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SYSTEMATICS AND ZOOGEOGRAPHY OF THE WORLDWIDE BATHYPELAGIC SQUID *BATHYTEUTHIS* (CEPHALOPODA: OEGOPSIDA)

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Systematics and Zoogeography of the Worldwide Bathypelagic Squid *Bathyteuthis* (Cephalopoda: Oegopsida)

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This work forms number 291 of the *Bulletin* series.

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Director, United States National Museum

Contents

Systematics and Zoogeography of the Worldwide Bathypelagic Squid *Bathyteuthis* (Cephalopoda: Oegopsida)[1]

Introduction

Study the deep-sea squid and see how he does only what he has to.
Carl Sandburg

Bathyteuthis abyssicola Hoyle has been recorded as an uncommon deep-sea species from widely scattered localities throughout the major oceanic regions of the world. In recent years the relatively large quantity of material that has accumulated allows a more thorough analysis of the systematics and distribution of *Bathyteuthis.* Newly described species and range extensions are represented in small collections from lower latitudes; however, the bulk of the material, useful in determining details of horizontal and vertical distribution, comes from the Antarctic Ocean.

The cephalopods of the open waters of the Southern or Antarctic Ocean and the shallower waters along the shores of the Antarctic Continent are very poorly known despite an impressive list of vessels and expeditions that have collected in these regions. Most of the species known in the Antarctic cephalopod fauna were described from collections made during the great era of exploration prior to World War I. Berry (1917) reviewed the literature and listed the species that occur south of 60° south latitude; with the addition of Berry's 5 new species the list at that time contained 17 species—11 species of the order Octopoda and 6 species of the suborder Oegopsida. Thiele (1921) and Odhner (1923), reporting on the collections of the German and Swedish Expeditions (both 1901–1903), added to the knowledge of the Antarctic fauna. Robson (1930, 1932) struggled with the complexities of the octopod fauna represented in the early collections of the *Discovery.* Dell (1959) reported on the cephalopod material collected during the British Australian New Zealand Antarctic Research Expedition (B.A.N.Z.A.R.E.) and listed the species that occur in the

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[1] Contribution no. 982 from the Institute of Marine Sciences, University of Miami and paper no. 65 from the *Dana* oceanographical collections. This paper was submitted in partial fulfillment of the requirements of the Degree of Doctor of Philosophy, University of Miami.

zoogeographical regions defined by Powell (1951) for the Southern Ocean. Dell listed 20 species of cephalopods in the Antarctic Province that is bounded in the north by the mean location of the Antarctic Convergence. The list included 12 species of octopods and 8 species of oegopsids (4 of them cranchiids). Every species that Dell listed, endemic or cosmopolitan, presents a systematic problem, and the distribution and biology of these forms have been virtually unknown.

Some other groups of the Antarctic marine fauna, however, have been studied more thoroughly, primarily because of the extensive program carried on by the *Discovery* office. More than 30 volumes of *Discovery* Reports have been prepared on the biology of Southern Ocean organisms. The systematics and distribution of planktonic and nektonic groups have been presented by Mackintosh (1934, 1937), Hardy and Gunther (1935), Fraser (1936), Baker (1954), Tebble (1960), Marr (1962), and many others.

In 1962 the Office of Antarctic Programs of the National Science Foundation initiated its program in oceanography by the deployment of the USNS *Eltanin* to the Southern Ocean. A biological collecting program of broad scope provided the opportunity to conduct detailed studies on the marine fauna of Antarctica. A grant to study the systematics and distribution of Antarctic cephalopods was awarded to G. L. Voss of the Institute of Marine Sciences, University of Miami. As the large collections were sorted and identified, it became increasingly clear that the cephalopod fauna of Antarctic waters was considerably more extensive and more complex than had been indicated by all previous surveys. Preliminary sorting and identification of the collections by the writer in the winter of 1965 revealed that approximately 30 species of the suborder Oegopsida occur in the Southern Ocean. Some of these species are relatively well known; some represent long extensions in range; several are undescribed. Nearly the same situation holds for the dozen or so nominal species of benthic octopods that are being studied by G. L. Voss. The finned octopods, a perpetual problem group, are represented by about a half-dozen species.

Recent additions to the cephalopod fauna of the Antarctic include the Batoteuthidae, a new family of oegopsids (Young and Roper, 1968), the second and third specimens of the curious *Promachoteuthis* Hoyle (Roper and Young, 1968), the second known specimen of *Cirrothauma murrayi* Chun, and new species in several oegopsid families (e.g., Cranchiidae, Histioteuthidae).

While new or rare species were being added to the fauna with the increasing collections, one species, *Bathyteuthis abyssicola* Hoyle, 1885, emerged as the overwhelmingly dominant species of pelagic cephalopod. It seemed to be common everywhere in the Antarctic Ocean, where it was captured over a great range of depths; often it was taken in what is considered great abundance for a deep-sea squid, with as many as two-dozen specimens in a single midwater tow. Although *B. abyssicola* has been recorded in the literature from several different localities in the Atlantic, Pacific, Indian, and Antarctic Oceans, it has been regarded as a rather rare bathypelagic squid that exhibits a world-wide distribution.

The overall objectives of the Antarctic Celphalopod Project are to delineate the Antarctic cephalopod fauna, to define the horizontal and vertical distributions of its components, and to determine its zoogeographic relationships with the faunas of adjoining regions. The systematics of the fauna is currently being worked out group by group, but it seemed that the ultimate objectives of the program could be achieved by first working out the distribution and zoogeographic relationships of a single species as a model for comparison in future studies on other species. *Bathyteuthis abyssicola* was the obvious choice for the initial study because of its numbers and because it occurs throughout the area of operations of the *Eltanin*.

In addition to the material from the Antarctic, a number of specimens of *Bathyteuthis* from the Atlantic, East Pacific, and Indian Oceans were available from the collections of the *Dana*, *Pillsbury*, *Velero*, *Anton Bruun*, *Chain*, and Bureau of Commercial Fisheries vessels.

The work that is presented here is divided into two major parts. The part on systematics presents a review of literature on *Bathyteuthis*, detailed descriptions of *B. abyssicola* and of two newly named species of *Bathyteuthis*, *bacidifera* and *berryi* (Roper, 1968), a comparison of the species, a determination of the familial relationships of the Bathyteuthidae, an analysis of *Ctenopteryx*, and a comparison of *Ctenopteryx* with *Bathyteuthis* to determine the validity of their inclusion in the same family. The final part of the sections on systematics comprises an examination of the geographical variation in Atlantic, East Pacific, and Antarctic populations of *B. abyssicola*.

The second part is a study of the distribution of *Bathyteuthis*. The bathymetric and geographic ranges of the species are established, and the physicochemical and biological factors that govern these distributions are analyzed. The occurrence and abundance of the Antarctic population are examined in relation to area, environmental conditions, season, and other species of pelagic squid. The size-group composition of the population and the distribution of growth stages are presented.

A detailed characterization of the Antarctic oceanic environment was a necessary prelude to the study of the distribution of *B. abyssicola* and of all other Southern Ocean species of cephalopods as well. *Eltanin* oceanographic data were available only in tabular form from Lamont Geological Observatory. Data in this form, however, are of little value to the biologist seeking an overall view of the physicochemical environment. Therefore, the oceanographic data were analyzed and compiled by hand as vertical sections of oceanographic parameters along meridians and latitudes. Seven groups of sections were constructed along meridians between 25° west longitude and 160° west longitude; a pair of sections was made along 60° south latitude from 25° W to 160° W. A brief survey of the major features of Antarctic oceanography is supplemented by the detailed examination of the vertical sections, and several previously suspected features of the oceanography of the Antarctic Ocean are verified.

The analysis of oceanographic parameters has provided the information necessary for the determination of the many facets of the horizontal and vertical distribution of *Bathyteuthis abyssicola*. Furthermore, now that this environmental information has been compiled, it can be used for determining and comparing the distributions of all pelagic species occurring in the Antarctic Ocean.

Studies of this nature are moderately common in the literature of biological oceanography. In the field of systematics and biology of the Cephalopoda, however, this approach has not been taken because few large collections of oceanic squid, and particularly of bathypelagic species, have been available for study. Therefore, analyses of geographic variation and ecological factors governing distribution are presented for a bathypelagic squid for the first time.

A work of this scope is accomplished only with the aid and cooperation of other people and organizations. The Antarctic Cephalopod Project is supported by the Office of Antarctic Programs, National Science Foundation (Grants GA 103 and GA 253 to G. L. Voss, Institute of Marine Sciences [IMS] Miami). The Department of Biology of the University of Southern California is responsible for the macrobiological collecting program aboard the *Eltanin;* I acknowledge the careful preservation and handling of specimens by the USC teams and their cooperation with Institute of Marine Sciences personnel who have participated in *Eltanin* cruises. S. Jacobs of the Lamont Geological Observatory made suggestions and supplied listings of the oceanographic data collected aboard *Eltanin*.

Additional material and assistance were available from several sources. J. Rosewater provided working space and facilities in the Division of Mollusks, U.S. National Museum, Smithsonian Institution, where I examined the type of *Benthoteuthis megalops* Verrill, 1885, and miscellaneous collections; I am grateful to him for reviewing the manuscript. R. H. Backus loaned specimens that I sorted from the cephalopod collections at the Woods Hole Oceanographic Institute. W. Clench and G. Mead gave access to the cephalopod specimens in the Museum of Comparative Zoology at Harvard. N. Tebble, Curator of Molluscs at the British Museum (Natural History), provided facilities for studying the type of *Bathyteuthis abyssicola* Hoyle, 1885. Cephalopod material collected during the *Dana* expeditions is available at the Institute of Marine Sciences through the Carlsberg Foundation, E. Bertelsen, Director. Specimens collected by U.S. Bureau of Commercial Fisheries vessels are on deposit at IMS through H. Bullis, Pascagoula, Mississippi. R. E. Young, IMS, loaned material of a new species from the *Velero* collections in California waters. E. McSweeny, W. Herrnkind, J. Walsh, and G. Hendrix of IMS participated in *Eltanin* cruises to collect material and make observations of Antarctic cephalopods. T. E. Bowman, U.S. National Museum, brought the quote by Sandburg to my attention. I am most grateful to all of these people and institutions for their aid.

Several members of the faculty at IMS read all or portions of the manuscript and gave helpful suggestions. I am indebted to A. J. Provenzano, C. R. Robins, F. M. Bayer, J. Fell, L. P. Thomas, L. J. Greenfield, S. Broida, and E. S. Iverson.

I am especially grateful to G. L. Voss for his suggestions and encouragement throughout this work, for the stimulation he has provided by his continuous interest in and support of my studies, and for his review of the manuscript.

Long discussions with R. E. Young have been particularly valuable; I appreciate his suggestions and enthusiasm for this work.

The illustrations of *Bathyteuthis* are the skillful work of Miss Constance Stolen; her patience and perceptiveness result in precise renditions of the material. I am most grateful for her assistance.

My wife, Ingrid, has compiled and plotted data, assisted in translations, and prepared the graphs and charts for reproduction; for this and for her encouragement I am grateful.

Material and Methods

Most specimens used in this study were taken by the USARP vessel *Eltanin*, but material was available from other sources as well. Specimens are referred to by ship and station number in the text and figures. The following list gives the sources of material by ship and by geographic area, and an example of the abbreviation of the reference number (ship and station).

Eltanin	Southern Ocean	Elt. 354
Dana	Atlantic, Bay of Panama	D1208 VI
Pillsbury	Gulf of Guinea	Pil. 300
Oregon	Western Atlantic	O 4296
Silver Bay	Western Atlantic	SB 2024
Pelican	Western Atlantic	Pel. 11
Chain	Atlantic	Ch. 17–18
Velero	San Pedro Basin, California	V 9661

The abbreviations used are standard, e.g., m for meters, mm for millimeters, etc. Abbreviations used in reference to morphometric dimensions are also standard in the teuthological literature; the most common is ML for mantle length. Others are explained in the legends or text. Definitions of these abbreviations are found in Voss (1963) and Roper (1966) so they need not be repeated.

All raw data, measurements and indices, and complete station data are on file in the Division of Mollusks, U.S. National Museum, Smithsonian Institution.

PART I.

SYSTEMATICS

Historical Résumé

The initial account by Hoyle of the cephalopods collected by HMS *Challenger* appeared in the narrative of the cruise that was published in May 1885. Hoyle's brief comments dealt primarily with the more unusual cephalopods captured, and a number of new genera and species were erected. One very curious decapod, according to Hoyle, was the small specimen taken in the Southern Ocean between Prince Edward and Crozet Islands by a dredge (trawl) haul that fished at 1600 fathoms (2900 m). Appropriately, he named this species *Bathyteuthis abyssicola.* The original description was brief, but, in conjunction with its accompanying illustration, it adequately established the species. Hoyle listed these important features (p. 272): body tapering to a blunt point; fins small, round; head broad, with prominent eyes; oral membrane with suckers; arms short with minute, biserially arranged suckers; tentacles with unexpanded clubs but gradually tapering to a point armed with numerous, very small suckers; pen resembling that of *Ommastrephes.*

Hoyle stated that the structure of this form seemed to adapt it for life in the great depths, justifying the belief that it actually came from the 1600-fathom depth reached by the trawl. He further stated (pp. 272–273) that the ". . . small fins are in marked contrast to those of pelagic species, while the small suckers and delicate tentacles are equally little fitted for raptorial purposes; but, on the other hand, the large circumoral lip would seem well suited for collecting nutritive matters from an oozy bottom."

Shortly after the narrative was published Hoyle brought out his diagnosis (1885a) of new species of cephalopods collected during the cruise of HMS *Challenger.* In this he not only described new species which had not been described in the narrative (primarily species of *Loligo* and *Sepia*), but also included the previously described *Promachoteuthis* and *Histiopsis.* However, *Bathyteuthis*, the only other new decapod in the *Challenger* collections, curiously was omitted.

The third catalog of Mollusca published by Verrill (1885) contained a number of new species of cephalopods that were captured by the U.S. Fish Commission Steamer *Albatross* in 1884 off southeastern New England. Among the new species were two small specimens that represented a new genus as well, which Verrill named *Benthoteuthis megalops.* As was his practice, he did not assign the new genus to a family.

Verrill gave detailed descriptions of the new genus and species, accompanied by a single illustration "of one of the types." Apparently this is the female, mantle length 57 mm, to which he referred several times in the text. I have examined the remains of the type in the U.S. National Museum; it bears the catalog number 39968, and it is a mature female. No additional mention is made in Verrill's text of the other specimen, number 39967.

Verrill mentioned (p. 402) that *Benthoteuthis* displays "marked embryonic or primitive characters," typified in the young stages of *Loligo* and *Ommastrephes*, that "are seen especially in the small size, posterior position and form of the fins; in the form of the body, head and mantle; in the small short arms, with the dorsal pair shortest; in the small simple suckers; in the want of differentiation of the tentacular club and the uniformity of its minute suckers."

Verrill thought that the affinities of the genus probably lay with the *Ommastrephes* group because of the "distinct eye lids and sinus, and by the character of the connective cartilages of the mantle." He also noted that the pen was like that of *Loligo*, but that the pen is apparently of little value in determining relationships of squids. It is curious that he should choose for showing affinities such a general and indecisive character in the oegopsids as the eyelid and such a singularly decisive familial character as the mantle-connective cartilages of *Ommastrephes*. Nowhere in Verrill's description is there an indication that the locking apparatus in *Benthoteuthis* resembles the strong, inverted T-structure of ommastrephids.

Shortly after the diagnosis on the *Challenger* cephalopods appeared, Hoyle published his preliminary report (1885b), which was identical to the earlier diagnosis (1885a) except for the inclusion of an introduction, a generic diagnosis, and a description of *B. abyssicola*. In addition, he gave a footnote (p. 282): "This [*Bathyteuthis*] seems to be at all events congeneric with a form which Professor Verrill has recently dredged in the North Atlantic, and named *Benthoteuthis megalops*."

In the generic synonymy Hoyle (p. 308) listed *Bathyteuthis* Hoyle, May 1885 and, as a synonym, *Benthoteuthis* Verrill, July 1885. This is the first mention of these two genera after their original descriptions. In synonymizing *Benthoteuthis*, Hoyle had to determine the month of publication; apparently he felt that no future conflict would exist over the dates, for he did not discuss the point in the text.

The generic characterization emphasized the blunt body shape, the small, rounded, subterminal fins, the simple, elongate mantle-connective, the large, very broad head with prominent eyes, the short arms with minute suckers in two rows, the large 7-pointed buccal membrane bearing 1 to 2 suckers, the long, slender tentacles with unexpanded clubs bearing numerous minute suckers, and the "*Ommastrephes*-like" anterior section of the gladius.

The specific description is an amplification of the generic diagnosis. Hoyle gave the following details: arm formula 4.3.2.1; arms only one-fourth as long as the body; delicate protective membranes on the arms; suckers spheroidal, nearly embedded, sucker rings smooth with 2–3 rows of conical papillae; hectocotylus lacking; club one-eighth as long as tentacle; club sucker rings smooth with two rows of papillae. Hoyle's accompanying illustration (fig. 2, p. 309) indicates that the specimen had undergone distortion during capture and preservation; this may account largely for the discrepancies in shape and proportion of fins, head, mantle, and arms noted by later authors, particularly Chun (1910) and Pfeffer (1912).

Hoyle's comprehensive report on the *Challenger* cephalopods appeared in 1886. The first section of this work is a synoptic listing of the recent cephalopods. The genus *Bathyteuthis* Hoyle, 1885, is listed under the family Ommastrephini Steenstrup, 1861, subfamily Ommastrephidae Gill, 1871, with *Benthoteuthis* Verrill, 1885, as its synonym. Hoyle listed two species in this genus: his own *Bathyteuthis abyssicola* and Verrill's *B. megalops*. Hoyle mentioned in the discussion the possibility that the two species might ultimately prove to be conspecific (p. 169); in the zoogeographic and bathymetric sections of this monograph, however, he continued to list them separately.

Hoyle, in an attempt to delimit the distributions of cephalopods, defined four major zoogeographic regions of the oceans and seven bathymetric zones between the surface and 3000 fathoms (5500 m). *B. megalops* occurred in the Atlantic Ocean region, 600–1073 fathoms (1100–1950 m); *B. abyssicola* inhabited the Indian and Southern Ocean regions at 1600 fathoms (2925 m).

In his discussion of bathymetric distribution, Hoyle stated that there is reason to regard *Bathyteuthis* and *Benthoteuthis* (which "obviously belongs to the same genus" [p. 232]) as deep-sea inhabitants. Hoyle drew attention to Verrill's observation of embryonic characters in this genus, but he considered these as characters that indicate a deep-sea habitat. In addition, he believed that the small fins were ill-adapted for pelagic existence, that the minute suckers were not fitted for raptorial purposes, and that the large buccal membrane was well suited for collecting food from an oozy bottom.

The generic diagnosis and the specific description are nearly "verbatim" duplications of those given in his preliminary report (Hoyle, 1885b) with the exception of two phrases. In the earlier work he stated it was impossible to determine if the gladius formed a terminal conus, while in the *Challenger* Report he said that the gladius was damaged in dissection but that it was still possible to determine that had no terminal conus as in *Ommastrephes* or *Taonius*. In the earlier report he had described the arm suckers as being arranged in two rows, but in the later work the statement had been altered to "two or four rows."

In stating that *B. abyssicola* and *B. megalops* might prove to be the same species, Hoyle noted the following differences (p. 169) : *B. abyssicola* lacks an angular sinus on the eyelid, has a large head, has suckers more nearly in two very irregular rows ("if slightly more [irregular they] might be regarded as four"). The type specimen is well illustrated on his plate 29, figures 1–7.

Hoyle stated his uncertainty to which family *Bathyteuthis* rightly belongs and suggested that the establishment of a new family might be necessary.

Hoyle (1886b) again listed *Bathyteuthis* (with *Benthoteuthis* as a synonym) and included both *B. abyssicola* Hoyle and *B. megalops* (Verrill) in the genus as he had done in the *Challenger* Report.

Hoyle reported upon the existence of cephalopods in the deep sea at the meeting of the British Association for the Advancement of Science held in September 1885. He considered *Cirroteuthis*, *Mastigoteuthis*, and *Bathyteuthis* as true representatives of the deep sea because they had not been captured prior to the days of deep-sea investigations, and Hoyle indicated that *Bathyteuthis* possessed structural peculiarities that fitted it for abyssal existence, some of which it shared with *Mastigoteuthis*. He did not enumerate these characters.

Goodrich (1892) published one of the first keys for the identification of oegopsid genera. He characterized *Bathyteuthis* by the features that he considered most diagnostic (p. 318) : "siphon without bridles, arms with four rows of smooth suckers, club of tentacle with many rows of minute suckers, small [eye] sinus, pen feather-shaped, suckers on the seven lobes of buccal membrane, fins subterminal, rounded."

Pfeffer (1900) erected and characterized the new family Bathyteuthidae. The familial name first appeared in the key to the families where it was separated out on the basis of its peculiar characters: free funnel, simple locking apparatus, *Loligo*-like gladius with free rhachis and leaflike vane, and in particular, the size, number and arrangement of suckers on the arms and clubs.

After a short diagnosis of the family, Pfeffer stated that it could not be said with certainty whether *Bathyteuthis* and *Ctenopteryx*, both of which he included within the family, truly constitute a natural group.

He described the two genera in some detail and gave partial synonymies; *Bethoteuthis* Verrill was listed as a synonym of *Bathyteuthis*

Hoyle. Pfeffer utilized the descriptions of both Hoyle and Verrill, and his description of *Bathyteuthis* is a composite of the two orignal descriptions. Species were listed with their synonyms and distributions. Here, for the first time, *Benthoteuthis megalops* Verrill, 1885, is synonymized with *Bathyteuthis abyssicola* Hoyle, 1885, although Hoyle had anticipated it earlier (1886). Pfeffer stated that it was difficult to say if Hoyle's and Verrill's specimens belong "exactly" to the same species (p. 173).

Chun's classic work on the eyes and light organs in deep-sea cephalopods (1903) was based on material gathered during the German Deep-Sea Expedition. He made a detailed study of the eye of *Bathyteuthis*. Chun placed *Benthoteuthis* in parentheses after *Bathyteuthis*, indicating that it was a synonym.

Hoyle (1904) reported on the cephalopods captured by the U.S. Fish Commission steamer *Albatross* during two cruises to the tropical eastern Pacific (1891 and 1899–1900). Two specimens of *Bathyteuthis abyssicola* were recorded from off Cape Mala, Gulf of Panama. No description of the specimens was given; however, a colored illustration was presented, made when the larger specimen was still fresh, and Hoyle commented about slight inaccuracies in the drawing (head and arms too large, nuchal mantle point too pointed). In addition, it should be noted that the eyes are too prominent, having been forced out through the eye openings, and that the fins are displaced posteriorly. All of these discrepancies are attributable to stresses of capture.

Hoyle's (1904a) key to the genera of recent dibranchiate cephalopods included *Bathyteuthis* and *Ctenopteryx* in the family Bathyteuthidae. Hoyle mentioned that the association of these two genera in the same family is rather artificial and that further information is necessary to determine their true relationships.

In the second supplement (1909) to this catalog, Hoyle listed Bathyteuthidae Pfeffer, 1900, and *Ctenopteryx*, and he gave the synonymy of *Ctenopteryx sicula* (Ruppell).

