii* was collected during May–November, no specimens were found in any winter samples. Similarly, this species was not identified from any sample taken south of Cape Hatteras but was found commonly in Gulf Stream waters from Virginia north. Yamamoto and Okutani (1975) reported young *Thelidioteuthis alessandrinii* (=*A. lesueurii*) absent from surface plankton samples, while present deeper, but we collected several specimens at the surface. Data ancillary to these surface samples indicate a temperature range of 17.6–20.9°C and a salinity range of $33.6–35.8 \times 10^{-3}$ for the young of this species.

Morphology of voucher specimens 2.8 mm ML: Mantle rounded, cup-shaped, devoid of photophores. Fins terminal, small, weakly muscled. Tentacles long, robust, without photophores. Eleven suckers, no hooks on club; proximal sucker small, next five enlarged almost to diameter of tentacle stalk, distal five small with several anlagen distally. No hooks or photophores on arms. Arm suckers few and large; no suckers on proximal portions of arms. Five suckers on Arms I, six suckers on Arms II (none on proximal one third), two suckers on Arms III. Arms IV very short with only a few sucker anlagen. Photophores absent on head. Eyes and buccal assemblage stalked with gelatinous material filling spaces between stalks.

3.8 mm ML: Mantle without obvious photophores. Fins small, rounded. Tentacles long, robust, without photophores. Fifteen suckers on club plus several distal anlagen, no hooks; all suckers large except proximal 1 and distal 2. Arm order II>I=III>>IV. Arm suckers large, few in number, none on proximal sections of arms. Eight suckers on Arms I, 12 on Arms II, 9 on Arms III, none on Arms IV. Head lacks detectable photophores. Eyes and buccal assemblage stalked with gelatinous material between stalks.

5.6 mm ML (Fig. 10A–C): Mantle short, broad, bluntly rounded posteriorly, muscular; MW = 83% ML; 12 photophores on ventral surface: four along anterior margin, four pairs that form two zig-zag rows posteriorly to the tip. Fins small, elongate, semilunar, posterior. Funnel tubular, base broad. Head broad, HW = MW. Two rows of five photophores on ventral surface of head in an arc from posterolateral corner to base of Arms IV. Arms long, robust, attenuate; arm order III>II>I>IV. Number of suckers on Arms I-15, II-16, III-22, IV-8; no hooks. Suckers relatively large, on long stalks. Tentacles long, robust to the attenuate tip. Suckers on club begin with one small proximal sucker, set apart from the rest. Manal suckers relatively large, biserial proximally, enlarge gradually to maximum diameter in third-sixth pairs, then diminish to tip; lateral suckers larger than medial suckers; about 27 suckers in total, no hooks. Six small spherical photophores embedded along the tentacular stalk.

8.2 mm ML (Fig. 10D): Mantle muscular, broadest anteriorly, tapers evenly to bluntly rounded posterior tip; MW = 64% ML. Eighteen small, spheroidal photophores on ventral surface of mantle in distinct pattern of transverse rows, anterior to posterior: 4,2,2,4,2,2,2. The posterior-most photophores form at the very tip as elevated knobs. Fins rounded, triangular, terminal; FL = 43% ML. Funnel large, base broad, tube extends to posterior level of eyes. Head large, HW > MW; eyes prominent, no ocular photophores. At least five photophores in arc on each side of ventral surface of head. Specimen damaged, so exact number of photophores on head and Arms IV cannot be determined. Arms very long, robust, attenuate; Arms I–III subequal, longer than IV. Armature on Arms I: one proximal sucker, five hooks, 13+ distal suckers; Arms II: 8–9 hooks, 14+ suckers; Arms III: 11 hooks, 16+ suckers; Arms IV: 0 hooks, about 20 suckers. Tentacles long, robust to tip. Club with four pairs biserial carpal suckers; four transverse rows with two medial hooks and two large marginal suckers each (i.e., eight hooks) on manus; 8 to 10 diminishing biserial suckers on dactylus. Low aboral keel extends from level of first manal row to tip of dactylus. Tentacular stalk with nine small embedded spheroidal photophores.

Remarks The early stages of *A. lesueurii* are easily confused with those of *Octopoteuthis* spp. (Figs. 16–17), because both are characterized by few large suckers on the tentacular clubs and by eyes and buccal assemblages on stalks embedded in gelatinous tissue. *Octopoteuthis* species, however, have a smaller number of suckers on the tentacular clubs. Bello (1992) presented a nomenclatural history of the names applied to this species.

Family Pyroteuthidae

Pyroteuthis margaritifera (Ruppell, 1844)

Voucher specimens 1.6 mm ML, ALB7206 sta. 15, USNM 816692; 1.9 mm ML, ALB7302 sta. 64, USNM 730520; 2.8 mm ML, station data missing; 3.8 mm ML, ALB7206 sta. 75, USNM 816693; 4.9 mm ML, ALB7302 sta. 42, USNM 816694; 7.3 mm ML, ALB7302 sta. 42, USNM 816694; 13.8 mm ML, WIE7410 sta. 94, USNM 816696.

Species distribution Although *P. margaritifera* appeared to be widely distributed based on presence or absence in samples, 27 of the 30 specimens considered here were collected in the southern Sargasso Sea. Paralarval specimens collected off New England and Nova

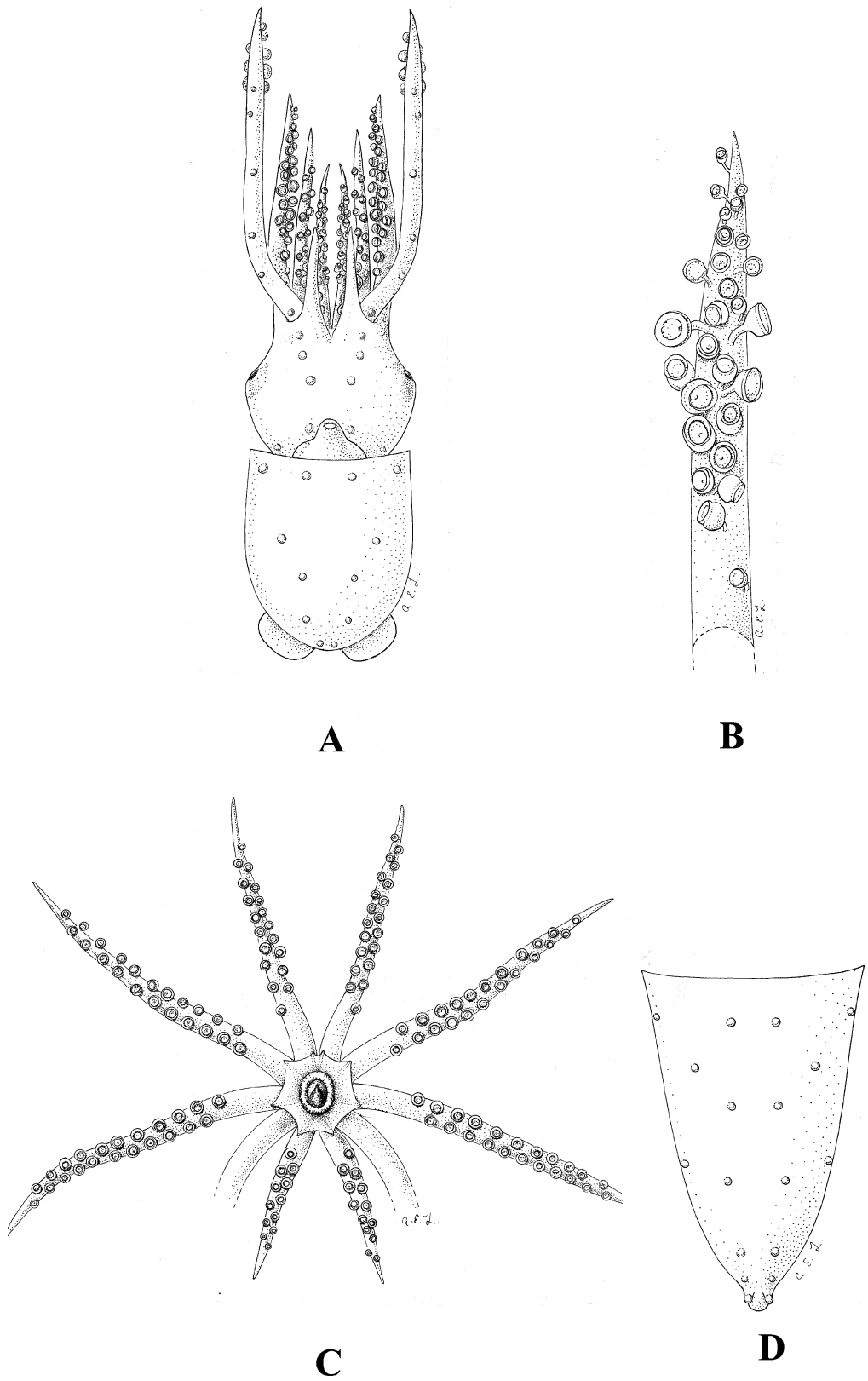

Figure 10

Ancistrocheirus lesueurii (d'Orbigny, 1842 in Ferussac & d'Orbigny 1834–1848). A, ventral view, 5.6 mm ML, USNM 730528, R/V *Albatross IV* sta. 7106-26; B, tentacular club, same specimen; C, oral view, same specimen; D, ventral mantle, 8.2 mm ML, USNM 730529, R/V *Albatross IV* sta. 7308-126.

Scotia probably were beyond their normal range, a result of northeastward transport by Gulf Stream meanders. This distribution contrasts with that of older specimens; *P. margaritifera* was very abundant in midwater net samples collected by Roper (1977) near Bermuda, off the middle U.S. Atlantic states (Lu and Roper, 1979), and off Nova Scotia (Vecchione, personal observ.).

Young *P. margaritifera* were taken during all seasons. Similar to the vertical distribution found in older individuals (Roper and Young, 1975), none of these planktonic specimens were collected at the surface.

Morphology of voucher specimens 1.6 mm ML: Anal light organs very small, separated, pigmented but non-reflective. Gill, intestinal, and posterior light organs undifferentiated. Eye light organs uncertain due to damage. Arms very short; Arms II and III with eight suckers, Arms I with six suckers, Arms IV with four buds. Tentacles missing (broken off). Eyes antero-lateral and tubular. Brachial/buccal crown tubular. Funnel very large.

1.9 mm ML (Fig. 11A–E): Anal light organs small, spherical, pigmented, reflective, and separated. Light organs absent on gill, intestinal, and posterior areas. Seven light organs or anlagen (probably numbers 2, 3, 4, 5, 6, 7, and 9; see Chun, 1910) detectable on each eye. Eye photophore 4 pigmented, 2,3,5 reflective (2–5 shown in Fig. 11C); others just anlagen tissue knobs. Arms I–III with about eight suckers, Arms IV with about six buds. Tentacles long with 8 to 10 suckers on clubs; tentacular stalk with a bend, or slightly swollen elbow, at proximal one third, marking site of photophore anlagen. Eyes, brachial crown, and funnel as above.

2.8 mm ML: Anal light organs posterior to anus, large, spherical, and separated. Gill light organs minuscule anlagen, non-pigmented, non-reflective. No indication of intestinal or posterior light organs. Nine eye light organs; 1, 6, and 8 non-reflective and non-pigmented, 9 primordial. Eyes directed antero-laterally. Arms relatively long, without hooks, 14 to 16 suckers on each. Arms IV much shorter than I–III. Tentacles missing (broken off). Mantle/gladius tip blunt, almost rounded. Funnel large, long. Fins small, round, broadly separated.

3.8 mm ML (Fig. 12): Anal light organs well developed, large, spherical, wide-set, slightly posterior to anus. Gill light organ anlagen visible only as spheres of differentiated tissue. Intestinal and posterior light organs not visible. Nine eye light organs, 1 and 8 non-pigmented and minute. All arms relatively long, no hooks, each arm has 12 to 18 suckers. Arm order III>II>I=IV. Tentacles long, clubs very short with 20 to 25 suckers, no carpal suckers, no hooks. Head broad. Funnel long. Fins round, paddle shaped. Mantle and gladius tip blunt.

4.9 mm ML: Anal light organs fully developed. Gill light organs pigmented and small, about one fourth diameter of anal light organs. Precursor of intestinal light organ a faint strand of stained tissue in inverted-V between gill light organs. Nine eye light organs plus two anlagen (10 and 11). Arms with 18 to 22 suckers, fourth ventral sucker on Arms IV transformed into hook. Tentacle clubs with about 45 suckers, including one small carpal sucker.

7.3 mm ML: Anal light organs large, well-developed. Gill light organs small. Intestinal light organs a single minute ring of differentiated tissue. Posterior visceral light organ a single very small anlage at terminal location. Nine eye light organs, plus two anlagen. Arms with 20 to 26 suckers, two hooks at seventh pair on Arms II, three hooks at fifth pair on Arms III. No hooks on Arms I and IV. Tentacular club without hooks but with 55 to 60 suckers and two enlarged carpal suckers two to three times the diameter of suckers on manus. Mantle and gladius tip elongate, pointed.

13.8 mm ML (Fig. 13A–D): Juvenile female. Anal light organs large, fully developed, posterior to anus. Gill light organs at base of gill small, fully developed, sub-spherical. Three intestinal light organs developed, not fused; central photophore large, oval, pearly colored; laterals small, spherical, bronze-colored. Three posterior visceral light organs: terminal photophore in tip of mantle small, well-developed, spherical, dark-pigmented; central and anterior photophores minute, round, unpigmented anlagen. Twelve eye light organs (nine large, three small), all reflective. Arm hooks in dorsal/ventral rows: Arms I-8/9; Arms II-8/8; Arms III-8/8; Arms IV-9/11. Tentacles longer than arms, slender, stalks with four embedded photophores. Four hooks on right tentacle, three on left in ventral median rows. Three enlarged carpal suckers larger than manal suckers. Mantle long, conical; gladius tip pointed and long. Head broad. Ventral and dorsal surfaces of head, arms, and bases of tentacles covered with very silvery reflective tissue.

Remarks Early stages of *P. margaritifera* are easily confused with those of *Pterygioteuthis* spp. They can be distinguished by the relative sizes of the anal and gill light organs (ALO>>GLO in *Pyroteuthis,* GLO = or> ALO in *Pterygioteuthis*) and the shape of the gill light organs (round in *Pyroteuthis,* with a protuberance in *Pterygioteuthis*).

Pterygioteuthis sp.

Voucher specimens 2.3 mm ML, ALB7206 sta. 13, USNM 816697; 3.5 mm ML, ALB7302 sta. 52, USNM 730524; 5.0 mm ML, ALB7302 sta. 79, USNM 730523; 6.0 mm ML, ALB7308 sta. 144, USNM 730525; 9.0 mm ML, ALB7308 sta. 144, USNM 730525.

Distribution Whereas Lu and Roper (1979) concluded that *P. gemmata* probably spawns during the spring in the middle U.S. Atlantic states, planktonic *Pterygioteuthis* were found throughout the year in our

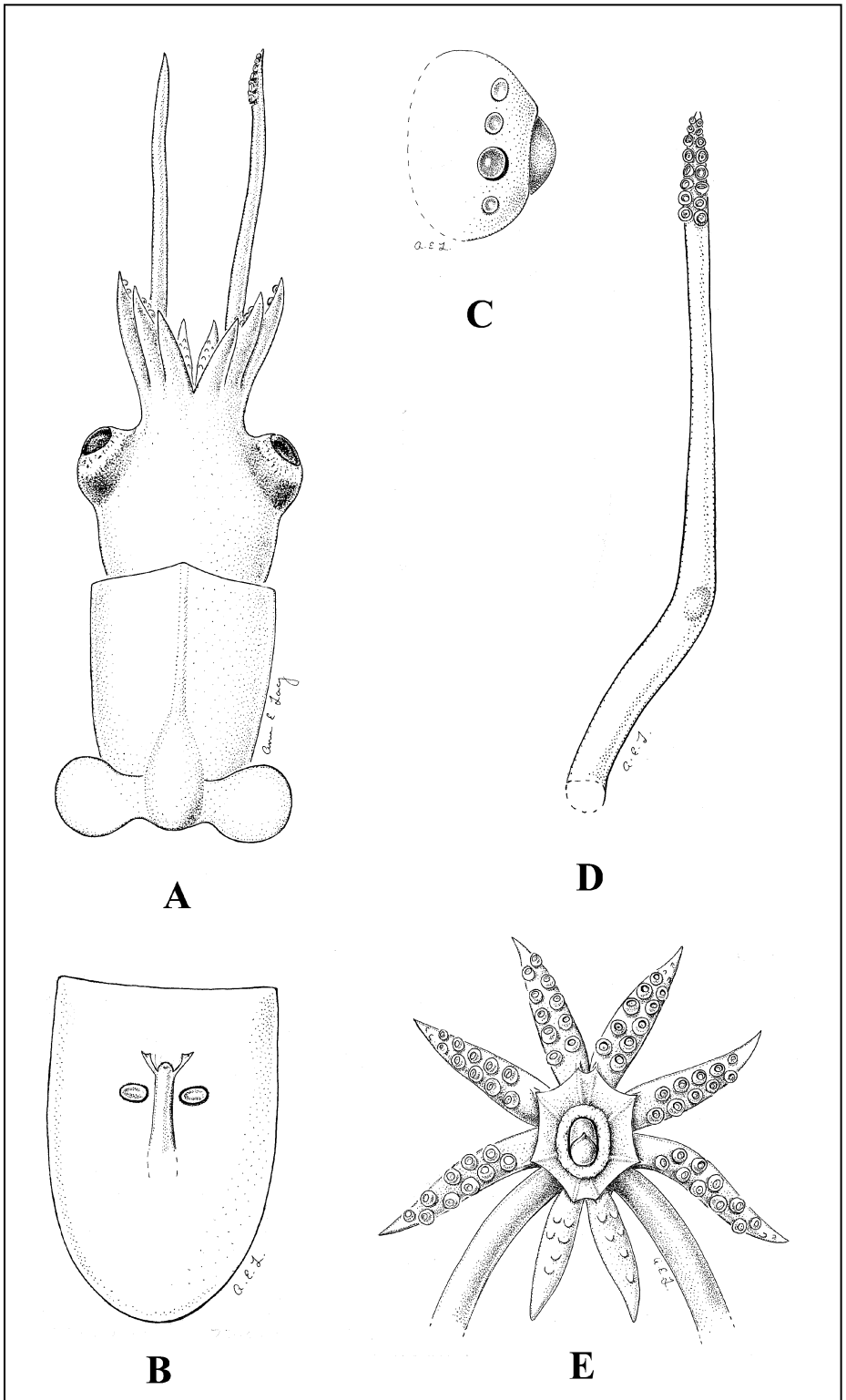

Figure 11

Pyroteuthis margaritifera (Ruppell, 1844). A, dorsal view, 1.9 mm ML, USNM 730520, R/V *Albatross IV* sta. 7302-64; B, visceral light organs, same specimen; C, vertical row of light organs on ventral surface of eye, same specimen; D, tentacle, same specimen; E, oral view, same specimen.

samples. This taxon also was collected throughout the study area. Yamamoto and Okutani (1975) reported that *P. giardi* off Japan was absent from surface plankton samples but present in the upper 200 m. Of our 17 specimens of *Pterygioteuthis* sp., only a single specimen was collected in a surface net. Species of this genus are mesopelagic, but may ascend to the lower epipelagic zone (Young, 1978; Nesis, 1987).

Morphology of voucher specimens 2.3 mm ML: Anal light organs already well-developed, silvery, pigmented. Gill light organs swollen, with minuscule black pigmented protuberance just developing. Intestinal and posterior light organs absent. Eyes directed antero-laterally; six to seven photophores. Arms I–III with eight suckers each, Arms IV very short and smooth, without suckers. Tentacle stalks long and robust, club tiny, terminal, with 15–20 suckers, none on carpus.

3.5 mm ML (Fig. 14A–B): Anal light organs small, close-set, pigmented, lens developed. Gill light organs well-developed elongate spheroids; minute pigmented protuberance on postero-dorsal surface. Intestinal light organ developing, non- pigmented. Posterior light organs not developed. Eye light organs damaged, probably nine large plus two small anlagen. Arms short; Arm order III>II>I>IV. Arms II and III with about 20 suckers on each, Arms I with 16, Arms IV with 10. Tentacles missing (broken off). Funnel short. Tip of mantle and gladius bluntly pointed. Head narrow.

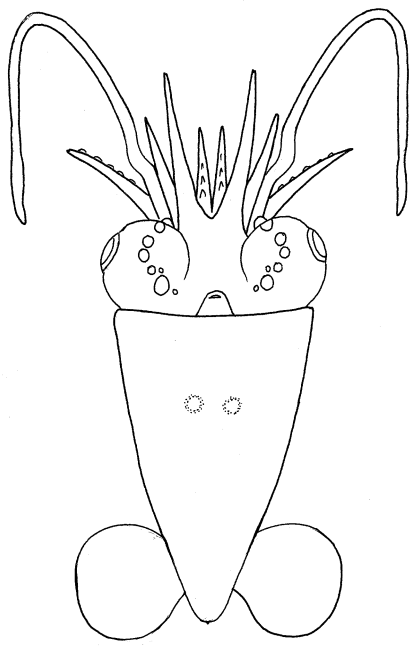

Figure 12

Pyroteuthis margaritifera (Ruppell, 1844). Ventral view, 3.8 mm ML, USNM 816693, R/V *Albatross IV* sta. 7206-75.

5.0 mm ML (Fig. 15A–B): Anal light organs large, well-developed. Gill light organs large spheres with very small black postero-dorsal protuberances. Intestinal light organ present, faintly pigmented. Posterior intestinal light organs not developed. Eyes directed laterally and adult-like. Nine large eye light organs, plus two small. Arm suckers: Arms I-16, Arms II-18, Arms III-18, Arms IV-10. Tentacle stalks very long, clubs very short with more than 40 suckers in four rows plus two to three carpal suckers. Tip of mantle plus gladius short, bluntly pointed.

6.0 mm ML: Anal light organs with reflective silver anterior, black posterior. Gill light organs oblong, light brown with black postero-dorsal protuberance. Intestinal light organ spherical and pigmented; posterior intestinal light organs not developed. Eyes lateral. Eye light organs damaged, nine large, plus two small, plus two anlagen. Arm suckers: Arms I-17, Arms II-16, Arms III-17, Arms IV-approx.15. Protective membranes very well-developed; trabeculae robust. Tentacles missing distally but enlarged chromatophore present at base. Tip of mantle and gladius pointed, beginning to elongate.

9.0 mm ML (Fig. 15C): Anal light organs large, half silvery, half black. Gill light organs large. Intestinal light organ well-developed, slightly ovoid, very black. Terminal intestinal posterior light organ present, small, black. Other two posterior light organs not present. Nine large eye light organs, plus four small. Hooks absent on arms; suckers on Arms I-24, Arms II-26, Arms III-23, Arms IV-17. Tentacles missing (broken off). Posterior mantle/gladius very pointed, adult-like.

Remarks Two species, *Pterygtioteuthis gemmata* and *P. giardi* occur in the western North Atlantic. Our material may include either or both species.

Family Octopoteuthidae

Octopoteuthis sp.

Voucher specimens 3.0 mm ML, KAI8201 sta. 47 USNM 884239; 6.0 mm ML, KAI8201 sta. 45, USNM 816716; 8.8 mm ML, BLM06W sta. A2, USNM 884240.