Chun (1910) covered the Bathyteuthidae in his monograph based on the cephalopods collected during the German Deep-Sea Expedition aboard the *Valdivia*; *Bathyteuthis*, in particular, was considered in detail.

Chun attempted to determine whether *Benthoteuthis megalops* Verrill or *Bathyteuthis abyssicola* Hoyle had priority; he decided that the question was answered by the notation "April, 1885" on page 399 of Verrill's paper which was published in the Transactions of the Connecticut Academy of Arts and Sciences. Since Hoyle's description was published in May in the narrative of the *Challenger* expedition, Chun considered that Verrill's *Benthoteuthis* had priority by one month. Therefore, Chun, in attempting to establish priority, introduced further uncertainty that, in spite of Hoyle's attempts to rectify the mistake, has persisted to the present, primarily because of the stature of Chun's monograph. Unfortunately, Chun used the printer's signature date, which indicates only the date that sheet 50 of Transactions of the Connecticut Academy of Arts and Sciences was run off the press. Signature dates are not necessarily valid dates of publication.

Chun quoted Pfeffer's original familial diagnosis and further stated that he retained the Bathyteuthidae not only on the basis of the known characters, but in addition on the basis of a number of unusual features of the internal structure of *Benthoteuthis*. Chun emphasized that until that time the only anatomical work had been on *Ctenopteryx* from the Mediterranean and that this knowledge should not be applied to *Benthoteuthis*. He differentiated these genera on the differences in size and structure of the fins and the absence of light organs in *Ctenopteryx*.

Chun's specimens were captured by the *Valdivia* in the Benguela Current south of the Cape of Good Hope, off northwest Sumatra, southwest of Ceylon, and north of the Chagos Archipelago. All of the specimens were small, ranging from 9 to 18 mm in mantle length. (The largest specimen probably belongs to the new species described from the Bay of Panama.)

Since two species are represented in Chun's material, it is impossible to know to which species the description refers except in sections where he mentioned individual specimens. Presumably most of the description, and especially that of the eye and internal anatomy, is based on the largest specimen (only 18 mm in mantle length). This probably is the only specimen of Chun's that belongs to the new species described from Panama.

The description of the species is extremely detailed and comprehensive, covering both external and internal features. Chun gave details concerning the consistency and gross structure of the skin and muscles. The funnel organ and olfactory papilla were described for the first time. Chun's observations of 1903 on the structure of the eye were included. He also commented on the structure and position of the light organs. From these observations he deduced that *Benthoteuthis* is a true deep-sea cephalopod.

In attempting to determine the relationships of the Bathyteuthidae within the Oegopsida, Chun decided that the family held a truly isolated position. He stated that the nature of the buccal membrane connectives to the arms corresponds to the condition in the Enoploteuthidae, Histioteuthidae, and Ommastrephidae, but that the form and position of the liver and pancreas preclude any close relationship.

(The value of these characters for determining relationships between the higher taxa is discussed below.) Finally Chun agreed that Pfeffer's placement of *Ctenopteryx* and *Benthoteuthis* in the same family should be upheld.

Hoyle's (1910) list of generic names included *Bathyteuthis* with *Benthoteuthis* as its synonym. In a footnote Hoyle gave the sources and dates of publication for the two monotypic genera.

Hoyle (1912) reported on the cephalopods captured by the Scottish National Antarctic Expedition's vessel *Scotia*. A single specimen of *Bathyteuthis* was taken off Coats Land at 71°22′S, 18°15′W. Hoyle listed the locality information and previous records but did not describe the specimen. Instead, he attempted to settle the nomenclatural disharmony that had persisted since *Bathyteuthis abyssicola* Hoyle and *Benthoteuthis megalops* Verrill had been erected in 1885. He chided Chun (1910) for using the sheet (signature) date, April 1885, to determine priority for Verrill's name, but he emphasized that if sheet dates are to be used, then *Bathyteuthis* would still have priority because the date on sheet 34 in which *Bathyteuthis abyssicola* was described is "1884." Hoyle apparently made an extensive investigation to determine that Verrill's paper was not released as separate signatures in April, May, and June but that it came out as a single unit in June or, more probably, in July 1885.

Pfeffer's extensive monograph (1912), based primarily on the Plankton-Expedition cephalopod material, gave a key to the families of the Oegopsida that included the family Benthoteuthidae. This key is more detailed than the one given in his synopsis (1900), although the basic arrangement and the characters used are the same. Pfeffer gave a detailed diagnosis of the family and discussed the similarities and differences of *Benthoteuthis* and *Ctenopteryx;* he concluded that the strong differences that exist between the adults are small or nonexistent in the young stages, and that these genera form a unit distinct from all other oegopsids.

At no point in the text did Pfeffer mention that he was altering the family name to Benthoteuthidae, nor did he give Bathyteuthidae as a synonym. In fact, even in his section on history and synonymy, he failed to mention the erection of the family Bathyteuthidae 12 years earlier in his "Synopsis der Oegopsiden Cephalopden."

Pfeffer, in a short sentence following his diagnosis of the genus *Benthoteuthis* (p. 324), casually stated that it need only be mentioned that, as Chun had determined, the generic name *Benthoteuthis* Verrill is one month older than *Bathyteuthis* Hoyle. Pfeffer apparently did not make his own investigation into the matter of priority but simply accepted the authority of Chun. (Perhaps this is understandable judging from Chun's contemporary prominence and stature as a scientist.) Pfeffer did include his use in 1900 of *Bathyteuthis* and *B. abyssicola* in the synonymy of *Benthoteuthis* and *B. megalops.*

Pfeffer's unexplained substitution of Benthoteuthidae for Bathyteuthidae is considered improper and not in the best interests of stability in nomenclature. It is generally regarded that a familial name, once properly erected, as the Bathyteuthidae was by Pfeffer himself in 1900, should not be changed because of subsequent alterations to the generic name (International Code, Art. 40). Of course, the problem in this case is resolved with the establishment of priority for *Bathyteuthis.*

Pfeffer presented a comparison of previously described and illustrated specimens, analyzed and explained the inconsistencies, and concluded that all specimens represent the same species which has nearly a worldwide distribution. Pfeffer gave a very detailed description of his specimens, which came from the western North Atlantic at 40.4°N, 57°W, the South Equatorial Current at 05.1°S, 14.1°W, and the Mediterranean. Apparently no details of the Mediterranean specimen are available except that it was deposited in the Hamburg Museum and apparently came from Messina. The validity of the record has been questioned by some subsequent compilers (e.g., Grimpe, 1922) of the Mediterranean cephalopod fauna. Pfeffer's plate 27, figures 12–15, presents illustrations of the specimens, but Pfeffer's caption to the figures is "*Benthoteuthis abyssicola* Verrill," an unfortunate combination of names. The specimen from Messina in the Hamburg Museum (figs. 14 and 15) has a mantle length of only 3 mm and does not resemble *Bathyteuthis;* it looks very much like the larva of *Ctenopteryx* illustrated by Naef (1923, figs. 116, 117). Since this specimen is the first of two doubtful records of *Bathyteuthis* in the Mediterranean and since *Ctenopteryx* is so common there, it is very probable that this larva has been misidentified. This matter is considered in detail in the discussion of Joubin's 1920 work. Figures 12 and 13 are the Atlantic specimens and look like *Bathyteuthis* larvae with mantle lengths of about 3 mm and 4.5 mm.

Berry (1912) presented some nomenclatural changes in the Cephalopoda and discussed briefly the problem of priority for *Bathyteuthis* or *Benthoteuthis.* He accepted Chun's reasoning that Benthoteuthidae should be the familial designation. Apparently Berry had not seen Hoyle's discussion (1912) that appeared in May, seven months prior to Berry's paper.

Joubin (1912) noted some of the more interesting cephalopods that were captured during the 1911 cruise of the *Princesse-Alice.* He recorded one specimen of *Benthoteuthis megalops* caught between 0 and

4500 m and stated that only one other sample, the original material from America, was known. Apparently Joubin was unaware of Chun's (1910) *Valdivia* specimens and of the nomenclatural controversy that persisted concerning *Benthoteuthis* and *Bathyteuthis*.

Massy (1916) listed some cephalopods from the Irish Atlantic Slope; the small collection contained a young specimen of *B. abyssicola* that was taken at 55°22′N, 11°40′W in 700–750 fathoms. This locality constitutes the northernmost record of *B. abyssicola*.

Massy (1916a) recorded *B. abyssicola* in her report on the cephalopod collections of the Indian Museum. Two small specimens (about 5 and 12 mm mantle length) were captured in the Bay of Bengal by the *Investigator*. The brief description noted the following features: 2 rows of suckers on arm IV, 3 to 4 irregular rows of suckers on arms I–III (2 rows on all of the arms of the larva); 4 blunt, widely separated teeth on the club suckers, 5 to 6 teeth on the arm suckers (4 to 5 in the larva); distinct photophores and pigment. Measurements are given for the larger specimen.

In his work on the paleobiology of dibranchiate cephalopods, nearly half of which concerns living forms as well, Abel (1916) mentioned *Bathyteuthis* and *Benthoteuthis* in his discussion of retention of larval characters in adult forms. In a number of highly specialized species of oegopsids that inhabit the deep sea, the terminal fin is divided even in the adult, whereas in almost all known young stages of Oegopsida the terminal fins are divided only during the larval life. The comments by Abel, a paleontologist, are undoubtedly based on the suggestions and observations of Verrill, Hoyle, Chun, and Pfeffer.

Naef (1916) listed the family Benthoteuthidae Pfeffer, 1900, and *Ctenopteryx sicula*. In his incorrect assignment of the family name, Naef erred in one of two ways. He intended to use either Bathyteuthidae Pfeffer, 1900, or Benthoteuthidae Pfeffer, 1912. It was not until 1912 that Pfeffer, without explanation but apparently following Chun's decision that *Benthoteuthis* had priority, made the unwarranted change in the family name. In his 1921 survey of Mediterranean dibranchiate cephalopods, Naef correctly listed the family Bathyteuthidae but erroneously referred it to Pfeffer's 1912 work, which included only Benthoteuthidae. This work again lists *Ctenopteryx* Appellof and adds *Bathyteuthis* Hoyle, probably on the basis of Pfeffer's (1912) record from the Mediterranean.

Berry (1917) listed Hoyle's *Scotia* specimen of *B. abyssicola* as a representative of the Antarctic cephalopod fauna in the historical section of his report of the Cephalopoda captured during the Australian Antarctic Expedition, 1911–1914.

Joubin (1920) reported on the cephalopods captured during the cruises of the *Princesse-Alice* from 1898–1910. One small specimen of *Benthoteuthis megalops*, only 7.5 mm from "mouth" to posterior end of body, was taken between the Azores and northern Portugal. Joubin's description was brief and dealt primarily with color observations. Another specimen, only 3.5 mm in length, was taken in the western Mediterranean and, according to Joubin, very closely resembled the specimen illustrated by Pfeffer (1912) on plate 27, figures 14 and 15. Joubin's specimen was smaller than Pfeffer's and Joubin felt that it belonged in the same series but listed it only as *Benthoteuthis* sp. in the event of a future reconsideration. Judging from the illustration it appears that Joubin's specimen, like Pfeffer's, is a larva of *Ctenopteryx*. Therefore, the only two records of supposed *Bathyteuthis* (reported as *Benthoteuthis*) in the Mediterranean actually represent *Ctenopteryx* larvae.

Further verification of this is found in Naef's (1923) discussion and illustrations of the juvenile stages of *Ctenopteryx siculus*. Joubin's *Benthoteuthis* sp. (pl. 12, fig. 9) and Pfeffer's *Benthoteuthis megalops* (mislabeled as "*Benthoteuthis abyssicola* Verrill," pl. 27, figs. 14 and 15) very closely resemble Naef's illustrations of the larvae of *Ctenopteryx siculus* (p. 253, figs. 116 and 117). In addition, all of these specimens come from the western Mediterranean, Messina, and Naples. The larvae illustrated by the three authors range in size from less than 2 mm to about 3.5 mm in mantle length and, taken together, represent a good growth series of larval *Ctenopteryx*.

Robson (1921) described *Chunoteuthis minima*, a new genus and species, which he placed in the family Benthoteuthidae. The description of the new genus and species is based upon a single larval specimen only 3 mm in length from the apex of the mantle to the base of the arms. Nothing in the description would lead one to believe that this form was a bathyteuthid instead of the larva of any number of other Oegopsida. Robson admitted that the specimen was the source of considerable trouble because it was very shriveled and many of the external features were obliterated. He could not align it with any known genus, and furthermore, "even its family relationships are very doubtful." Nevertheless, he saw fit (p. 432) to "assign it to the Benthoteuthidae on the strength of its general superficial appearance"! Robson's entire presentation is the absolute epitome of the fallacious belief held by some earlier workers that every specimen in a collection, regardless of size or condition, must have a name applied to it.

Nothing can be ascertained from the description concerning the true identity of this larval form. The type in the British Museum

(NH) has been examined by G. L. Voss; it is hard and unmanageable and its identity cannot be determined.

The illustration reveals nothing that would qualify *Chunoteuthis* as a bathyteuthid; the arms and tentacles are too long and slender, no "web" connects the basal parts of the arms, the clubs are too expanded, and the arm suckers are too prominent. *Chunoteuthis* almost certainly is not a bathyteuthid.

Unfortunately, Robson's name has to be reckoned with since he considered the specimen a bathyteuthid. The only recourse is to proclaim *Chunoteuthis minima* Robson, 1921, a *nomen dubium*.

Thiele (1921) reported on the Cephalopoda obtained during the German South-Polar Expedition, 1901–1903. Specimens of *Ctenopteryx sicula* and *Benthoteuthis megalops* were included, which he placed in the Benthoteuthidae following Chun and Pfeffer. Two specimens 11 mm in mantle length were referred without doubt to *B. megalops;* one was captured in the South Atlantic at 35°10′S, 02°33′E, while the other came from northwest of Prince Edward Island at 43°04′S, 36°22′E. A third specimen was questionably referred to this species; it was taken south of the Cape Verde Islands at 05°27′N, 21°41′W.

Naef's work on fossil cephalopods (1922) included a classification of both fossil and Recent cephalopods. The family Bathyteuthidae was listed as the first family under the suborder Metateuthoidea Oegopsida Naef, 1916. The genera *Bathyteuthis* and *Ctenopteryx* were listed.

Grimpe (1922) erected several new taxa in association with the Bathyteuthidae. He listed as the first group in the oegopsids Bathyteuthina, a new "family group" that included the Bathyteuthidae Pfeffer, 1900. In addition, he erected two new subfamilies, the Ctenopteryginae and the Bathyteuthinae. The former contained only *Ctenopteryx*, while the latter included *Bathyteuthis* and *Indoteuthis* Grimpe, 1922, p. 45 (an improper replacement name for *Chunoteuthis* Robson, 1921; see discussion under Grimpe, 1925). Grimpe considered that it might be a juvenile *Bathyteuthis*. No diagnoses are given for the new taxa. Grimpe gave the distribution of species in seas around Europe. *B. abyssicola* is recorded from the northwest Atlantic and from the Mediterranean with question, apparently querying Pfeffer's (1912) record.

Naef's monograph (1923) has devoted a chapter (p. 251) to the Bathyteuthidae that includes a detailed diagnosis and discussion of the family, a generic diagnosis of *Ctenopteryx*, and a detailed description of *C. siculus*. Apparently Naef had no specimens of *Bathyteuthis abyssicola*, for he referred readers to Chun's (1910) coverage, upon which he must have relied heavily for his information about the genus.

Naef again listed the Bathyteuthidae as being erected by Pfeffer in 1912 instead of 1900. In the first volume of the monograph, Naef (1921a, p. 48) listed the families and genera of cephalopods and gave Benthoteuthidae Pfeffer, 1900, and *Benthoteuthis* Verrill, 1885. It is curious that Naef always confused the dates of the familial synonyms.

Naef emphasized that although *Ctenopteryx* and *Bathyteuthis* are not close relatives, they show special relationships to each other that are best expressed by retaining them in one family; together they represent a common contrast to all other oegopsids.

According to Naef, the characters of the family are partly juvenile characters, and in part they may be regarded as primitive for the entire Oegopsida. In particular, Naef gave the shape of the gladius and the subterminal fins as general juvenile characters, and the occurrence of suckers on the buccal membrane and the suckers on the arms in four rows and on the clubs in many rows as primitive characters in all oegopsids. He gave a number of other characters which, though less clearly understood, indicated the primitive nature of the Bathyteuthidae.

Naef presented his ideas on the phylogeny of the Cephalopoda in a phylogenetic bush (p. 795). He showed the Bathyteuthidae arising obscurely with the rest of the Oegopsida and coming off as the oegopsid family closest to the Myopsida. Finally, Naef gave a systematic review of the dibranchiates (p. 809) in which he included the Bathyteuthidae as the first family in the Oegopsida, with two genera *Bathyteuthis* and *Ctenopteryx*.

Odhner (1923) reported on the small collection of cephalopods taken by the Swedish Antarctic Expedition, 1901–1903. He recorded one damaged specimen of *B. abyssicola* 50 mm long (total length?) which "agreed in all details with the illustration of Chun." The specimen was captured at 48°27′S, 42°36′W. He gave the range of the species in the subantarctic area based on the *Challenger*, *Valdivia*, and *Scotia* specimens. Although he gave no discussion, Odhner apparently based his decision to use the name *Bathyteuthis abyssicola* on the arguments presented in Hoyle's rejection (1912) of Chun's statement of priority for *Benthoteuthis megalops*.

A major report on the cephalopods collected by the Prince of Monaco was published by Joubin in 1924. Three specimens of *Benthoteuthis megalops* were recorded from the Azores-Portugal region of the eastern Atlantic. Again, Joubin added little to the description of the species except the statement that the head is more darkly colored than illustrated by Chun. In addition, Joubin stated that the little white pearls (photophores) at the bases of the arms are replaced by masses of dark chromatophores. This character is quite variable, however, and depends upon the age and the state of preservation of the specimens. Throughout his work Joubin utilized only the name *Benthoteuthis megalops*, apparently relying on Chun's and Pfeffer's usage.

The final section of Grimpe's major work on the cephalopod fauna of the North Sea (1925) consists of an annotated systematic review. The scheme of classification is similar to that given in his work of 1922 including the use of the "provisional family-group" Bathyteuthina, Bathyteuthidae Pfeffer, 1900, and the subfamilies Ctenopteryginae and Bathyteuthinae. Grimpe maintained that the differences between *Ctenopteryx* and *Bathyteuthis* were so considerable as to warrant their subfamilial separation. In the footnote to *Bathyteuthis*, Grimpe fully concurred with Hoyle's arguments for priority of that genus.

Referring to the myopsid-reminiscent characters of *Bathyteuthis* and *Ctenopteryx* mentioned by Chun (1910) and Naef (1921a), Grimpe placed the family at the beginning of the Oegopsida in the special family-group Bathyteuthina to indicate that a certain relationship exists between it and the Myopsida.

The footnote for *Indoteuthis* emphasizes the brevity and inconclusiveness of Robson's description of *Chunoteuthis* (1921) and Grimpe questioned the placement of the form and, in fact, the reality of the genus. Grimpe (1922) had changed the name to *Indoteuthis* because it too closely resembled *Chunioteuthis* Grimpe, 1916, a cirrotuthid octopod. A change of this nature, however, is illegal under the Code of Nomenclature; *Indoteuthis* is a junior objective synonym of *Chunoteuthis*, which is a *nomen dubium*.

Massy (1928) briefly described *B. abyssicola* in her report of the cephalopods of the Irish coast. Massy first listed the specimen in 1916; it was taken at 50°22′N, 11°40′W by the *Helga* in a midwater otter trawl that fished in 700–750 fathoms. The larva, only 3.5 mm in mantle length, had distinct light organs and pale reddish coloration. Massy gave the distribution and vertical range from the literature.

The first description of the male reproductive system of *Bathyteuthis* was presented by Robson (1932a) who used the name *Benthoteuthis*. Robson found two male specimens in the cephalopod material obtained by the RRS *Discovery;* only the larger one (40 mm mantle length) was mature. The "most striking" external feature, Robson noted, was the total absence of hectocotylization, and in this feature *Benthoteuthis* agrees with "essentially abyssal forms." He gave a very brief description of the genitalia but deferred a more detailed discussion until a later date. Robson concurred with Chun that the ink-sac is much reduced and must be regarded as atrophied.

Robson's report on the vast collections of decapod cephalopods taken by the *Discovery* never appeared, so we have no additional details on the structure of the male genitalia. Furthermore, we have no clarification of Robson's statement (p. 375), ". . . it will be seen that the specimens obtained by the *Discovery* are probably not referable to *B. megalops*, the single species hitherto described." Since Robson's *Discovery* specimens came from the same Antarctic localities (ca 55°S, 52°W) that have been thoroughly collected by the *Eltanin* as well, it is doubtful if they represent anything other than *Bathyteuthis abyssicola*.

Thiele (1935) listed the family Bathyteuthidae and gave a short diagnosis for the family and for *Bathyteuthis* (with *Benthoteuthis* as as synonym) and *Ctenopteryx*. He mentioned Robson's (1921) *Chunoteuthis minima* as a bathyteuthid and Grimpe's (1922) subsequent changing of the generic name to *Indoteuthis*.

Allen (1945), reporting on the planktonic cephalopod larvae of eastern Australia, split off the family Ctenopterygidae from the Bathyteuthidae based on the literature and on one larval specimen of *Ctenopteryx sicula*. Apparently, she had no specimens of *Bathyteuthis* and relied entirely on the description of this form in Hoyle's *Challenger* report. Although Allen's decision was based on totally irrelevant taxonomic characters, current information indicates that she was correct in her elevation of Grimpe's subfamilial designation. This is discussed in more detail in the section in which *Ctenopteryx* and *Bathyteuthis* are compared.

In a posthumous publication Robson (1948) reported on the cephalopods caught during the *Arcturus* Expedition of 1925. Contrary to his previous publications, Robson used the family name Bathyteuthidae and listed ten specimens of *B. abyssicola* taken around the Galapagos and Cocos Islands of the eastern Pacific.. He stated that he was in agreement with Naef and Grimpe in believing that Hoyle's *B. abyssicola* had priority over Verrill's *Benthoteuthis megalops*.

Robson described one small specimen (mantle length 7.0 mm) as *Bathyteuthis* sp. which he believed differed from *B. abyssicola* in "head and body-shape and in general proportions . . ." (p. 117). Then he stated, "On the whole the features agree fairly well with *abyssicola*." Fortunately, on this occasion he was unwilling to base the type of a new species on such a young and immature specimen. The *Bathyteuthis* sp. probably falls within the normal range of variation for *abyssicola*, particularly if it differs only in shape and general proportions, features that are readily altered by rigors of capture and preservation.

Voss (1956) reviewed the extensive collections made in the Gulf of Mexico by the U.S. Bureau of Commercial Fisheries R/V *Oregon*.