Distribution The 30 young *Octopoteuthis* sp. reported here are of particular interest because adults and advanced juveniles are seldom captured in nets. Whereas *Octopoteuthis* spp. were rare in midwater-net samples examined by Cairns (1976), Clarke (1977), Roper (1977), and Lu and Roper (1979), stomach contents from sperm whales indicate that this genus is comparatively common in the North Atlantic (Clarke, 1977). The relative frequency of *Octopoteuthis* in the plankton samples we examined, as well as those reported by Okutani and McGowan (1969) from the California Current, indicates

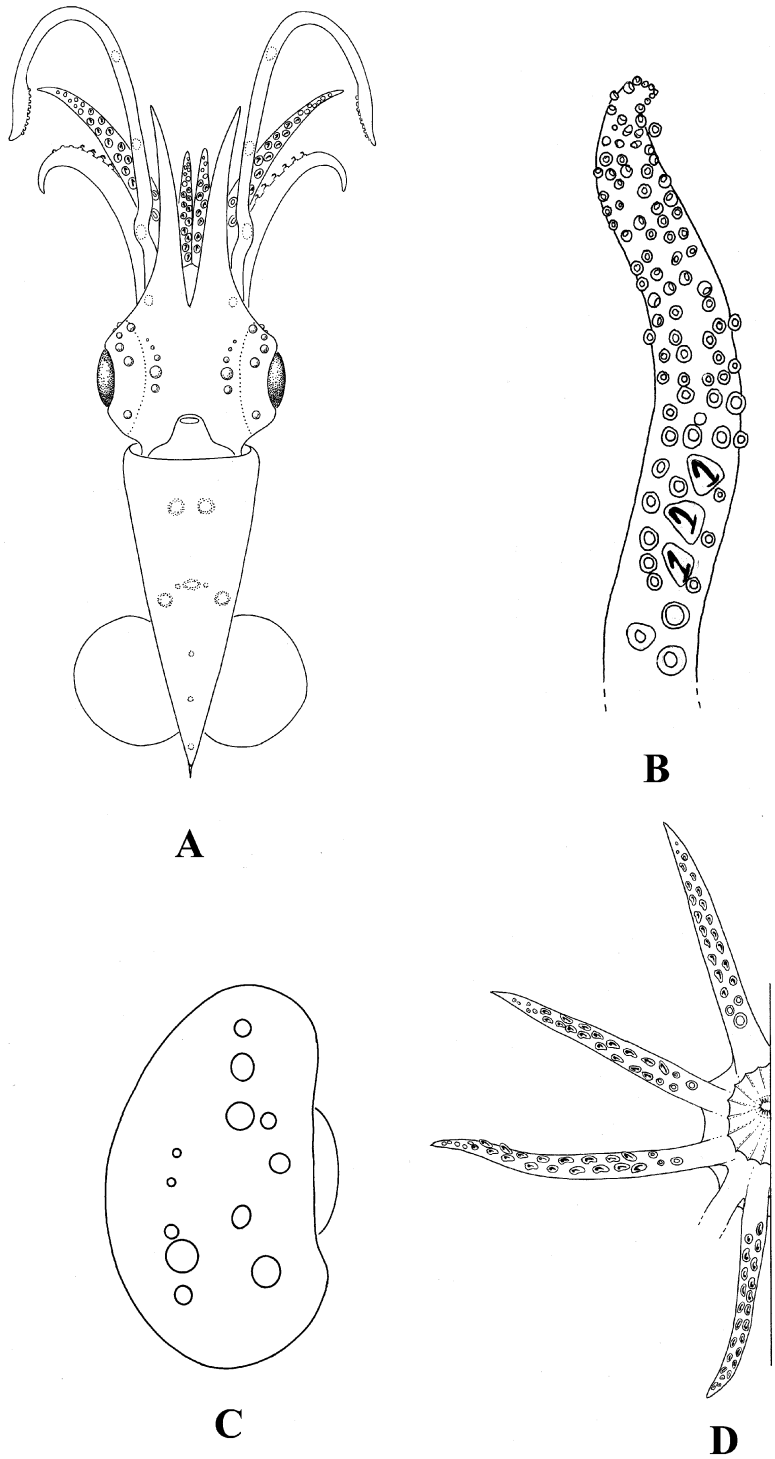

Figure 13

Pyroteuthis margaritifera (Ruppell, 1844). A, ventral view, 13.8 mm ML, USNM 816696, R/V *Wieczno* sta. 7410-94; B, tentacular club, same specimen; C, pattern of light organs on ventral surface of eye, same specimen; D, left half of oral view, same specimen.

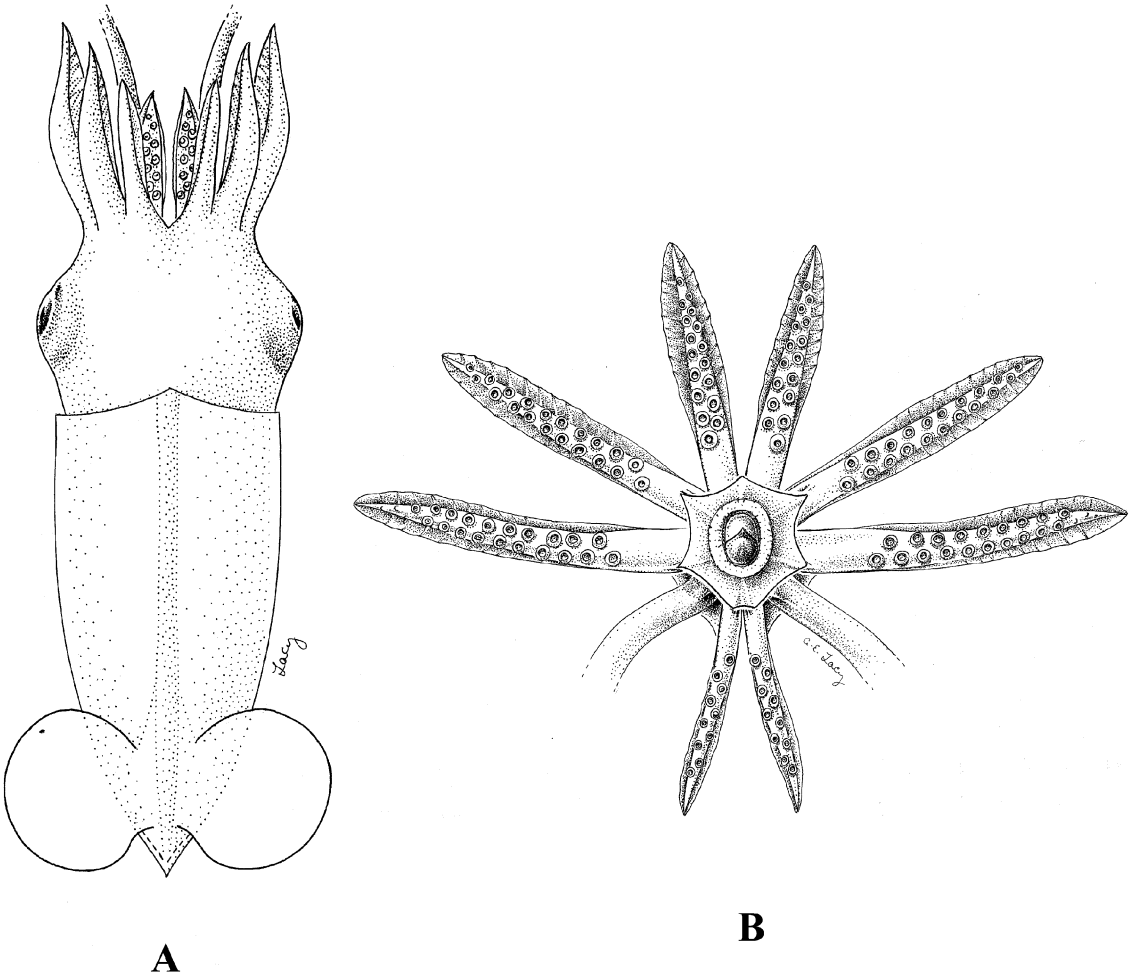

Figure 14

Pterygioteuthis sp. A, dorsal view, 3.5 mm ML, USNM 730524, R/V *Albatross IV* sta. 7302-52; B, oral view, same specimen.

that sampling for the young may be an adequate approach to a rough estimation of comparative abundance of this taxon, as has been done with other cephalopods (e.g. Kubodera and Okutani, 1977). *Octopoteuthis* sp. was widespread in our samples but never abundant; it was found in 27 samples but never more than two specimens in any one sample. It was collected throughout the year and throughout the western North Atlantic. However, 24 of 30 specimens were taken in the southern Sargasso Sea. Specific identities cannot be determined for our specimens, because four nominal species of *Octopoteuthis* are known to occur in the temperate and subtropical western North Atlantic (Stephen and Jefferts, 1992).

Morphology of voucher specimens 3.0 mm ML (Fig. 16): Mantle short, broad, round posteriorly; MW about 75% of ML. Fins terminal, very short, broad, laterally ovoid; FL about 33% of ML; FW of both fins about 45% of ML. Tentacles long, robust proximally, thin distally with eight suckers. From proximal to distal, first two suckers minute, next two strikingly large (>tentacle diameter), followed by two intermediate in size, one slightly smaller, then one minute terminal sucker. Arms long, attenuate, with swollen areas at tips (anlagen to light organs). Biserial suckers on arms developing into hooks, some well-developed. Eyes and buccal assemblage stalked, with stalks embedded in gelatinous tissue of anterior head.

6.0 mm ML (Fig. 17): Mantle thin walled, muscular, conical, widest at anterior opening, tapers to blunt tip; MW 60% of ML. Fins very muscular, fused along dorsal midline of mantle; blunt mantle tip extends very slightly beyond posterior border of fins. Fins longest at point of fusion with mantle; FL 60% of ML. Fins very broad, oval, FW 112% of ML. Funnel long, tapers to narrow opening that reaches mid-level of head, poste-

rior to eyes; HW 60% of ML. Eyes on antero-laterally directed stalks; buccal stalk elongate. Eye and buccal stalks embedded in gelatinous matrix. No photophores nor photophore anlagen present on mantle or head. Arms long, attenuate; arm order II>III>I>IV, (most tips broken). Arms II and III, especially, are very robust in proximal half. Arms with biserial globular suckers that develop into hooks; hooks and suckers present on Arms II and III, suckers only on I and IV. Arm tips with swellings that are anlagen to photophores. Tentacles with robust stalks, but not nearly as muscular as arms; TL approximately equal to length of Arm I, longer than IV, considerably shorter than II and III. Club region unexpanded; two to three minute biserial suckers on proximal club, followed by two enormous suckers, each with a diameter greater than that of the tentacle where they are attached. Proximally are two more enlarged suckers, then one intermediate and one small sucker at the bluntly rounded tip of the club. No sucker anlagen occur on the tip. All sucker rings have relatively narrow openings and very broad walls. Anlagen of photophores on ink sac beginning to differentiate as a different appearance of the ventral-most reflective tissue.

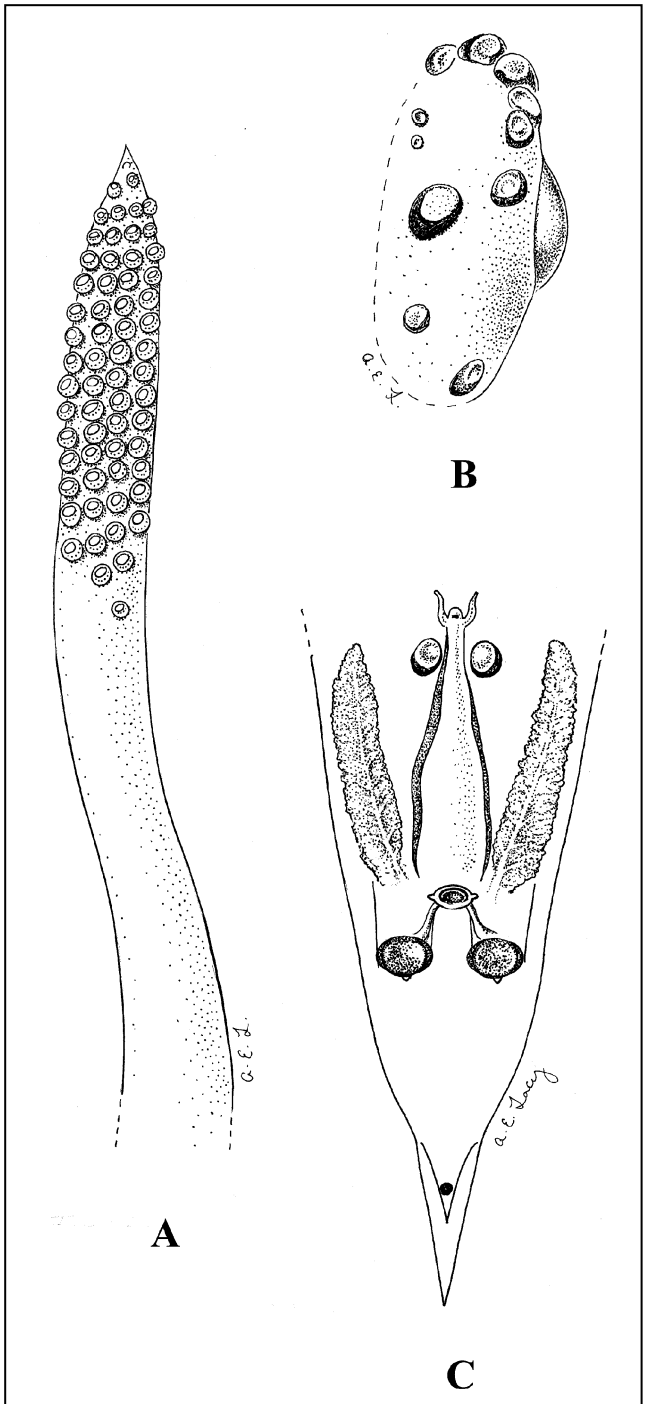

Figure 15

Pterygioteuthis sp. A, tentacular club, 5.0 mm ML, USNM 730523, R/V *Albatross IV* sta. 7302-79; B, light organs on ventral surface of eye, same specimen; C, visceral light organs, 9.0 mm ML, USNM 730525, R/V *Albatross IV* sta. 7308-144.

8.8 mm ML: Fin length (6.3 mm) 72% of ML. Fin width (about 12 mm) 136% of ML. Tentacles missing, but long shreds of tissue remain. Biserial hooks on all arms. Arm tips damaged, apparently from abrasion, causing loss of photophores. Eyes and buccal assemblage stalked, embedded in gelatinous tissue.

Remarks Octopoteuthid development has been described in detail by Stephen (1985). Generic identifications can be determined easily for even the smallest paralarvae because of the huge suckers on the tentacular clubs (but see *Ancistrocheirus*); large post-paralarvae collected in plankton samples can be identified based on adult characteristics: absence of tentacles, presence of arm hooks and arm-tip photophores, large fin size, and body photophores. Very small specimens differ greatly from the adults because they lack the arm-tip photophores and the greatly enlarged fins, and they possess functional tentacles. The general appearance of Octopoteuthidae is quite similar to the early stages of Ancistrocheiridae, but they are distinguished by differences in armature of the tentacles.

Family Onychoteuthidae

Onychoteuthis cf. banksii (Leach, 1817)

Voucher specimens 2.0 mm ML, Z7802, sta. 20, USNM 884235; 3.6 mm ML, KAI8201 sta. 75; 5.4 mm ML, KAI8201 sta. 78, USNM 884236.

Species distribution The 94 specimens of *Onychoteuthis cf. banksii* in this study constitute the most abundant species collected except for the loliginids and the ommastrephids. This species was found in oceanic waters throughout the study area and was collected from February through August. Most of the specimens came

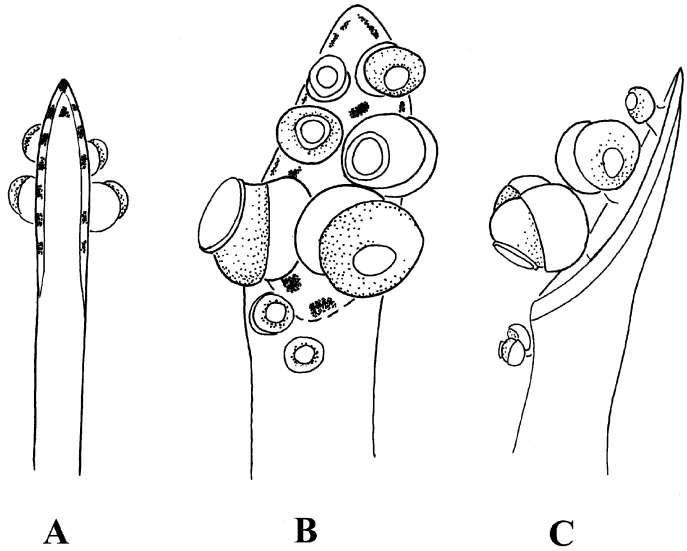

Figure 16

Octopoteuthis sp. A–C, aboral, oral, and lateral view of club, 3.0 mm ML, USNM 884239, R/V *Kaiyo-Maru* sta. 8201-47.

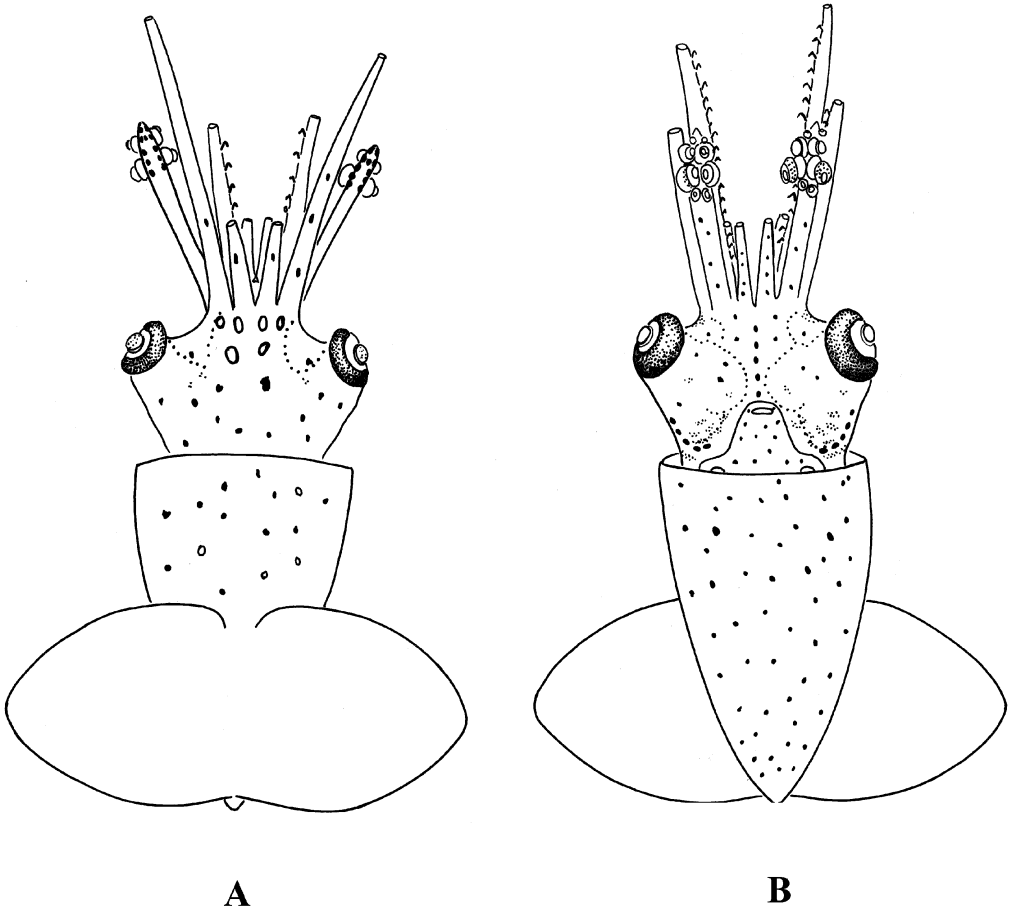

Figure 17

Octopoteuthis sp. A, dorsal view, 6.0 mm ML, USNM 816716, R/V *Kaiyo-Maru* sta. 8201-45; B, ventral view, same specimen.

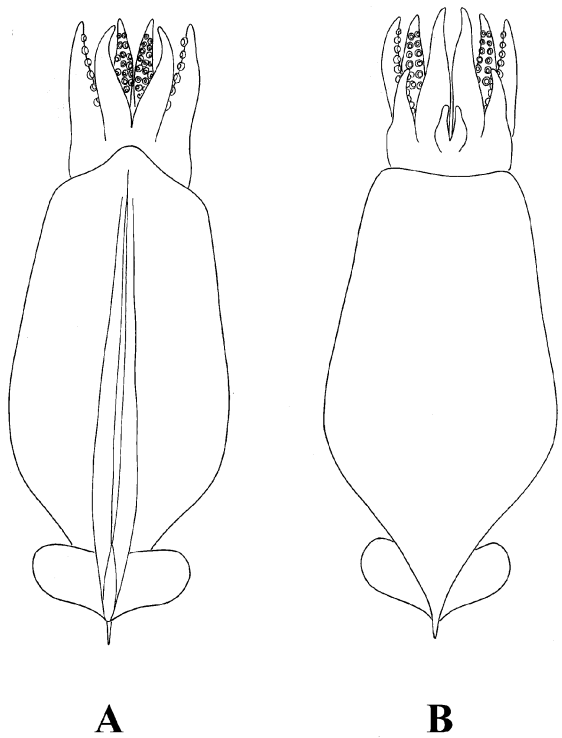

Figure 18

Onychoteuthis cf. banksii (Leach, 1817). A, dorsal view, 2.0 mm ML, R/V *Kaiyo-Maru* sta. 8201-75; B, ventral view, same specimen.

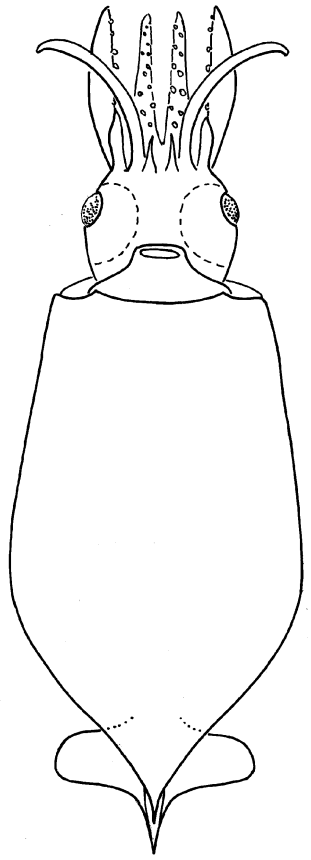

Figure 19

Onychoteuthis cf. banksii (Leach, 1817). Ventral view, 5.4 mm ML, KAI8201 sta. 78, USNM 884236.

from the Sargasso Sea, although a few were collected in Gulf Stream waters. Specimens from surface samples were collected only at high salinities ($S > 35.5 \times 10^{-3}$) and relatively high temperatures (18.2–28.8°C). Although *O. cf. banksii* was collected in 56 samples, all but three samples contained only one to three specimens (maximum=7). Thus the presumed "shoaling" by young juveniles of this species (Clarke, 1966) was not found within the planktonic size range (2–7 mm ML) available to us.

Morphology of voucher specimens 2.0 mm ML (Fig. 18): Mantle very elongate, narrow, muscular; MW = 42% ML. Posterior third of gladius and mantle bent ventrally. Posterior "spike" of gladius extends beyond very small, paddle-shaped, laterally directed fins. Funnel very large, well-developed, covers much of postero-ventral surface of head, extends anteriorly to level of lenses of eyes. Head narrow; HW = 28% ML, dominated by large, sessile, laterally oblong eyes. Arms III and IV not well developed, Arms II>I. Five suckers on Arms I, six on Arms II. Tentacles slightly longer than arms, with eight suckers. No hooks on clubs nor light organs on viscera or eyes.

3.6 mm ML: Head completely retracted inside mantle, which is tightly sealed around head; only arms and tentacles protrude. Posterior third of gladius bent ventrally, and "spike" bent back dorsally. Fins small, round, well-developed. Arms III and IV mere protuberances. Arms I and II and tentacles short, stubby, all approximately of equal length. Suckers on arms and tentacles small, 12 each on Arms I and II and tentacles. Tentacular suckers appear to be biserial.

5.4 mm ML (Fig. 19): Head narrow, partially withdrawn into mantle; HW 24% ML. Eyes lateral, relatively large. Mantle opening constricted to about two-thirds maximum mantle width; MW at opening 39% ML, MW at widest part in posterior half of mantle = 48% ML. Fins well-developed, broadly heart-shaped, FL = 14% ML, FW = 33% ML. Gladius tip still protrudes as "spike" beyond posterior end of mantle and fins; spike length = 9% ML. Arm formula: I=II>>III>>IV. Arm suckers small, numerous on Arms I and II, few on Arms III, none on Arms IV. Tentacles slightly longer than longest arms.

Small biserial suckers along entire oral surface of tentacles, a few in central region beginning to elongate into hooks. Nuchal folds not yet developed. Intestinal light organs undeveloped.

Remarks Young (1972) presented evidence that "*O. banksii*" in the western North Atlantic might represent a species complex of at least two species, but this has not yet been confirmed. If this is so, then our specimens may include more than one species. Furthermore, *Ancistroteuthis lichtensteinii* (Ferussac, 1835) now is known to be more abundant in the western Atlantic Ocean than previously recognized (Vecchione, personal observ.). Paralarval morphology of *Onychoteuthis* from Hawaiian waters indicates that a complex of very similar species is present there as well (Young and Harman, 1987). Clarke (1992) presented additional observations on paralarval onychoteuthids.

Onykia carriboea Lesueur, 1821

Voucher specimens 1.5 mm ML, ALB7302 sta. 25, USNM 817004; 4.0 mm ML, TRI130, sta. 6, USNM 816717; 7.5 mm ML, KAI8201, sta. 64, USNM 884241.

Species distribution The young of this neustonic squid were collected in oceanic waters throughout the western North Atlantic and during all seasons. In the surface samples for which we have ancillary data, this species was taken at temperatures above 27.5°C and salinities greater than 35×10^{-3}. Of the 51 specimens we examined, 16 were collected in a single 10-min neuston tow at 35°30′N, 74°00′W in the Gulf Stream off Cape Hatteras.

Morphology of voucher specimens 1.5 mm ML: Mantle very stout, MW = 83% ML; rounded posteriorly, no point or rostral spike. Fins tiny, terminal, truncate-rounded. A line of chromatophores extends along dorsal midline of mantle. Funnel muscular, tube reaches posterior level of eyes. HW = 60% ML; eyes prominent, antero-laterally directed. Dorsal surface of head covered with several large chromatophores; one medium-sized chromatophore at base of dorsal arms. Arms I and II short, stubby, bluntly attenuate; suckers biserial, minute, few in number. Arms III minute, pointed and Arms IV merely blunt buds; no suckers. Tentacles longer than Arms II, slightly more slender, armed with a few biserial minute suckers along the stalk, club undifferentiated, sucker anlagen minute, numerous.

4.0 mm ML (Fig. 20A–B): Mantle broad, bluntly pointed posteriorly; tip does not extend beyond level of fins; MW = 50% ML. Dorsal surface of mantle, head, and arms thickly covered with large and small chromatophores in two layers, the smaller overlying the larger. Small, retracted chromatophores scattered over ventral surface of mantle, head, and Arms IV. Fins well-developed, short, terminal, round, FW = 47% ML; FL = 19% ML. Eyes very large, lateral, completely covered with reflective tissue. Arm suckers biserial, decrease in size distally. Arm formula: II>III>I>IV. Tentacle length greater than Arms II. Tentacle suckers along proximal oral surface of stalk are biserial, become triserial, decrease in size and become quadraserial distally.

7.5 mm ML: Mantle, funnel, arms, and tentacles all covered dorsally and ventrally with numerous small chromatophores. A few large chromatophores on dorsal surface of head. No nuchal folds. Mantle muscular. Fins subterminal, round, and large. Conus of gladius extends as a very short "spike" beyond posterior junction of fins and mantle. No hooks on tentacles. Arms short but robust, II>III>I>IV. Arm suckers biserial, darkly pigmented, well-developed along entire length of arms. Sucker counts: Arms I-12, Arms II-22, Arms III-18, Arms IV-10. Left tentacle missing. Length of right tentacle nearly equals Arms III. Tentacle suckers also darkly pigmented, all approximately equal in size but slightly smaller than arm suckers, quadraserial, numerous, covering all except base of oral surface of tentacle. Numerous sucker anlagen at distal tip of tentacle.

Remarks Tsuchiya and Okutani (1992) hypothesize that some *Onykia* might be the young stages of *Moroteuthis*.

Family Gonatidae

Gonatus fabricii (Lichtenstein, 1818)

Voucher specimen 6.9 mm ML, ALB7404 sta. 15, USNM 730519.

Species distribution *Gonatus* was common only on *Kaiyo-Maru* cruise 8201 in February–March 1982, with six specimens collected. Two additional specimens were collected on separate cruises over the continental shelf, one in March and one in August. All specimens came from boreal slope water north of the Gulf Stream at the extreme northern part of our study area.

Morphology of voucher specimen 6.9 mm ML (Fig. 21A–C): Mantle moderately long, bluntly rounded posteriorly: MW = 47% ML. Mantle chromatophores elongate: row of 13 to 14 encircle mantle just posterior to opening, three pairs along posterior half of dorsal midline, two pairs lateral to midline pairs, one very large chromatophore at base of each fin, a few others scattered on lateral and ventral surfaces. Fins subterminal, very small, wide, rounded; FW = 35% ML, FL = 10% ML. Funnel broad, robust, extends to mid-point of eyes. Eyes large, with ventral half covered with golden reflective tissue; diagonally directed anteriorly. Head short, broad; HW = 42% ML. Arms I–III well developed, especially II; Arms IV very short, much less developed than other arms. Arm formula: II>I=III>>IV. Basal two pairs of suckers on Arms I–III biserial; suckers increase to three to four rows at midpoint, then decrease to two rows of precursors at tips. Suckers on Arms IV biserial, minute. Arm sucker counts: I-32, II-36, III-36, IV-12.

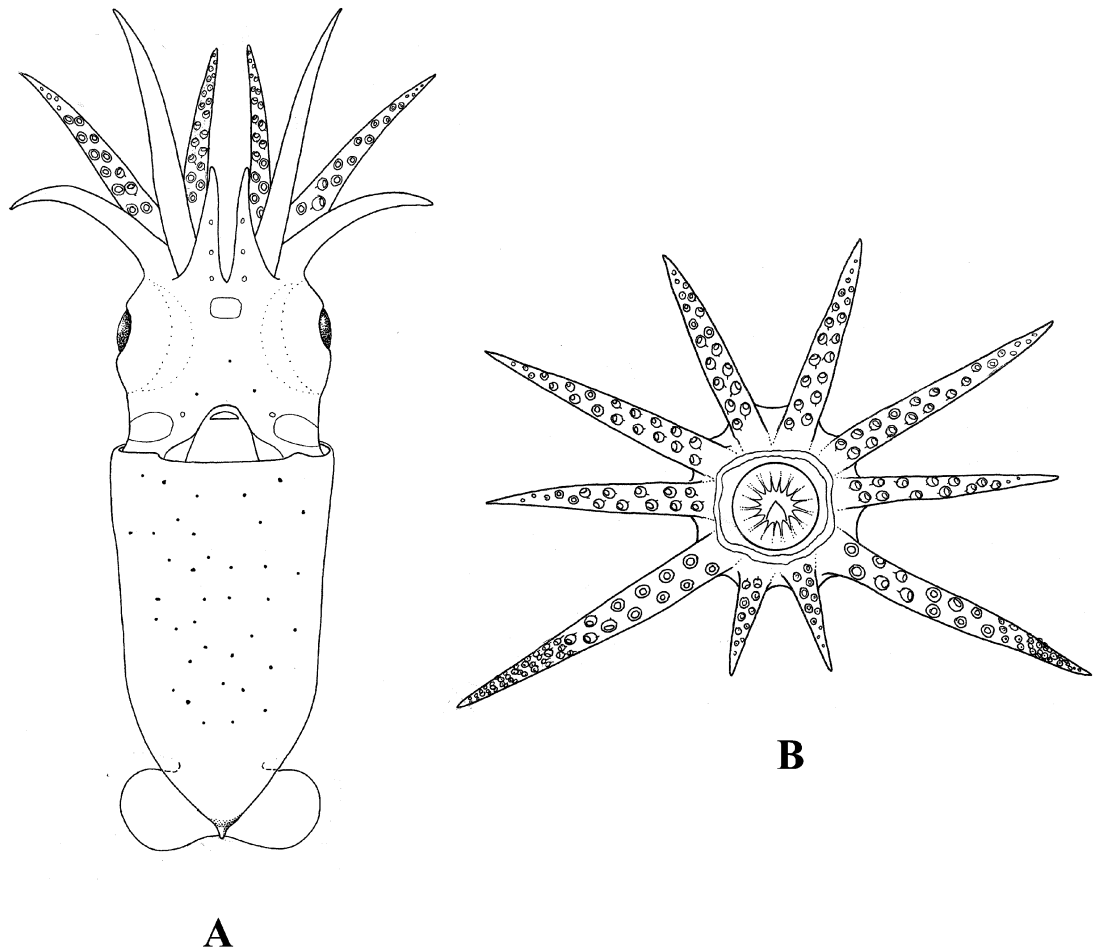

Figure 20

Onykia carriboea Lesueur, 1821. A, ventral view, 4.0 mm ML, USNM 816717, R/V *Trident* sta. 130-6; B, oral view, same specimen.

Tentacles very long, robust, prominent; oral surface covered with more than 75 very small suckers that extend from near proximal base to distal tip. Proximal suckers widely spaced in two rows, then become closely packed in three then four rows. No evidence of enlarged suckers or hook development.

Remarks *Gonatus fabricii* is common in Arctic-Subarctic waters of the western North Atlantic. A boreal-zone eastern Atlantic species, *G. steenstrupi,* has been reported as far west as Newfoundland (Kristensen, 1981). Based on the known distributions of the adults, the *Gonatus* reported here probably are *G. fabricii.* Falcon et al. (2000) found that the most useful characters to distinguish between the paralarvae of the two species are the shape of the dorsal pad of the funnel organ (lateral sides straight in *G. fabricii*; curved in *G. steenstrupi*) and chromatophores on the ventral surface of the head (a pair slightly anterior to the ocular axis present in *G. fabricii*; absent in *G. steenstrupi*).

Family Histioteuthidae

Histioteuthis spp.

Voucher specimens 1.6 mm ML, ALB7302 sta. 57, USNM 730527; 3.2 mm ML, ALB7302 sta. 87, USNM 730526.

Distribution Several species of this genus are found in the western North Atlantic (Voss, 1969; Voss et al., 1992a). We collected *Histioteuthis* throughout the year in plankton samples, but these specimens are not identifiable to species. The 11 specimens of *Histioteuthis* in this study probably include several species because the development of characters is quite different for about the same mantle length, e.g., fin shape and dimensions. Seven specimens came from the southern Sargasso Sea and the other four were associated with the Gulf Stream in the central and northern regions of the study area. Based on midwater trawling in the middle U.S. Atlantic states, Lu and Roper (1979) concluded that *H. reversa*

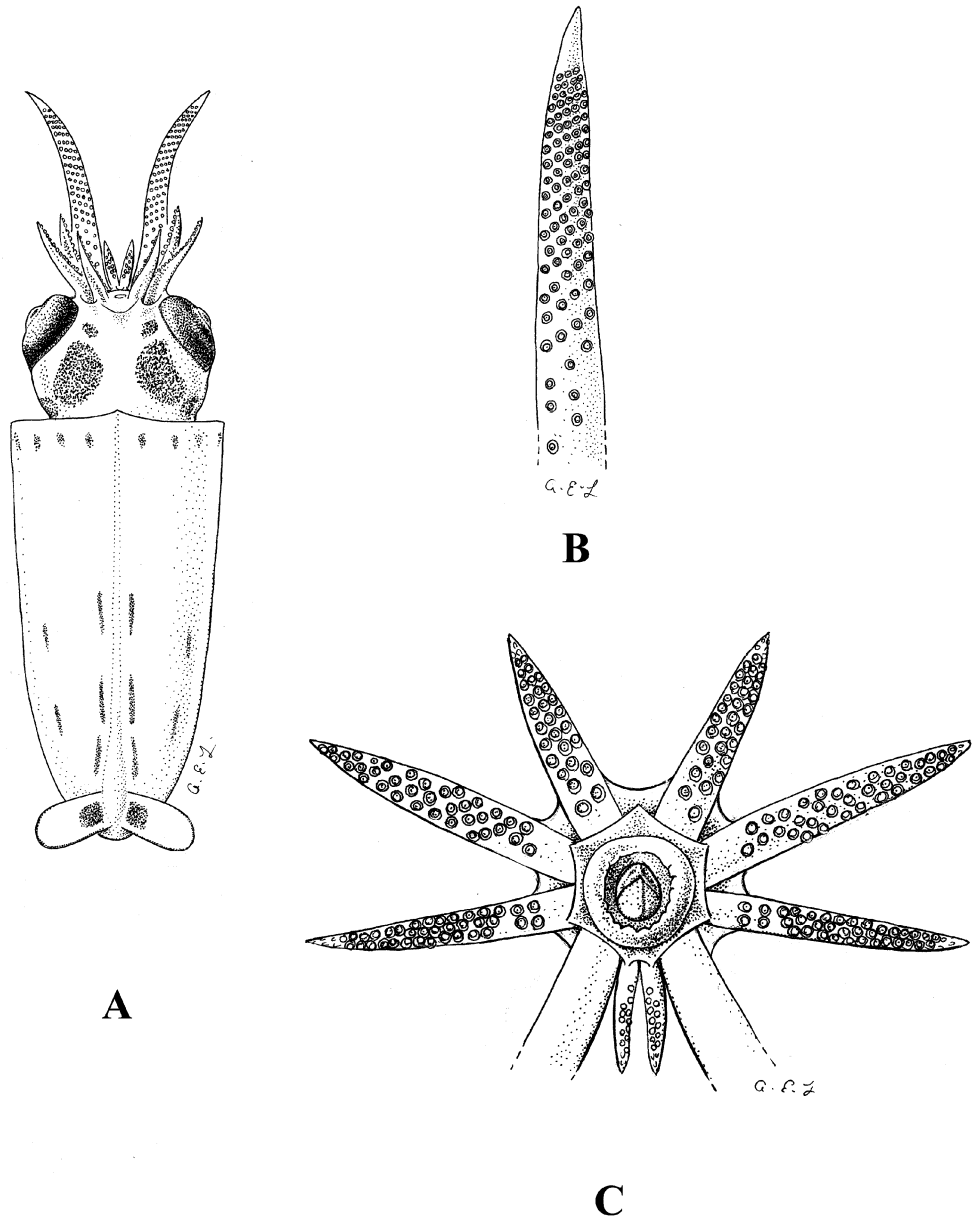

Figure 21

Gonatus fabricii (Lichtenstein, 1818). A, dorsal view, 6.9 mm ML, USNM 730519, R/V *Albatross IV* sta. 7404-15; B, tentacular club, same specimen; C, oral view, same specimen.

probably spawns in the spring. Clarke (1966) suggested that, because the young of *Calliteuthis* (=*Histioteuthis*) *reversa* usually are collected close to land, this species spawns on the continental slope.

Morphology of voucher specimens 1.6 mm ML (Fig. 22A): Mantle muscular, very short, broad. Fins very small in proportion to mantle, close-set, wide, rounded only at tips. Funnel very large, muscular, broad; extends anteriorly nearly to base of arms. Head narrow, long. Eyes "sub-tubular," dorso-ventrally elongate, antero-laterally directed. Arms I and II robust, attenuate, each with 12 suckers, central six somewhat enlarged and globular. Arms III small with eight suckers, only two to four slightly enlarged. Arms IV very short with two minute suckers. Tentacles missing distally (broken off) but proximal stalks robust.

3.2 mm ML (Fig. 22B–E): Mantle muscular, very broad, rounded, much longer dorsally than ventrally; MW = 70% ML. Fins attached to each other, round, muscular, large; extend posteriorly well beyond man-

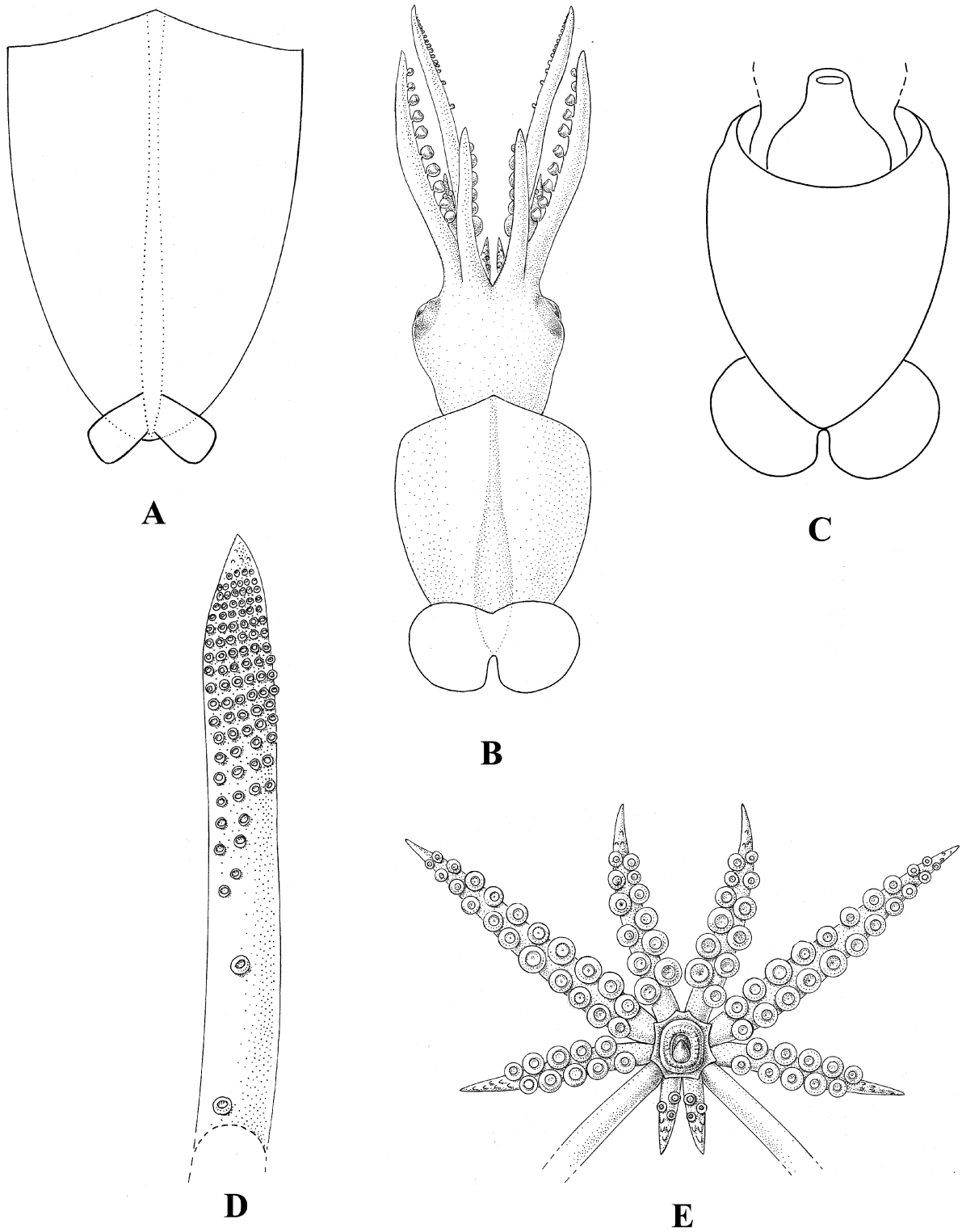

Figure 22

Histioteuthis spp. A, dorsal view of mantle, 1.6 mm ML, USNM 730527, R/V *Albatross IV* sta. 7302-57; B, dorsal view, 3.2 mm ML, USNM 730526, R/V *Albatross IV* sta. 7302-87; C, ventral view of mantle, same specimen; D, tentacular club, same specimen; E, oral view, same specimen.

tle; FW = 56% ML; FL = 31% ML. Reddish chromatophores thickly distributed on mantle, head, and funnel, especially on dorsal surfaces. Funnel very large, broad, but tapers to small opening. Head narrower than mantle, eyes "sub-tubular," antero-laterally directed. Arms long, slender, tapered, bluntly attenuate. Arm formula: II>I>III>IV. Arms III only about two-thirds the length of II. Arm suckers large and few, except for Arms II which have much smaller suckers. Arms I with 18 to 20 suckers, proximal six pairs enlarged; Arms II with 24 suckers, seven pairs enlarged; Arms III with 16 to 18 suckers, five pairs slightly enlarged; Arms IV very short with four to six small suckers plus a few anlagen. Enlarged suckers very globular, spherical, with narrow openings. Tentacles robust, long, about one-fourth longer than Arms II, suckers very small, proportionately few. Tentacular stalk with two single suckers near base; pairs of suckers begin sparsely at mid-stalk, then increase in numbers, first as pairs, then in more than two rows, up to six to eight rows across distal manus where suckers become smaller; minute suckers and anlagen buds only at dactylus.

Remarks One useful feature to recognize *Histioteuthis* is the much smaller size of the tentacular suckers compared with the arm suckers. Species common in the western North Atlantic Ocean include: *reversa*, *corona*, *arcturi* and *bonnellii* (Vecchione, 2001).

Family Bathyteuthidae

Bathyteuthis abyssicola Hoyle, 1885

Voucher specimen 4.3 mm ML, ALB7302 sta. 59, USNM 730514.

Species distribution Our three specimens add little to what is known of the paralarval distribution of this species presented by Roper (1969).

Morphology of voucher specimen 2.8 mm ML (Fig. 23A–C): Mantle muscular, relatively narrow, very blunt posteriorly, MW = 46% ML. Fins widely separated, minute, paddle-shaped, attached laterally to mantle anterior to tip. Funnel very large, long; tube extends at least to anterior level of eyes. Head small, short. Eyes antero-laterally directed, semi-stalked, with very large, bulbous red lenses. Numerous small red-brown chromatophores closely packed over all surfaces of mantle and head. Elongate ink sac completely enveloped in golden bronze reflective tissue. Arms very short, stubby, connected by web in proximal half; approximate order IV>III>II>I. Arm suckers on distal two-thirds of arms biserial but with the appearance of one zigzag row, six suckers on each arm. Tentacles very long, robust, blunt at tips. Club very small, confined to tips of tentacles; 18 minute suckers in two rows.

Remarks Our three specimens, especially the described voucher, constitute among the smallest specimens of this species to be described. The development and distribution of this species have been described by Roper (1969).