Table I.—*Synopsis of previous records of* Bathyteuthis

Author	*Location*	*Area*	*Number of specimens*	*Mantle length millimeters*	*Depth reached by gear, meters*	*Gear*	*Vessel or expedition*
Hoyle, 1885	46°16′S 48°27′E	Southern Ocean between Prince Edward and Crozet Islands	1	[1] 40	2900	bottom trawl	*Challenger*
Verrill, 1885	39°45′N 71°18′W	Off Martha's Vineyard	1	[2] 57	1960	large beam trawl	*Albatross*
	39°49′N 70°26′W	Off Martha's Vineyard	1	–	1100	large beam trawl	*Albatross*
Hoyle, 1904	06°30′N 81°44′W	Off Cape Mala, Gulf of Panama	1	23	1010	large beam trawl	*Albatross*
	07°06′N 79°48′W	Off Cape Mala, Gulf of Panama	1	–	2140	large beam trawl	*Albatross*
Chun, 1910	36°23′S 17°38′E	Benguela Current, off Cape Agulhas	1	9	2500	vertical net	*Valdivia*
	05°23′N 98°48′E	Indian Ocean, off NW Sumatra	1	9	800	vertical net	*Valdivia*
	04°56′N 78°15′E	Indian Ocean, SW of Ceylon	2	9–11	2000	vertical net	*Valdivia*
	04°05′S 73°24′E	Indian Ocean, N of Chagos Archipelago	1	18	2000	vertical net	*Valdivia*
Hoyle, 1912	71°22′S 18°15′W	Off Coates Land	1	–	4210	–	*Scotia*
Pfeffer, 1912	40.4°N 57°W	North Atlantic, Gulf Stream	1	3	–	plankton net	Plankton Exp.
	05.1°S 14.1°W	Atlantic Ocean, S Equatorial Current	1	4.5	400	plankton net	Plankton Exp.
Massy, 1916, 1928	50°22′N 11°40′W	North Atlantic off British Isles	1	3.5	1280–1375	midwater otter trawl	*Helga*
Massy, 1916a	07°21′N 85°07′E	Southern Bay of Bengal	1	ca 5	0–3650	–	*Investigator*
	09°08′N 87°25′E	Southern Bay of Bengal	1	12	0–870	–	*Investigator*
Joubin, 1920	43°04′N 19°42′W	North Atlantic Ocean	1	larva	0–100	Richard net	*Princesse Alice*, 1909

Thiele, 1921	35°10′S 02°33′E	South Atlantic Ocean	1	11	3000	vertical net	German South Polar Exp.
	43°04′S 36°22′E	South Indian Ocean	1	11	2500	vertical net	
	05°27′N 21°41′W	S of Cape Verde Island	1	9	1500	vertical net	
Odhner, 1923	48°27′S 42°36′W	South Atlantic Ocean	1	[4] 50	2500	plankton net	Swedish Antarctic Exp.
Joubin, 1924	35°09′N 21°21′W	Azores	1	30	0–3500	Bouree net	*Princesse Alice*, 1911
	31°45′N 20°17′W	Madeira	1	larva	0–3000	Bouree net	*Princesse Alice*, 1912
Robson, 1932	55°48.5′S 52°35′W	Southern Ocean	[5] 1	40	1200–1300	–	*Discovery I*
	–	Southern Ocean	1	53	–	–	*Discovery I*
	–	Southern Ocean	1	"immature"	–	–	*Discovery I*
Robson, 1948	00°40′N 88°51′W	NE of Galapagos Island	1	5–22	1280	Petersen trawl	*Arcturus*
	00°17′N 90°02′W	NE of Galapagos Island	1		550	Petersen trawl	*Arcturus*
	02°00′S 89°30′W	SE of Galapagos Island	1		730	tow net	*Arcturus*
	03°52′N 86°43′W	South of Cocos Island	3		1000	tow net	*Arcturus*
	04°50′N 87°00′W	South of Cocos Island	2		1100	tow net	*Arcturus*
	00°17′S 91°34′W	Galapagos Island	1		1280	Petersen trawl	*Arcturus*
	00°42′N 91°47′W	Galapagos Island	1		1100	tow net	*Arcturus*
	00°17′S 91°34′W	Galapagos Island	[3] 1	7	1280	Petersen trawl	*Arcturus*
Voss, 1956	28°28′N 87°18′W	Gulf of Mexico	1	44	1400	40′ flat trawl	*Oregon*

[1] Type of *Bathyteuthis abyssicola*.
[2] Type of *Benthoteuthis megalops*.
[3] Identification uncertain.
[4] Total length excluding tentacles.
[5] Robson apparently had a number of *Discovery* specimens but mentioned only these.

B. abyssicola was represented by one specimen 44 mm in mantle length. Voss gave a detailed description of the specimen and in his remarks mentioned the possibility of the presence of two species of *Bathyteuthis* based on the presence or absence of light organs, a feature that generally merits specific distinction.

Dell (1959) worked up the B.A.N.Z.A.R.E. cephalopod collections. Although no specimens of *B. abyssicola* were captured during the expedition, Dell included the species in his comprehensive list of the cephalopod fauna of the Antarctic Province.

Powell's (1960) compilation of Antarctic and Subantarctic Mollusca lists the family Bathyteuthidae and *Bathyteuthis* Hoyle with the type locality in the Southern Ocean. Powell listed only Odhner's (1923) record for the range of the species in these waters and omitted the Antarctic and Subantarctic specimens recorded by Hoyle (1912), Thiele (1921), and Robson (1932).

A. H. Clarke (1962) gave the distribution of *B. abyssicola* as cosmopolitan in temperate and tropical seas at depths of 0–2000 fathoms (0–3660 m); apparently he overlooked all the records from boreal waters.

M. R. Clarke (1966), in a work published since the present research was completed, reviewed the previous records of *B. abyssicola* and gave additional records from the collections of the *Discovery II*. Clarke estimated the vertical range and ecological conditions occupied by the species.

Roper (1968) gave preliminary descriptions of two new species of *Bathyteuthis; B. bacidifera* and *B. berryi* are described in greater detail in the present work, and information about their distribution is included.

Family BATHYTEUTHIDAE Pfeffer, 1900

Bathyteuthidae Pfeffer, 1900, p. 152, 171.—Chun, 1903, p. 68.—Hoyle, 1904, p. 33; 1904a, p. 3, 14; 1909, p. 271.—Chun, 1910, p. 185.—Berry, 1912, p. 645.—Hoyle, 1912, p. 282.—Naef, 1921, p. 535; 1922, p. 298.—Grimpe, 1922, p. 45.—Naef, 1923, p. 251, 809.—Grimpe, 1925, p. 95.—Thiele, 1935, p. 970.—Robson, 1948, p. 116.—Voss, 1956, p. 142.—Powell, 1960, p. 185.

Benthoteuthidae Pfeffer, 1912, p. xx, 323.—Berry, 1912, p. 645.—Naef, 1916, p. 14.—Joubin, 1920, p. 57.—Thiele, 1921, p. 453.—Naef, 1921a, p. 48.—Joubin, 1924, p. 74.

Not Benthoteuthidae—Robson, 1921, p. 432 (for *Chunoteuthis minima*).

TYPE-GENUS.—*Bathyteuthis* Hoyle, 1885.

DIAGNOSIS.—Mantle-funnel locking apparatus simple with straight ridge and groove; buccal connectives attach dorsally to arms IV; club short, unexpanded, with more than four rows (8–10) of numerous, small suckers; arms with two, increasing to more than two rows (4) of irregularly arranged suckers; lappets of buccal membrane with small suckers; fins subterminal; gladius simple with long, narrow rhachis, broad, thin vane and open, thin terminus (no conus).

Genus *Bathyteuthis* Hoyle, 1885

Bathyteuthis Hoyle, May 1885, p. 272; 1885b, p. 282, 308; 1886, p. 36, 167, 232, 236; 1886a, p. 247; 1886b, p. 1064.—Goodrich, 1892, p. 318.—Pfeffer, 1900, p. 172.—Chun, 1903, p. 69, 71, 77, 85–90.—Hoyle, 1904, p. 33; 1904a, p. 3, 14; 1909, p. 271.—Chun, 1910, p. 186.—Hoyle, 1910, p. 408; 1912, p. 282.—Pfeffer, 1912, p. 324.—Berry, 1912, p. 645.—Abel, 1916, p. 93.—Massy, 1916, p. 114; 1916a, p. 241.—Naef, 1921, p. 535; 1922, p. 298.—Grimpe, 1922, p. 45.—Naef, 1923, p. 795, 809.—Odhner, 1923, p. 1.—Grimpe, 1925, p. 95, 101.—Massy, 1928, p. 30.—Thiele, 1935, p. 970.—Allen, 1945, p. 328.—Robson, 1948, p. 116.—Voss, 1956, p. 142.

Benthoteuthis Verrill, July 1885, p. 401.—Hoyle, 1885b, p. 282, 308; 1886, p. 36, 167, 169, 232.—Chun, 1910, p. 185, et. seqq.—Hoyle, 1910, p. 408.—Joubin, 1912, p. 396.—Pfeffer, 1912, p. 324, et. seqq. (pars).—Berry, 1912, p. 645.—Abel, 1916, p. 93.—Joubin, 1920, p. 57 (pars).—Thiele, 1921, p. 453.—Naef, 1921a, p. 48.—Joubin, 1924, p. 74.—Robson, 1932, p. 375.

?*Chunoteuthis* Robson, 1921, p. 432 (nomen dubium).—Grimpe, 1922, p. 45; 1925, p. 95, 102.—Thiele, 1935, p. 970.

?*Indoteuthis* Grimpe, 1922, p. 45 (replacement for *Chunoteuthis* Robson, 1921; not *Chunioteuthis* Grimpe, 1916); 1925, p. 95, 102.—Thiele, 1935, p. 970.

TYPE-SPECIES.—*Bathyteuthis abyssicola* Hoyle, 1885. By monotypy.

DIAGNOSIS.—Tentacular clubs with 8–10 rows of numerous, minute suckers; arms I–III with 2–4 rows of irregularly placed suckers; arms IV with 2 rows of suckers; fins short, round, subterminal; eyes directed anteriorly; color a deep maroon; simple photophore at aboral base of arms I–III; arms I–III connected by a broad "web"; integumentary layers thick, honey-combed, semigelatinous; liver with large oil chambers; hectocotylus absent.

Bathyteuthis abyssicola Hoyle, 1885

PLATES 1–5

Bathyteuthis abyssicola Hoyle, May 1885, p. 272–3, fig. 108; 1885b, p. 282–3, 309–10, fig. 2; 1886, p. 36, 168–9, 203, 213, 229, pl. 29, figs. 1–7; 1886a, p. 247.—Pfeffer, 1900, p. 173.—Hoyle, 1904, p. 33, pl. 1, fig. 2; 1909, p. 271.—Chun, 1910, p. 186.—Hoyle, 1910, p. 408; 1912, p. 273, 282.—Pfeffer, 1912, p. 327, et seqq.—Massy, 1916, p. 114; 1916a, p. 241.—Berry, 1917, p. 7.—Grimpe, 1922, p. 45.—Odhner, 1923, p. 1.—Grimpe, 1925, p. 95, 101.—Massy, 1928, p. 30.—Thiele, 1935, p. 970.—Allen, 1945, p. 328.—Robson, 1948, p. 117.—Carcelles, 1953, p. 226.—Voss, 1956, p. 142, fig. 11d.—Dell, 1959, p. 104.—Powell, 1960, p. 185.—Clarke, A. H., 1962, p. 75.—Clarke, M. R., 1966, p. 166.

Benthoteuthis megalops Verrill, July 1885, p. 402–3, pl. 44, fig. 1.—Hoyle, 1885b, p. 282; 1886, p. 36, 169.—Chun, 1910, p. 185–199, pl. 24–27.—Hoyle, 1910, p. 408; 1912, p. 282.—Joubin, 1912, p. 396.—Pfeffer, 1912, p. 325–331, pl. 27, figs. 12–13 (as "*Benthoteuthis abyssicola* Verrill") (pars; figs. 14, 15= *Ctenopteryx*).—Joubin, 1920, p. 57, pl. 13, fig. 4.—Thiele, 1921, p. 453.—Joubin, 1924, p. 74.—Robson, 1932, p. 375, figs. 1–2.—Johnson, 1934, p. 161.

Bathyteuthis megalops—Hoyle, 1886, p. 36, 213, 229; 1886a, p. 247.
Not *Benthoteuthis* sp.—Joubin, 1920, p. 57, pl. 12, fig. 9 (=*Ctenopteryx*).
?*Chunoteuthis minima* Robson, 1921, p. 432, pl. 65, fig. 2 (nomen dubium).—Thiele, 1935, p. 970.
?*Indoteuthis minima*—Grimpe, 1922, p. 45 (replacement for *Chunoteuthis*).
?*Bathyteuthis* sp. Robson, 1948, p. 117, fig. 1.

DIAGNOSIS.—Protective membranes low, fleshy, no enlarged trabeculae; tentacles and clubs relatively short; arm suckers relatively few; sucker rings with 8–18 protuberances; gills short, narrow.

List of Material

Antarctic Ocean

The majority of specimens that were captured by the *Eltanin* in the Southern Ocean were taken by 10′ Isaacs-Kidd midwater trawls; they are listed below followed by the few that were taken by other types of gear. Complete station data are recorded in Savage and Caldwell (1965) and "University of Southern California" (1966).

Eltanin *Sta. No.*	*Number of males*	*Size range ML, millimeters*	*Number of females*	*Size range ML, millimeters*	*Depth of capture, meters*
97	–	–	3	31–40	1830
99	3	10–21	2	11–19	1210
		5 larvae, size range 8.5–11 mm			
110	1	43	1	48	2891
123	2	38–44	1	48	2439
125	2	36–38	2	19–27	1830
132	2	41–43	–	–	1219
133	–	–	2	32–44	2196
137	5	28–41	5	22–53	1556
142	1	19	1	54	1830
148	–	–	1	20	1226
149	1	32	1	37	2105
154	13	33–46	7	31–56	2105
175	–	–	3	15–38	2893
190	–	–	3	21–36	2891
213	2	14–21	–	–	550
		1 larva, 6 mm			
215	1	13	1	17	1220
235	3	19–41	1	32	1830
247	1	49	1	41	1830
248	6	28–40	6	42–45	1370
252	1	42	3	13–46	1570
262	1	35	–	–	2400
274	1	75	4	31–55	1875
275	–	–	2	36–40	1885
296	1	37	–	–	1880

Eltanin *Sta. No.*	*Number of males*	*Size range ML, millimeters*	*Number of females*	*Size range ML, millimeters*	*Depth of capture, meters*
310	–	–	2	13–43	1425
313	–	–	–	–	810
		2 larvae, 6 mm			
325	–	–	1	11	933
354	9	25. 5–47	5	42–54	2150
355	3	41–49	1	49	2440
		1 larva, 9 mm			
360	1	37	2	12–55	1680
361	2	15–38	2	25–50	2100
		1 larva, 7 mm			
364	–	–	1	47	713
368	–	–	2	19–20	914
381	5	28–48	–	–	1870
382	10	20–42	5	18–56	1280
383	4	22–44	4	15–43	1695
388	5	22–37	2	25–37	1420
392	1	44	3	45–52	2330
449	–	–	1	35	1610
571	–	–	1	49	1491
580	1	29	–	–	2743
592	–	–	–	–	2562
		1 larva, 9 mm			
597	2	24–40	–	–	1922
605	1	35	–	–	1510
626	–	–	1	55	1647
668	–	–	1	33	1280
683	1	33	–	–	1690
687	1	35	2	22–48	2214
691	–	–	1	47	1510
692	–	–	2	26–32	1034
714	–	–	1	22	1097
718	1	23	2	41–43	1065
737	–	–	1	51	2575
741	1	17	–	–	2325
742	3	13–21	1	16	864
		2 larvae, size range 8–12 mm			
743	1	17	4	13–29	1830
		1 larva, 9 mm			
767	1	37	–	–	1373
771	3	32–42	1	45	2400
778	–	–	2	12–16	1251
		1 larva, 10 mm			
779	2	34–41	3	31–48	1910
782	2	14–36	4	34–52	2860
789	2	27–31	1	50	2196
792	2	12–45	2	27–33	1481
793	3	19–40	–	–	2260
796	–	–	1	52	2475
		1 larva, 7 mm			

Eltanin *Sta. No.*	*Number of males*	*Size range ML, millimeters*	*Number of females*	*Size range ML, millimeters*	*Depth of capture, meters*
802	4	28–40	3	42–49	1603
812	1	34	5	30–53	823
832	–	–	2	39–46	2200
836	5	28–48	2	35–45	2055
846	4	20–42	2	35–63	1866
847	6	34–47	3	15–41	1991
850	2	15–23	3	43–46	1785
852	–	–	2	11. 5–48	2917
854	–	–	1	26	1285
855	2	22–53	1	25	2320
858	7	30–52	5	31–56	2099
864	–	–	3	24–39	1285
866	1	13	1	14	1127
867	2	36–43	5	31–55	2642
874	2	12–16	1	24	1391
877	1	25	–	–	1719
891	1	19	–	–	1347
949	–	–	1	33	1028
1038	–	–	1	47	1281
1057	–	–	1	25	812
1099	1	22	–	–	956
1106	1	37	–	–	769
1107	1	16	–	–	714
1132	–	–	2	45–49	1603
1133	1	38. 5	6	45–61	685
1137	1	36	–	–	626
1162	–	–	1	20	803
1163	–	–	1	28	626
1170	4	11–14	4	11–13	1080
1185	1	46	1	36	2200
1187	2	31–46	2	36–56	1550
		2 unmeasured males			
1195	1	41	–	–	1650
1201	10	14. 3–49	10	18–46	1120
1214	1	49	3	17–21	2150
1216	2	17–34	2	15–16	1000
1218	2	15–38	3	15–42	1850
1224	–	–	1	34	1600
1236	2	23–24	–	–	900
1262	2	12–21	3	12–21	1230
1269	10	14–45	7	15–27	1248
1270	2	16–38	–	–	933
1286	1	26	4	34–38	2500
1287	4	15–40	4	28–37	2269
1288	1	15	2	13–39	2620
		1 larva, 10 mm			
1299	1	24	2	17–21	1190
1302	1	15	–	–	685
1303	3	16–39	4	15–45	1281

Eltanin *Sta. No.*	*Number of males*	*Size range ML, millimeters*	*Number of females*	*Size range ML, millimeters*	*Depth of capture, meters*
1304	1	12	1	16	864
1307	6	18–50	–	–	1373
1319	–	–	6	37–48	1867
1320	1	47	4	33–58	2288
1323	2	20–48	2	36–41	2560
1324	7	26–46	8	21–49	1958
1327	7	33–46	2	37–45	2060
1328	6	18–46	5	35–48	1775
1358	2	41	4	35–44	1702
1359	1	17	3	30–52	2416
1361	1	46	1	22	1903
1364	8	22–35	3	22–37	1848
1365	3	21–43	2	34–56	2434
1376	–	–	1	13	705
		1 larva, 10 mm			
1383	9	15–49	4	18–54	914
1384	1	21	1	32	1262
1388	2	22–27	3	19–40	942
1389	1	46	–	–	1710
1392	–	–	3	16–35	897
1393	4	15–34	2	22–43	1537
1396	–	–	1	46	2525
1448	6	22–42	1	17	2275
1454	1	20	–	–	825
1456	2	40–43	2	49–54	1000
1462	4	23–29	1	21	1010
1470	1	32	–	–	1800
1471	1	32	–	–	311
1473	1	21	–	–	415

The following specimens were collected in Blake trawls, beam trawls, and dredges.

Eltanin *Sta. No.*	*Number of males*	*Size range ML, millimeters*	*Number of females*	*Size range ML, millimeters*	*Depth of capture, meters*
230	1	44	–	–	1150
353	1	45	1	37	3642
450	–	–	1	54	1110
462	–	–	1	48	3404
870	1	18	–	–	5014
1117	–	–	1	46	4813
1148	2	34–35	–	–	4850
1199	1	41	–	–	4374
1292	–	–	1	34	4941
1363	1	36	2	16–32	2763

Atlantic and Eastern Pacific Oceans

Sex	*ML*	*Ship Sta.*	*Location*	*Date*	*Depth, meters*	*Gear*
M	56 mm	Pel. 11	27°52′N 79°45′W	11 III 56	430	40′Otter trawl
F	49 mm	Ch. 17–18	Sargasso Sea	61		10′ IKMT
F	47 mm	D3981 I	19°16′S 01°48′W	19 II 30	500	E 300
F	45 mm	SB 2024	28°26.5′N 80°11.5′W	27 IV 60	36	10′ scallop dredge
M	44 mm	O 4296	07°55′N 53°55′W	22 III 63	914	65′ shrimp trawl
F	39 mm	Pil. 20	04°56′N 00°13′E	27 V 64	1650–2125	10′ IKMT
F	38 mm	Ch. 17–13	05°N 15°W	IV 61	750	10′ IKMT
F	37 mm	Ch.(RHB) 978	01°44′S 27°44′W	27 II 63	1000–3500	10′ IMKT
F	36 mm	D3996 I	15°41′S 05°50′W	25 II 30	2000	E 300
M	33 mm	D4000 I	00°31′S 11°02′W	4 III 30	500	E 300
F	30 mm	D1208 XIV	06°48′N 80°33′W	16 I 22	1550	S 150
M	25 mm	Pil. 300	02°05′N 04°50′E	24 V 65	2000–3000	10′ IKMT
M	24 mm	D1208 XV	06°48′N 80°33′W	16 I 22	1300	S 150
M	24 mm	D1208 XV	06°48′N 80°33′W	16 I 22	1300	S 150
F	23 mm	D4003 I	08°26′N 15°11′W	9 III 30	3000	E 300
F	22 mm	D1208 XV	06°48′N 80°33′W	16 I 22	1300	S 150
?	20 mm	Pil. 37	04°00′N 02°46′W	29 V 64	490	10′ IKMT
M	19 mm	D3998 VIII	07°34′S 08°48′W	1 III 30	2000	S 150
F	19 mm	D1209 I	07°15′N 78°54′W	17 I 22	1750	S 150
M	17 mm	Pil. 39	04°24′N 03°00′W	30 V 64	300	10′ IKMT
M	17 mm	Pil. 21	05°07′N 00°05′E	27 V 64	1150–1450	10′ IKMT
L[1]	16 mm	D4000 VI	00°51′S 11°02′W	4 III 30	3000	E 300
F	16 mm	D1162 II	13°35′N 30°11′W	6 XI 21	200	S 200
F	15 mm	D1162 II	13°35′N 30°11′W	6 XI 21	200	S 200
M	15 mm	D1022	39°51′N 48°20′W	16 IX 13	1500	P 200
F	14 mm	D1165 VIII	12°11′N 35°49′W	9 XI 21	1500	S 150
L	14 mm	D3998 XI	07°34′S 08°48′W	1 III 30	500	S 150
L	13 mm	D3998 II	07°34′S 08°48′W	1 III 30	200	S 150
L	13 mm	D1209 III	07°15′N 78°54′W	17 I 22	1250	S 150
L	12 mm	D4003 IV	08°26′N 15°11′W	9 III 30	1500	S 150
L	12 mm	D4003 IV	08°26′N 15°11′W	9 III 30	1500	S 150
L	11 mm	Pil. 300	02°05′N 04°50′E	24 V 65	2000–3000	10′ IKMT
L	10 mm	D4003 V	08°26′N 15°11′W	9 III 30	1000	S 150
L	9 mm	D3998 X	07°34′S 08°48′W	1 III 30	1000	S 150
L	9 mm	D4201 XIX	47°02′N 31°45′W	27 VI 31	1500	S 200
L	8 mm	D4005 III	13°31′N 18°03′W	12 III 30	1500	S 150
L	8 mm	D3996 II	15°41′S 05°50′W	25 II 30	1500	S 150

[1] L refers to larval or juvenile specimens of undetermined sex.