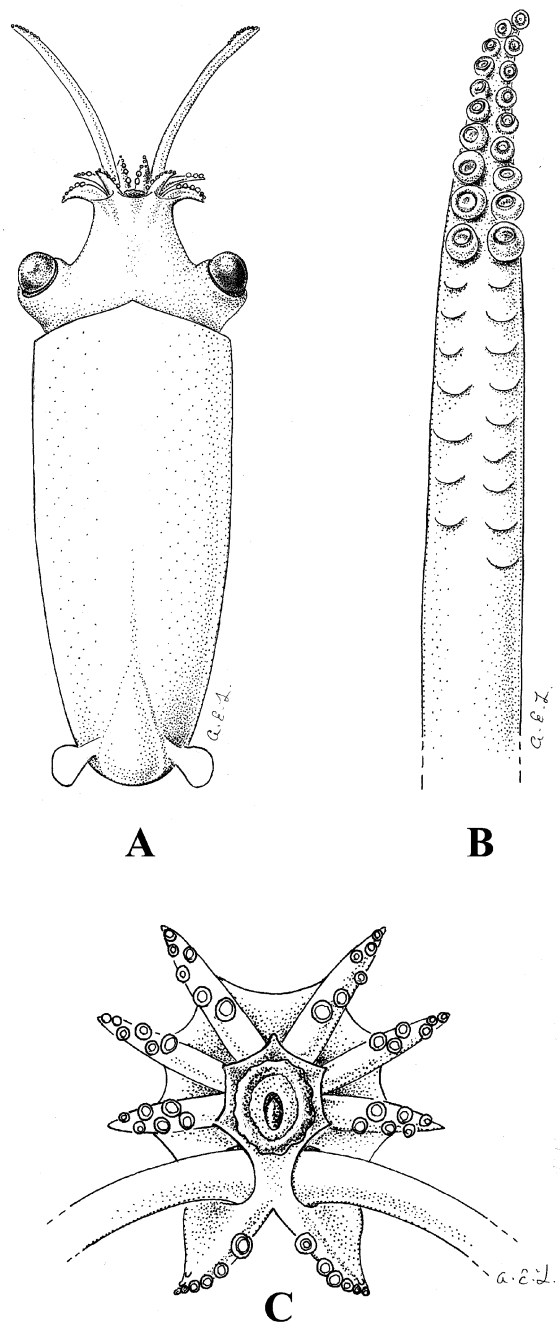

Figure 23

Bathyteuthis abyssicola Hoyle, 1885. A, dorsal view, 4.3 mm ML, USNM 730514, R/V *Albatross IV* sta. 7302-59; B, tentacular club, same specimen; C, oral view, same specimen.

Family Chtenopterygidae

Chtenopteryx sicula (Verany, 1851)

Voucher specimens 2.2 mm ML, ALB7302 sta. 45A, USNM 816718; 3.2 mm ML, ALB7302 sta. 5, USNM 816719; 3.5 mm ML, ALB7302 sta. 34, USNM 816720; 3.6 mm ML, ALB7302 sta. 69, USNM 730522.

Species distribution Little is known of the life history or ecology of this unusual species (Clarke, 1966; Roper and Young, 1975). The 37 specimens we collected provide some insight into the ecology of the paralarvae. These specimens were widely distributed both in time and in space; they were collected throughout the western North Atlantic Ocean and during all seasons. Although never particularly abundant (the maximum number of specimens taken in a single tow was six) the presence of this species in 23 samples from six cruises indicates the ubiquitous distribution of *C. sicula*. These results contrast with the paucity of adult *C. sicula* in trawl surveys.

Morphology of voucher specimens 2.2 mm ML: Mantle large, muscular, broad, tapers to a point posteriorly; mantle much longer than head and arms combined. Fins minute, terminal flaps. Funnel large, robust, muscular, extends to level of mid-eye. Head short, dorso-ventrally compressed. Eyes prominent, tubular, sub-spherical, slightly dorso-ventrally elongate. Tentacles short, robust. Clubs terminal, broad, round, nearly equal in diameter to eyes, with about 25 suckers in round cluster of five to six suckers across. Arms IV longest. Arms II and III subequal, very short, stubby at bases; sudden attenuate papilla-like tips; two to three suckers. Arms I are minute papillae, just developing. Digestive gland sub-spherical. Ink sac well-developed, spherical, with concentration of bronze reflective tissue on ventral surface (precursor to photophore).

3.2 mm ML: Fins very small, with short bases, but extend well posterior to mantle tip; about 10 short muscular supports (ribs) extend from muscular bases, connected by thin, easily torn membrane. Funnel very large, robust; extends anterior to base of arms. Head very short. Eyes tubular, directed antero-laterally, slightly elongate dorso-ventrally. Tentacle stalks robust, longer than arms. Clubs terminal, expanded, round, with about 20 suckers and a papilla-like dactylus. Arms short with attenuate tips and few very small suckers. Digestive gland globular, slightly elongate dorso-ventrally. Photophore anlage a round, reflective, bronze patch at ventral tip, ringed with black.

3.5 mm ML: Fins terminal and lateral, extend far posteriorly beyond mantle tip; joined at posterior tip of mantle to form a deep notch. Series of about 12 muscular supports ("ribs") connected by thin membranous tissue that is easily torn, giving comb-like appearance to fins.

3.6 mm ML (Fig. 24): Tentacular clubs with attenuate dactylus that contains a few sucker anlagen. Otherwise similar to smaller specimens described above.

Remarks Naef (1923) and Clarke (1966) presented a series of life history stages of *C. sicula*.

Family Brachioteuthidae

Brachioteuthis sp.

Voucher specimens 3.0 mm ML, KAI8201 sta. 77, USNM 884237; 6.4 mm ML, BLM07W sta. J1, USNM 884238.

Distribution The 10 specimens of *Brachioteuthis* captured in this study were scattered among seven cruises. Thus, although rarely taken, paralarvae occur during each season throughout the western North Atlantic Ocean.

Morphology of voucher specimens 3.0 mm ML: Mantle long, relatively broad, sac-like, muscular; MW = 57% ML. Mantle covered with chromatophores. Fins very small, separate, postero-lateral, elongate flaps; FW = 17% ML. Neck long, very narrow; neck length equals 33% ML, neck width equals 10% ML. Head bulbous, long, broad; dorsal hump posterior to eyes; HL = 33% ML, HW = 30% ML. Eyes strongly oval in antero-ventral axis. Tentacles prominent, stalks robust, clubs slightly expanded, tips somewhat attenuate; 13 to 15 minute manal suckers in two to three rows; dactylus with anlagen only. TL = 73% ML; tentacle width = 13% ML. Arms I and II very short, II longer. Arms III and IV merely anlagen, papillae-like. Arms I with 0–1 suckers, Arms II with one to two very small suckers; several anlagen.

6.4 mm ML: Neck length about 25% ML. Tentacles long, robust; clubs expanded with drawn out dactyli. Numerous (about 60) small suckers in up to six series across clubs at widest part, numerous anlagen distally. Arms very short; arm formula: II>>I=III>IV. Few (0–4) suckers on arms. Eyes sessile, antero-ventrally elongate. Fins small, round.

Remarks Two species of *Brachioteuthis*, *B. riisei,* and *B. beani* are reported in the region covered by our study, but specimens are so rare in collections that the systematics of the family are not well known, even at the adult level. Consequently, we are not able to assign specific identifications to our material. See Roper and Sweeney (1992) for illustrations of paralarval *Brachioteuthis*. Shea (1995) presented information on taxonomy and distribution of paralarval *Brachioteuthis* spp. in the central North Atlantic.

Family Ommastrephidae

Illex sp.

Taxonomy The development of *Illex* was described in detail by Roper and Lu (1979) and Vecchione (1979b), based on the MARMAP and BLM specimens, respectively. Roper and Lu (1979) used the MARMAP specimens from the middle U.S. Atlantic states to com-

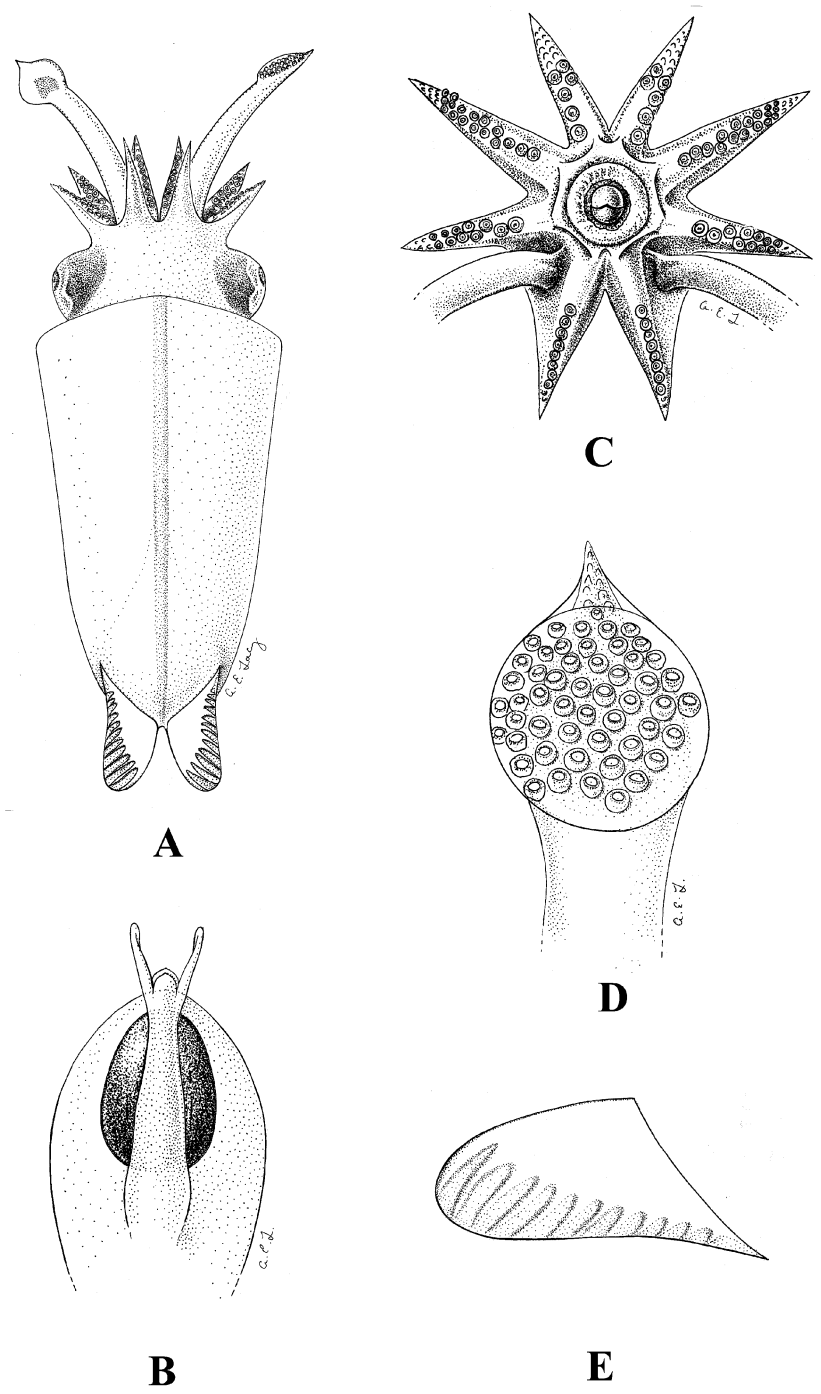

Figure 24

Chtenopteryx sicula (Verany, 1851). A, dorsal view, 3.6 mm ML, USNM 730522, R/V *Albatross IV* sta. 7302-69; B, visceral light organ, same specimen; C, oral view, same specimen; D, tentacular club, same specimen; E, fin, same specimen.

pare the morphology of paralarval *Illex* with the other genera of ommastrephids likely to be found in the western North Atlantic. The characters that are most useful for identification of *Illex* are: 1) all eight suckers at the tip of the fused tentacles (proboscis) are small and of equal size, that is, the two lateral suckers are not en-

larged as in some other genera of ommastrephids; and 2) the fused tentacles are relatively short and robust (tentacle length index = 25.0–71.0). Furthermore, no photophore development occurs on either the eyes or the digestive gland. The stages in the development of *Illex* sp. are presented in Vecchione (1979b).

Distribution Roper and Lu (1979) and Vecchione (1979b) also presented preliminary reports on the planktonic distribution of *I. illecebrosus*. These authors independently reached similar conclusions that the general distribution of planktonic *I. illecebrosus* was centered in the slope water between the shelf edge and the Gulf Stream. However, they reached different conclusions on the seasonality of young *I. illecebrosus*. Lu and Roper (1979) originally felt that the smallest specimens occurred only in winter and spring based on collections from a restricted area in the middle U.S. Atlantic states. However, after finding additional small rhynchoteuthion paralarvae from a broader area, Roper and Lu (1979) concluded that spawning takes place over an extended period, perhaps year-round. Based on a relatively large sample size, Vecchione (1979b) concluded that the winter-spring specimens are *I. illecebrosus*, but the summer specimens are too distinct ecologically to be assigned to *I. illecebrosus* without additional seasonal and regional captures. Two other *Illex* species, *I. oxygonius* and *I. coindetii,* are known from the western North Atlantic Ocean and could be included. Furthermore, Vecchione (1979a) believed that the predominant abundance of planktonic *I. illecebrosus* along the shelf break and continental slope and the absence of eggs in the plankton samples supported earlier proposals that this species spawns on the slope, perhaps in contact with the bottom. *Illex illecebrosus* has since been shown to be a pelagic spawner (O'Dor et al., 1982) with a large gelatinous egg mass. The egg mass could easily be pushed aside by the pressure wave of a bongo sampler and thus not be collected. Spawning on the bottom at the continental slope, therefore, is not a likely explanation for the observed distribution of planktonic *Illex*.

More recent data, including our specimens from *Kaiyo-Maru* cruise 8201, indicate a close relationship between *Illex* paralarval distribution and the interface between the slope water and the Gulf Stream (Dawe and Beck, 1985; Rowell and Trites, 1985; Vecchione and Roper, 1986; Dawe and Stephen, 1988; Perez and O'Dor, 2000). Our specimens from the *Kaiyo-Maru* cruise were collected at stations with a wide range of surface temperatures, about 7–20°C. However, at all of these stations, temperature values converged to 13–18°C at 150–200 m depth (see Vecchione and Roper, 1986). Because the samples were collected by oblique tows between 0–200 m, we do not know the precise depths at which the specimens were collected.

The distribution of *I. illecebrosus* in the BLM samples was very similar to that of pteropod species known to migrate vertically to depths of 200 m or more (Vecchione and Grant, 1983). Furthermore, almost all of the BLM specimens came from subsurface samples; relatively few were collected at the surface (Vecchione, 1979b). O'Dor et al. (1982) suggested that *I. illecebrosus* spawns at the interface between slope water and the Gulf Stream. This interface would be encountered at the deep end of the depth range sampled in our study. The temperatures and salinities at depths of 150–200 m at the KAI8201 stations from which we have planktonic *I. illecebrosus* indicate that this is a region of isopycnal mixing at σt of approximately 26.7 (Vecchione and Roper, 1986), between what Wright and Parker (1976) refer to as the "slope-water thermostad" and Gulf Stream water.

Further support for this relationship between *Illex* paralarval distribution and the slope water/Gulf Stream interface has been presented by Hatanaka et al. (1985), based on logged entries of field identifications of all specimens from *Kaiyo-Maru* cruise 8201. Rowell and Trites (1985), described paralarval distribution in the area of overlap of *I. illecebrosus* and *I. oxygonious* distribution between Cape Canaveral and Cape Hatteras. In addition, the few specimens of paralarval *Illex* that were taken in the surface samples on *Columbus Iselin* cruise 7802 also came from the interface between slope water and the Gulf Stream. Our own long-term research in the waters off Ft. Pierce, Florida, confirms that *Illex* paralarvae occur only in the narrow band of "transitional" water that lies just shoreward of the Florida Current (Gulf Stream) against the outer boundary of the Florida Coastal Water mass (slope water) (Adams, 1997).

The absence of *Illex* specimens in both surface and subsurface samples from unmixed slope water during the VIMS winter cruise to the Norfolk Canyon area (see Ruzecki, 1979 for water-mass analysis), reinforces the hypothesis that it is the interactions between the slope water and the Gulf Stream that are of critical importance to *Illex* spawning, paralarval distribution, and recruitment. Because the physical characteristics of the "slope-water thermostad" and the Gulf Stream remain relatively unchanged year-round, prolonged or non-seasonal spawning by *I. illecebrosus* is quite possible, as suggested by Lu and Roper (1979).

Remarks Based on the distribution of the specimens discussed in Roper and Lu (1979) and Vecchione (1979b), both reports probably described the northern species, *Illex illecebrosus*. Two other species have been reported from the warmer waters of western North Atlantic, *I. oxygonius* and *I. coindetii* (Roper et al., 1969). Therefore, until comparisons can be made among specimens of known parentage, the morphological characters agreed upon by Roper and Lu (1979) and by Vecchione (1979b) must be considered to be of generic

importance. Two recent studies have elucidated the systematics of *I. coindetii* (Roper and Mangold, 1998) and of the entire genus of *Illex* (Roper et al., 1998).

Rhynchoteuthion Type A′

Distribution Twenty-seven specimens identified as rhynchoteuthion Type A′ under-represent the relative abundance of this taxon; 124 additional rhynchoteuthion paralarvae could be identified only as Ommastrephidae, but undoubtedly these included many specimens of rhynchoteuthion Type A′. Rhynchoteuthion Type A′ was collected during all seasons, but taxonomic difficulties preclude definite statements about temporal or spatial distribution. As noted below, rhynchoteuthion Type A′ probably is *Ommastrephes bartramii*. This typically oceanic taxon was found over bottom depths as shallow as 85 m, a result of cross-shelf transport involving Gulf Stream eddies (Vecchione and Grant, 1983). Such transport, together with mixing of shelf and oceanic water masses, is reflected in the very broad salinity range (S = 32.6–36.6 $\times 10^{-3}$) for specimens collected in surface samples. The temperature range for this taxon at the surface was limited to 18.2–25.3°C. On the transect from Bermuda to Rhode Island (cruise CI7802), rhynchoteuthion Type A′ was collected only near the offshore edge of the Gulf Stream. Similarly, off Nova Scotia (cruise KM8201) this species was taken predominantly at the southernmost stations, again indicating a tendency to be concentrated at the offshore edge of the Gulf Stream.

Taxonomy Roper and Lu (1979) described larvae as "rhynchoteuthion Type A′" from the MARMAP collections, which were similar to Yamamoto and Okutani's (1975) "Type A." The two lateral suckers at the tip of the fused tentacles are enlarged, two to three times the diameter of the remaining six suckers. The length of the fused tentacles is short to moderate (tentacle length index = 30.0–70.0). A reflective patch is located on the ventral surface of each eye, and a small, round, well-defined light organ is located near the anterior end of the intestine, between the intestine and the ventral surface of the digestive gland. This combination of characters leads to the suggestion that this is the paralarval form of *Ommastrephes*. Young and Hirota (1990) described development of Pacific *Ommastrephes bartramii*, but no visceral photophore was present. Detailed descriptions and illustrations of rhynchoteuthion Type A′ paralarvae in the mantle length range of 1.00–7.25 mm are given in Roper and Lu (1979). Wormuth et al. (1992) presented some additional information.

Remarks Goldman and McGowan (1992) reported the summer distribution of rhynchoteuthion paralarvae off the Florida Keys, based on discrete-depth samples. They found that the peak of rhynchoteuthion abundance occurred at the Gulf Stream front. The most abundant type was Type A′, which tended to be caught at shallower depths than Type B′. Similarly, Saito and Kubodera (1993) found vertical separation of rhynchoteuthion types in the vicinity of the Kuroshio Current off Japan.

Rhynchoteuthion Type B′ (revised)

Distribution This morphotype was found throughout the year and probably is distributed throughout the study area. As noted for the other ommastrephids in this study, rhynchoteuthion Type B′ occasionally was transported into the continental shelf waters to depths as shallow as 46 m.

Taxonomy Roper and Lu (1979) described as "Rhynchoteuthion Type B′" larvae that they thought belong to *Ornithoteuthis antillarum*. We now believe that some rhynchoteuthion Type B′ include paralarvae of *Sthenoteuthis* and possibly of *Hyaloteuthis*. Refer to Roper and Lu (1979) for the detailed description and illustration of rhynchoteuthion Type B′ from which the following is summarized. Rhynchoteuthion characterized by having the two lateral suckers on the tip of the fused tentacles (proboscis) equal in size or slightly larger than the remaining six suckers, but not enlarged to twice the diameter of the small suckers. The fused tentacles are very thin, narrow, and moderately long to very long (tentacle length index = 54.0–137.0). A single relatively large, round, raised photophore occurs on the ventral surface of each eye. A distinct round photophore is present between the intestine and the digestive gland. The variability in relative sizes of suckers and tentacles indicates possible inclusion of multiple species in rhynchoteuthion Type B′.

Harman and Young (1985) described paralarvae of *Sthenoteuthis oualaniensis* from Hawaiian waters that are very similar to Roper and Lu's (1979) Type B′. Two species belong to this genus: *S. pteropus* which occurs broadly in the tropical/subtropical Atlantic Ocean from approximately 40°N to 30°S and *S. oualaniensis*, a widespread species throughout the tropical Pacific and Indian oceans. Thus it seems safe to assume that the species represented here includes *S. pteropus*. Ommastrephids in our study area, besides *Illex* spp., *O. bartramii*, and *S. pteropus*, include *Ornithoteuthis antillarum* and *Hyaloteuthis pelagica*. The latter two species also may be included in rhynchoteuthion type B′.

Remarks Among the ommastrephids that we have identified, almost as many specimens were rhynchoteuthion Type B′ (21), as were rhynchoteuthion Type A′ (27). Thus, a substantial number of the 124 unidentified rhynchoteuthion specimens in this study are likely to include *Sthenoteuthis*, *Ornithoteuthis*, and *Hyaloteuthis*. Contrary to inferences from sampling for adults (Clarke, 1966), *O. antillarum* probably is not particularly rare in the western North Atlantic based on observations from submersibles (Vecchione and Roper, 1992), from which *O. antillarum* is seen frequently.

Family Chiroteuthidae

Chiroteuthis sp.

Voucher specimen 5.6 mm ML, ALB7302 sta. 71, USNM 730518.

Distribution Only three specimens were collected, so nothing can be ascertained about the distribution except where they were caught.

Morphology of voucher specimen 5.6 mm ML (Fig. 25): Mantle long, narrow, thin-walled, with scattered chromatophores; tapers abruptly to anterior insertion of fins, extends posteriorly into long spike-like tail (broken). Fins short, broad, elliptical. Tip of gladius broken (tail missing). Funnel short, narrow, weakly developed. Neck long, cylindrical, semi-gelatinous, with a few scattered chromatophores; about 3.4 mm long from dorsal mantle margin to posterior edge of eyes. Head small, narrow. Eyes occupy entire anterior portion of head, bulge ventrally; antero-ventral surface of eyes covered by large chromatophores. Eye light organs not distinguishable. Brachial crown displaced dorsally. Arms very short, stubby. Arm formula I=II>IV>>III (Arms III present only as minute anlagen). Arms I and II each with two relatively large suckers that occupy entire oral surface. One sucker each on Arms IV. Tentacles very long, robust; oral surface covered with minute suckers, beginning with one "large" proximal sucker, two to three times diameter of other tentacular suckers, at base of stalk, then a single small sucker, followed distally by six pairs of equal-sized suckers. Manus suckers in two rows proximally, increasing rapidly to three then four rows; suckers end abruptly at dactylus where only minute, very closely packed precursors occur; manus suckers total about 70. Digestive gland bulbous, elongate, vertically oriented; precursor of light organ present as 2-tone bronze reflective tissue on ventral half; ventral-most part set off from upper part by dark ring.

Remarks Paralarval chiroteuthids are referred to as a "doratopsis" stage. Doratopsis paralavae also occur in *Planktoteuthis*, *Asperoteuthis*, and *Grimalditeuthis*. The most common species in our study area is *C. veranyi*, but *C. capensis* and *C. joubini* have been reported from the area as well (Passarella and Hopkins, 1992). Vecchione et al. (1992) described tail morphology of a *Chiroteuthis* paralarva (not *C. veranyi*) collected in the western Atlantic by submersible. Young (1992) provided detailed descriptions and comparisons of Hawaiian doratopsis paralarvae.

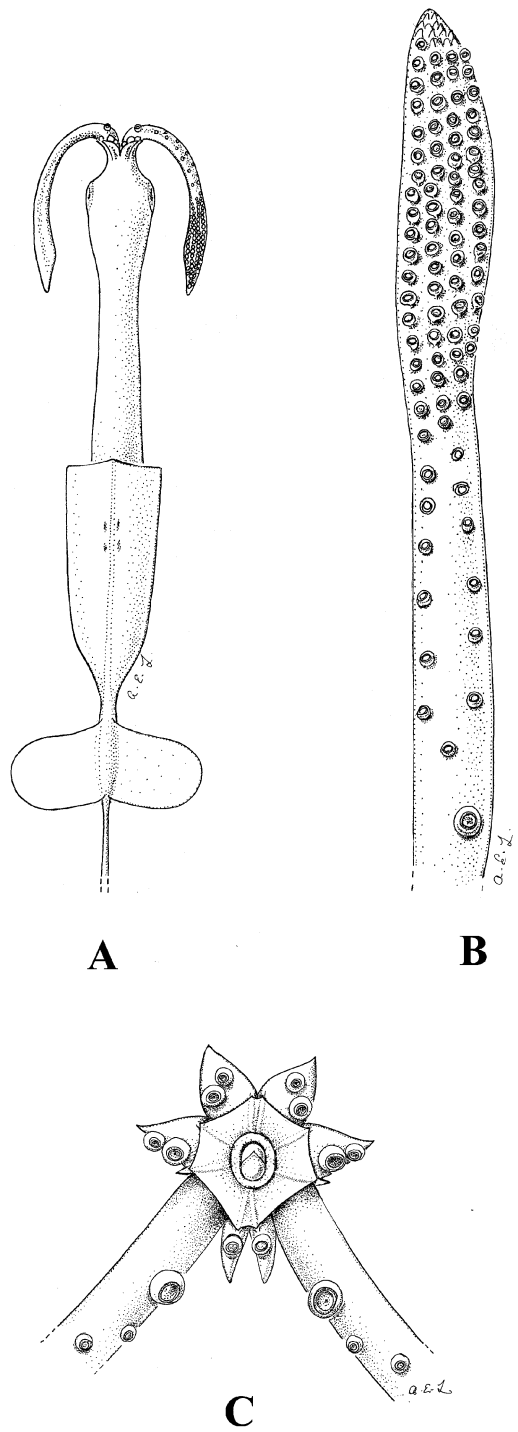

Figure 25

Chiroteuthis sp. A, dorsal view, 5.6 mm ML, USNM 730518, R/V *Albatross IV* sta. 7302-71; B, tentacular club, same specimen; C, oral view, same specimen.

Family Mastigoteuthidae

Mastigoteuthis hjorti Chun, 1913

Voucher specimen 6.0 mm ML, ALB7302 sta. 71, USNM 730521.

Species distribution Nothing can be inferred about the distribution of this species based on the two specimens collected at a single station. Adults, however, appear to be cosmopolitan in tropical and subtropical waters of all major oceans, although the species is not found in Hawaiian waters.

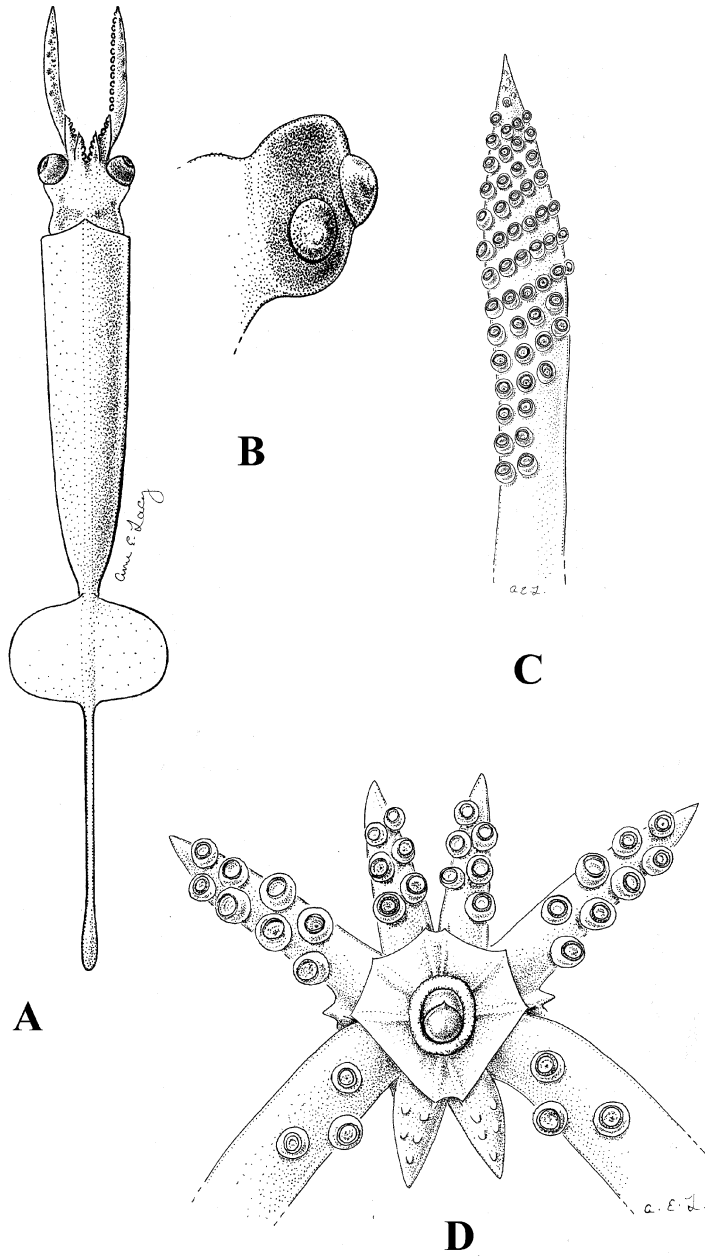

Figure 26

Mastigoteuthis hjorti Chun, 1913. A, dorsal view, 6.0 mm ML, USNM 730521, R/V *Albatross IV* sta. 7302-71; B, ocular light organ, same specimen; C, tentacular club, same specimen; D, oral view, same specimen.

Morphology of voucher specimen 6.0 mm ML (Fig. 26): Mantle long, narrow; tapers gradually to anterior insertion of fins. Fins evenly rounded; fin length about 25% of ML (exclusive of tail); tail very long, spike-like, nearly three times as long as fins. Skin mostly rubbed off but fragments around fins have scattered tubercles. Head small, eyes protrude antero-laterally; one light organ on ventral surface of each eye. Arm formula: II>I>IV>>III (Arms III present only as minute anlagen buds). Tentacles long, robust, about four times the length of Arms II. Clubs with about 54 small suckers in two rows proximally, graded to six rows along "manus." Suckers end abruptly, followed by a number of sucker anlagen on dactylus.

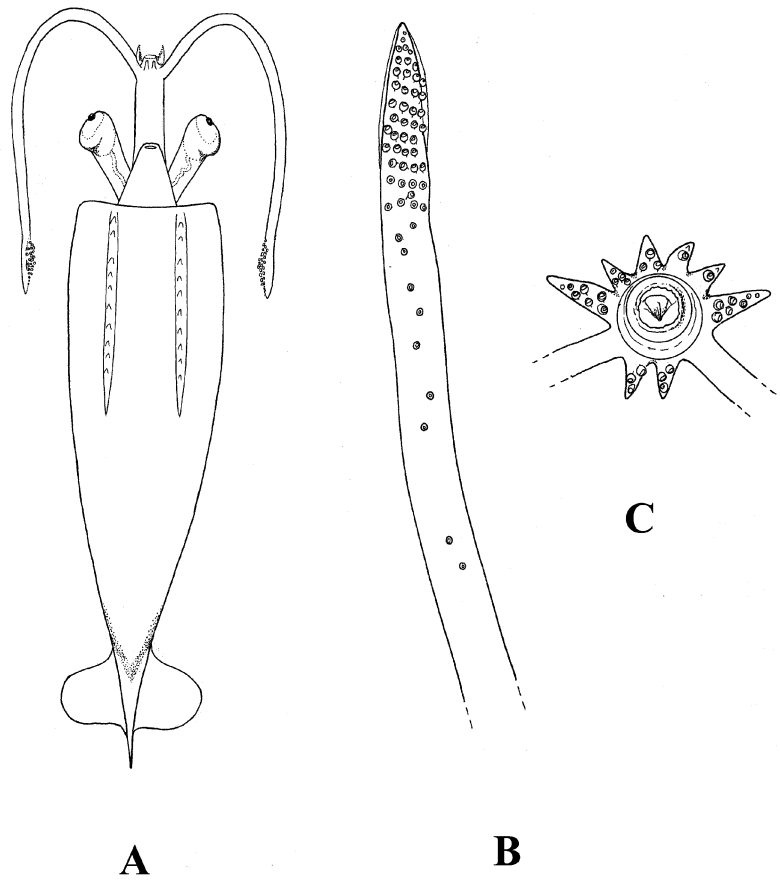

Figure 27

Leachia lemur (Berry, 1920). A, ventral view, 13.8 mm ML, USNM 816942, R/V *Columbus Islen* sta. 7802-20; B, tentacular club, same specimen; C, oral view, same specimen.

Remarks The presence of a photophore on each eye suggests identification of these *Mastigoteuthis* as *M. hjorti*, which has two ocular photophores as subadults.

Family Cranchiidae

The comparative morphology and systematics of larval cranchiids have been examined in detail by Voss (1980) and Voss et al. (1992b). Our material includes specimens of *Leachia lemur* (Berry, 1920) (Fig. 27), *Teuthowenia megalops* (Prosch, 1849) (Fig. 28), *Helicocranchia cf. papillata* (Voss, 1960) (Fig. 29), and ? *Taonius/Galiteuthis* sp.

Leachia lemur (Berry, 1920)

Voucher specimen 13.8 mm ML, CI7802 sta. 20, USNM 816942.

Species distribution Generic distribution circumglobal in tropical, subtropical waters; *L. lemur* occurs in the North Atlantic Subtropical Region, west of about 50°W (north and south Sargasso Sea) (Voss et al., 1992b). Our 11 specimens were collected only in winter.

Morphology of voucher specimen 13.8 mm ML (Fig. 27): Mantle elongate, sharply tapered posteriorly; gladius broad posteriorly then tapers to short, stout, sharp spike; muscular tissue of mantle ends near anterior borders of fins; MW = 28% ML. Fins small, transversely elliptical, length equals width on each fin. Single, narrow, tubercular, cartilaginous strip on ventral mantle extends posteriorly from each funnel-mantle fusion; occupies about 35% of ML; tubercles simple, a single point, two points, and three points aligned transversely with axis of strip. Funnel very large. Head *per se* minute, but dominated by very large antero-lateral, transparent, tubular eye stalks and very long, narrow muscular arm-crown stalk. Eyes relatively small, dorso-ventrally elliptical; small patch of golden

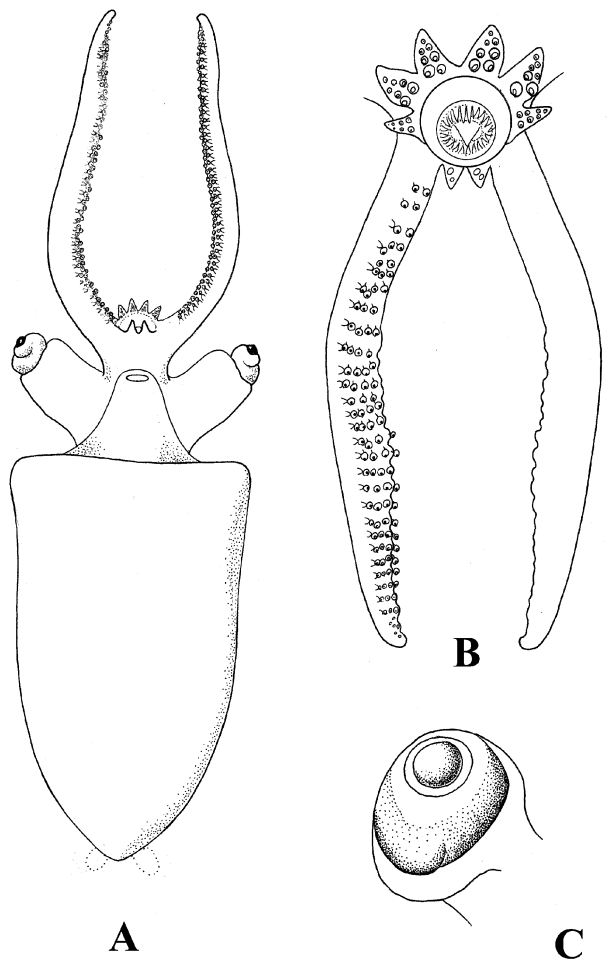

Figure 28

Teuthowenia megalops (Prosch, 1847). A, ventral view, 6.2 mm ML, USNM 816721, R/V *Albatross IV* sta. 7203-59; B, oral view, same specimen; C, eye with ocular light organ anlage, same specimen.

reflective tissue developed on ventral surface, anlagen of two photophores barely detectable. Arms minute, order III>>IV>II>I; seven suckers on Arm III, globular grading to tiny, three on IV and one to four or "variable" each on I and II. Tentacles extremely long, robust: TL = 52% ML. Clubs not expanded; suckers develop at extreme proximal area of tentacular stalk with a zig-zag line of nine minute suckers followed distally by the tiny manal suckers in four rows, and minute anlagen at the tip.

Remarks Paralarval *Leachia* have been referred to as a "*Pyrgopsis*" stage. The simplicity of the tubercles on the ventral mantle cartilaginous strips, as well as the geographical localities of captures, lead us to identify this species as *L. lemur*. The smallest specimen of *Leachia* identified in our samples was 12.5 mm ML.

Teuthowenia megalops (Prosch, 1847)

Voucher specimen 6.2 mm ML, ALB7203 sta. 59, USNM 816721.

Species distribution *Teuthowenia megalops* is found in the North Atlantic Ocean in subarctic and highly productive areas of the North Temperate region (Voss, 1985). Paralarvae in the present material were collected only in the winter.

Morphology of voucher specimen 6.2 mm ML (Fig. 28): Mantle stout sac-like, blunt posteriorly. Fins (broken) very small, separate. Funnel very large, broad. No tubercles on funnel-mantle fusion at this stage. Head small, but eye stalks stout, relatively short; eyes small, dorso-ventrally elliptical, reflective tissue developing, very slight ventral rostrum. Arm-crown stalk short, stout. Arms very small, order I=II>>III=IV. Arms I and

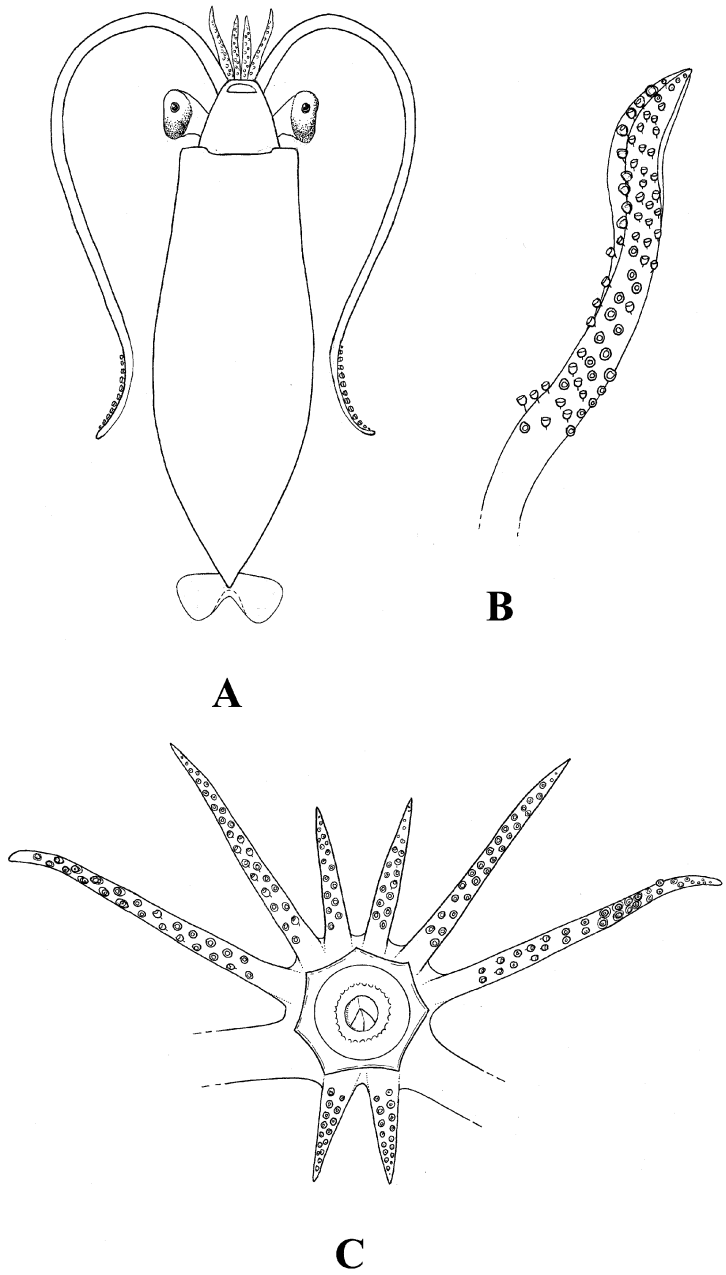

Figure 29
Helicocranchia cf. *papillata* (Voss, 1960). A, ventral view, 15.6 mm ML, USNM 816722, R/V *Albatross IV* sta. 7206-74; B, tentacular club, same specimen; C, oral view, same specimen.

II stout, conical with 5–6 suckers, globular grading to small; Arms III and IV very small, conical; two to three minute suckers and two to four sucker anlagen on III, one to two sucker anlagen on IV. Tentacles moderately large, stalks covered with suckers from proximal base in two rows that rapidly become four rows along stalk to near tip. Large chromatophores are typical for this species, beginning at early paralarval stages.

Remarks This species is the only *Teuthowenia* that occurs in the western North Atlantic region sampled by the programs from which we have material. Voss (1985) described in great detail all growth stages and the distri-

bution of this species. *Teuthowenia megalops* commonly is seen from submersibles off New England (Vecchione and Roper, 1992).

Helicocranchia cf. papillata (Voss, 1960)

Voucher specimens 5.5 mm ML, ALB7206 sta. 44, USNM 816723; 15.6 mm ML, ALB7206 sta. 74, USNM 816722.

Species distribution *Helicocranchia papillata* is a warm-water form distributed widely in the western North Atlantic Subtropical Region, Caribbean Sea, and Gulf of Mexico (Voss et al., 1992b). Our specimens were caught only in the summer in the eastern and southernmost area of our samples.

Morphology of voucher specimens 5.5 mm ML: Mantle elongate, thin walled, muscular, bluntly rounded at tip; MW = 33% ML. Fins subterminal to mantle, wide, paddle shaped, inserted on short, stout shield-shaped posterior rostrum of gladius; FL = 13% ML; FW = 35% ML. Funnel very large; extends to level of buccal mass. Head small. Eyes covered with reflective tissue, dorso-ventrally elongate, with developing ventral rostrum; eyes on short, stout stalks. Arm crown short. Arms short, order II>I>III>>IV; Arms IV merely conical buds. Sucker number on arms: 6 on Arm I, 11 to 12 on Arm II, 6 on Arm III. No enlarged suckers on Arms III at this stage. Tentacles long, robust; TL = at least 65% ML; minute suckers extend entire length of tentacular stalk, none enlarged at this stage.

15.6 mm ML (Fig. 29): Posterior tip of rostrum of gladius broad, rounded; dorsal rostrum shield-shaped or lanceolate; posterior borders of fins united by thin membrane. Funnel huge, extends beyond level of buccal mass. Dorsal element of funnel organ with swollen round limbs and apex; one short, sharp papilla on apex and on each limb; ventral pads oval. Eyes large, on short stalks; with prominent ventral rostrum. Arms small, order III>II>I>>IV; Arms III with four pairs of enlarged suckers in distal third, beginning with eighth pair. Tentacles very long, robust proximally, tapered distally; a few suckers enlarged along ventral row of manus; TL > ML.

Remarks This species is identified as *Helicocranchia* based on the arrangement of the fin attachment to the broad, short rostrum of the gladius, the funnel organ shape and papilla size, and the enlarged suckers on Arms III and the club (in the larger specimen).

Other Cranchiidae

Distribution These are general comments on our unidentified cranchiids. The scarcity of cranchiids in these samples, especially the "*Pyrgopsis*" stage of *Leachia* spp., is somewhat surprising. Based on other studies (Okutani, 1974; Clarke and Lu, 1975; Roper and Young, 1975; Young, 1975; Lu and Roper, 1979), these taxa should be relatively common in the near-surface plankton. However, we collected only 11 specimens of *Leachia lemur*, all in the "*Pyrgopsis*" stage of development. Other cranchiids were quite rare, with five or fewer specimens of each taxon.

The cranchiids were among the few taxa which appeared to be seasonal in distribution. *Leachia lemur*, *Teuthowenia megalops*, and ?*Taonius* were collected only in the winter, whereas *Heliocranchia cf. papillata* was collected only in summer in the southernmost region. Although *Leachia lemur* was found throughout the western North Atlantic, no cranchiids were collected in waters over the continental shelf. In the samples from *Columbus Iselin* cruise 7802 and *Kaiyo-Maru* cruise 8201, young *Leachia lemur* appear to be concentrated near the offshore edge of the Gulf Stream.

Family Octopodidae

Octopodid spp.

General comments on identification Recent work on paralarval octopod systematics, especially Pacific species, has shown that chromatophore patterns and sucker arrangements are promising characters for identification of species (Young and Harman, 1989; Hochberg et al., 1992). The systematics of all octopodids however, still is in serious need of revision.

Sixty octopodids were collected in our study. In spite of morphological diversity among these specimens, we are unable to identify them to species due to taxonomic problems such as bleaching of chromatophores that are important species-distinctive characters. However, two basic morphotypes were evident.

Voucher specimens *Octopus* sp.-type (all arms subequal in length): 1.9 mm ML, ALB7302 sta. 74, USNM 816724 (Fig. 30); 7.4 mm ML, ALB7404 sta. 18, USNM 816866 (Fig. 31); 7.9 mm ML, WIE7410 sta. 11, USNM 816865. "*Macrotritopus*"-type (Arms III greatly elongated and enlarged): 2.4 mm ML, DE7219 sta. 129, USNM 816867 (Fig. 32); 6.6 mm ML, WIE7410 sta. 94, USNM 730507 (Fig. 33).