Description.—The mantle is short and broad; it is widest just posterior to the mantle opening. The mantle tapers gradually to a bluntly rounded tip, giving it a bullet-shaped outline (pl. 1). In adults the greatest mantle width is about 48% of the mantle length, and the average width is 44%. The margin of the mantle opening has three small, anteriorly projecting triangular lobes that mark the articulation points of the two ventral mantle-funnel locking cartilages and the single dorsal mantle-nuchal cartilage. The wall of the mantle is relatively thick and muscular, although in individuals that have recently spawned there may be some degradation of the muscle tissue and a thinning of the mantle wall.

The integumentary layers on the mantle form a thick sheath (pl. 2b). The outermost integument consists of small, closely aligned patches that give the skin a velvet-like appearance when observed in natural size. Under magnification, however, the outer integument looks like a very fine-meshed knotless net. Though somewhat variable, the meshes are primarily pentagonal, occasionally hexagonal. The margins of the web-units are very thin and membranous and stand perpendicular to the plane of the mantle wall. These margins of the web are deeply colored by maroon-brown pigment. One or two chromatophores of the same color lie in the thin membrane that underlies and interconnects the walls of the web.

A thin sheet containing chromatophores lies immediately beneath the outer reticular layer. The sheet of chromatophores overlies a relatively thick, watery-gelatinous, transparent, unpigmented layer. This gelatinous layer is supported by a network of ridges that are of greater density than the nearly fluid contents of the pockets made by the intersections of the supporting reticulation. These pockets are also pentagonal but are larger than those of the outer layer of integument. Two additional layers of maroon chromatophores are located beneath the gelatinous layer. A thick elastic layer of connective tissue and fibers binds the integumentary layers to the muscles of the mantle wall. A few small widely spaced chromatophores lie even in the connective tissue very close to the muscular wall of the mantle.

The fins are small and nearly circular in outline (pl. 1). The bases of the fins are separated posteriorly by the blunt termination of the mantle; they are broadly separated anteriorly by the dorsal surface of the mantle. The bases of the fins are robust and muscular but radially the fin muscle becomes thin and weak, so that the borders of the fins are thin, nearly membranous. The margins of the fins are damaged even in the best-preserved specimens. The rounded anterior fin lobes protrude well forward of the bases of the fins; the rounded posterior lobes extend beyond the end of the mantle.

The funnel is long and narrow; it extends nearly to the level of the posterior edge of the eye opening (pls. 1B; 2A). Between the components of the locking apparatus the posteroventral margin of the funnel is broadly U-shaped and is weakly muscled. The tube of the funnel is long and narrow; the opening is small. The collar of the funnel is thin-walled and weakly developed; it does not form a strong anterior fold. The funnel retractor muscles are strong and robust. They extend posteriorly from the dorsal wall of the funnel and the bases of the locking-apparatus components to the posterior end of the mantle where they flare and insert along the shell-sac and the mantle wall. The bridles of the funnel are broad, thin, weak bands deeply embedded in the posterior depression of the funnel groove. Integument and subcutaneous gelatinous connective tissue blend the funnel smoothly with the surface of the head around the collar and along the lateral borders of the funnel tube. The anterior end of the funnel, however, lies free in the funnel groove. A small pore lies in the midline of the funnel groove; a tube leads dorsally from the pore, through the gelatinous tissue, and between the bridles. I am conducting a separate study of this previously unreported structure which occurs in several oegopsid families.

The cartilaginous components of the funnel-making locking apparatus belong to the simple type. The funnel component is a long, narrow structure with a smooth median sulcus that is deep and narrow anteriorly but shallow and flaring posteriorly (pl. 2A, E). The funnel component is bordered anteriorly and laterally by a thin, membranous lip that fuses posteriorly with the thin, posteroventral edge of the funnel. The mantle component of the locking apparatus is a simple straight ridge that is most pronounced and distinct in its anterior half; it diminishes and broadens posteriorly until it is flush with the inner wall of the mantle (pl. 2A, D).

The dorsal member of the funnel organ is a broad, inverted, Y-shaped glandular structure (pl. 2F). The diagonal limbs are long, slender, unsculptured, and rounded posteriorly. The median (anterior) limb is short and blunt; it terminates with an erect, spatulate spire that protrudes from the dorsal wall into the chamber of the exhalant tube.

The ventral members of the funnel organ are elongate, rounded pads (pl. 2F). The median border of each is nearly straight and the lateral border is broadly curved. The anterior and posterior ends are rounded.

The funnel valve is a large semicircular flap that extends across the dorsal surface of the funnel tube just posterior to the opening of the funnel (pl. 2F). A deep pocket is formed by the fusion of the lateral and posterior borders of the funnel valve with the dorsal wall of the funnel tube.

The head is broad and short (pl. 1). The huge, anteriorly directed eyes give the head a distinctly swollen appearance. The head narrows markedly at the base of the brachial crown just anterior to the eye openings. The dorsal and ventral surfaces of the head are nearly flat and the head tapers anteriorly into the brachial crown. No nuchal crests or folds occur in the region of the neck.

The nuchal component of the mantle-nuchal locking apparatus is a strong, elongate, cartilaginous structure with a straight median ridge bordered on each side by a smooth sulcus (pl. 1c). The edge of the nuchal component is bordered by a broad membranous skirt. The cartilaginous mantle component of the nuchal lock is complementary in structure to the nuchal component. A deep median sulcus is bordered on each side by a long, straight ridge. The mantle component lies directly ventral to the anterior terminus of the gladius, and its form is imposed by the chitinous rhachis that has a deep median groove ventrally and is supported by strong, rodlike edges.

The olfactory papillae lie on the posterior ventrolateral surface of the head just anterior to the collar. They are short, small, slightly swollen, lobate, or flaplike structures that lie beneath the anterior border of the mantle.

The integumentary layers on the head are similar to those on the mantle. The gelatinous layer is particularly thick on the dorsal and posterior regions of the head. In general, the pigmentation on the head and arms is more concentrated than it is on the mantle, so that the color is a dark maroon.

A small, simple photophore is located at the base of each of the first, second, and third arms (pl. 5A, E). No trace of a photophore is present at the bases of the ventral arms. The photophore is readily visible on smaller specimens as a dark, elongate, rounded patch, often with a pale central spot. In larger specimens, however, the light organs become less distinct because they are partially overgrown with integument and gelatinous tissue. The organs arise in one of the deeper chromatophore layers where they are surrounded by an area of maroon pigment which gradually diminishes away from the organ. In long-preserved specimens that have become bleached, the photophores usually are indistinguishable.

The arms and tentacles extend from the base of the narrow brachial crown. The arms are short, subequal in length. The arm formula occurring with the greatest frequency is 4.3.2.1, followed by 4=3=2.1 and 4.3=2.1. The length of the arms is measured from the basal portion of the sucker-bearing area to the tip of the arm. The measurement on the ventral arms may be misleading in some specimens, because the sucker-bearing portion may originate more distally than on the remaining three pairs of arms, giving the impression that the fourth arms are shorter. Generally, however, the fourth pair of arms is the longest or equals in length the third and/or second arms. The first pair of arms is always the shortest.

The four pairs of arms are connected by a fleshy web (pl. 3A, B) that is an extension of the integumentary layers of the head and arms. The web that connects the first arms is the deepest, and web depth decreases gradually between the first and second, the second and third, and the third and fourth arms. No web exists between the fourth arms. The web between the third and fourth arms is the continuation of the lateral membrane (or "tentacular sheath") along the dorsal aboral angle of the fourth arms. This thick, fleshy web makes the arms look shorter and the head (anterior to the eye opening) longer than they actually are.

The arms are elongate cones, thick at the bases and evenly tapered to the tips (i.e., not sharply attenuate). Swimming keels and membranes exist on the aboral surfaces of the arms, but they occur only as fleshy ridges rather than as distinct, muscular (or membranous) keels. The keel on the dorsal arms is a raised fleshy ridge along the distal half of the arm. The keel on the second arms is noticeable proximally as a thickened ridge that becomes raised and thinner distally. The greatest development of a true swimming keel occurs on the third arms where the keellike ridge is raised and relatively thin (though still fleshy) along the distal three-fourths of the arm. On the ventral arms the lateral membranes, which partially envelop the tentacular stalks during swimming, are moderately developed, although they too are fleshy, particularly proximally, and not membranous as in most other oegopsids.

All arms in *B. abyssicola* are supplied with protective membranes (pl. 3A) that are extremely variable; they are thick and fleshy. Typical thin, muscular, strutlike trabeculae are lacking. The membranes appear to be the result of the fusion of the edges of flattened trabeculae. The membranes arise abruptly on the oral surface of the first three pairs of arms, about in line with the base of the proximalmost sucker. Along the proximal two-thirds to three-fourths of the first three pairs of arms the protective membranes are well developed and the edges stand well above the level of the suckers. Distally, however, the membranes become merely low ridges that form the oral angles of the arms primarily; suckers stand well above the borders of the membranes. Borders of the protective membrane may be straight, gently undulate, or scalloped to varying degrees. The protective membranes of the fourth arms are very weakly developed along their entire length.

The oral surfaces of the arms are covered with numerous, small suckers that are irregularly arranged in up to four longitudinal rows particularly on the dorsal three pairs of arms (pl. 3A). One or two suckers arise proximally close to the midline of the arm; these may be in a single row or slightly biserial. The next several pairs of suckers are generally clearly distributed in two biserial, often well-separated rows. It is difficult to determine exactly how many longitudinal sucker rows exist, because about a third to halfway out the arms the distribution of suckers becomes irregular. Generally, however, the rows can be separated down the midline of the arm where no suckers occur so that on each side a band of biserially arranged, closely packed suckers occurs that continues toward the tip. When the sucker stalks on each side of the midline emerge from the oral surface of the arms they are in biserial arrangement, but beneath the surface their bases arise nearly in line. The sucker arrangement on the ventral arms usually remains uncomplicated with a normal biserial distribution. Close to the arm tips the suckers diminish in size and number. The sucker-bearing portion of the arm terminates proximal to the extreme tip of the arm, and the last traces of the protective membranes fuse in the middle; a sudden decrease in the diameter of the arm occurs distal to this point. The extreme tip of the arm may be entirely devoid of suckers, or one or two minute suckers may be present (pl. 3c). In either case the tip is short, almost blunt.

The texture of the arms is the same as that of the head and mantle; the arms are covered with the reticulate integument and the subcutaneous gelatinous layer.

The tentacles are extremely long, thin and muscular (pl. 1). They range in length from about 100% to 130% of the mantle length. (These values may vary considerably depending on the amount of contraction at the time of fixation.) The tentacular stalks are nearly round in cross section except along the flat to slightly concave oral surface. The longitudinal concavity or depression extends nearly the entire length of the tentacular stalk; it is less pronounced toward the base of the stalk. Occasionally a slightly raised ridge appears in the depression, but this is a factor of contraction of muscles during fixation.

The tentacular club is relatively short, narrow, and unexpanded (pl. 4A); it belongs to the simple type and is not divided into distinct regions of carpus, manus, and dactylus. The club occupies from about 20% of the mantle length in younger specimens up to about 30% in adults. The club length is about 20% of the tentacle length. The tentacular stalk maintains about the same diameter along its entire length to the base of the club, but the club tapers gradually to a blunt termination. The sucker-bearing portion of the club is covered with numerous, minute, closely packed suckers. The suckers originate with a single sucker proximally; the next few suckers are slightly scattered and set apart, but the suckers increase in number rapidly and become very closely packed. Suckers are evenly distributed over the club so that no clearly defined pattern of rows exists; however, eight to ten longitudinal rows of suckers occur on the sucker-bearing surface for nearly the entire length of the club. Suckers decrease in numbers only at the very proximal and distal ends of the club.

The sucker-bearing portion of the club terminates in a bluntly rounded area of suckers. An extremely small, papilla-like tip protrudes distal to the sucker-bearing area and is continuous with the aboral surface of the club (pl. 4B). A few minute knobs are located on the proximal portion of the terminal papilla; these knobs probably are precursors to suckers. Possibly the terminal papilla represents the growing portion of the tentacular club.

No protective membranes exist along the borders of the club; only a slight, pigmented line outlines the sucker-bearing portion of the club, especially in its proximal half. A thin, low keel originates on the dorsal aboral surface of the tentacular stalk just proximal to the first (proximalmost) sucker of the club. The keel extends distally and broadens gradually in the distal third of the club; it terminates near the tip of the club just proximal to the end of the sucker-bearing area. No additional keels or membranes are present.

The suckers on the club are small and numerous; about 525 suckers, the largest 0.14 mm in diameter at the aperture, occur on the club of a specimen 56 mm in mantle length. The diameter of the sucker apertures in adults varies between 0.08 and 0.14 mm, depending upon the size of the specimen. Some variation in dentition occurs, but in general about 8–12 teeth and knobs are set around the aperture. The teeth that occur on the distal half of the border generally are truncate, longer than broad, and widely separated, although occasionally the teeth will be shorter, almost square, or rounded, or very occasionally, triangular. The larger suckers of a club from a specimen 28 mm in mantle length (Elt. 1201; pl. 4J) have about 8–12 points around the aperture; those with 8 or 9 points have 4 to 5 long, truncate, widely spaced teeth and 4 to 5 small, rounded bumps or knobs; those with 11 or 12 points have 6 teeth and 5 to 6 knobs. Sometimes two teeth will be closely set and very narrow as though earlier in ontogeny they had been a single tooth that split in two. Larger specimens have club suckers with a few more enlarged teeth so that rings with 9–13 points may have 5–8 long, truncate teeth and 4 to 5 knobs (pl. 4K). Some large teeth are notched on the ends, and sometimes the notch is so deep that the tooth will have two small, pointed cusps. The largest specimen in the collection, 75 mm in mantle length, has as many as 17 protuberances around the aperture; of these, 7 are proper teeth, truncate to rounded and a little more closely packed than usual, while the remainder are merely low knobs that give a scalloped appearance to the posterior half of the border of the ring. Occasionally large suckers will have nearly smooth or scalloped apertures.

The sucker rings from the arms of a specimen 56 mm in mantle length are described first. The outer rings on the suckers of the arms bear 3 to 4 concentric rows of small chitinous papillae (pl. 4H). The papillae are minute knobs on the outer margin and gradually increase in length on the rows toward the aperture. The innermost row that borders the aperture has numerous, small, elongate papillae that project into the aperture and give the appearance of being small teeth on the inner sucker rings. Together the teeth of the inner sucker ring and the papillae of the outer ring make a double-rowed armature.

The inner chitinous sucker rings are subglobular; the walls are broadest distally, and they taper to their narrowest dimension proximally. The sucker rings on the first arms bear 9–15 small, truncate to rounded teeth. The maximum diameter of the apertures is about 0.20 mm. The largest sucker ring aperture on the second arms is also 0.20 mm. The dentition of the rings is variable. The larger rings have about 12–18, usually 14–16 small, low, truncate, subtruncate, or slightly pointed teeth. The inconsistency in dentition holds for smaller suckers also, but they generally have about 9–12 teeth. The sucker rings may be nearly smooth or scalloped, or they may have truncate or pointed teeth. The suckers on the third arms have maximum ring apertures of about 0.20 mm. The rings bear from 9–18 very small teeth, which are generally truncate, but sometimes rounded in shape. The sucker rings on the fourth arms are about 0.16 mm in maximum diameter, and they bear between 8 and 18 teeth, more frequently 10–14. Generally the smaller rings have fewer teeth but this does not always hold; one medium-sized ring had 18 closely spaced teeth. Normally the larger suckers have 10–14 teeth. The teeth usually are truncate to slightly rounded with their bases set apart, but occasionally the teeth will be very closely packed. A few rings are nearly smooth to slightly scalloped.

Since dentition varies slightly with the size of the animal, the following description of suckers from a specimen 38 mm in mantle length is given.

The diameter of the outer ring from the largest sucker on arm I is 0.22 mm and of the inner ring aperture 0.16 mm (pl. 4C). The largest rings have 12 teeth and the medium-sized rings have 9–10. The teeth are always small; they are more elongate and truncate in the distal portion of the ring and shorter, more rounded, and knoblike proximally. The teeth on the larger rings often are separated at their bases by the widths of several teeth; teeth are widely spaced on the smaller rings. The rings from the first arms of a specimen of 28 mm mantle length bear eight teeth: four long, truncate, widely spaced teeth distally and four small, round, widely set knobs proximally (pl. 4D). These rings measure 0.12 to 0.14 mm in diameter.

The outer ring has 3 to 4 concentric rows of chitinous knobs that become elongate and toothlike on the inner row. The outer ring fits closely around the aperture of the inner ring; in this position the inner row of toothlike knobs serves as an additional row of teeth that are very closely associated with the teeth of the inner ring.

On the second arms the outer rings measure 0.24 mm and the inner rings 0.14 mm (pl. 4E). There are 9 to 10 teeth around the aperture. The teeth are generally short, truncate to rounded in shape; some are worn so that the tips are concave.

The largest suckers on arm III have outer rings 0.24 mm in diameter and inner rings 0.16 mm in diameter. The larger inner rings bear about 12 evenly spaced teeth (pl. 4F), while the smaller rings have 8 teeth that are more elongate and widely spaced than those of the larger rings.

The diameter of the outer ring of the largest sucker on the fourth arm is 0.28 mm and of the inner ring 0.20 mm. On the largest inner rings appear 12 to 14 small, widely spaced truncate to rounded teeth (pl. 4G); 9 teeth appear on the medium-sized rings where the 3 to 4 distalmost teeth tend to be more elongate than the others.

The suckers on the buccal lappets possess outer rings that measure 0.18 mm in diameter and inner ring apertures that measure 0.12 mm across. The 9 to 10 teeth on the inner ring are widely spaced and elongate, particularly along the distal border (pl. 4I).

The buccal membrane is large, fleshy, and rugose (pl. 3A). The buccal connectives are attached to the dorsal, dorsal, ventral, dorsal oral edges of arms I–IV respectively (pl. 3B). The buccal lappets bear from 0 to 3 minute suckers that have 8–12 teeth on the chitinous rings (pl. 4I). The significant geographical variation that occurs in the number of buccal suckers is discussed in detail later.

The buccal mass, comprised of the muscular bulb that encases the mandibles, radula, and other mouth parts, is relatively smaller in *B. abyssicola* than in other oegopsids (e.g., ommastrephids, enoploteuthids, gonatids). The beaks (pls. 3D, E) are small; they are darkly pigmented where the rostra are exposed, but the pigmentation lightens on the lamellae. The rostrum of the upper beak is curved and sharply pointed; the curved jaw angle has a slight protuberance. The insertion plate of the palatine lamella is nearly two times longer than high and the posterior end is angled. The rostrum of the lower beak is relatively blunt and forms nearly a right angle with the long, narrow rostral lamella. The gular lamella is broad; it is bluntly rounded posteriorly.

The radula consists of seven transverse rows of pointed teeth and two rows of elongate lateral plates (pl. 3F). The rhachidian has a broad, low base; the median cusp is moderately long and bluntly pointed. No lateral cusps exist, but the basal, concave, lateral borders of the rhachidian are often set with irregular protuberances. Some of these may approach the size of lateral cusps, but still they remain as protuberances and are not cusps. The first lateral teeth are broadly crescent-shaped with convex medial and concave lateral borders; the blunt cusp is about as long as that of the rhachidian. The second laterals are long, slender and crescent-shaped; the cusps are slightly longer and more pointed than the first laterals or the rhachidian. The basal lateral borders of the first and second lateral teeth are also marked with slight irregularities or small protuberances, but these are not incipient cusps. The third lateral teeth are very long, slender, scythe-shaped; they terminate in moderately sharp points. The lateral plaques are elongate plates set on the radula ribbon at about 45° to the long axis of the radula. The long sides are concave and the ends are bluntly rounded. In other specimens the plates become very knobby or irregular, or they may even be divided into two or more small masses.

The gladius is embedded in the inner surface of the mantle wall. The circular muscles of the mantle are continuous over the gladius so that it is not visible in the dorsal midline. The anterior end of the rhachis lies on the inner surface of the mantle covered only by a thin sheath. At its anterior tip the rhachis is covered by a thin cartilaginous band. This band and the exposed rhachis posterior to it make up the mantle component of the mantle-nuchal locking apparatus. Immediately posterior to the nuchal locking apparatus the gladius is bound to the inner surface of the mantle wall by a strong, thick muscle that is an extension of the inner portion of the collar muscle. This sheath spreads posteriorly and ventrally and envelops the liver in a strong muscular sheath. The strong dorsoanterior band is continuous ventral to the mantle, but it diminishes posteriorly, so that the fibers of the liver sheath attach to the shell-sac along the lateral edges of the rhachis. The remainder of the gladius is visible in the shell-sac posteriorly extending from the heavy muscle band to the termination.

The powerful funnel retractor muscle passes posteriorly over the ventrolateral surface of the liver, and in the region dorsal to the branchial heart it flattens out into a broad sheet. Dorsally it merges with the fibers of the liver sheath and attaches to the shell-sac along the edge of the rhachis and vane of the gladius. The funnel retractor sheath attaches to the lateral wall of the mantle.

The vane of the gladius arises from the rhachis at a point in line with the branchial hearts. The vane broadens gradually posteriorly and curves ventrolaterally with the mantle wall. The visceral dome and the visceral-pericardial coelom lie directly ventral to the vane and are attached to the shell-sac with weak connective tissue. The relationship of the posterior end of the gladius with the tip of the mantle is difficult to ascertain, because the mantle tip always seems to be violently contracted. The contractions push the vane of the gladius anteriorly and ventrally in a series of irregular folds.

The rhachis of the gladius is very long and narrow (pl. 2G). The free portion of the rhachis accounts for over half the length of the gladius. The lateral edges of the rhachis are strong, straight, cylindrical rods that are joined dorsomedially by a concave strip. A deep groove lies between the lateral rods; anteriorly the groove of the rhachis holds portions of the muscles of the collar and liver-sheath that are attached to the shell-sac. In the posterior half of the gladius the rods of the rhachis converge and taper gradually until they disappear in the posterior end of the vane.

The vane is a thin, blade-shaped structure that arises at about the midpoint of the gladius. It broadens gradually to its widest point posteriorly then quickly terminates in a bluntly rounded tip. No conus is present. The anterior portion of the vane is nearly flat, but the broader posterior section is deeply concave, conforming with the shape of the tapering mantle. Considerable variation exists in the shape of the vane.

The spermatophores (pl. 2H) are 4.5–7 mm in total length, depending upon the size of the male. The proportions of the components, however, remain relatively constant. The sperm mass occupies about 68–72% of the total length; the cement body makes up 6–8% of the length, and the ejaculatory apparatus occupies the remaining 20–25%. The base of the ejaculatory apparatus is goblet-shaped; the basal section is a thickened collar that fuses with the cigar-shaped cement body.

No hectocotylus exists.

HOLOTYPE.—British Museum (Natural History); BM 1890, 1.24.15.