Species distribution The few "*Macrotritopus*"-type octopods were widely scattered both in time and in space. Young *Octopus*-type octopods are very common in plankton samples, although usually not abundant (e.g. Rees, 1950; Silas, 1968; Lu and Roper, 1979). In the present study, these octopodids were collected on 11 of 21 cruises. Furthermore, they were found in all sampled areas where bottom depths were greater than 100 m and during all seasons. Octopodids comprised the fifth most abundant "taxon" (60 specimens) in our collections and were found in both surface and subsurface samples. At the surface, they were collected at 19.2–22.5°C and at S = 33.2–36.4 × 10^{-3}.

Remarks Uncertainty existed about the identity of the "*Macrotritopus*"-type octopods for many years.

Rees (1954) suggested they probably were the young of *Scaeurgus unicirrhus* (d'Orbigny, 1840). Boletzky (1977b), however has reared *S. unicirrhus* and found that it does not have a "*Macrotritopus*" paralarva. Hanlon et al. (1979) captured and raised a "*Macrotritopus*" which proved to be *Octopus defilippi* Verany, 1851. It is possible however that this morphotype is characteristic of more than one octopodid species.

Family Tremoctopodidae

Tremoctopus violaceus Chiaie, 1830

Voucher specimens 2.3 mm ML, WIE7410, sta. 94, USNM 730508; 7.5 mm ML, ALB7302, sta. 71, USNM 816868.

Species distribution Thirty-six specimens were taken in the southern Sargasso Sea in February and July; a single additional specimen came from the continental shelf off New England in the summer.

Morphology of voucher specimens 2.3 mm ML (Fig. 34): Mantle short, broad, covered with small, evenly spaced chromatophores. Large internal chromatophores on viscera visible through dorsal mantle. Funnel extends to base of Arms IV. Head short, broad, with 12 large chromatophores on dorsal surface. Arms I disproportionately enlarged, length greater than ML; all but distal two suckers are large, globular; third from base greatly enlarged, about two times diameter of next largest. Proximal three to four suckers on Arms I uniserial, remainder biserial. Arms II–IV much shorter; thinner, with small suckers, uniserial proximally, but biserial toward tips. Arm formula I>>>II>IV>>III. Sucker counts: Arms I-15, Arms II-6, Arms III-2, Arms IV-5. Narrow web connects all arms, deepest between Arms I, proportionally shallower with each pair ventrally. Single row of large chromatophores on aboral surface of each arm; one large chromatophore on base of each sucker.

7.5 mm ML: Two pairs of pores on head: one pair between bases of Arms I and II, one pair at bases of Arms IV on each side of funnel opening. Mantle plump, triangular; mantle opening very wide, extends dorsally to level with eye lens. Head wider than mantle opening. Eyes large; occupy entire lateral surface of head. Funnel large, tapers to anterior of eyes, tip free. Arms I and II extremely long. Arm formula: I>II>>IV>III. Suckers on all arms small, numerous, biserial, widely separated. Deep web connects dorsal arms and Arms I and II.

Remarks Thomas (1977) reviewed the genus *Tremoctopus* and described the development of the two recognized species, *T. violaceus* and *T. gelatus*, both of which are found in the western North Atlantic Ocean. Of these species, *T. violaceus* is by far the most common, and our 10 specimens have the characteristics of *T. violaceus*. Hochberg et al. (1992) provide illustrations of all growth stages and references to detailed descriptions.

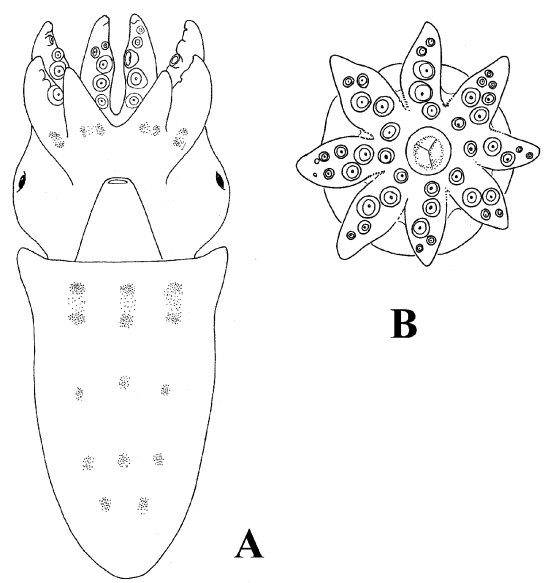

Figure 30

Octopus sp.-type (all arms subequal in length). A, ventral view, 1.9 mm ML, USNM 816724, R/V *Albatross IV* sta. 7302-74; B, oral view, same specimen.

Family Argonautidae

Argonauta argo Linnaeus, 1758/*Argonauta hians* Lightfoot, 1786

Voucher specimens 1.9 mm ML (juvenile female), WIE7410, sta. 89.1, USNM 730515; 1.5 mm ML (?mature male), ALB7106, sta. 33, USNM 730516; 13 mm ML (immature female), CI7802, sta. BRI2, USNM 816869.

Species distribution Argonauts are surface dwellers that are cosmopolitan in tropical and subtropical waters (Roper and Young, 1975). The specimens collected in these plankton surveys included adult females with "shells" (= egg cases), belonging to two species, *A. argo* and *A. hians*. Most of the 13 specimens, though, were either males or immature females without shells and thus could not be identified to species. Argonauts were found during all seasons and in all areas, except from the northernmost cruise off New England and Nova Scotia. Specimens from surface samples were limited to a relatively narrow range of temperatures (18.5–22.3°C) but were found across a broad range of salinities ($S=33.1–36.7 \times 10^{-3}$). The low-salinity captures occurred on the continental shelf (minimum bottom depth 65 m) during September 1976.

Morphology of voucher specimens 1.9 mm ML (juvenile female) (Fig. 35A–B): General appearance very similar to paralarval *Octopus*-type octopodid. Mantle

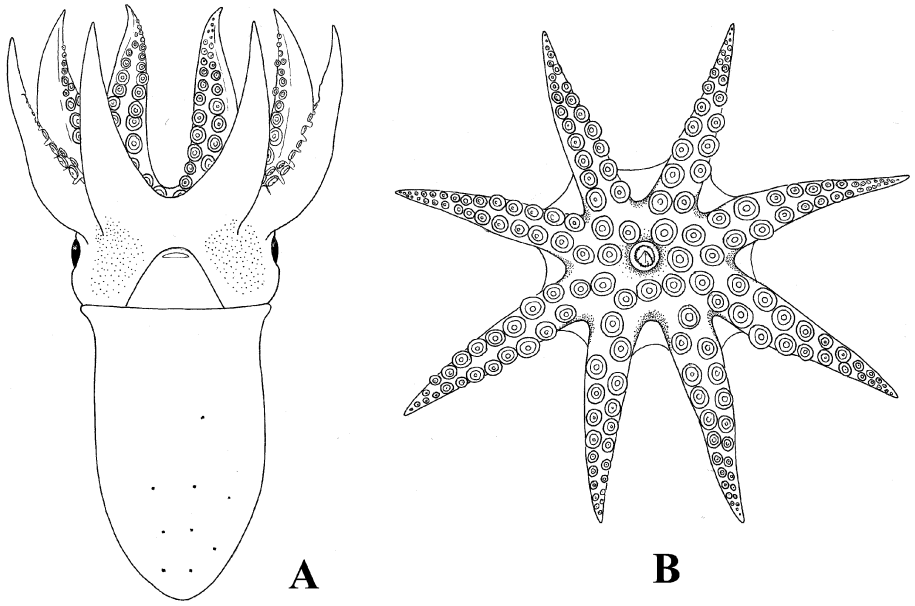

Figure 31

Octopus sp.-type (all arms subequal in length). A, ventral view, 7.4 mm ML, USNM 816866, R/V *Albatross IV* sta. 7404-18; B, oral view, same specimen.

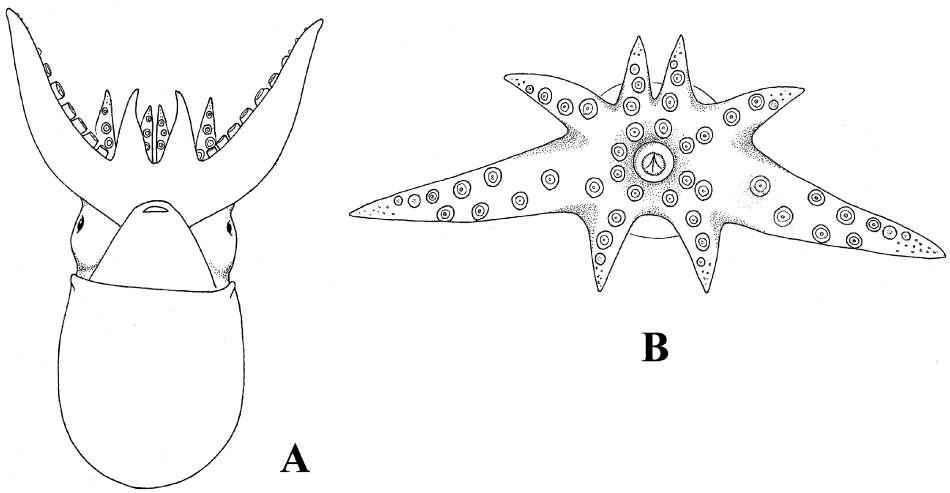

Figure 32

"*Macrotritopus*"-type (arms III greatly elongated and enlarged). A, ventral view, 2.4 mm ML, USNM 816867, R/V *Delaware II* sta. 7219-129; B, oral view, same specimen.

short, very broad, widest at anterior end. Head short, wider than mantle. Eyes large, protrude laterally, covered with silvery reflective tissue. Funnel moderately large, extends to anterior level of eyes, tip not yet free. Arms very short, with eight to nine suckers each, biserial. Arms I longest, distal elongations are devoid of suckers, probably a condition as precursor to the shell-secreting modifications of Arms I of female ("shell web"). Arms all connected by shallow web.

1.5 mm ML (male, possibly mature) (Fig. 35C): Much like immature specimen described above but without naked elongations to Arms I and with left Arm III hecto-

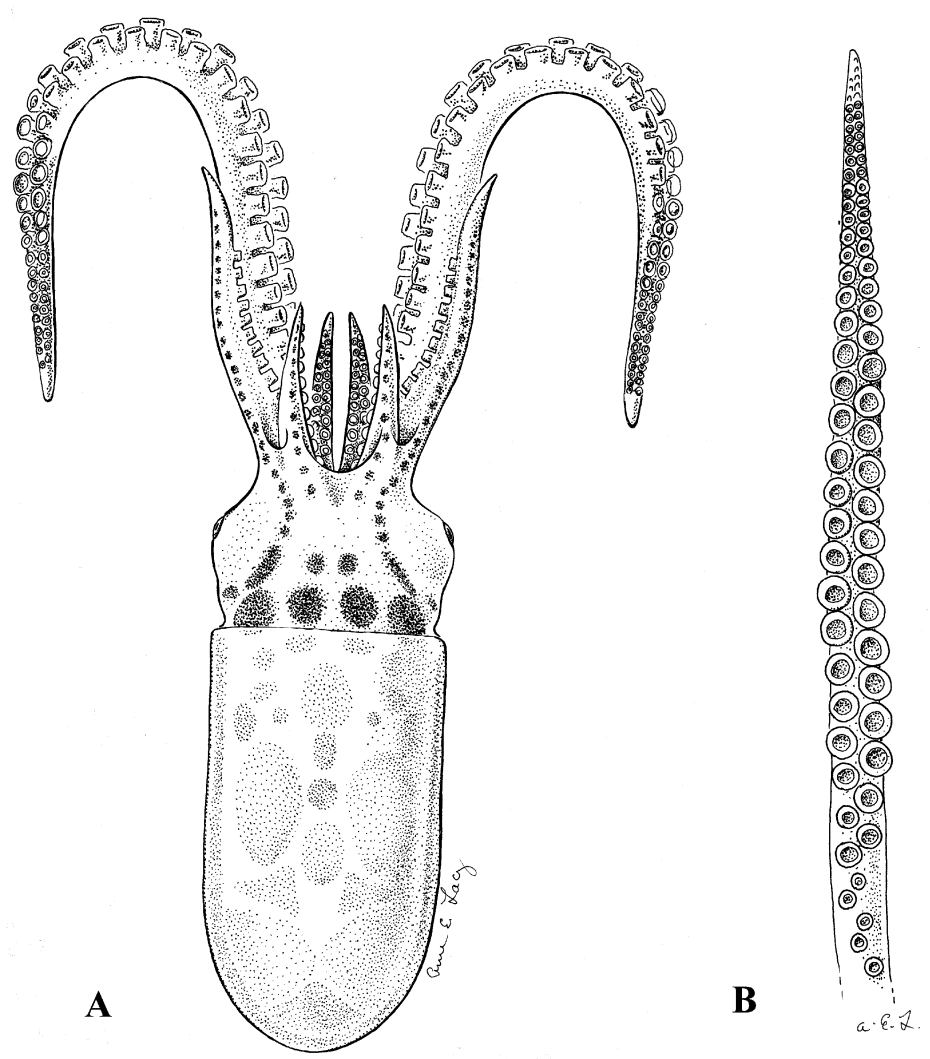

Figure 33

"*Macrotritopus*"-type (arms III greatly elongated and enlarged). A, dorsal view, 6.6 mm ML, USNM 730507, R/V *Wieczno* sta. 7410-94.

cotylized and contained in a large sac (right Arm III was hectocotylized on one specimen). All arms and hectocotylus sac connected by web.

13 mm ML (immature female) (Fig. 36): Mantle very muscular, conical, very broad at anterior margin; attaches to head at postero-dorsal border of eyes. Funnel very large, muscular, extends to base of Arms IV; funnel tip free, but membrane from dorsal edge of Arms IV connects to funnel just posterior to the tip. Eyes very large, bulge laterally. All outer surfaces of mantle, funnel, head, and arms are covered with numerous dense, small chromatophores. Arms II–IV long, slender, subequal in length; each has a single small basal sucker followed by biserial suckers, very numerous, closely-packed, the proximal three to four pairs particularly large; suckers toward the distal tip minute and very thickly set. Arms I very long, thick, much longer than others, but much contorted and twisted in preservation due to strong contraction of "shell web." Basal one to two suckers small, next four pairs noticeably enlarged, following pairs with reduced diameters. Suckers extremely minute distally with longitudinal series widely separated; distal tip devoid of suckers, a ridge-like supporting structure for "shell web." "Shell web" begins as narrow membrane at base of Arms I, broadens noticeably at level where suckers become small (about the fifth to sixth pair), then becomes very expanded in distal one third of arm (full extent and dimension cannot

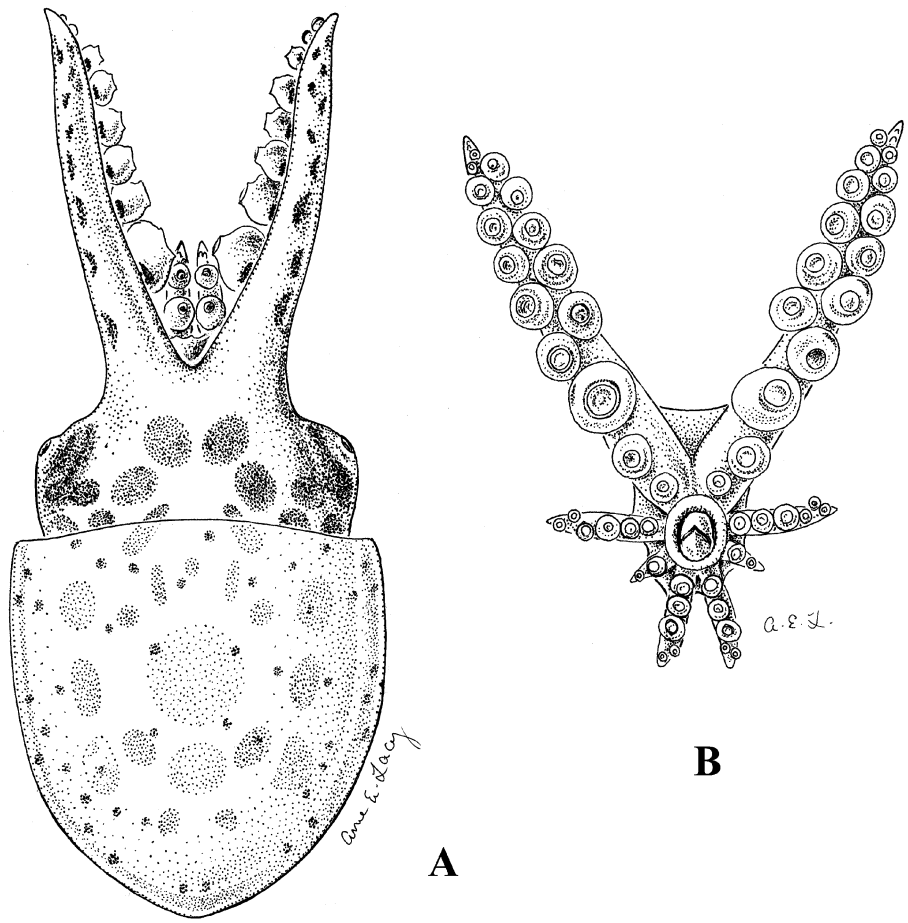

Figure 34

Tremoctopus violaceus Chiaie, 1830. A, dorsal view, 2.3 mm ML, USNM 730508, R/V *Wieczno* sta. 7410-94; B, oral view, same specimen.

be described because "shell webs" are very tightly contracted and covered with dense chromatophores). Ovaries developing, ova extremely minute. Viscero-pericardial membrane covered with dark chromatophores.

Remarks Argonauts are sexually dimorphic and are the only octopod species of which mature adults are commonly collected in plankton samples. One of the most distinctive features of *Argonauta* paralarvae is the presence of a "pit-like" locking apparatus on the funnel. Additional descriptions and illustrations are available in Hochberg et al. (1992), Naef (1928), and Grimpe (1928).

Distributional patterns

A conceptual framework for consideration of the distribution of micronekton, such as young cephalopods, was developed by Haury et al. (1976). They proposed scales of temporal and spatial variability appropriate for various size categories of pelagic organisms. They suggested that the range of spatial (geographical or linear) scales important for micronekton was roughly hundreds of meters to hundreds of kilometers, whereas the important temporal scales ranged from hours to tens of thousands of years. Our data allow us to examine the distribution of young cephalopods within this range of spatial scales and on a temporal scale of a few hours to several years.

Replication of zooplankton collections by repeated, consecutive tows actually represents an interaction of short-term temporal and small-scale spatial variability. Although several attempts at such replication were made during the BLM and MARMAP programs, only three of these "replicate" data sets collected cephalopods. Thus, we have these data only for the most

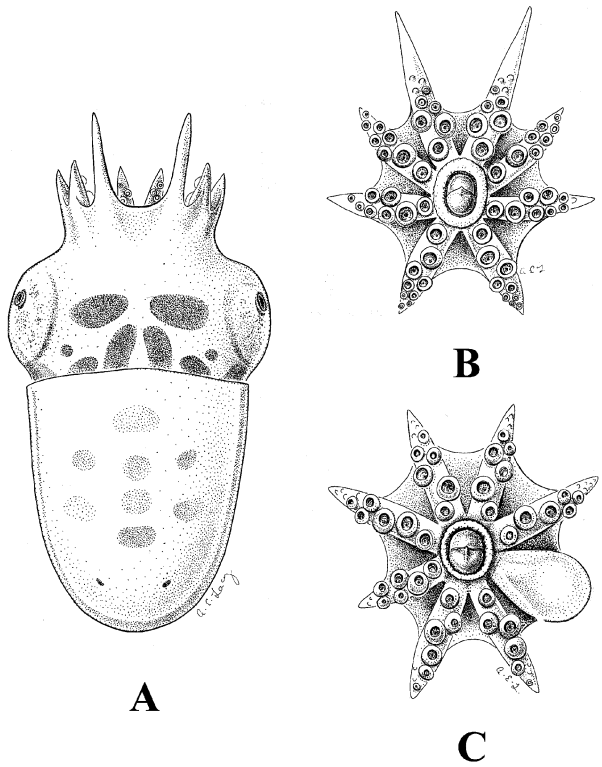

Figure 35

Argonauta argo Linnaeus, 1758/*Argonauta hians* Lightfoot, 1786. A, dorsal view, 1.9 mm ML (juvenile female), USNM 730515, R/V *Wieczno* sta. 7410-89.1; B, oral view, same specimen; C, oral view, 1.5 mm ML (?mature male), USNM 730516, R/V *Albatross IV* sta. 7106-33.

abundant taxon, the loliginids. The high variance in abundance of loliginids (relative to mean abundance) among these "replicates" highlights a serious unresolved problem in field studies of the early life histories of cephalopods. Okutani and McGowan (1969) and Bower et al. (1999) found similarly high variability among consecutive tows. If, as seems likely, such variability represents spatial patchiness, sampling should be designed around either more numerous tows of shorter duration to sample smaller volumes of water, in order to resolve small-scale variability, or long-duration tows to filter extremely large volumes of water, in order to eliminate small-scale variability. However, even the most abundant species seem under represented in samples of any size when compared with ecologically similar fishes and shrimps. An investigator consequently must be prepared to examine many small-volume samples that do not contain cephalopods in order to resolve small-scale variability. In any case, this variability means that, regardless of the scale being considered, a large number of samples must be included in any discussion of the details of the distribution of paralarval cephalopods. Such details were not a goal of this paper.

In contrast to the distinct pattern of diel variability which Vecchione (1981) found for *Loligo pealeii* in surface samples, time series of oblique subsurface tows showed no consistent diel patterns, either for *L. pealeii* (Fig. 5) or for enoploteuthids and ommastrephids (Fig. 37). The patterns in Fig. 37 were tested for periodicity using the nonparametric Runs Test (Siegel, 1956) and the null hypothesis of randomness could not be refuted. Random variability in the time series of oblique samples does not fit the assumptions of diel vertical migration to and from the surface. This suggests that diel changes in the inferred abundance of juvenile cephalopods in surface samples (e.g., Okutani, 1968) may actually result from changes in visual avoidance of the sampler, rather than from vertical migration by these very young stages. The determination of when a species begins diel vertical migration awaits analyses based on high-resolution sets of discrete-depth samples and most likely will vary from species to species (e.g., Shea, 1995).

In spite of these problems with small-scale and short-term variability, the large size of the data set that we have assembled allows us to look for seasonal and interannual temporal patterns as well as mesoscale to large-scale spatial patterns. Both winter and summer samples are available from the southern Sargasso Sea. Two years of data from quarterly cruises over the continental shelf and slope of the middle U.S. Atlantic states are available, as well as from six other shelf and slope cruises that cover a period of six years. The shelf data extend from Nova Scotia to Cape Canaveral. Furthermore, the winter oceanic samples extend from the Bahamas nearly to Newfoundland. Thus, despite some serious sampling problems, such as a lack of completely standardized sampling methods, we feel that the coverage is adequate to elucidate some patterns.

Many of the taxa for which we have the most data were collected throughout the year (Table 2). The taxa that appeared to have distinct seasonal distributions probably reproduce seasonally and included most of the neritic species (e.g., the loliginids collected north of Cape Hatteras) and, surprisingly, the young of two meso-bathypelagic cranchiids. Taxa with uncertain seasonality included those that were collected on only one cruise (e.g., *Mastigoteuthis hjorti*) and those with the most difficult taxonomic problems (such as the loliginids collected south of Cape Hatteras).