TYPE LOCALITY.—Between Prince Edward Island and the Crozets Islands at 46°16′S 48°27′E. HMS *Challenger*, 30 December 1873.

DISTRIBUTION.—Bathypelagic in the Southern Ocean and in the productive waters of the East Pacific, Atlantic, and Indian Oceans. Ranges between 300 and 3000 m, mostly 1000–2500 m (see Part II).

MORPHOMETRY.—Measurements of various body parts have been made to determine allometric relationships and variability of proportions that occur in *Bathyteuthis abyssicola* during growth. All measurements are compared with the standard of size, the mantle length, which is plotted as the abscissa. Measurements were made on 121 specimens of *B. abyssicola* from the Southern Ocean. These specimens represent about one-fourth of the total sample population that was available at this stage of the study; the sample consists of 53 males and 68 females of all available sizes taken throughout the study area. The following measurements were made: mantle length, mantle width, head length, head width, basal fin length, total fin length, fin width, tentacle length, club length, arm lengths (I–IV). The values of these measurements are plotted as the ordinate against mantle length on scatter diagrams (figs. 1 to 13).

The plots of all of the characters, with the exception of tentacle length and club length, show little spread in the values, and the relations of mantle length to the other variates appear to be linear. The broader spread of points on the scattergrams for tentacle length especially and less so for club length (figs. 7, 8) reflects a condition of preservation rather than of irregular or unordered growth. The elastic tentacles are subject to contraction or stretching, depending on the condition of the specimen at fixation. Even so, a more or less linear growth is indicated for the tentacles (fig. 7). Clubs make up a small proportion of tentacle length so they do not readily show the effects of preservation.

Club length vs. tentacle length is plotted (fig. 9); a linear relationship is indicated here, too, although in the extreme upper and lower range of sizes club lengths appear to be plateaus. These may be a result of the conditions of preservation, or they may reflect a natural sigmoidal pattern of growth.

Allometric growth appears to occur as a general feature in the squids that have been studied in this regard. *Chiroteuthis* exhibits an extreme growth pattern in which drastic changes in proportions occur between the "Doratopsis" stage and adulthood. Also, Adam (1952, p. 63) has demonstrated that the fins and ventrolateral arms of males of *Alloteuthis africana* cease to grow allometrically above a certain size (age). In *B. abyssicola* the allometric relationships of mantle width, head width, and fin width, for example, may be slightly altered at the maximum size of the species, although too few very large specimens are available currently to substantiate this. Therefore, within the extent of these data, *B. abyssicola* exhibits well-defined allometric growth curves.

DISCUSSION.—I have examined the holotypes of both *Bathyteuthis abyssicola* Hoyle, 1885, and *Benthoteuthis megalops* Verrill, 1885. Hoyle's type in the British Museum (NH) is in fair condition only, but no particular points are in question about this specimen from the Southern Ocean. Light organs cannot now be detected at the bases of the arms, but, as mentioned in the preceding description in reference to recently preserved material, this is a feature of preservation and is not due to the absence of the photophores.

The type of *Benthoteuthis megalops*, deposited in the U.S. National Museum, is in poor condition; it has dried up in the past and now is hard and unmanageable. That it is conspecific with the Atlantic form of *Bathyteuthis abyssicola*, however, is still verifiable.

The nomenclatural problem that exists between *Bathyteuthis abyssicola* and *Benthoteuthis megalops* seems not to have arisen until Chun (1910) announced that Verrill's *Benthoteuthis megalops* had priority. Actually, *Benthoteuthis* was synonymized with *Bathyteuthis* in the same year that the two genera were introduced; Hoyle (1885c, p. 282) considered Verrill's specimens at least congeneric with *Bathyteuthis* and, further, determined that *Benthoteuthis megalops* was not published until July 1885, while *Bathyteuthis abyssicola* appeared in May 1885. In his *Challenger* Report, Hoyle (1886, p. 169) suggested that *B. abyssicola* and *B. megalops* were conspecific, but he retained them as separate species (p. 36). Again in 1886a (p. 274) Hoyle listed the two species of *Bathyteuthis*. Pfeffer (1900, p. 173) synonymized *B. megalops* with *B. abyssicola*, although not without some uncertainty. In 1903 Chun referred to "*Bathyteuthis* (*Benthoteuthis*)" (p. 85) and from then on to *Bathyteuthis*, a clear indication that he considered *Benthoteuthis* a synonym. But Chun (1910, p. 186) changed his mind and claimed that *Benthoteuthis megalops* Verrill had priority over *Bathyteuthis abyssicola* Hoyle by one month on the basis of the April 1885 signature date on the sheet that contained Verrill's description. Shortly thereafter, however, Hoyle (1912, p. 282) emphatically opposed Chun's decision claiming that Verrill's work was not published in separate sheets. "Therefore, under the most favourable construction, it cannot possibly have appeared before June, and careful inquiries which I made at the time led me to the conclusion that it did not make its appearance till July" (p. 283).

Since that time the usage of the names seems to have been more a matter of preference than of priority.

I have made an exhaustive search through the records of the Smithsonian Institution Library, the Yale University Library, and the Connecticut Academy of Arts and Sciences in an effort to determine the exact date of publication of Verrill's *Benthoteuthis megalops*. I have found no evidence to prove that the description was published in the nomenclatural sense prior to June 1885. *Bathyteuthis abyssicola* Hoyle, 1885 (May), therefore, must take priority.

Bathyteuthis bacidifera Roper, 1968

PLATES 6–10; 12 G,H

?*Benthoteuthis megalops*, Chun, 1910, p. 185–199, pls. 24–27 (pars; station 221, 18 mm specimen only).—Pfeffer, 1912, p. 325–331 (pars; using Chun's description).

Bathyteuthis bacidifera Roper, 1968, p. 163, pls. 1–4.

DIAGNOSIS.—Protective membranes on arms lacking; long, free, finger-like trabeculae present; tentacles and clubs relatively long; suckers on arms numerous; sucker rings with 18–34 protuberances; gills long, broad.

List of Material

Sex	*ML, millimeters*	*Ship Sta.*	*Location*	*Date*	*Depth, meters* [1]	*Gear*
HOLOTYPE:						
F	37	Elt. 34	07°47′S 81°23′W	7 VI 62	683	10′ IKMT
PARATYPES:						
F	37	Elt. 34	07°47′S 81°23′W	7 VI 62	683	10′ IKMT
F	34	Elt. 54	18°23′S 72°39′W	16 VI 62	1373	10′ MW Beam
M	28	Pil. 510	06°54′N 79°57′W	3 V 67	[2] 3182	40′ otter
F	26	D1208 XIV	06°48′N 80°33′W	16 I 22	1550	[3] S 150
OTHER MATERIAL:						
F	19	D1203 XIII	07°30′N 79°19′W	11 I 22	1000	S 100
M	17	D1208 VIII	06°48′N 80°33′W	16 I 22	750	S 100
M	12	D1209 III	07°15′N 78°54′W	17 I 22	1250	S 150
M	11.5	D1208 VI	06°48′N 80°33′W	16 I 22	1250	S 150
F	11.5	D1203 XVI	07°30′N 79°19′W	11 I 22	750	S 150
L [4]	10	Elt. 34	07°47′S 81°23′W	7 VI 62	683	10′ IKMT
F	9	D1203 XII	07°30′N 79°19′W	11 I 22	1250	S 150
L	6	D1208 XVI	06°48′N 80°33′W	16 I 22	1050	S 150

[1] Estimated depth of capture.

[2] Bottom depth fished by otter trawl.

[3] Stramin tow-net of 150 cm diameter.

[4] L refers to larvae.

DESCRIPTION.—The mantle is short, broad, and bullet-shaped with gently curving sides; it has approximately the shape of a truncated ellipse, terminating in a bluntly rounded tip (pl. 6). The mantle width is about 50% of the mantle length. The location of the mantle-funnel locking apparatus is indicated ventrally on each side of the mantle opening by a small triangular projection. The anterior projection on the dorsum of the mantle is a blunt lobe. The muscle that makes up the wall of the mantle is moderately thick and well developed. The integumentary layers are relatively thick, similar to those of *B. abyssicola*; they are bound to the mantle wall by a semigelatinous, fibrous matrix of connective tissue.

The fins are short, small, and paddle-like; they are nearly circular in outline (pl. 6). The fins are subterminal; the bases are separated posteriorly by the blunt end of the mantle and anteriorly by the broad dorsal surface of the mantle. The bases of the fins are thick and muscular, but the margins are thin and fragile, almost membranous; they are easily torn so that the actual outline of the fins is difficult to determine. The anterior and posterior fin lobes project well beyond the bases of the fins and the posterior lobes extend beyond the end of the mantle.

The funnel is broad at the base and tapers anteriorly (pls. 6B; 7A). The exhalant opening extends nearly to the level between the posterior margins of the eye openings. The posterior border along the base of the funnel is deeply concave between the funnel components of the locking apparatus. The funnel retractor muscles are strong and robust. The bridles are weak, thin bands of muscle.

The collar is a simple, thin-walled band of muscle that passes dorsally from the base of the funnel to the nuchal lock.

The funnel and the collar are bound to the head by the integument and the subcutaneous, semigelatinous connective tissue so that only the anterior portion of the tube is free. The funnel groove is short and relatively shallow.

A small median orifice in the integumentary tissue occurs near the posterior end of the funnel groove, dorsal to the exhalant tube (pl. 7F). The orifice marks the opening of a narrow tube that passes dorsally through the gelatinous tissue and between the median edges of the bridles. This unusual structure, which occurs in some other groups, is currently being investigated.

The funnel component of the locking apparatus is a long, narrow, cartilaginous structure of the simple type (pl. 7A, B). The rounded posterior end is broader than the rounded anterior end. The sulcus of the component is smooth and relatively shallow; it is slightly deeper and narrower anteriorly. A narrow, membranous lip outlines the structure. The mantle component of the locking apparatus is a simple, low ridge; it is highest and most pronounced anteriorly and diminishes posteriorly (pl. 7A, C).

The dorsal member of the funnel organ is an inverted Y-shaped structure (pl. 7E). The posterolateral limbs are long, narrow, and rounded; the anterior limb is short, broad, and blunt. A long, flattened papilla protrudes from the apex of the anterior limb. The lateral borders of the organ are slightly concave, while the medial borders form a curved, open V. The ventral members are elongate, oval patches. The funnel valve consists of a free, semicircular flap anteriorly and a muscular base posteriorly that forms a flat, deep pocket against the dorsal wall of the funnel.

The head is short and broad; it is rounded and swollen laterally by the huge, bulbous eyes that are directed anterolaterally. The eyes constitute a very large proportion of the head. Anterior to the eye openings the head narrows abruptly where the base of the brachial crown originates. The head appears longer than it actually is because the web that interconnects the arms is continuous with the integument of the head. The eye openings are circular; an optic sinus is lacking. The olfactory papillae are minute projections located on the posterolateral curvature of the head. The dorsal and ventral surfaces of the head are flattened across the median areas, but they curve laterally. Nuchal folds or crests are lacking.

The nuchal component of the nuchal-mantle locking apparatus is long and narrow with rounded ends (pl. 7D). It is bordered by a thin, narrow, membranous skirt. A distinct cartilaginous ridge lies in the midline; a narrow deep sulcus lies along each side. These features conform to the cartilaginous mantle component that has a deep median sulcus with a high ridge on each side; this is formed by the anterior end of the rhachis of the gladius.

A small, flat, ovoid photophore is located near the base of each of the dorsal six arms (pls. 6A; 10A). The light organs are embedded in the integument and, as in *B. abyssicola*, are more difficult to detect in large, darkly pigmented specimens. The simple organs consist of a white or cream-colored central area encircled by a darkly pigmented ring that is broadest posteriorly. In young specimens the photophores are readily visible as raised, light or pearly organs (pl. 10A); the pigmented ring is much less pronounced than in larger forms.

The arms are relatively short and conical; the tips are pointed but not attenuate. The ventral three pairs of arms are subequal in length; the dorsal arms are always the shortest. The most frequent arm formula is 4.3=2.1 followed by 4=3=2.1.

A deep web joins the four pairs of arms; it extends out about one-third the length of the arms (pls. 8A; 10B, D), except between the ventral arms where no web occurs. The web is a continuation of the integument of the head and arms, so it is relatively thick and fleshy, not membranous. Because of this the web makes the head appear longer and the arms shorter than they actually are. The section of web between the third and fourth arms continues out the fourth arm as the broad lateral keel or "tentacular sheath."

All arms have aboral swimming keels or membranes. The keel on the dorsal arms occurs as a low, fleshy ridge along the distal third of the arms. The dorso- and ventrolateral arms have relatively well-developed keels along their distal two-thirds. The lateral keel of the fourth arms has been described above.

The most distinctive feature of *B. bacidifera* is the structure of the protective membranes that occur on all arms. Protective membranes in the usual sense are lacking along the proximal half of the arms and are replaced by long, fleshy, finger-like or rodlike projections that roughly resemble thick, blunt cirri (pls. 8 A, B; 10 B, D). A trace of a low membrane occurs between the bases of the projections, or trabeculae. The trabeculae are not strong muscular rods, but are soft and fleshy, nearly semigelatinous, i.e., the same consistency as the normal protective membranes of *Bathyteuthis*. The trabeculae attain their maximum dimensions immediately distal to their origin at the bases of the arms. The ventral trabeculae of the dorsal three pairs of arms are longer and more robust than those along the dorsal edges. Distally the trabeculae become shorter, broader, and more lobate which gives a scalloped effect to the protective membrane that is fully developed on the distal quarter of the arms. The protective membranes are normal toward the arm tips. The ventral arms have fewer, smaller, less strongly developed trabeculae that give way almost immediately to scalloped protective membranes.

The comblike rows of trabeculae appear early in ontogeny and are present even in the smallest larva (6 mm ML) in the present sample. In fact, this feature alone permits definite identification of the larvae of this species.

The oral surfaces of the arms are covered with numerous small to minute suckers arranged in irregular rows. The arrangement of suckers is biserial at the bases of the arms but quickly becomes irregularly 3- to 4-rowed along the middle portion of the arm (pls. 8A,B; 10B,D). The suckers become extremely numerous and closely packed in the distal quarter of the arms, and toward the tips they become minute. Suckers do not occur on the extreme distal tips of the arms. The arrangement of suckers on the ventral arms is nearly the normal biserial distribution.

The tentacles are very long, thin, and muscular; they are about 125–150% of the mantle length. The tentacles are nearly round in cross section except along the oral surface which is flattened and has a shallow, narrow depression running the entire length of the tentacular stalk.

The tentacular club is relatively long, narrow, tapering and simple with no differentiation into carpus, manus, or dactylus (pl. 9A). The club is about 25–30% of the mantle length in smaller specimens and 30–35% in the large specimens; the club makes up about 23–27% of the tentacle length. The sucker-bearing portion of the club is covered with numerous, minute, closely packed suckers that originate proximally as one or two scattered suckers. The suckers increase very rapidly in number distally and are so numerous and closely packed that a definite linear pattern is not obvious, but there are about 8–10 suckers across the club. Suckers decrease in numbers only at the extreme end of the club. The left club of the holotype has approximately 615 suckers. Although the club tapers gradually posteriorly it terminates abruptly in a blunt tip. In smaller specimens the tip is slightly drawn out. This papilla-like tip bears minute granules that appear to be precursors of suckers. The tips of the clubs of the two larger specimens (37 mm ML) are blunt nubs with only a very few nonchitinous suckers; no papilla-like growing tips exist, so these clubs may be approaching the maximum size for these specimens.

No protective membranes occur along the lateral borders of the club. A narrow, weak swimming membrane arises on the dorsolateral surface of the tentacular stalk just proximal to the sucker-bearing region; it runs the length of the club and terminates just short of the tip.

The apertures of the largest inner sucker rings from the first arms of the holotype measure 0.12–0.14 mm in diameter and possess 20–34 (average 24) minute teeth (pl. 9B, C). Medium-sized suckers have around 16 teeth. In general the teeth are small, short, and closely packed; they are long and truncate distally and grade to stubby knobs proximally. The teeth on some rings are so closely packed that their lateral edges are in contact; these teeth tend to be rounded to knobby and not truncate.

The maximum diameter of the sucker apertures on the second arms is 0.14–0.16 mm. These rings bear 20–23 (average 22) teeth (pl. 9D). The small, short teeth are truncate to rounded in shape distally and grade to knobs proximally. Smaller rings tend to have only rounded or knobby teeth. Occasionally a tooth will be broad (about two times wider than its neighbors) or long (about two times longer than broad).

The third arms have sucker apertures with maximum diameters of 0.16 mm. Around the aperture are 21–25 (average 23) small, closely packed truncate (separate) or rounded (borders touching) teeth (pl. 9F). Smaller rings have about 16 teeth. The apertures of the suckers from the third arms of a 26 mm specimen are 0.10 mm in diameter and bear about 20–22 closely packed protuberances. The most distal 4 or 5 teeth are relatively long and robust and are bluntly rounded. The four lateral teeth on each side are reduced in size and these grade into the eight blunt knobs that occur on the proximal part of the ring.

The apertures of the largest suckers from the fourth arms are 0.14 mm in diameter and bear 18–26 (average 21) short, closely packed, truncate teeth that are longer distally, blunter and stubby proximally (pl. 9G).

The largest sucker rings from the tentacular club are 0.08–0.10 mm in diameter and bear 8–10 extremely small, widely spaced, truncate teeth that are elongate on the distal half of the aperture and knoblike on the proximal half (pl. 9I).

The aperture of the tentacular club sucker from the specimen 27 mm in ML is 0.06 mm in diameter and bears about eight small protuberances: four relatively long, bluntly rounded, evenly spaced teeth on the distal border; two slender, blunter teeth on the lateral border; and two short, blunt, widely spaced knobs on the proximal border.

The suckers of the buccal lappets of the holotype have aperture diameters of 0.08–0.10 mm, and they possess 8 to 12 widely spaced, minute, truncate teeth (pl. 9H). The apertures from the 26 mm specimen measure 0.06 mm in diameter.

During ontogeny there is an increase in the number of teeth on the sucker rings; plate 10F, G, H, shows rings with 7, 13, and 18 teeth from specimens of 11, 16, and 29 mm ML.

The large, fleshy, rugose buccal membrane has seven points; the buccal connectives have an attachment formula of DDVD (pl. 8F). From one to five minute suckers occur on each of the buccal lappets (pl. 8A). The suckers are about 0.06–0.10 mm in diameter across the aperture and bear 8–12 truncate to rounded teeth (pl. 9H).

The buccal mass and the beaks are very small for the size of the animal. The rostra of the beaks are black but the pigmentation decreases markedly on the lamellae. The rostra are strong but the lamellae are very weak, thin, and fragile. The rostrum of the upper beak is long, curved, and sharply pointed (pl. 8C). The jaw angle at the junction of the rostrum and the rostral lamella is nearly a right angle, and the anterior border of the rostral lamella is slightly convex. The dorsal outline of the palatine lamella is nearly flat, not curved; the ventral outline is nearly semicircular. The rostrum of the lower jaw is short and blunt; the jaw angle is a smooth curve (pl. 8D). The rostral lamella is long; the insertion plate of the gular lamella is broad and, posteriorly, it is subangular.

The radula has seven transverse rows of pointed teeth and two rows of marginal plates (pl. 8E). The rhachidian has a broad, low base and the median cusp is relatively short, triangular, and bluntly pointed. No secondary (lateral) cusps occur on the rhachidian, but the concave borders of the tooth are occasionally interrupted with small, ragged protuberances. The first lateral has a long, low base and a moderately long, pointed cusp. The second lateral has a long, sharply pointed, crescent-shaped cusp. The third lateral has a very long, slender, scythe-shaped cusp. The marginal plates vary considerably in shape but are generally irregularly rectangular.

The rhachis of the gladius is long and slender (pl. 7G). The anterior tip is thin and weak, but almost immediately the lateral edges are rolled under to form strong, heavy rods that extend posteriorly nearly the entire length of the gladius. The rods taper gradually along the vane and terminate just anterior to the end of the gladius. The rhachis is free for more than half the length of the gladius. No median ridge or rod occurs. The vane is very thin, weak, and fragile, almost membranous. From its origin at the rhachis the vane broadens and becomes wide posteriorly, terminating suddenly in a very blunt, rounded, weak tip. No conus exists.

The entire animal is maroon colored. The pigmentation is darker on larger specimens, particularly in the region of the head and arms; there the color may mask the photophores. On younger, paler specimens, however, the photophores are readily seen. The tentacles alone lack pigmentation.

Spermatophores from the only mature male available (28 mm ML) are 3.8–4.4 mm in length (pl. 12 G,H). The sperm mass is 63–66% of the total length of the spermatophore, the cement body is 17–20% and the ejaculatory apparatus is 15–20%. The cement body is cigar-shaped and elongate with a slightly flaring lip anteriorly. The base of the ejaculatory apparatus is barrel-shaped.

No hectocotylus is present.

HOLOTYPE.—United States National Museum, number 576148.

TYPE LOCALITY.—Off northern Peru at 07°47′S 81°23′W. USNS *Eltanin* Sta. 34, 683 m, 7 June 1962.

DISTRIBUTION.—Bathypelagic in the productive waters of Eastern Pacific Equatorial Water Mass and possibly in the Indian Ocean Equatorial Water Mass (based on Chun's [1910] single specimen).

ETYMOLOGY.—The specific name *bacidifera* is a neo-Latin word meaning "bearing little rods"; this is derived from the old Latin *baculum*, a staff, stick or rod, the diminutive *-idium*, and *-fer*, a suffix meaning bear, carry. The name alludes to the outstanding characteristic of the species, the rodlike trabeculae.

Morphometry.—Although relatively few specimens of *B. bacidifera* are available, they represent a broad range of sizes from larvae of 6 mm to fully ripe adults of 37 mm mantle length. Standard measurements have been made to determine the gross features of growth of *B. bacidifera* and to compare these features with *B. abyssicola.* The morphometric values are plotted as pluses (+) on the scattergrams for *B. abyssicola* (figs. 1 to 13); this allows a direct comparison of the morphometric characteristics of the two species. In *B. bacidifera,* as in *B. abyssicola,* the data indicate that the growth of the body parts that were analyzed is allometric with respect to mantle length.

Discussion.—The *Dana* and *Eltanin* material used in this work show that *B. abyssicola* and *B. bacidifera* are sympatric in the tropical eastern Pacific Ocean. Certain statements in the literature indicate that the two species may also be sympatric in the equatorial waters of the Indian Ocean. Reports of specimens from these two areas may refer to either species or both. In most instances, however, it is difficult to determine the identity of the material.

Chun (1910) had five specimens of *Bathyteuthis* taken by the *Valdivia*; four were captured in the Indian Ocean Equatorial Water Mass. The specimens ranged from 9–18 mm mantle length. In a separate section on the details of arm structure, Chun noted that the largest specimen lacked the protective membrane between the strong muscle supports (trabeculae) and that the trabeculae looked like cirri. All smaller specimens had well-developed protective membranes. Therefore, Chun's largest specimen probably represents *B. bacidifera,* while the remainder of the specimens probably refers to *B. abyssicola.* Unfortunately, it is impossible to be sure to which species Chun's description refers except in sections where he mentions particular specimens. Since the largest specimen is only 18 mm in mantle length, probably most of the description applies to it, especially the descriptions of the eye and internal structures.