The BLM cruises collected 25 taxa from a total of 44 taxa for the entire study. Neritic taxa, such as *Loligo pealeii*, *Illex illecebrosus*, and *Semirossia tenera*, were taken with approximately the same seasonal patterns during both years. However, interannual differences in the oceanic taxa collected were extreme (Table 3). Only *Abraliopsis*

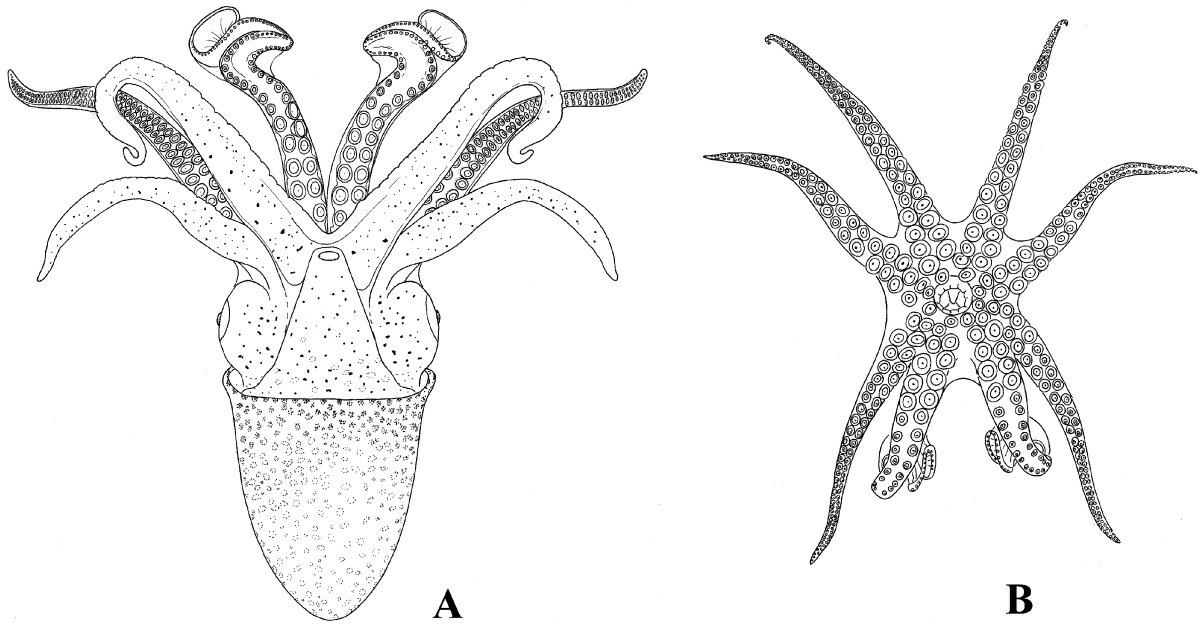

Figure 36

Argonauta argo Linnaeus, 1758/*Argonauta hians* Lightfoot, 1786. A, ventral view, 13 mm ML (immature female), USNM 816869, R/V *Columbus Islen* sta. 7802-BRI2; B, oral view, same specimen.

pfefferi and *Pterygioteuthis* sp. were caught during both years. Therefore, although ample evidence existed that cross-shelf intrusions occurred throughout both years (Vecchione and Grant, 1983), either the chances of cross-shelf transport varied for most cephalopod species or the sampling program failed to collect many species at one time or another. Many more taxa were collected during the expanded sampling of the second year, but a few taxa were found only during the first year.

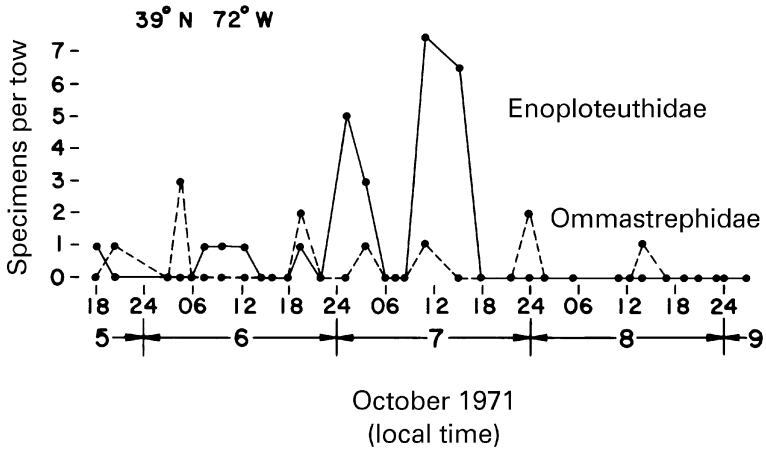

Figure 37

Time series of oblique subsurface tows in October cruise for captures of Enoploteuthidae and Ommastrephidae. Note absence of consistent diel patterns.

Cross-shelf transport is determined largely by the dynamics of the Gulf Stream which vary from year to year. Further, meanders, eddies, and rings of the Gulf Stream are associated with the formation of patchy environments that can be important to distribution and growth of species in the western North Atlantic, young *Illex* for example. Because meso-scale distribution is so patchy, macro-scale distribution sometimes might be masked in cruises with a grid sampling design, since meso-scale spatial conditions might change during the course of the sampling. We interpret the interannual variability as further evidence that extensive sampling is necessary to estimate distribution of young cephalopods, especially of rarely caught species.

The dominant features that control faunal distributions in the western North Atlantic Ocean are the continental shelf and the Gulf Stream. Mesoscale spatial vari-

Table 2

Patterns of seasonal distribution.

Taxa collected throughout the year:	Taxa collected only in winter:	Taxa of uncertain seasonality:
Semirossia tenera	*Stoloteuthis leucoptera*	*?Spirula spirula*
Abralia cf. veranyi	*Leachia lemur*	unidentified Loliginidae
Abraliopsis cf. pfefferi	*Teuthowenia megalops*	*Selenoteuthis scintillans*
Pyroteuthis margaritifera	Taxa not collected in winter:	*Gonatus fabricii*
Ptyerygioteuthis sp.	*Lolliguncula brevis*	*Bathyteuthis abyssicola*
Octopoteuthis sp.	*Loligo pealeii*	*Mastigoteuthis hjorti*
Onychoteuthis cf. banksii	*Ancistrocheirus lesueurii*	*?Taonius/Galiteuthis* sp.
Onykia carriboea	*Discoteuthis?* sp.	*?Bathythauma lyromma*
Histioteuthis spp.	*Helicocranchia cf. papillata*	
Chtenopteryx sicula	"*Macrotritopus*"	
Brachioteuthis sp.		
Illex sp.		
rhynchoteuthion Type B′		
Chiroteuthis sp.		
unidentified octopods		
Tremoctopus violaceus		
Argonauta spp.		

Table 3

Seasonal and interannual differences in BLM collections.

	Fall		Winter		Spring		Summer	
Taxon	Nov '75	Nov '76	Feb '76	Mar '77	Jun ' 76	May '77	Sep '76	Aug '77
Unidentified octopod	X		X				X	
"*Macrotritopus*"		X						
Argonauta argo/Argonauta hians							X	
Semirossia tenera				X	X	X		X
Stoloteuthis leucoptera				X				
Lolliguncula brevis								X
Loligo pealeii	X	X			X	X	X	X
Illex sp.								X
Illex illecebrosus		X		X	X	X		
rhynchoteuthion Type A′								X
rhynchoteuthion Type B′								X
unidentified rhynchoteuthion								X
oegopsid sp. A		X	X					
Abraliopsis cf. pfefferi							X	X
Abralia cf. veranyi								X
Pterygioteuthis sp.				X			X	X
Ancistrocheirus lesueurii	X					X		X
Histioteuthis spp.						X		
Brachioteuthis sp.						X		
Octopoteuthis sp.				X				
?Discoteuthis sp.								X
Gonatus fabricii								X
unidentified oegopsid								X
Total taxa per cruise	3	4	2	5	3	6	5	14
Total taxa per season	6		7		6		16	

Table 4

Patterns of geographical distribution.

Taxa found throughout the western North Atlantic:
- *Abralia cf. veranyi*
- *Abraliopsis cf. pfefferi*
- *Pyroteuthis margaritifera* (see comments in text)
- *Pterygioteuthis* sp.
- *Octopoteuthis* sp.
- *Onychoteuthis cf. banksii*
- *Onykia carriboea*
- *Histioteuthis* spp.
- *Chtenopteryx sicula*
- *Brachioteuthis* sp.
- *Leachia lemur*
- unidentified octopods

Taxa limited to southern portion of study area:
- *Pyroteuthis margaritifera* (see comments in text)
- *Chiroteuthis* sp.
- *Helicocranchia cf. papillata*
- *Tremoctopus violaceus*

Taxa limited to southern and middle portions of study area:
- *Argonauta* spp.

Taxa limited to northern and middle portions of study area:
- *Illex illecebrosus*
- *Teuthowenia megalops*
- *Gonatus* sp.
- Note–no taxa were found only in northern portion of study area.

Taxa of uncertain distribution:
- *Spirula spirula*
- *Semirossia tenera*
- *Stoloteuthis leucoptera*
- Loliginidae (including *Loligo* spp.)
- *Selenoteuthis scintillans*
- *Ancistrocheirus lesueurii*
- *?Discoteuthis* sp.
- *Bathyteuthis abyssicola*
- Ommastrephidae
- *Mastigoteuthis hjorti*
- *Bathothauma lyromma*
- *"Macrotritopus"*

ability in the distribution of planktonic cephalopods was greatest perpendicular to these features rather than latitudinally (Table 4). This contrasts with the situation in the eastern North Atlantic (Lu and Clarke, 1975) where latitudinal variability in cephalopod distribution was great. Latitudinal variability would not be expected to be so great in the western Atlantic, because the entire Gulf Stream system acts as a strong dispersal agent for subtropical and temperate offshore neritic and oceanic species. Furthermore, our samples from boreal water were quite limited, as were samples from the southernmost area sampled. Perhaps if this study had been extended northward (and even southward into the Caribbean Sea), distributional variability associated with latitude might become a more important factor.

Across-shelf transport of paralarvae of tropical, oceanic species probably is limited by the maximum depth at which these species occur in the water column. Zooplankton that migrate vertically to depths greater than the bottom depth on the shelf typically are excluded when Gulf Stream eddies transport the oceanic plankton community onto the shelf (Vecchione and Grant, 1983). Species that are strictly neustonic also are usually excluded, because the direction of the surface flow of shelf water is predominantly offshore (Vecchione, 1979b). Therefore, in our study area, the planktonic cephalopods can be separated into two distinct groups based on the depth of the water column (Fig. 38). One group is confined to water with depths greater than

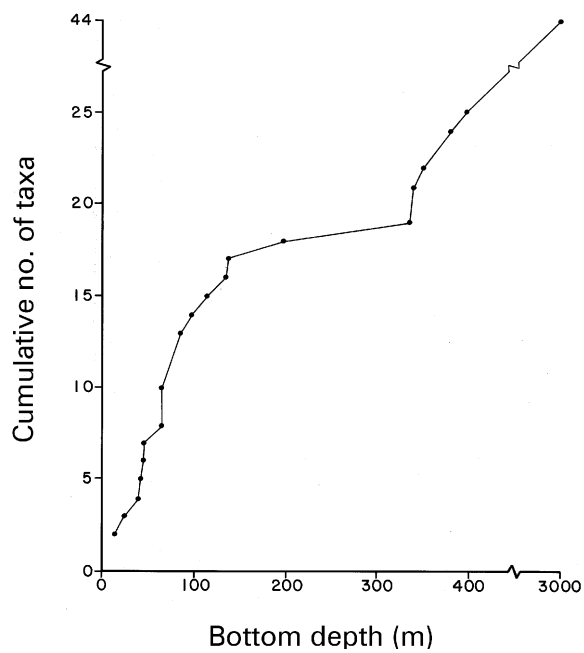

Figure 38

Cumulative number of planktonic cephalopod taxa collected relative to increasing bottom depth. Two distinct groups were found, separated at the shelf/slope interface.

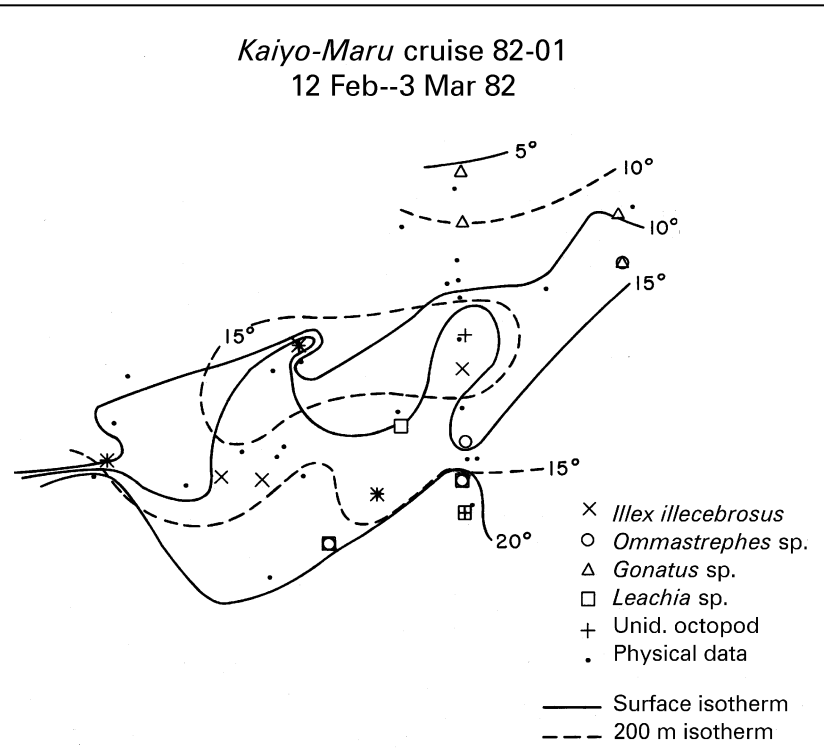

Figure 39

Kaiyo-Maru cruise 8201. Station locations, surface and 200 m isotherms, and the occurrence of the five most abundant cephalopod taxa. See Fig. 1 for specific location.

350 m (i.e., offshore of the shelf break, which in the western North Atlantic occurs at about 200 m depth); this group includes neustonic species such as *Onykia carriboea* and species that probably are deep in the water column, at least during part of the day (e.g., *Histioteuthis* spp., *Chiroteuthis* sp., and *Bathyteuthis abyssicola*). The second group is found over shallower bottom depths and includes the species that spawn on the continental shelf (e.g., the loliginids and *Semirossia tenera*) and those species that probably spend most of their time at intermediate depths of 50–200 m (e.g., ommastrephids and the enoploteuthid group of families) and consequently are subject to transport onto the shelf.

The other pattern of spatial segregation indicated by the data was the distribution of species across the Gulf Stream. Many species seemed to be associated in one way or another with this feature (Figs. 39 and 40). Species such as *Illex* spp. are found predominantly along the shoreward edge of the Gulf Stream in the strong thermal gradient between slope water and the Gulf Stream, whereas rhynchoteuthion Type A′ and *Leachia lemur* often are caught along the offshore edge of the Gulf Stream in the more poorly defined interface with Sargasso Sea water (Vecchione and Roper, 1986).

Strong vertical gradients exist in physical parameters such as temperature, salinity, ambient light, and dissolved oxygen, both on the continental shelf and offshore. Therefore, discrete-depth sampling is required to delimit the dimensions of a species' niche along these gradients. Our only discrete-depth data are from the surface tows, for which temperature and salinity were measured concurrently. These data indicate broad overlapping ranges of temperature and salinity for many species captured in surface waters (Fig. 41). Surface tows may have sampled the extreme end of the range. Or, vertical migration may have caused some individuals to cross water-mass boundaries into the surface layer where conditions were not within the preferred ranges for the species. For example, most *Illex* were collected in subsurface samples, but the few that were collected at the surface indicated a tolerance for very broad ranges of temperature and salinity. Probably temperature and salinity were much less variable at the depths at which most *Illex* were caught. Similar explanations may be true for the other taxa presented in Fig. 41.

A comparison of the results of this study with other studies of cephalopod species distributions is difficult because of the taxonomic problems discussed above

and inherent to varying degrees in virtually all studies. However, comparisons of relative abundance at the family level can be made. We used Spearman's nonparametric correlation coefficient (Siegel, 1956) to compare the rank-order of family abundance of our data with those of other studies of planktonic cephalopods and of trawling studies from the North Atlantic Ocean. The results were as follows:

Study	Type	Location	Spearman's r
Sanchez and Moli, 1985	plankton	Mediterranean	.754
Guerra et al., 1985	plankton	E Atlantic	.733
Cairns, 1976	trawling	NW Atlantic	.732
Okutani and McGowan, 1969	plankton	E Pacific	.640
Dawe and Stephen, 1988	plankton	N Atlantic	.601
Dawe and Stephen, 1988	trawling	N Atlantic	.528
Okutani, 1968	plankton	W Pacific	.523
Yamamoto and Okutani, 1975	plankton	W Pacific	.511
Lu and Roper, 1979	trawling	NW Atlantic	.503
Roper, 1977	trawling	NW Atlantic	.430
Clarke, 1977	trawling	NE Atlantic	.351
Kubodera and Jefferts, 1984	plankton	N Pacific	.327

Thus, the rank-order of family abundance that we found was most similar to that of the study of planktonic cephalopods off the Mediterranean coast of Spain by Sanchez and Moli (1985). Our results were least similar to those of Kubodera and Jefferts (1984) from the northern North Pacific Ocean, where the planktonic cephalopods are very strongly dominated by gonatids. The studies by Guerra et al. (1985) and Cairns (1976) in the eastern and western North Atlantic Ocean, respectively, show a close similarity to our results. Interestingly, though, our results were more similar to those of the plankton studies from the Pacific Ocean (Okutani, 1968; Okutani and McGowan, 1969; Yamamoto and Okutani, 1975) than to several other trawling studies from the North Atlantic Ocean. One conclusion is that it seems there are some families of cephalopods for which plankton net methods sample quite differently from trawling methods. In fact, different midwater trawling techniques provide different rank orders of captures within the same geographical region, as pointed out in comparative studies by Roper (1977) and Wormuth and Roper (1983). Clearly, additional carefully structured comparative studies are necessary in order to determine the most effective techniques to sample different taxonomic groups and different life history stages.

Octopoteuthids and chtenopterygids, for instance, are rare in trawl collections but comparatively common in plankton samples. The frequency of octopoteuthid remains taken in sperm whale stomachs has been compared with their scarcity in trawl samples to emphasize the difficulty in sampling for oceanic cephalopods (Clarke, 1977). For species in families that are relatively common in plankton samples, early-life-history studies, similar to the familiar ichthyoplankton surveys of fisheries science, may be the most reliable method of gathering data on distribution and abundance. An example of the utility of such methods is Kubodera and Okutani's (1981) study of Pacific gonatids.

The enoploteuthid group of families and onychoteuthids rank among the 10 most abundant families in all of these studies, using both trawling and plankton methods. Furthermore, Young et al. (1985) showed that it is possible to collect and to identify enoploteuthid eggs. Consequently, it may be possible to sample enoploteuthid species adequately throughout all their developmental stages using different selective sampling

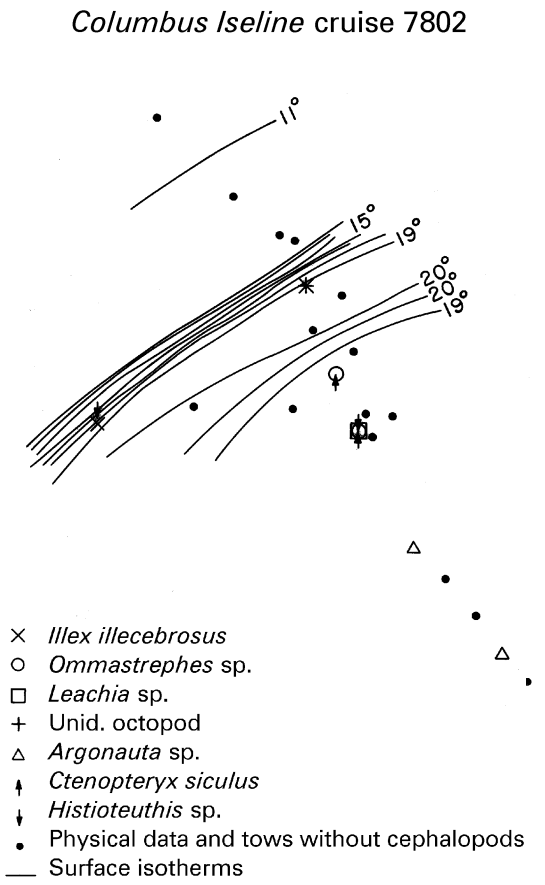

Figure 40

Columbus Islen cruise 7802. Station locations, surface isotherms, and the occurrence of the seven most abundant cephalopod taxa. See Fig. 1 for specific location.

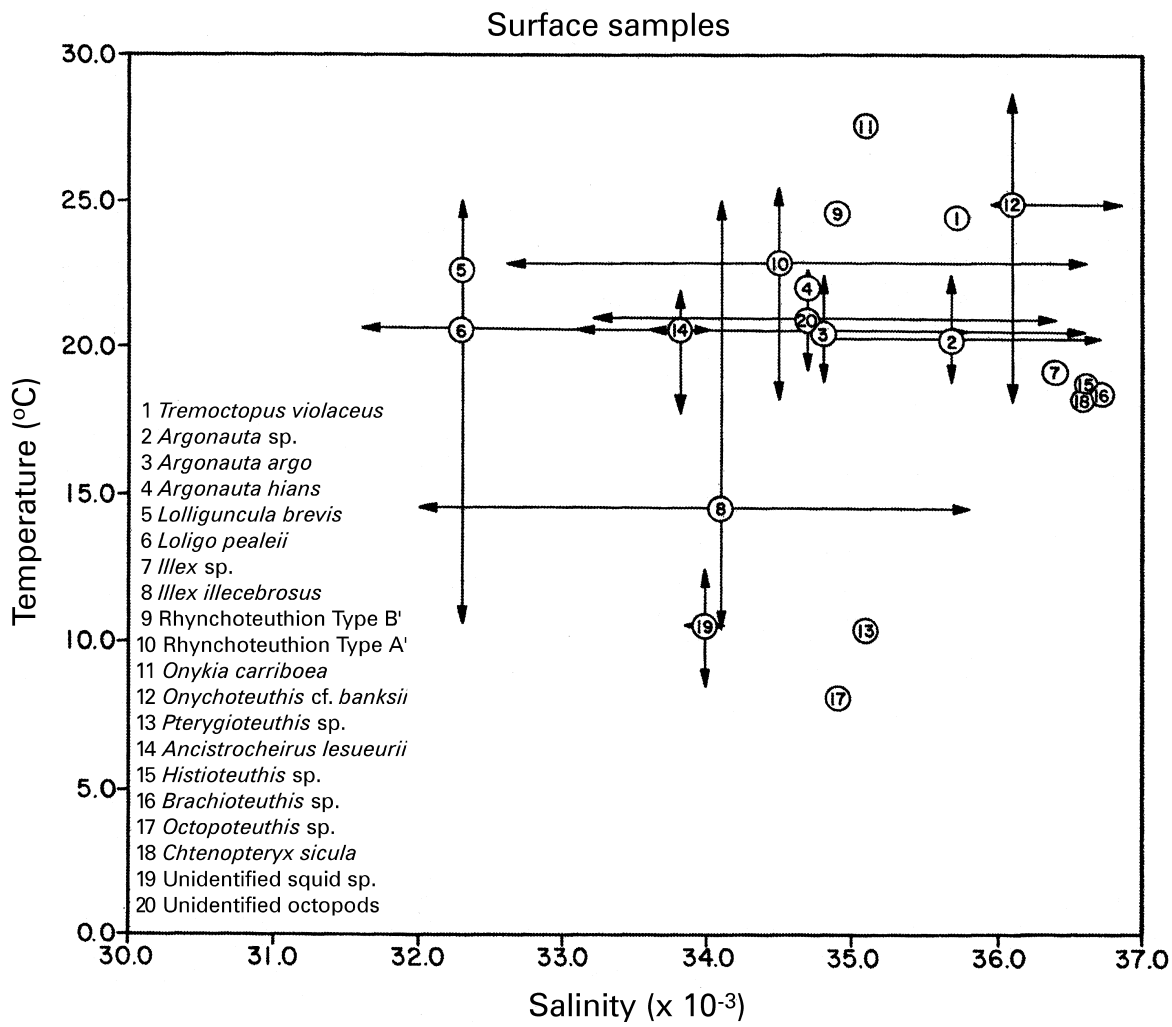

Figure 41

Median and range of surface temperature and surface salinity for captures of cephalopod taxa in neuston samples.

techniques. These species should be considered as likely candidates for studies of the population dynamics of oceanic squids (e.g., Bigelow, 1991).