Pfeffer (1912) had three larval specimens that he considered to be *Bathyteuthis* (*Benthoteuthis*). The specimen from the Mediterranean was a larva of *Ctenopteryx* (see Historical Résumé). The two remaining specimens were from widely separated localities in the Atlantic. Since the two larvae were only 3 and 4.5 mm mantle length, it seems unlikely that Pfeffer could have derived his detailed description from them. For the greater part, it appears that Pfeffer's information is based on Chun's description. Pfeffer's specimens from the Plankton Expedition were undoubtedly *B. abyssicola,* but since most of his description is based on Chun's work, it necessarily includes a mixture of both species. Pfeffer stated that the protective membranes of larval specimens disappear in older specimens and that only the cross-struts (trabeculae) remain as a comblike structure reminiscent of the ambulacral stalks of some asteroids. Therefore, Pfeffer's description, like Chun's must be considered a mixture of the characters of two species. Both of these works, nevertheless, are still usable in a general way because they do not deal with the characters (other than the trabecula-comb) that distinguish *B. abyssicola* from *B. bacidifera.*

Naef's conclusions about *Bathyteuthis*, which he stated are based primarily on Chun's and Pfeffer's descriptions, are not adversely affected because he dealt with taxa on the generic and familial levels. Works that would be affected are those based on material taken from localities where *B. bacidifera* is known to occur: the equatorial waters of the Indian and eastern Pacific Oceans. Reports that may include specimens of *B. bacidifera* are by Hoyle (1904), Massy (1916), and Robson (1921, 1948).

Hoyle's (1904) description of *B. abyssicola* from the Panama region gives no hint that would help in determining the identity of his specimen. The illustration is not particularly diagnostic either, but the second left arm (one of the five arms shown) looks as though it has distinct trabeculae; these are connected at their ends by a membrane and are not long. The tentacles look very long in the illustration and when their measurements are reduced to natural size (38 mm) they are 1 mm longer than the longest tentacle of *B. abyssicola* from the Antarctic; they are also somewhat longer than the tentacle of *B. bacidifera.* The long tentacles may be due to preservation or to an illustrator's error. No other specific features can be seen in the illustration and it is not possible to determine with certainty to which species of *Bathyteuthis* Hoyle's specimen belongs.

Massy's (1916a) brief description of two small *B. abyssicola* from the southern part of the Bay of Bengal is not detailed enough to indicate if it should apply to *B. bacidifera*, and no illustrations are given. Trabeculae would be developed even in these small specimens, but Massy did not mention them. The arm suckers have 4, 5, and 6 teeth, and the suckers on the very short clubs have 4 teeth.

In the absence of trabeculae, these features may refer the specimens to *B. abyssicola*, but this cannot be stated with certainty, because Chun's and Pfeffer's descriptions imply an ontogenetic occurrence of trabeculae in older specimens; Massy could have believed that her specimens were too small to have trabeculae.

Robson's (1921) supposed bathyteuthid from the Indian Ocean must be ignored, because no information whatsoever can be gleaned from the description or the specimen (see Historical Résumé).

The *Arcturus* captured 11 small specimens in the eastern tropical Pacific in the region of the Galapagos and Cocos Islands. Robson

(1948) considered 10 of them to be *B. abyssicola;* the remaining specimen (7 mm ML) he called *Bathytheuthis* sp. primarily on the basis of different body proportions. Robson recognized that considerable variation exists in specimens referred to *B. abyssicola*, but he did not illustrate or adequately describe his specimens. Therefore, it is impossible to know if these specimens should be referred to *B. abyssicola* or to *B. bacidifera*.

In conclusion, only one specimen mentioned in the literature probably can be referred to *B. bacidifera:* Chun's specimen of 18 mm ML from *Valdivia* Sta. 221, 04°05′S 73°24′E, in the Indian Ocean.

Occurrence in relation to physical parameters.—The specimens of *B. bacidifera* all were captured in open nets that were calculated to have fished at depths ranging from 683 meters to 1550 meters. The depths of capture for the *Dana* specimens have been calculated by the method suggested by Bruun (1943); since no wire angles were taken during *Dana* tows, Bruun calculated that the fishing depth is one-third the length of the wire for less than 1000 meters of wire out and one-half the length of the wire for more than 1000 meters of wire out. The *Dana* specimens were taken as follows: two at 750 meters, one each at 1000 and 1050 meters, three at 1250 meters and one at 1550 meters. Three *Eltanin* specimens were taken in an Isaacs-Kidd Midwater Trawl (IKMT) that fished around 683 m, and a fourth came from 1373 m. It is extremely unfortunate that so few tows were taken during the period that the *Eltanin* was working southward along the eastern Pacific boundary. It is also unfortunate that Robson's eleven *Arcturus* specimens from the Galapagos region and Hoyle's two *Albatross* specimens from the Gulf of Panama are not specifically identifiable from the descriptions.

The temperature-salinity relationships of *B. bacidifera* are plotted on figure 44. The zone of captures falls within the envelope of the Eastern Pacific Equatorial Water Mass. The range of the depths of capture corresponds to the band of the salinity minimum (34.55‰ to 34.61‰) where the temperature ranges from just above 3° C in deeper water to nearly 6° C in the shallower portion of the range. The density values increase with depth from sigma-t=27.20 to 27.60. In addition, the oxygen concentration of the water layer between 200 to 2000 m is extremely low, between 0.1 ml/L and 2.0 ml/L; it represents a very broad oxygen minimum layer. The lowest values (0.1–0.5 ml/L) occur at the shallowest depths (ca 200–700 m) so *B. bacidifera*, with depth-of-capture values of 0.47 to 1.47 ml/L, lies just below the oxygen minimum layer.

The narrow band along the eastern boundary of the tropical Pacific water mass is an area of high organic productivity (fig. 60). *B. bacidi-*

fera apparently inhabits the water layer immediately beneath the zone of high productivity, an adaptive advantage commensurate with its anatomical adaptions for a relatively sluggish, upper bathypelagic existence.

Chun's largest specimen (18 mm ML) from the Indian Ocean, which may be *B. bacidifera*, was captured in the Indian Ocean Equatorial Water Mass in a plankton net that was towed vertically from 2000 meters. Granting that *Bathyteuthis* normally lives below 500 meters, the temperature-salinity values (Tressler, 1963; Fell, 1965) indicate that Chun's specimen came from temperatures and salinities as low as 2° C and 34.7‰ at 2000 m to as high as 10° C and 35.1‰ at 500 m. The oxygen concentration in shallower portions of this zone ranges from less than 0.5 ml/L at around 500 m to 1.0 ml/L at 1000 m; in deeper portions it rises to about 2.5 ml/L at about 2000 m. If the distribution of *B. bacidifera* in the Indian Ocean Equatorial waters is governed by similar physicochemical parameters as this species in the Eastern Pacific Equatorial Water it would be found below about 500 m. Oxygen values in the two oceans (ca 0.5–1.5 ml/L) coincide between 750–1500 m and temperatures (ca 3.8°–6° C) coincide between 1000 and 1750 m. Salinities are high in Indian Equatorial water so there is no overlap of values, but sigma-t values of 27.20 to 27.60 in the eastern Pacific are found between 750 and 1500 m in Indian equatorial waters.

Further consideration of the distribution of *B. bacidifera* is given in the main section on distribution.

Bathyteuthis berryi Roper, 1968

PLATES 11–12 A–F

Bathyteuthis berryi Roper, 1968, p. 169, pls. 5–7.

DIAGNOSIS.—Protective membranes on arms present, well developed and fleshy proximally, no free trabeculae; suckers on arms extremely numerous, sucker rings with 10–14 protuberances; gills long and broad.

DESCRIPTION.—The mantle is very plump and robust; it is bullet-shaped in outline (pl. 11). The widest part of the mantle is about at the midpoint, and the mantle width is 50% of the mantle length. The mantle opening is slightly narrower and the margin bears low, ventrolateral lobes. The mantle remains broad for much of its length, then tapers and terminates posteriorly in a broad, bluntly rounded tip.

The fins are short, rounded, and widely separated posteriorly by the blunt tip of the mantle (pl. 11). Anterior insertions are very broadly separated by the dorsal surface of the mantle. Anterior and posterior fin lobes are about of equal dimensions.

List of Material

Sex	*ML, millimeters*	*Ship Sta.*	*Location*	*Date*	*Depth, meters*[1]
HOLOTYPE:					
M	49	V 8714	33°14′45″N 118°37′20″W	7 VI 63	1200
PARATYPES:					
M	23	V 10540	29°05′04″N 118°12′00″W	6 IV 65	1300
M	20	V 10377	33°25′00″N 118°50′45″W	24 II 65	1100
F	19	V 10976	32°35′00″N 120°35′06″W	17 II 66	1300
OTHER MATERIAL:					
M	19	V 11169	31°40′25″N 120°22′42″W	31 VII 66	1300
L[2]	17	V 9905	29°28′14″N 119°02′58″W	8 VIII 64	800
L	16	V 9661	33°08′20″N 119°12′35″W	14 IV 64	1000
L	16	V 8700	33°15′30″N 118°33′45″W	25 VI 64	800
L	14	V 9056	33°12′42″N 118°32′15″W	14 XI 63	1100
L	13	V 10973	32°37′45″N 120°24′30″W	16 II 66	850
L	12	V 10730	33°27′40″N 118°52′50″W	26 IX 65	1000
L	11	V 10973	32°37′45″N 120°24′30″W	16 II 66	850
L	10	V 11189	32°25′06″N 118°08′20″W	4 VIII 66	5–900
L	9	V 8349	33°26′38″N 118°54′15″W	7 XII 62	1000

[1] Estimated depths of capture. All specimens were captured by a 10′ Isaacs-Kidd midwater trawl.

[2] L refers to larval or juvenile specimens of undetermined sex.

The funnel is very large, prominent, and long; it extends anteriorly to a point in line with the anterior borders of the eye openings. The posterior part of the funnel and the collar are bound to the posteroventral and posterolateral surfaces of the head with integument and gelatinous, subcutaneous tissue. The funnel groove is very shallow, almost nonexistent. A small pore lies at the base of the funnel groove where the dorsal part of the funnel fuses with the head.

Cartilaginous funnel components of the locking apparatus are simple and elongate with a smooth, shallow, median sulcus. The mantle component is a simple, straight ridge that articulates with the funnel lock.

The dorsal member of the funnel organ is an inverted, roughly Y-shaped structure with short, broad limbs. A spatulate papilla extends anteriorly from the anterior limb of the Y-structure. The ventral pads have straight, diagonal anterior borders, nearly parallel sides and narrow, rounded posterior borders. A thin, broad funnel valve is present.

The head is long and narrow; it is flattened dorsoventrally. The eyes are very large and are directed anterolaterally. The borders of the eye openings are circular; they lack an optic sinus. A minute, stubby olfactory papilla occurs on each side of the posterolateral surface of the head just anterior to the nuchal region. Nuchal folds and crests are absent.

The nuchal component of the mantle-nuchal locking apparatus is long and narrow with three longitudinal grooves: a narrow, shallow, median groove and two broader, deeper, lateral grooves. The median groove complements the low, thin, median ridge of the mantle component of the locking apparatus. The lateral grooves receive the rolled edges of the rhachis of the gladius that partially make up and provide support for the mantle component.

The head narrows considerably anterior to the eyes where it forms the base of the brachial crown. A single, small, simple photophore is embedded in the chromatophore layer of the subcutaneous tissue at the base of each of the dorsal three pairs of arms. Photophores are characterized by a darkly pigmented ring that is generally broadest posteriorly and a central mass that is much more lightly pigmented. Photophores in the holotype are embedded and not easily seen, but the photophores in the juvenile and larval specimens contrast more with the background pigmentation, are slightly raised, and are more readily seen.

The arms are long, slender and drawn out into attenuate tips (pl. 11). All arms are of nearly equal length in the holotoype, so the arm formula for adults is 4=3=2=1.

A moderately deep web joins the bases of the four pairs of arms. The depth of the web decreases from the dorsal to the ventral pairs, and no web occurs between the fourth arms.

Low aboral swimming keels occur on the dorsal three pairs of arms, with those of the third arms the best developed. The web between the third and fourth arms extends distally along the fourth arms as the lateral membrane or "tentacular sheath."

Protective membranes occur on all arms. They are particularly well developed at the basal portion of the arms where they are thick, fleshy, and ruffle-like (pl. 11A). The thickened ruffles diminish quickly distal to the bases of the arms, and the protective membranes extend distally as low, even keels. Protective membranes on the fourth arms are considerably less developed than on the dorsal three pairs. No distinct or separate trabeculae support the protective membranes.

The oral surfaces of the arms are covered with extremely numerous small to minute suckers (pl. 11A). The proximal suckers are quite small, and widely spaced; they originate in a single row, then soon increase in size and split off into two widely separated rows. About one-third of the way out the arms, the suckers become smaller and more closely packed and the rows become irregularly arranged so that occasionally 3–4 suckers occur across the oral surface of the arms. On the distal one-third to one-fourth of the arms, the suckers grade smaller, become very closely packed, and are exceedingly numerous. On the ventral arms, the sucker rows do not become so irregular and the suckers are not nearly so numerous as on the dorsal three pairs of arms. Suckers extend to the extreme distal tips of all the arms.

About 275 suckers occur on each of the dorsal six arms of the holotype. The dorsal arms may have very slightly fewer, and the ventral arms have around 150 suckers each. A specimen 23 mm ML (*Velero* 10540) has 175–185 suckers on arms I–III and 110 on arms IV. A specimen 12 mm ML (*Velero* 10730) has 62–75 suckers on arms I–III and 48 suckers on arms IV.

Inner sucker rings from the arms bear 10–14 very low, small, rounded or subtriangular, knoblike teeth (pl. 11C–F). Outer rings are made up of concentric rows of tiny chitinous bumps or pebbles.

Both tentacles are missing from the holotype, probably having been lost during capture. In fact, the tentacles are broken off all but one specimen that is available at this time. The specimen (*Velero* 10976) is a juvenile 19 mm in mantle length. The single complete tentacle is long (ca 20 mm) and robust. The club is short (ca 4.5 mm), unexpanded, simple; no keels or membranes are present and no discrete divisions into manus, carpus or dactylus exist (pl. 11B). About 7 to 8 rows of very small suckers are distributed across the distal half of the club; fewer rows occur proximally. Between 150 and 200 suckers are present at this stage. The extreme distal portion of the club is reduced to a small, papilla-like tip with a few minute bumps that are probably precursors to future suckers. Inner sucker rings from the 19 mm specimen (*Velero* 10976) are extremely small, and it is difficult to determine the dentition. Rings varied from being nearly smooth or slightly scalloped to having a few minute, low, subtriangular teeth as shown in plate 11G, although the figure may exaggerate the size of the teeth. The outer ring consists of concentric, pebbled rows.

The buccal membrane is broad and heavily rugose. The seven buccal lappets are long and bear 4 to 6 small suckers; the inner chitinous rings of the suckers have around 10 small, low, papilla-like teeth (pl. 11H). The connections of the buccal membrane attach to the dorsal oral edges of arms I, II, and IV and to the ventral oral edge of arm III.

The beaks are small and are darkly pigmented only on the rostra (pl. 12C, D). Lamellae are lightly pigmented and fragile. The rostrum of the upper beak is strong, sharply curved, and hooklike. The jaw angle is nearly a right angle. The rostrum of the lower beak is short and blunt; the jaw angle is obtuse.

The radula has seven transverse rows of teeth and two rows of lateral platelets (pl. 12A). The rhachidian tooth has a broad base and a broad, bluntly pointed median cusp. The concave lateral borders of the cusp are very slightly irregular with minute denticles. The first lateral tooth has a straight, blunt cusp about as long as the rhachidian cusp; the concave lateral border has a few small, irregular denticles. The second lateral tooth has a long, straight pointed cusp. The third lateral has a very long, thin, scythe-shaped cusp. The marginal platelets are irregularly shaped oblong structures.

The rhachis of the gladius is very long and slender; it makes up 60% of the total length of the gladius (pl. 12B). No median ridge occurs along the gladius, but the lateral edges are rolled under to form strong rodlike supports to the rhachis. These rods extend posteriorly, decreasing in diameter, nearly to the tip of the gladius. The rhachis is U-shaped in cross section. The anterior tip of the rhachis is very thin and flaplike. The vane is very broad, thin, membranous and paddle-shaped. The rounded posterior border of the vane curves ventrally and forms a shallow cuplike terminus. The gladius lacks a conus.

Most of the pigmentation is bleached out of the holotype, but the smaller specimens exhibit the maroon coloration typical of *Bathyteuthis*.

The holotype is a mature male with fully developed spermatophores in Needham's sac. A hectocotylus is lacking. Spermatophores are about 8 mm in total length; the sperm mass occupies about 72% of the total length, the cement body about 8% and the ejaculatory apparatus about 20% (pl. 12E, F). The cement body is an elongate, vase-shaped structure with a flaring lip or collar where it joins with the narrow base of the short, bell-shaped end of the spiral filament. About one-third to one-fourth of the sperm mass is slightly pigmented.

The gills are long and broad; counts and measurements were made on the gills of six specimens ranging from 16–49 mm ML. Gill filaments number from 19–21. The index of gill length to mantle length ranges from 43 to 53 (mean 48.6), that of gill width to mantle length from 7.5 to 15.7 (12.5), and that of gill width to gill length from 17 to 30 (25.5).

Holotype.—University of Southern Cailfornia. U.S.C. *Hancock* collections, AHF cephalopod type number 10.

Type Locality.—Catalina Basin, 10.9 miles SSW of West End Light, Catalina Island at 33°14′45″N 118°37′20″W. *Velero* Sta. 8714, about 1200 m., June 1963.

Distribution.—Bathypelagic in the waters off Southern California.

Etymology.—The specific name *berryi* is given in honor of Dr. S. Stillman Berry who has contributed a lifetime of study to malacology and teuthology.

Discussion.—*B. berryi* was not discovered and described until after this manuscript was completed. The present description, an amplification of the original (Roper, 1968), and pertinent parts of the original discussion are inserted here for the sake of completeness.

R. E. Young has compiled the capture data for the specimens of *B. berryi* that are currently available from the *Velero* collections in southern California waters. The specimens were distributed in 100 m increments as follows: 1 from 100–200 m, 1 from 300–400 m, 3 from 800–900 m, 5 from 1000–1100 m, and 5 from 1100–1200 m. The 1200 m level is the maximum depth sampled during the program. The two individuals from shallow water were taken in tows that had been preceded by tows that had fished at depths greater than 1000 m. It is reasonably safe to assume that these specimens were contaminants that had stuck in the net from the preceding deep tows. It seems likely also that only the shallow segment of the population of *B. berryi* was sampled at depths of 800–1200 m and that the bulk of the population lives below 1200 m.

The three species of *Bathyteuthis* may be distinguished on the basis of several features, the most prominent of which are presented in the following list:

Character	*abyssicola*	*bacidifera*	*berryi*
Free trabeculae	absent	present	absent
Protective membranes	present	absent	present
Arm suckers [1]	few (100)	numerous (150)	extremely numerous (275)
Sucker ring dentition (Arms)	8–18, truncate	18–34, truncate	10–14, subtriangular
Arms	short, blunt	short, blunt	long, attenuate
Gills	short, narrow	long, broad	long, broad
Spermatophore proportions [2]	68–72; 6–8; 20–25	63–66; 17–20; 15–20	72; 8; 20
Tentacles and clubs	short	long	missing from material

[1] The numbers in parentheses represent the approximate number of suckers on each of the six dorsalmost arms from specimens of about the same size (49 mm ML).

[2] The size of the sperm mass, cement body, and ejaculatory apparatus respectively expressed as a percentage of the total length of the spermatophores.

The most striking and easily recognized character of *bacidifera* is the presence of long, finger-like trabeculae on the arms that have no interconnecting protective membrane. This feature is apparent even on the smallest larva available (6 mm ML) and readily separates the species. Both *abyssicola* and *berryi* possess thick, fleshy protective membranes. Considerable variation exists in the membranes, but they are always present and connect unmodified trabeculae.

B. berryi is most readily distinguished from *abyssicola* by the extreme abundance of suckers on the arms and by long, wide gills. (The significance of gill size is discussed in a later section.) The arms of the holotype of *berryi* are 5–7 mm longer than the arms of *abyssicola* of the same mantle length (49 mm), and they are more attenuate. This trend holds in all specimens available. When material with tentacles in tact becomes available, differences in the clubs may be found. Although it is difficult to demonstrate quantitatively with the limited number of specimens on hand, the mantle of *berryi* appears to be slightly more plump that that of *abyssicola*.

Comparison of *Bathyteuthis abyssicola* and *Bathyteuthis bacidifera*

Morphological Comparison

The most striking and readily observable difference between *Bathyteuthis bacidifera* and *B. abyssicola* is the possession of long, free, finger-like trabeculae on the arms of *B. bacidifera*. *B. abyssicola* lacks this feature entirely, although its protective membrane differs from most other oegopsids by being thick, fleshy (semigelatinous), and unsupported by strong trabeculae. The protective membrane of *abyssicola* exhibits considerable individual variation; the border may vary from straight and smooth to gently undulating or scalloped, but a comblike row of trabeculae does not occur. The free trabecular rods of *bacidifera* are well developed on the smallest specimens observed (6 mm ML), so there is no danger of confusing even the larvae of the two species. The erection of a separate species might be warranted on the basis of this feature alone, but other less spectacular specific characters do exist.

The clubs of *bacidifera* are longer and bear more suckers than do those of *abyssicola* of the same size. For example, the clubs of the holotype of *bacidifera* (37 mm ML) and of an *abyssicola* of 57 mm ML are nearly equal in length, but *bacidifera* has about 615 suckers on the club while *abyssicola* has around 525 suckers. An analysis of club lengths is presented in the following section.

The gills of *bacidifera* are measurably larger than those of *abyssicola* and they tend to have a greater number of filaments. Geographic variation exists in the gill size of *abyssicola* from different areas but little overlap occurs with *bacidifera*. A detailed analysis of gill size appears in the section on geographical variation.

Within species, sucker dentition varies slightly with the size of the specimen and with the size of the suckers on an individual specimen.

Between species, however, there are greater, consistent differences in sucker dentition; *bacidifera* has a greater number of teeth on the arm suckers than does *abyssicola*. Suckers of *abyssicola* of 28 mm ML have about eight protuberances around the aperture. Of these, the four distal ones are long, truncate, widely set teeth, and the four proximal ones are small, blunt, widely set knobs. On specimens of 38 mm ML the number of teeth increases to 9–14 (usually 12) with the distal 4–7 teeth long, truncate to rounded, and widely spaced and the proximal teeth knoblike. Smaller suckers from the same specimen have fewer teeth. In specimens 56 mm ML the arm suckers bear from 8–18 teeth depending on the diameter of the ring. The larger rings generally average 10–14 widely spaced protuberances with long, truncate to rounded distal teeth and short, blunt proximal knobs. Occasionally a medium-sized ring will have more very closely packed teeth than normal (up to 18).

B. bacidifera of comparable size to *B. abyssicola* has slightly smaller sucker apertures but a greater number of protuberances. The larger sucker rings of the holotype (37 mm ML) have 18–26 (average 22) teeth. The teeth on the distal half are short, truncate to rounded, and closely packed, and they grade proximally into small, very closely packed knobs. The teeth on some rings are so closely packed that their lateral edges are in contact. Medium-sized teeth have about 16 protuberances. Exceptionally closely packed teeth and teeth on medium-sized rings tend to be rounded and knobby, not truncate. Rarely, teeth will be about twice as wide as normal or about two times longer than broad.

During ontogeny teeth are added rapidly to the rings of *bacidifera*, but during comparable growth in *abyssicola* the number of teeth becomes stabilized (pls. 10 F–H; 9 B–D, F, G; 4 C–G; 5 G–I). This should serve warning about placing too much emphasis on sucker dentition without considering the age (size) of the specimens.

The dentition of suckers from the tentacular clubs and the buccal lappets does not seem to differ so noticeably between the two species. Again, dentition varies but both species have about the same number of points on the sucker rings; both club suckers and buccal suckers have 8–12 teeth and knobs.

Table II summarizes the diameters of arm, club, and buccal lappet suckers for the two species of *Bathyteuthis*. The suckers of *abyssicola* tend to be slightly larger than those of *bacidifera*.

TABLE II.—*Range and average of diameters of inner sucker rings from* B. abyssicola *and* B. bacidifera

[Measurements in millimeters]

Species	*ML*	*Arm suckers range; mean*	*Club suckers*	*Buccal suckers*
abyssicola	56	0.16–0.20; 0.19	0.12–0.14	–
abyssicola	38	0.14–0.20; 0.168	0.12	0.12
bacidifera	37	0.12–0.20; 0.145	0.08–0.10	0.08–0.10
abyssicola	22–28	0.12–0.18; 0.155	0.08–0.10	–
bacidifera	26	0.10–0.16; 0.13	0.06	–
abyssicola	10–19	0.10–0.16; 0.125	0.10	0.06–0.10
bacidifera	17	0.10–0.10; 0.10	–	–

Morphometric Comparison

The plots for mantle width in relation to mantle length show the same proportional increase in both species of *Bathyteuthis* (fig. 1). The two largest specimens of *bacidifera* are 37 mm in ML; one has a mantle width of 19 mm while the other is 15 mm. The narrower width falls well within the range for *abyssicola* of about the same ML; the greater width is one or two mm wider than would be expected in *abyssicola* of the same size, but the specimen, the holotype (pl. 6), is a fully ripe female swollen with eggs. With the material at hand *bacidifera* does not seem to differ greatly from *abyssicola* in mantle width.

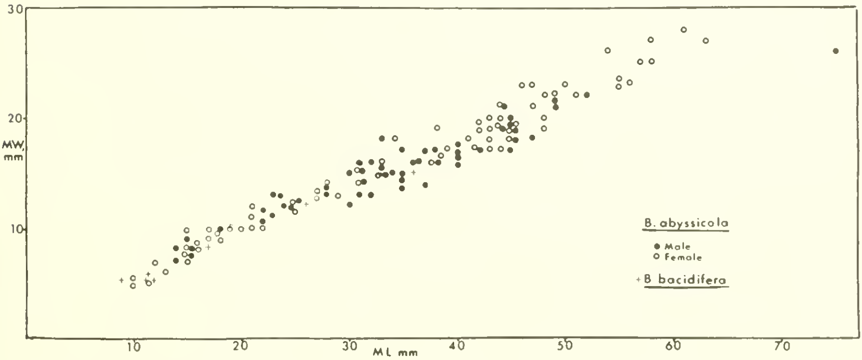


FIGURE 1.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. mantle width.

The plot for the length of the head of *abyssicola* and *bacidifera* shows narrow limits in specimens of less than 30 mm mantle length. Above 30 mm the head length becomes slightly more variable, but in general it continues the trend established in younger specimens. The head lengths of all sizes of *bacidifera* lie within the range of points for *abyssicola* (fig. 2).

A comparison of the plots of head width against mantle length shows that the head of small *bacidifera* may be slightly narrower than that of *abyssicola* (fig. 3). In larger specimens the widths of the heads of the two species converge.

The lengths of the fins may differ in larger specimens of the two species of *Bathyteuthis*. Only four specimens of *bacidifera* measure between 19 and 37 mm ML; these have basal fin lengths that range up to 20% greater than the basal fin lengths of *abyssicola* in the same size range (fig. 4). The plot of fin width against mantle length for *abyssicola* indicates that the fin width becomes more variable beyond a mantle length of 30 mm (fig. 5). The comparable plot for *bacidifera* shows that the two largest specimens (37 mm ML) and the specimen of 19 mm ML have fin widths that lie near the upper limit of fin width for the same size *abyssicola*. No significant difference is noted in the plot for fin width vs. fin length (fig. 6).

Tentacle length is a difficult character to evaluate because the elastic tentacles are subject to greater expansion and contraction during fixation than any other body part. A fair approximation of true tentacle length, however, may be made when a large number of specimens is measured and plotted as in the case of *abyssicola* from the Antarctic. When the plots for tentacle length vs. mantle length are compared, it is noted that the tentacles of the few specimens of *bacidifera* tend to be longer than the majority of *abyssicola* (fig. 7). Specimens of *bacidifera* 12 mm in ML have tentacles about 30% longer than the tentacles of *abyssicola*. At a mantle length of 37 mm the tentacle length of *bacidifera* is about 18% greater than in *abyssicola*.

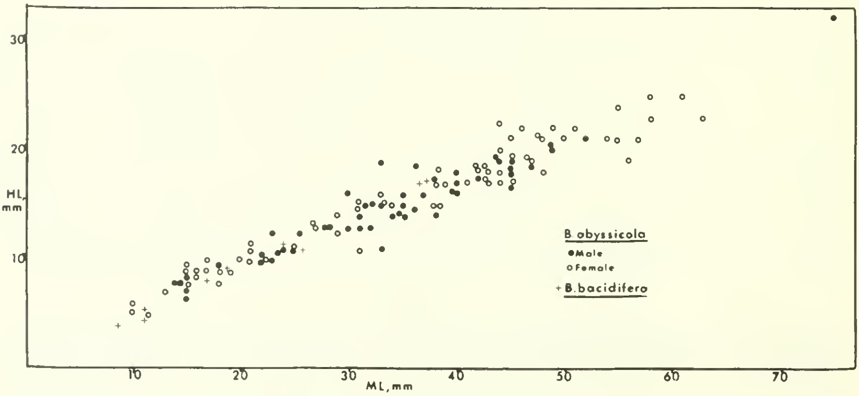


FIGURE 2.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. head length.

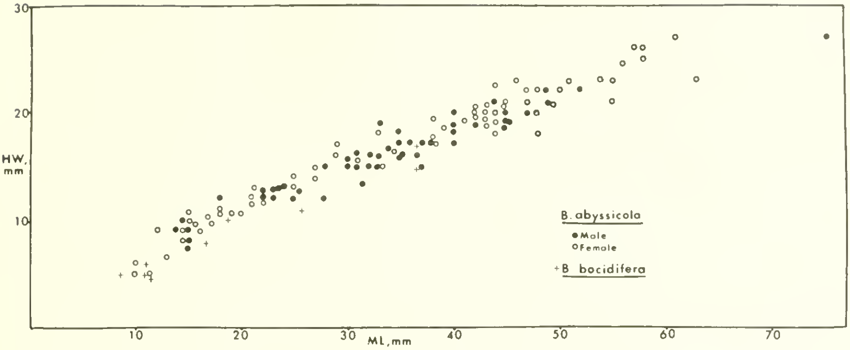


FIGURE 3.—*Bathytheuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. head width.

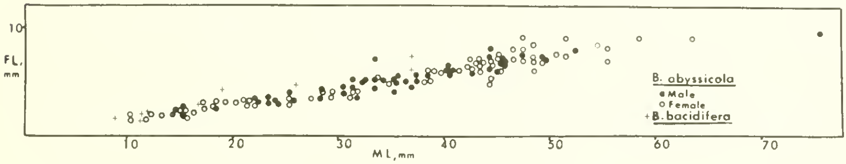


FIGURE 4.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. basal fin length.

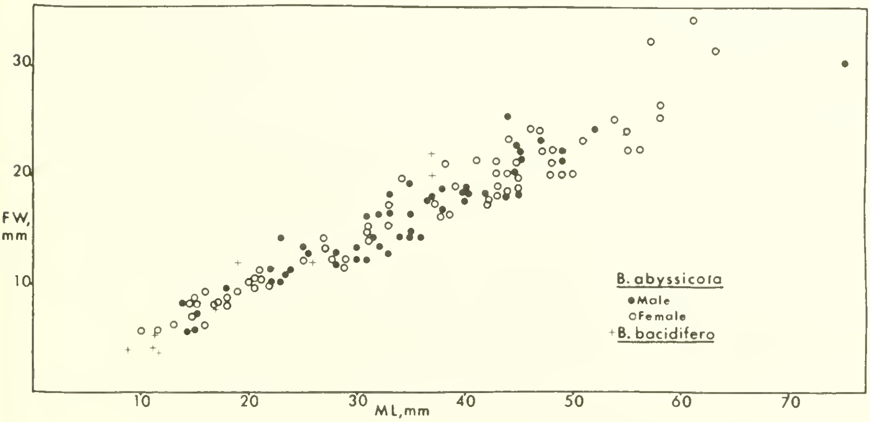


FIGURE 5.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. fin width.

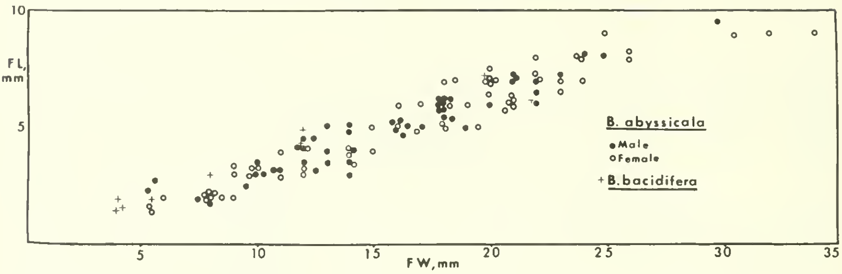


FIGURE 6.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of fin width vs. basal fin length.

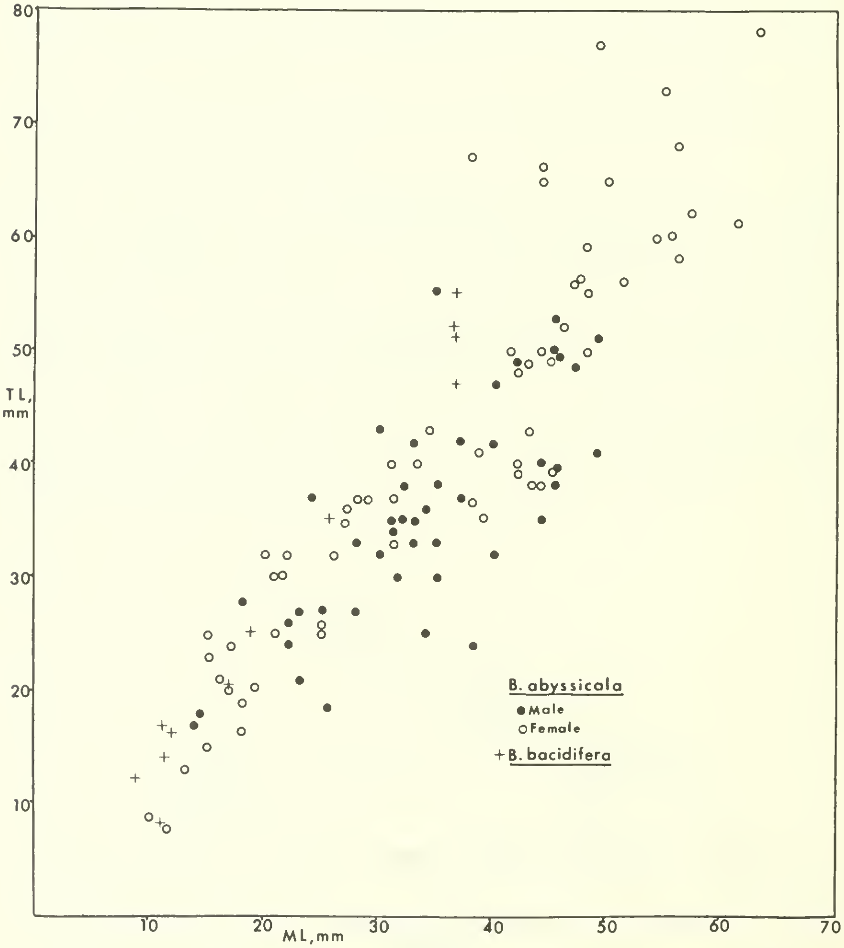


FIGURE 7.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. tentacle length.

Comparison of club length vs. mantle length indicates that the clubs of *bacidifera* tend to be about 25–30% longer than those of *abyssicola* of the same size (fig. 8).

The proportion of club length to tentacle length overlaps in the two species but the plot for *bacidifera* occurs in the upper range of values of *abyssicola* (fig. 9). A specimen of *bacidifera* of 15 mm ML would have a tentacle length of about 20 mm and a club length of 4.5 mm, while a specimen of *abyssicola* with the same tentacle length would have a mantle length of 19 mm and a club length of 3.5 mm.

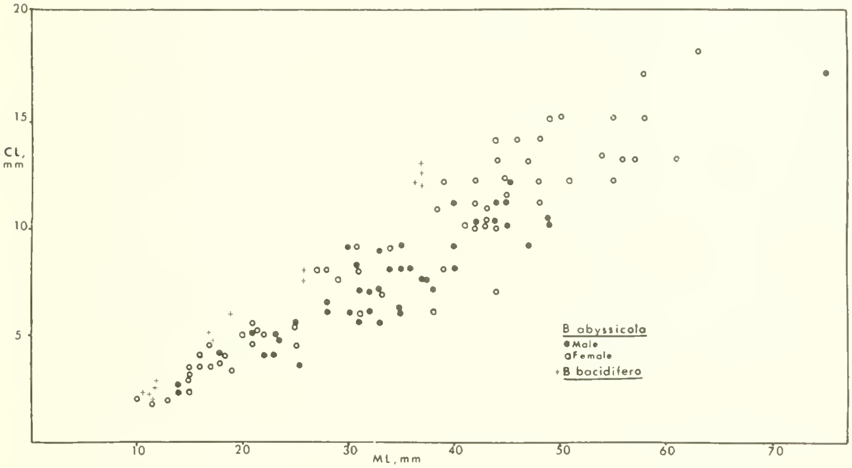


FIGURE 8.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. club length.

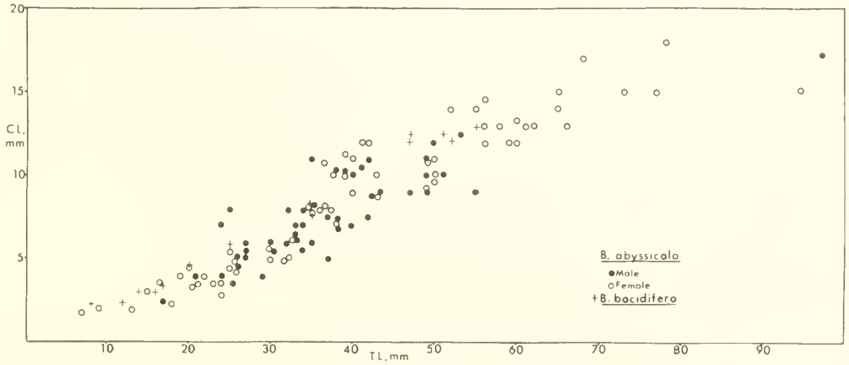


FIGURE 9.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of tentacle length vs. club length.

No difference in the lengths of the arms occurs between the two species (figs. 10–13). The predominant arm formula in each species is 4.3.2.1. In *abyssicola* of 37 mm ML the fourth arms average about 15.5% longer than the first arms; in *bacidifera* of the same size the fourth arms are 16% longer than the first arms.

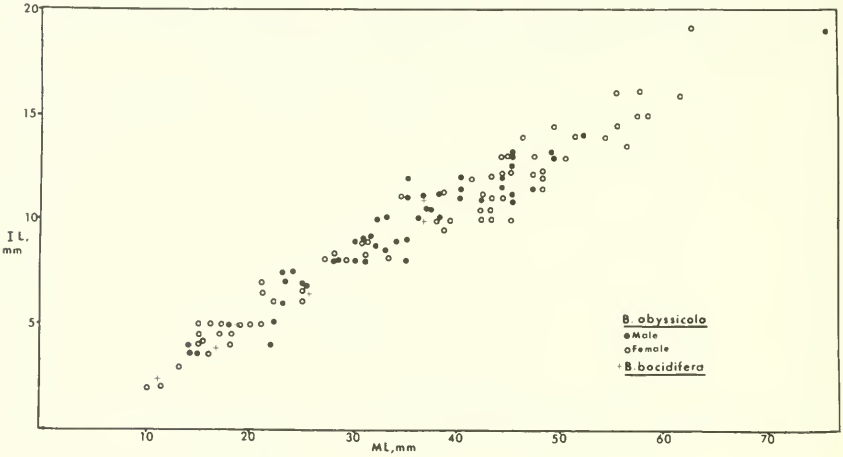


FIGURE 10.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. Arm I length.

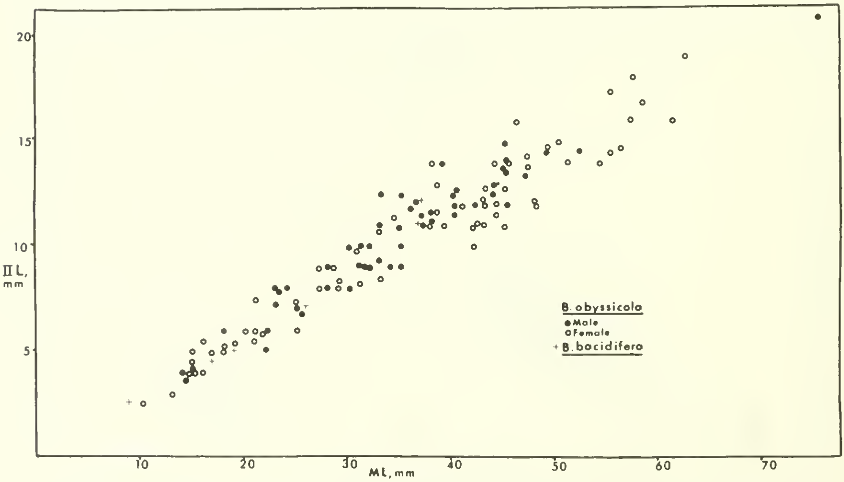


FIGURE 11.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. Arm II length.

In summary, little difference appears to occur in the overall proportions of the two species. The larger specimens of *bacidifera* have fins that are approximately 20% greater in basal length and less so in width than the average for *abyssicola* of comparable sizes. These differences,

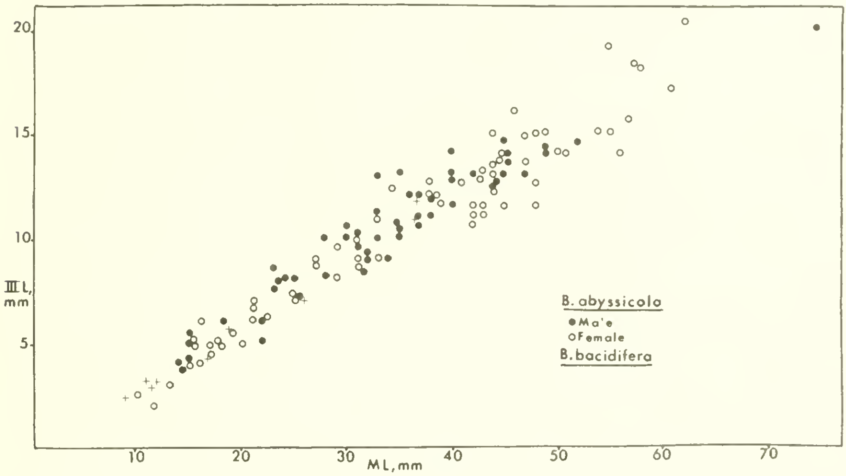


FIGURE 12.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. Arm III length.

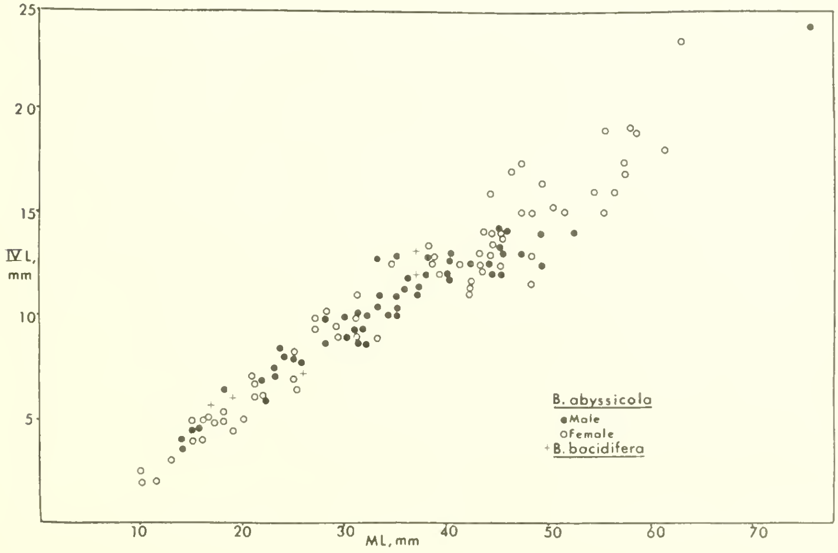


FIGURE 13.—*Bathyteuthis abyssicola, B. bacidifera:* scatter diagram of mantle length vs. Arm IV length.

however, may be too close to the limits of the range of variation of fin length and width for *abyssicola*, and because of the small sample size of *bacidifera*, may not be significant.

Differences in proportions are noted with the lengths of the tentacles and especially of the clubs; the club is 28–30% longer in *bacidifera* than the average for *abyssicola* of the same mantle lengths. Therefore, both species exhibit nearly the same characteristics of proportional growth.

Key to the species of *Bathyteuthis*

1. Protective membranes on arms low to well developed, fleshy, with straight to gently scalloped borders; trabeculae not free, enlarged, or elongate . . . 2
   Protective membranes reduced or lacking; trabeculae free, elongate, rodlike; arm suckers numerous, rings with 18–34 protuberances; gills long, broad. ***B. bacidifera*** Roper, 1968
2. Arm suckers relatively few, rings with 8–18 protuberances; arms short, blunt; gills short, narrow . . . . ***B. abyssicola*** Hoyle, 1885
   Arm suckers extremely numerous, rings with 10–14 protuberances; arms long, attenuate; gills long, broad . . . . ***B. berryi*** Roper, 1968

Geographical Variation in *Bathyteuthis;* Interspecific and Intraspecific Variation of Taxonomically Important Characters

Buccal Suckers

The Bathyteuthidae and the Ctenopterygidae are the only families of Oegopsida known to possess suckers on the oral surface of the lappets of the buccal membrane. It is primarily (though not exclusively) because of the possession of this character that *Bathyteuthis* and *Ctenopteryx* had been brought together in the past under the Bathyteuthidae. Both Naef (1923) and Grimpe (1925) considered that the buccal suckers, four rows of arm suckers, and many rows of club suckers are primitive characters within the Oegopsida, and they placed the Bathyteuthidae first in the suborder immediately adjacent to the Myopsida.