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Literature Cited

Adams, C. L.
1997. Developmental taxonomy and distribution of paralarval squids from the Florida Current. M.Sc. Thesis, Florida Institute Technology, Melbourne, FL, 177 p.

Beardsley, R. C., and J. Hart.
1978 A simple theoretical model for the flow of an estuary onto a continental shelf. J. Geophys. Res. 83:873–883.

Bello, G.
1992. On the validity, authorship, and publication date of the specific name *Ancistrocheirus lesueurii* (Cephalopoda: Ancistrocheiridae). Veliger 35(2):141–145.

Bigelow, K. A.
1991. Age and growth of three species of squid paralarvae from Hawaiian waters, as determined by statolith microstructures. M.Sc. Thesis, Univ. Hawaii, 78 p.

Bishop, J. M., and J. E. Overland.
1977. Seasonal drift on the Middle Atlantic shelf. Deep-Sea Res. 24:161–169.

Boicourt, W. C.
1982. Estuarine larval retention mechanisms on two scales. *In* V. S. Kennedy (ed.), Estuarine Comparisons, p. 445–457. Acad. Press, N.Y.

Boletzky, S.v.
1974. The "larvae" of Cephalopoda: A review. Thalassia Jugosl 10:45–76.
1977a. Post-hatching behavior and mode of life in cephalopods. Symp. Zool. Soc. Lond. 38:557–567.
1977b. Le developpement embryonnaire de *Scaeurgus unicirrhus*: contribution a l'etude du "*Macrotritopus* problem" (Mollusca, Cephalopoda). Rapp. P. V. Réun. Comm. Intl. Explor. Sci. Mer Med. 24(5):53–63.

Bower, J. R., M. P. Seki, R.E. Young, K. A. Bigelow, J. Hirota, and P. Flament.
1999. Cephalopod paralarvae assemblages in Hawaiian Islands waters. Mar. Ecol. Prog. Ser. 185:203–212.

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

Chun, C.
1910. Die Cephalopoden. Oegopsida. Wiss. Erg. Deu. Tiefsee-Exped. "*Valdivia*" 1898–1899 18(1):1–401, atlas 61 plates.

Clarke, M. R.
1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol. 4:93–300.
1977. Beaks, nets and numbers. Symp. Zool. Soc. Lond. 38:89–126.
1992. Onychoteuthidae. *In* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S.v. Boletzky (eds.), "Larval" and juvenile cephalopods: a manual for their identification, p. 127–137. Smithson. Contrib. Zool. 513, 282 p.

Clarke, M. R., and C. C. Lu.
1975. Vertical distribution of cephalopods at 18°N, 25°W in the North Atlantic. J. Mar. Biol. Assoc. UK 55:165–182.

Cohen, A.
1976. The systematics and distribution of *Loligo* (Cephalopoda, Myopsida) in the western North Atlantic, with descriptions of two new species. Malacologia 15:299–367.

Dawe, E. G., and P. C. Beck.
1985. Distribution and size of short-finned squid (*Illex illecebrosus*) larvae in the Northwest Atlantic from winter surveys in 1969, 1981 and 1982. J. Northwest Atl. Fish. Sci. 6:43–55.

Dawe, E. G., and S. J. Stephen.
1988. The cephalopod assemblage of the Gulf Stream system east of 60°W. Malacologia 29:235–245.

Falcon, L. I., M. Vecchione, and C. F. E. Roper.
2000. Paralarval gonatid squids (Cephalopoda: Oegopsida) from the Mid-North Atlantic Ocean. Proc. Biol. Soc. Wash. 113(2):532–541.

Goldman, D. A., and M. F. McGowan.
1992. Distribution and abundance of ommastrephid squid paralarvae off the Florida Keys in August 1989. Bull. Mar. Sci. 49(1–2)(1991):614–622 [publication date, 27 January 1992].

Grant, G. C.
1977. Seasonal distribution and abundance of the Chaetognatha in the lower Chesapeake Bay. Estuarine Coastal Mar. Sci. 5:807–824.

Grant, G. C., and J. E. Olney.
1979. Lower Bay zooplankton monitoring program: An introduction to the program and results of the initial survey of March 1978. Virginia Inst. Mar. Sci. Spec. Sci. Rep. 93:1–92.

Grimpe, G.
1928. Uber zwei jugendliche Mannchen von *Argonauta argo* L. Zool. Jahrb. 45:77–98.

Griswald, C. A., and J. Prezioso.
1981. *In-situ* observations on reproductive behavior of the long-finned squid, *Loligo pealei*. Fish. Bull. 78:945–947.

Guerra, A., G. Perez-Gandaras, and E. Morales.
1985. Juvenile planktonic cephalopods from NW Africa. Vie Milieu 35:169–170.

Haefner, P. A.
1964. Morphometry of the common Atlantic squid, *Loligo pealei*, and the brief squid, *Lolliguncula brevis* in Delaware Bay. Chesapeake Science 5:138–144.

Hanlon, R. T., S. v. Boletzky, T. Okutani, G. Perez-Gandaras, P. Sanchez, C. Sousa-Reis, and M. Vecchione.
1992. Myopsida. *In* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky (eds.), "Larval" and juvenile cephalopods: a manual for their identification, p. 37–53. Smithson. Contrib. Zool. 513, 282 p.

Hanlon, R. T., R. F. Hixon, and J. W. Forsythe.
1979. The "macrotritopus problem" solved: *Octopus defilippi* raised from a wild-caught, pelagic *Macrotritopus*. Bull. Am. Malacol. Union 1979:70.

Harman, R. F., and R. E. Young.
1985. The larvae of ommastrephid squids (Cephalopoda, Teuthoidea) from Hawaiian waters. Vie Milieu 35(3/4):211–222.

Hatanaka, H., A. M. T. Lange, and T. Amaratunga.
1985. Geographical and vertical distribution of short-finned squid (*Illex illecebrosus*) larvae in the northwest Atlantic. Northwest Atl. Fish. Organ. Sci. Council Stud. 9:93–100.

Haury, L. R., J. A. McGowan, and P. H. Wiebe.
1976. Patterns and processes in the time-space scales of plankton distributions. *In* J.H. Steele (ed.) Spatial pattern in plankton communities, p. 277–327. Plenum Press, N.Y.

Hochberg, F. G., M. Nixon, and R. B. Toll.
1992. Octopoda. *In* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky (eds.), "Larval" and juvenile cephalopods: a manual for their identification, , p. 213–280. Smithson. Contrib. Zool. 513, 282 p.

Kristensen, T. K.
1981. The genus *Gonatus* Gray, 1849 (Mollusca: Cephalopoda) in the North Atlantic. A revision of the North Atlantic species and description of *Gonatus steenstrupi* n. sp. Steenstrupia 7(4):61–99.

Kubodera, T., and K. Jefferts.
1984. Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the northern North Pacific. Bull. Nat. Sci. Mus. Ser. A (Zool.) 10:91–106.

Kubodera, T., and T. Okutani.
1977. Description of a new species of gonatid squid, *Gonatus madokai*, n. sp., from the northwest Pacific with notes on morphological changes with growth and distribution in immature stages (Cephalopoda: Oegopsida). Venus 36:123–151.
1981. *Gonatus middendorffi*, a new species of gonatid squid from the northern North Pacific, with notes on morphological changes with growth and distribution in immature stages (Cephalopoda: Oegopsida). Bull. Nat. Sci. Mus. Ser. A (Zool.) 7:7–26.

Lu, C. C., and M. R. Clarke.
1975. Vertical distribution of cephalopods at 40°N, 53°N, and 60°N at 20°W in the North Atlantic. J. Mar. Biol. Assoc. UK 55:143–163.

Lu, C. C., and C. F. E. Roper.
1979. Cephalopods from Deepwater Dumpsite 106 (western Atlantic): vertical distribution and seasonal abundance. Smithson. Contrib. Zool. 288:1–36.

McConnathy, D. A., R. T. Hanlon, and R. F. Hixon.
1980. Chromatophore arrangements of hatchling loliginid squids (Cephalopoda, Myopsida). Malacologia, 19:279–288.

Middleton, R. W., and J. A. Musick.
1986. The abundance and distribution of the family Macrouridae (Pisces: Gadiformes) in the Norfolk Canyon area. Fish. Bull. 84:35–62.

Naef, A.
1923. Die Cephalopoden: Systematik. Fauna Flora Golfes Neapel 35:149–863.
1928. Die Cephalopoden, Embryologie. Fauna Flora Golfo Napoli 35(2):346–357.

Nesis, K. N.
1987. Cephalopods of the world. Squids, cuttlefishes, octopuses, and allies. T.F.H. Publications, New Jersey, 351 pages. [English transl. by B.S. Levitov of K.N. Nesis, Abridged manual to the cephalopods of the world ocean, 1982, with additions and corrections]

O'Dor, R. K., N. Balch, E. A. Foy, R. W. M. Hirtle, D. A. Johnston, and T. Amaratunga.
1982. Embryonic development of the squid, *Illex illecebrosus*, and effect of temperature on development rates. J. Northwest Atl. Fish. Sci. 3(1):41–45.

Okutani, T.
1968. Studies on early life history of decapoden mollusca-III. Systematics and distribution of larvae of decapod cephalopods collected from the sea surface on the Pacific coast of Japan. Bull. Tokai Reg. Fish. Res. Lab. 55:9–57.
1974. Epipelagic decapod cephalopods collected by micronekton tows during the EASTROPAC expeditions, 1967–1968 (systematic part). Bull. Tokai Reg. Fish. Res. Lab. 80:29–118.

Okutani, T., and J. A. McGowan.
1969. Systematics, distribution, and abundance of the epipelagic squid (Cephalopoda, Decapoda) larvae of the California Current April 1954 — March 1957. Bull. Scripps Inst. Oceanogr. Univ. Calif. 14:1–90.

Passarella, K. C., and T. L. Hopkins.
1992. Species composition and food habits of the micronektonic cephalopod assemblage in the eastern Gulf of Mexico. Bull. Mar. Sci. 49(1–2)(1991):638–659 [publication date, 27 January 1992].

Perez, J. A. A., and R. K. O'Dor.
2000. Critical transitions in early life histories of short-finned squid, *Illex illecebrosus* as reconstructed from gladius growth. J. Mar. Biol. Assoc. UK 80(3):509–514.

Piatkowski, U., W. Welsch, and A. Ropke.
1993. Distribution patterns of the early life stages of pelagic cephalopods in three geographically different regions of the Arabian Sea. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in fisheries biology , p. 417–431. Tokai Univ. Press, Tokyo.

Pritchard, D. W.
1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. J. Mar. Res. 11:106–123.

Rees, W. J.
1950. The distribution of *Octopus vulgaris* Lamarck in British waters. J. Mar. Biol. Assoc. UK 29:361–378.
1954. The *Macrotritopus* problem. Bull. Br. Mus. (Nat. Hist.) Zool. 2:67–100.

Roper, C. F. E.
1969. Systematics and zoogeography of the worldwide bathypelagic squid *Bathyteuthis* (Cephalopoda: Oegopsida). U.S. Nat. Mus. Bull. 291:1–210.
1977. Comparative captures of pelagic cephalopods by midwater trawls. Symp. Zool. Soc. Lond. 38:61–87.

Roper, C. F. E., and C. C. Lu.
1979. Rhynchoteuthion larvae of ommastrephid squids of the western North Atlantic, with the first description of larvae and juveniles of *Illex illecebrosus*. Proc. Biol. Soc. Wash. 91:1039–1059.

Roper, C. F. E., and K. M. Mangold.
1998. Systematics and distributional relationships of *Illex coindetii* to the genus *Illex* (Cephalopoda; Ommastrephidae). *In* P. G. Rodhouse, E. G. Dawe, and R. K. O'Dor (eds.), Squid recruitment dynamics, p. 13–26. FAO Fisheries Technical Paper, 376, FAO, Rome, 273 p.

Roper, C. F. E., and M. J. Sweeney.
1992. Brachioteuthidae. *In* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky (eds.), p. 157–159. "Larval" and juvenile cephalopods: a manual for their identification. Smithson. Contrib. Zool. 513:1–282.

Roper, C. F. E., and G. L. Voss.
1983. Guidelines for taxonomic descriptions of cephalopod species. Mem. Nat. Mus. Vic. 44:48–63.

Roper, C. F. E., and R. E. Young.
1975. Vertical distribution of pelagic cephalopods. Smithson. Contrib. Zool. 209:1–51.

Roper, C. F. E., C. C. Lu, and K. Mangold.
1969. A new species of *Illex* from the Western Atlantic and distributional aspects of other *Illex* species (Cephalopoda: Oegopsida). Proc. Biol. Soc. Wash. 82:295–322.

Roper, C. F. E., C. C. Lu, and M. Vecchione.
1998. A revision of the systematics and distribution of *Illex* species (Cephalopoda: Ommastrephidae. *In* N. Voss, M. Vecchione, R. Toll, and M. J. Sweeney (eds.), Systematics and biogeography of cephalopods, p. 405–423. Smithson. Contrib. Zool. 586(1–2), 599 p.

Roper, C. F. E., M. J. Sweeney, and C. Nauen.
1984. Cephalopods of the world. An annotated and illustrated catalog of species of interest to fisheries. FAO Fish. Synop. 125 Vol. 3, 277 p.

Rowell, T. W., and R. W. Trites.
1985. Distribution of larval and juvenile *Illex* (Mollusca: Cephalopoda) in the Blake Plateau region (northwest Atlantic). Vie Milieu 35:149–161.

Ruzecki, E. P.
1979. On the water masses of Norfolk Canyon. Ph.D. dissertation, Univ. Virginia, Charlottesville, 281 p.

Saito, H., and T. Kubodera.
1993. Distribution of ommastrephid Rhynchoteuthion paralarvae (Mollusca, Cephalopoda) in the Kuroshio region. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in fisheries biology, p. 457–466. Tokai Univ. Press, Tokyo.

Sanchez, P., and B. Moli.
1985. An annotated list of cephalopod larvae collected off the Mediterranean coast of Spain. Vie Milieu 35:171–173.

Shea, E. K.
1995. The early life histories of three families of cephalopods (Order Teuthoidea) and an examination of the concept of a paralarva. M.Sc. thesis, College William and Mary, Williamsburg, VA, 133 p.

Sherman, K., A. Solow, J. Jossi, and J. Kane.
1998. Biodiversity and abundance of the zooplankton of the Northeast Shelf ecosystem. ICES J. Mar. Sci. 55:730–738.

Siegel, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., NY, 312 p.

Silas, E. G.
1968. Cephalopoda of the west coast of India collected during the cruises of the research vessel *Varuna*, with a catalogue of the species known from the Indian Ocean. Mar. Biol. Assoc. India Symp. Ser. 3:277–359.

Stephen, S. J.
1985. The distribution of larvae of the genus *Octopoteuthis* Ruppell, 1844 (Cephalopoda, Teuthoidea). Vie Milieu 35:175–179.

Stephen, S. J., and K. Jefferts.
1992. Octopoteuthidae. *In* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky (eds.), "Larval" and juvenile cephalopods: a manual for their identification, p. 165–166. Smithson. Contrib. Zool. 513, 282 p.

Sweeney, M. J., and C. F. E. Roper.
1998. Classification, type localities, and type repositories of recent Cephalopoda. *In* N.A. Voss, M. Vecchione, R.B. Toll, and M.J. Sweeney (eds.), Systematics and biogeography of cephalopods, p. 561–599. Smithson. Contrib. Zool. 586, 599 p.

Sweeney, M. J., C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky (eds.).
1992. "Larval" and juvenile cephalopods: a manual for their identification. Smithson. Contrib. Zool. 513, 282 p.

Thomas, R. F.
1977. Systematics, distribution, and biology of cephalopods of the genus *Tremoctopus* (Octopoda: Tremoctopodidae). Bull. Mar. Sci. 27:353–392.

Toll, R. B.
1983. The lycoteuthid genus *Oregoniateuthis* Voss, 1956, a synonym of *Lycoteuthis* Pfeffer, 1900 (Cephalopoda: Teuthoidea). Proc. Biol. Soc. Wash. 96(3):365–369.

Tsuchiya, K., and T. Okutani.
1992. Growth stages of *Moroteuthis robusta* (Verrill, 1881) with the re-evaluation of the genus. Bull. Mar. Sci. 49(1–2) (1991): 137–147 [publication date, 27 January 1992].

Vecchione, M.
1979a. Planktonic molluscan faunal structure across a large scale environmental gradient. PhD. dissertation, College William Mary, Williamsburg, VA, 153 p.
1979b. Larval development of *Illex* Steenstrup, 1880, in the northwestern Atlantic, with comments on *Illex* larval distribution. Proc. Biol. Soc. Wash. 91:1060–1075.
1981. Aspects of the early life history of *Loligo pealei* (Cephalopoda; Myopsida). J. Shellfish Res. 1:171–180.
1982. Morphology and development of planktonic *Lolliguncula brevis* (Cephalopoda: Myopsida). Proc. Biol. Soc. Wash. 95:602–609.
1986. The international symposium on the ecology of larval molluscs: Introduction and summary. Bull. Am. Malacol. Union 4:45–48.
1988. *In-situ* observations on a large squid spawning bed in the eastern Gulf of Mexico. Malacologia, 29:135–141.
1991. Observations on the paralarval ecology of a euryhaline squid, *Lolliguncula brevis* (Cephalopoda: Loliginidae). Fish. Bull. U.S. 89:515–521.
2001. Cephalopods of the continental slope east of the United States. American Fisheries Society Symposium, 25:153–160.

Vecchione, M., and G. C. Grant.
1983. A multivariate analysis of planktonic molluscan distribution in the Middle Atlantic Bight. Continental Shelf Res. 1:405–424.

Vecchione, M., and C. F. E. Roper.
1986. Occurrence of larval *Illex illecebrosus* and other young cephalopods in the slope water/Gulf Stream interface. Proc. Biol. Soc. Wash. 99:703–708.
1992. Cephalopods observed from submersibles in the western North Atlantic. Bull. Mar. Sci. 49(1–2)(1991):433–445 [publication date, 27 January 1992].

Vecchione, M., B. H. Robison, and C. F. E. Roper.
1992. A tale of two species: tail morphology in paralarval *Chiroteuthis* (Cephalopoda: Chiroteuthidae). Proc. Biol. Soc. Wash. 105(4):683–692.

Verrill, A. E.
1882. Report on the cephalopods of the northeastern coast of America. U.S. Bur. Fish. Rep. 1879:211–455.

Villanueva, R., and P. Sanchez.
1993. Cephalopods of the Benguela Current off Namibia: new additions and considerations on the genus *Lycoteuthis*. J. Nat. Hist. 27:15–46.

Voss, N. A.
1969. A monograph of the Cephalopoda of the North Atlantic. The family Histioteuthidae. Bull. Mar. Sci. 19:713–867.
1980. A generic revision of the Cranchiidae (Cephalopoda; Oegopsida). Bull. Mar. Sci. 30:365–412.
1985. Systematics, biology and biogeography of the cranchiid cephalopod genus *Teuthowenia* (Oegopsida). Bull. Mar. Sci. 36:1–85.

Voss, N. A., S. J. Stephens, and Zh. Dong.
1992a. Histioteuthidae. *In* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky (eds.), p. 73–91. "Larval" and juvenile cephalopods: a manual for their identification. Smithson. Contrib. Zool. 513, 282 p.
1992b. Cranchiidae. *In* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky (eds.), "Larval" and juvenile cephalopods: a manual for their identification, p. 187–210. Smithson. Contrib. Zool. 513, 282 p.

Wormuth, J. H., and C. F. E. Roper.
1983. Quantitative sampling of oceanic cephalopods by nets: problems and recommendations. Biol. Oceanogr. 2(2–4):357–377.

Wormuth, J. H., R. K. O'Dor, N. Balch, M. C. Dunning, E. C. Forch, R. F. Harman, and T. W. Rowell.
1992. Ommastrephidae. *In* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky (eds.), "Larval" and juvenile cephalopods: a manual for their identification, p. 105–119. Smithson. Contrib. Zool. 513, 282 p.

Wright, W. R., and C. F. Parker.
1976. A volumetric temperature/salinity census for the Middle Atlantic Bight. Limnol. Oceanogr. 21:563–571.

Yamamoto, K., and T. Okutani.
1975. Studies on early life history of decapoden Mollusca-V. Systematics and distribution of epipelagic larvae of decapod cephalopods in the northwestern waters of Japan during the summer in 1970. Bull. Tokai Reg. Fish. Res. Lab. 83:45–96.

Young, R. E.
1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithson. Contrib. Zool. 97, 159 p.
1975. *Leachia pacifica* (Cephalopoda, Teuthoidea): spawning habitat and function of the brachial photophores. Pac. Sci. 29(10):19–25.

1978. Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. Fish. Bull. 76(3):583–615.

1992. Chiroteuthids and related paralarvae from Hawaiian waters. Bull. Mar. Sci. 49(1–2)(1991):162–185 [publication date, 27 January 1992].

Young, R. E., and R. F. Harman.

1985. Early life history stages of enoploteuthin squids (Cephalopoda: Teuthoidea: Enoploteuthidae) from Hawaiian waters. Vie Milieu 35:181–201.

1987. Descriptions of the larvae of three species of the *Onychoteuthis banksii* complex from Hawaiian waters. Veliger 29(3):313–321.

1989. Octopodid paralarvae from Hawaiian waters. Veliger 32(2):152–165.

1998. Phylogeny of the "enoploteuthid" families. *In* N. Voss, M. Vecchione, R. Toll, and M. J. Sweeney (eds.), Systematics and biogeography of cephalopods, p. 257–270. Smithson. Contrib. Zool. 586(1–2), 599 p.

Young, R. E., and J. Hirota.

1990. Descriptions of *Ommastrephes bartramii* paralarvae with evidence of spawning in Hawaiian waters. Pac. Sci. 44(1):71–80.

Young, R. E., R. F. Harman, and K. M. Mangold.

1985. The common occurrence of oegopsid squid eggs in near-surface oceanic waters. Pac. Sci. 39(4):359–366.