The large number of specimens of *Bathyteuthis* available in this study makes it possible to examine the occurrence of buccal suckers over the geographic ranges of the species and to determine the value of these suckers as a taxonomic character at the species level.

1. *Bathyteuthis abyssicola*—Antarctic

B. abyssicola from the Antarctic exhibits a variety of combinations of suckers on each of the buccal lappets. An individual may have 0, 1, 2, or 3 suckers on each lappet. Very seldom do all seven lappets of an individual bear the same number of suckers, except when 0 suckers occur. For instance, a specimen may have 0 suckers on two lappets, 1 sucker on each of three lappets, and 2 suckers on the remaining two lappets. Clearly a large number of combinations of 0–3 suckers on 1 to 7 lappets is possible. Tables III and IV show the combinations that are known to occur in *B. abyssicola* from Antarctic waters.

At the outset of this study, it appeared that the distribution of suckers on the buccal lappets was entirely random, but as larger numbers of specimens were examined it seemed that a certain degree of accuracy was attained in predicting the sex of specimens by noting the presence (combination) or absence of suckers on the lappets. (The male of *abyssicola* has no differentiated hectocotylus.) A sample of 123 specimens, 69 females and 54 males, displays six combinations of numbers of suckers on the buccal lappets (Table III); the table records the combinations of numbers of suckers only and does not consider the number of individual lappets that bear a particular number of suckers. Twelve of the females, 17.4% of the female sample, had 0 suckers on any of the lappets, while 53.7% of the males lacked buccal suckers; but 47.8% of the females and 33.4% of the males had the 0, 1 combination of suckers, in which 1 sucker is present on one to six of the lappets. The 0, 1, 2 combination included 13.1% of the females and 9.3% of the males. Fourteen females (20.3%) but only one male (1.8%) had a combination of 1, 2 suckers. One male had 1 sucker on each lappet and one female had a combination of 0, 2, 3.

In comparing sucker combinations of males and females it is noted that nearly two-and-a-half times as many males as females have 0 suckers on the buccal lappets. The combinations 0, 1 and 0, 1, 2 are predominated by females in a ratio of two females to one male, although the 0, 1 combination is much more abundant.

One-third of the total sample has 0 suckers, and 41.5% has only 1 sucker on some of the lappets and none on others. Therefore, about 75% of the sample population has 0 or 0, 1 suckers. About 12% of the sample is represented in the 0, 1, 2 and 1, 2 categories.

In general males tend to have lappets that bear fewer suckers; about 87% have 0 or 0, 1 suckers, and only about 11% have some lappets with 2 suckers. About 65% of the females have 0 or 0, 1 suckers and the remaining 35% have combinations that include 2 suckers.

Table IV represents a sample of specimens that have 0, 1 suckers in all possible combinations of lappets from six lappets with 0 suckers and one lappet with 1 sucker to one lappet with 0 suckers and six with 1 sucker. Females have a broad range of combinations that includes all possibilities. About 30% have six lappets with 0 suckers and one lappet with 1 sucker and 25% have the reverse order. The combinations of 2 and 5 and 3 and 4 are nearly evenly distributed in the remaining 45% of the sample. The situation in males is striking: 75%

of the sample has only one lappet with 1 sucker and six lappets with 0 suckers; 16.6% has more lappets with 0 than with 1 sucker, and only 8.3% has six lappets with suckers, one without. Therefore, over 90% of the males have more lappets with 0 suckers than with 1 sucker. In contrast, females have no predominance of numbers of lappets with 0 or 1 suckers; there are as many lappets without suckers as there are with suckers. Applying these figures to Table III, it is found that 13.5 (=75%) of the 18 males with 0, 1 suckers would have only one lappet with 1 sucker and six lappets with 0 suckers. This further strengthens the indication that males have fewer lappets with suckers and, in addition, they have fewer suckers.

Figure 14 gives the plots of combinations of buccal suckers for males and females against mantle length. The graph is a visual reinforcement of the points brought out in the preceding discussion. In addition, it shows a weak trend toward an increase in numbers of suckers (and number of lappets with suckers) with increasing mantle length. The 0 and 0, 1 categories are represented by a broad range of sizes for males

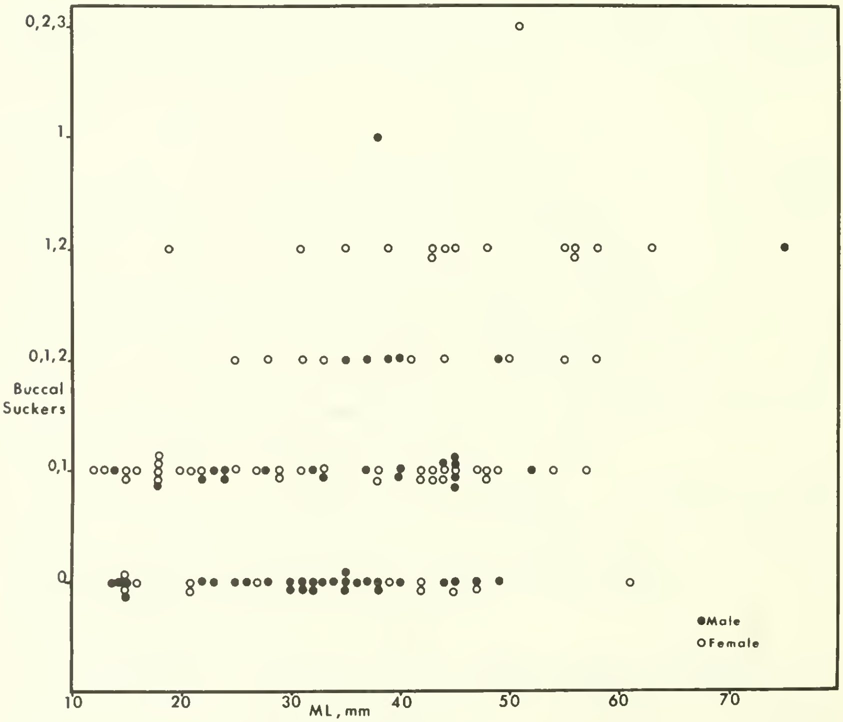


Figure 14.—Combinations of suckers on buccal lappets; *Bathyteuthis abyssicola*, Antarctic Ocean.

and females. Males predominate in the 0 category where 13.8% (7.4% of the total male sample) are less than 20 mm ML and the remainder are grouped in the 22 to 49 mm range with 55.3% (29.6%) concentrated between 30–40 mm. About 50% (28.7%) of the females in this category range from 39–61 mm and 25% are less than 20 mm. In the 0, 1 category males range from 14 to 52 mm in mantle length, and 83% (27%) of them are fairly evenly distributed through the 22–45 mm range. Females range from 12 to 57 mm in this category with 30% (14.5%) at less than 20 mm and 33% (16%) between 42 and 49 mm. In the 0, 1, 2 group 80% (13.8%) of the males are between 35–40 mm, the remaining, 1 specimen, is 49 mm. Females range evenly between 25 and 58 mm mantle length. The 1, 2 category contains only one male which is 75 mm in mantle length (the largest *B. abyssicola* on record). Females in the 1, 2 category range from 19 to 53 mm; only one specimen is smaller than 31 mm; 71% (17%) are larger than 43 mm. Therefore, in the sample of 123 specimens there is a trend toward increasing numbers of suckers with increasing mantle lengths.

In conclusion, it is apparent that considerable variation exists in the occurrence and numerical distribution of suckers on the buccal lappets. There are, however, trends in occurrence and distribution that are associated with sex and size (age) of the specimens.

TABLE III.—*Number of suckers on the buccal lappets of* B. abyssicola *from Antarctic waters. Sample number 123; 69 females, 54 males*

Sucker combination	*Number* ♀	*Percent* ♀	*Number* ♂	*Percent* ♂	*Ratio* ♀ : ♂	*Percent of total population*
0	12	17.4	29	53.7	1:2.4	33.3
0, 1	33	47.8	18	33.4	1:0.55	41.5
0, 1, 2	9	13.1	5	9.3	1:0.55	11.4
1, 2	14	20.3	1	1.8	1:0.07	12.2
1	0	0	1	1.8	–	.8
0, 2, 3	1	1.4	0	0	1:0	.8

TABLE IV.—*Frequency of occurrence of 0, 1 suckers on combinations of lappets;* B. abyssicola, *Antarctic*

Number lappets, 0 suckers	*Number lappets, 1 sucker*	*Number* ♀	*Percent* ♀	*Number* ♂	*Percent* ♂
6	1	6	30	9	75
5	2	2	10	1	8.3
4	3	2	10	1	8.3
3	4	3	15	0	0
2	5	2	10	0	0
1	6	5	25	1	8.3

2. *Bathyteuthis abyssicola*—Eastern Pacific

Seven specimens of *B. abyssicola* from the eastern Pacific exhibit five combinations of numbers of buccal suckers. The smallest specimen, 13 mm ML, has 1, 2 suckers while the remaining specimens (16–30 mm ML) have 2, 3; 3, 4; 3, 4, 5; or 4, 5 combinations of suckers (fig. 15). The indication is that suckers are added very rapidly to the lappets during growth, following the general trend of *B. bacidifera* from the same waters. Slight overlap of buccal sucker combinations occurs between *abyssicola* from the eastern Pacific and from the Southern Ocean. When overlap does occur between populations, a significant difference exists in the size of specimens that share a number-combination. *B. abyssicola* of 13 mm ML from the eastern Pacific has the 1, 2 combination of suckers; several Antarctic specimens have this combination (12% of the total sample), but only one is less than 31 mm ML. Three eastern Pacific *abyssicola*, 18, 19, and 22 mm in ML, have a 2, 3 combination and a single Antarctic specimen, 51 mm, has a 0, 2, 3 combination; this specimen has the highest combination of suckers of all the specimens from Antarctic waters. The 20–30 mm size range in *abyssicola* from the eastern Pacific has combinations of 3, 4, and 5 suckers; the same size group from the Antarctic has 0; 0, 1; and 0, 1, 2 (2 specimens) combinations.

3. *Bathyteuthis abyssicola*—Atlantic

The combination of buccal suckers of 20 specimens of *abyssicola* from the Atlantic are plotted on figure 15. Again, the trend toward increased numbers of suckers with increasing size of the animal is apparent. The 11 specimens below 23 mm ML (9 below 20 mm) have the combinations 1, 2; 1, 2, 3; or 2, 3; the smallest size within each category increases with increasing numbers of suckers. Nine specimens range in size from 33 to 49 mm ML; two-thirds of these have combinations of 3, 4, 5, 6, and 7 suckers and five of these six have no fewer than 4 suckers on each lappet.

B. bacidifera and *abyssicola* from the eastern Pacific apparently attain larger numbers of suckers at smaller sizes than does *abyssicola* from the Atlantic. That is, the 3, 4, 5 combination is found on a 30 mm ML specimen in the eastern Pacific and a 38 mm specimen from the Atlantic; the 4, 5 combination is found on a 25 mm *bacidifera* and a 22 mm *abyssicola* from the eastern Pacific and on 45 and 47 mm specimens of *abyssicola* from the Atlantic.

Half of the Atlantic *abyssicola* are 20 mm or less in ML and none of the specimens exhibit the 0; 0, 1; or 0, 1, 2 combinations. In Antarctic *abyssicola* 86% of the sample population falls into these three categories and 75% into the 0 or 0, 1 groups; 15.5% of the 0 and 0, 1 specimens are under 20 mm while no specimens under 25 mm occur in the 0, 1, 2 group. Both populations have specimens in the 1, 2 group: only one Antarctic specimen is less than 31 mm ML (19 mm); only one Atlantic specimen is greater than 19 mm ML (39 mm). Except for the slight overlap in the 1, 2 group these two populations of *abyssicola* are distinct in the number-combinations of suckers on the buccal lappets.

4. *Bathyteuthis bacidifera*—Eastern Pacific

B. bacidifera is represented by nine specimens that exhibit six combinations of numbers of suckers on the buccal lappets (fig. 15). (This does not include the combinations of numbers of lappets with a particular number of suckers.) There is a tendency toward increased numbers of suckers in larger specimens; only the three larger specimens (24 and 37 mm ML) have combinations that include 4 or 5 suckers (4, 5 and 2, 3, 4). Only one of the small specimens has 3 suckers, while the remaining individuals have combinations 0, 1; 0, 1, 2; 1, 2.

The smaller specimens (less than 20 mm ML) overlap somewhat with *abyssicola* from the Antarctic except that *bacidifera* has no representatives with 0 suckers and *abyssicola* has none under 20 mm

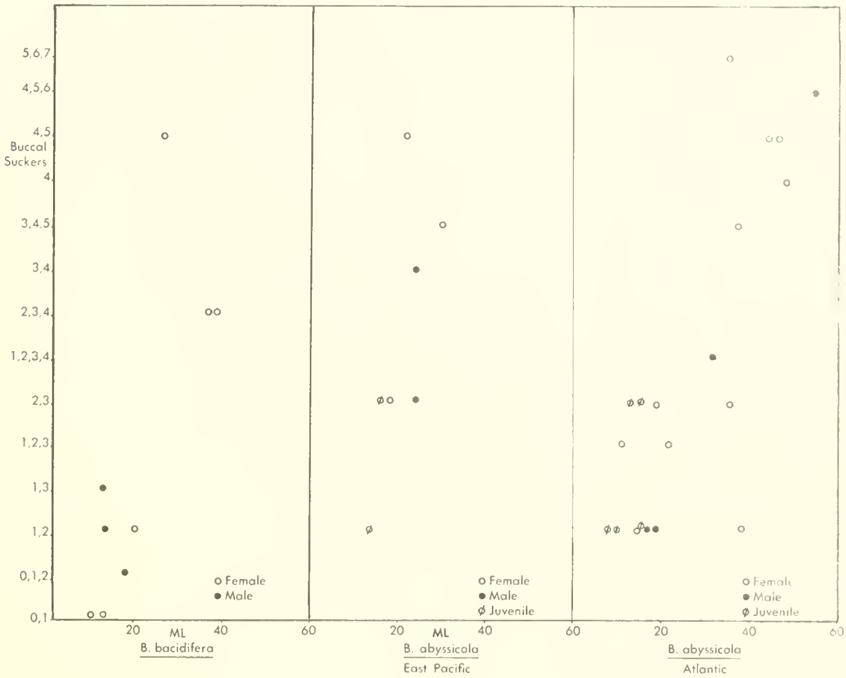


FIGURE 15.—Combinations of suckers on buccal lappets of *Bathyteuthis*.

with 0, 1, 2 and none at all with 1, 3. Antarctic *abyssicola* is not represented by any specimens that have 4 or 5 suckers on their lappets; only one specimen had as many as 3 suckers. Therefore, *bacidifera* appears to possess a greater number of suckers on buccal lappets than does *abyssicola* from Antarctic waters.

The preceding discussion about the suckers on the buccal lappets of *Bathyteuthis* points out that variability exists in this character not only between species and populations but also between individuals of the same population. The general trend is toward an increase in numbers of suckers with increase in size and for populations in lower latitudes to have a significantly greater number of suckers on the lappets. *B. abyssicola* from the Antarctic exhibits the least tendency toward increased numbers of buccal suckers with increased size, and in addition very seldom ever has more than two suckers on any single lappet and often has no buccal suckers at all. In contrast, larger specimens of *abyssicola* from the Atlantic may have combinations of 4, 5, 6, and 7 lappet suckers, and the smallest specimens available have at least some suckers. In the eastern Pacific populations of *abyssicola* and *bacidifera* the data are less complete, but the trend is indicated.

Significance of Buccal Suckers

Possession of suckers on the buccal lappets apparently is a specialization to an environmental pressure and not a primitive character as suggested by Naef; the character is variable enough to meet particular narrower demands of the environment. It is suggested here that the specialization is an adaptation associated with the acquisition of a particular type of food in the deep sea habitat of *Bathyteuthis.*

Contrary to Chun's suggestion (1910), I feel that characters associated with the digestive system of oegopsids (other than basic structures) are poorly suited for use in determining relationships of families. Structures and procedures for obtaining food would seem to be necessarily susceptible to adaptation to various environmental requirements. Recent cephalopods show a wide range of adaptations of the mechanical means for obtaining particular foods and of the physiological processes required for handling these special foods. Buccal suckers may be one of these adaptations.

Bathyteuthis is a true deep-sea cephalopod, exhibiting a number of modifications to the deep-sea habitat. As such, it must be derived from a shallower living form. If suckers on the buccal lappets do reflect the primitive condition in the Oegopsida as suggested by Naef, it seems more probable that they would be found on a generalized, shallow-living form rather than on a specialized, deep-sea form. They are not found in shallow-water forms. The possession of suckers on the buccal lappets by the Bathyteuthidae would be an example of the retention of this primitive character in a deep-sea form only, with no trace of the character in other groups.

Naef (1923) believed the buccal suckers to be a primitive character possessed by *Protodecapus*, a prototype. He placed the Metateuthoidea at the base line leading to Metateuthoidea Oegopsida and Metateuthoidea Myopsida; the Myopsida and Oegopsida separate as equal entities. At the base of the bush of recent Oegopsida, Naef split off the Bathyteuthidae (including *Ctenopteryx*) and placed it closest to the Myopsida. Then, at the same point he derived the Cranchiidae, Chiroteuthidae, Brachioteuthidae, and Joubiniteuthidae in one line at the top of the order, the Ommastrephidae and Thysanoteuthidae on another, and finally all the rest of the oegopsids in the middle between the Chiroteuthidae and Bathyteuthidae. Since the forerunner of recent oegopsid families was supposed to have had buccal suckers and since the Bathyteuthidae has buccal suckers, the character had to be lost just prior to the appearance of all the other groups of Oegopsida.

Naef's scheme, while possible, is not the only explanation that can be offered. Several possibilities exist: (1) Buccal suckers could be present if the Bathyteuthidae arose from the base of the myopsid stem soon after the myopsids and oegopsids separated. (2) The Bathyteuthidae could have split off very early from the oegopsid main line, and the Myopsida could have arisen from the base of the Bathyteuthidae. Both of these situations could explain the presence of buccal suckers either as a primitive character retained from the *Protodecapus* metateuthoid stem and lost to the remaining Oegopsida, or as a new character that appeared after the separation of the remaining Oegopsida. (3) Another possibility allows the buccal suckers to be an independently derived, convergent character. This situation would not require a closer relationship of the Myopsida and Bathyteuthidae than can be reconciled on the basis of existing information. The first two suggestions would imply an immediate and rapid divergence of the groups in structure and habitat: the Myopsida to a neritic and sublittoral (epibenthic) existence and the Bathyteuthidae to a bathypelagic existence. Naef's suggestion allows for the separation of the suborders prior to the loss of buccal suckers to all oegopsids except Bathyteuthidae. The idea of convergence of the buccal suckers is compatible with the very specialized nature of both of these groups.

Number of Arm Suckers

Bathyteuthis from different geographical areas show differences in the numbers of suckers on the arms. Figure 16 shows the numbers of suckers on each of the arms against mantle length for specimens of *B. abyssicola* from Antarctic, Atlantic, and eastern Pacific waters and of *bacidifera* from the eastern Pacific. Figure 17 shows the average number of suckers on each arm of Antarctic *abyssicola* and of *bacidifera.*

1. *Bathyteuthis abyssicola*

B. abyssicola from areas other than the Antarctic tends to have more suckers than the Southern Ocean form. The numbers of suckers for Atlantic and eastern Pacific *abyssicola* fall between those of *bacidifera* and Antarctic *abyssicola* (fig. 16). In specimens below about 17–20 mm ML considerable overlap occurs in numbers of suckers, but in larger specimens a trend toward more suckers exists in Atlantic and eastern Pacific specimens. In fact, specimens of *abyssicola* from the eastern Pacific closely approach *bacidifera* in numbers of suckers. Since the number of observations on the two forms is small, however, I shall not place much emphasis on the apparent differences other than to mention that geographical variation exists in this character.

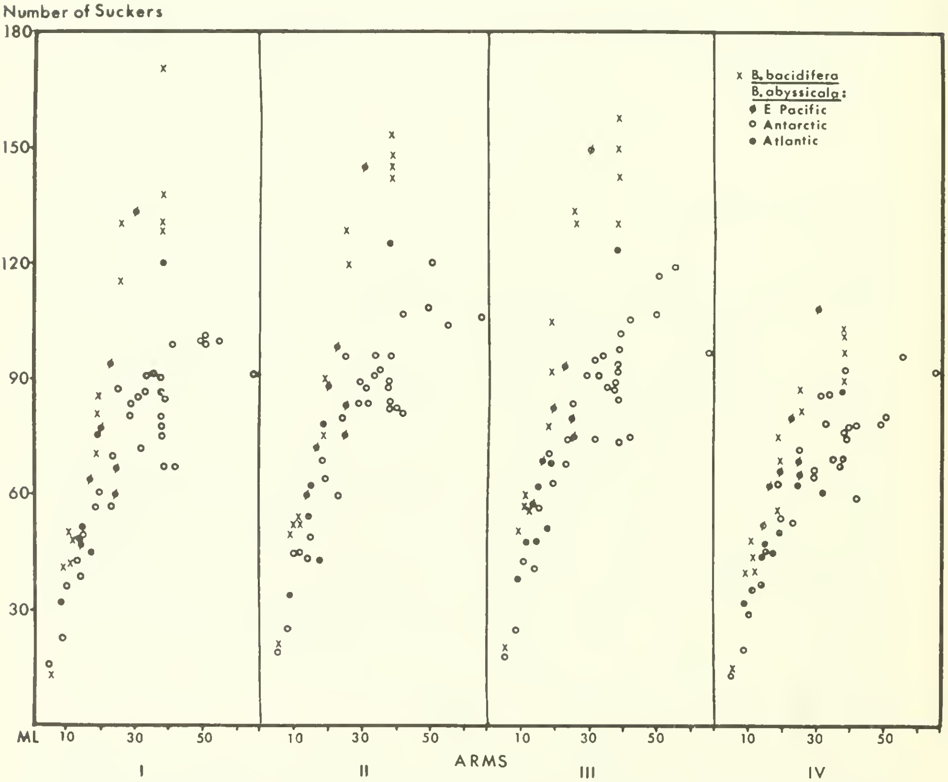


FIGURE 16.—Number of suckers on the arms of *Bathyteuthis abyssicola* from the Antarctic, Atlantic, and eastern tropical Pacific Oceans and of *B. bacidifera.*

2. *Bathyteuthis abyssicola* vs. *B. bacidifera*

The difference in numbers of suckers is most pronounced between *abyssicola* from Antarctic waters and *bacidifera* from eastern Pacific equatorial waters. *B. bacidifera* has a greater number of suckers on each of the arms except in very young specimens (fig. 17). Larvae of both species at about 6 mm ML have nearly the same number of suckers, but during the next 3–6 mm of growth *bacidifera* adds suckers more rapidly than *abyssicola*, so that the first three pairs of arms have from one-third to nearly one-half more suckers, and the fourth arms have nearly twice as many (Table V). With continued increase in mantle length the divergence in numbers of suckers increases gradually in the first three pairs of arms from about 40% more to 75% more suckers in *bacidifera* than in *abyssicola*. The fourth arms of *bacidifera*

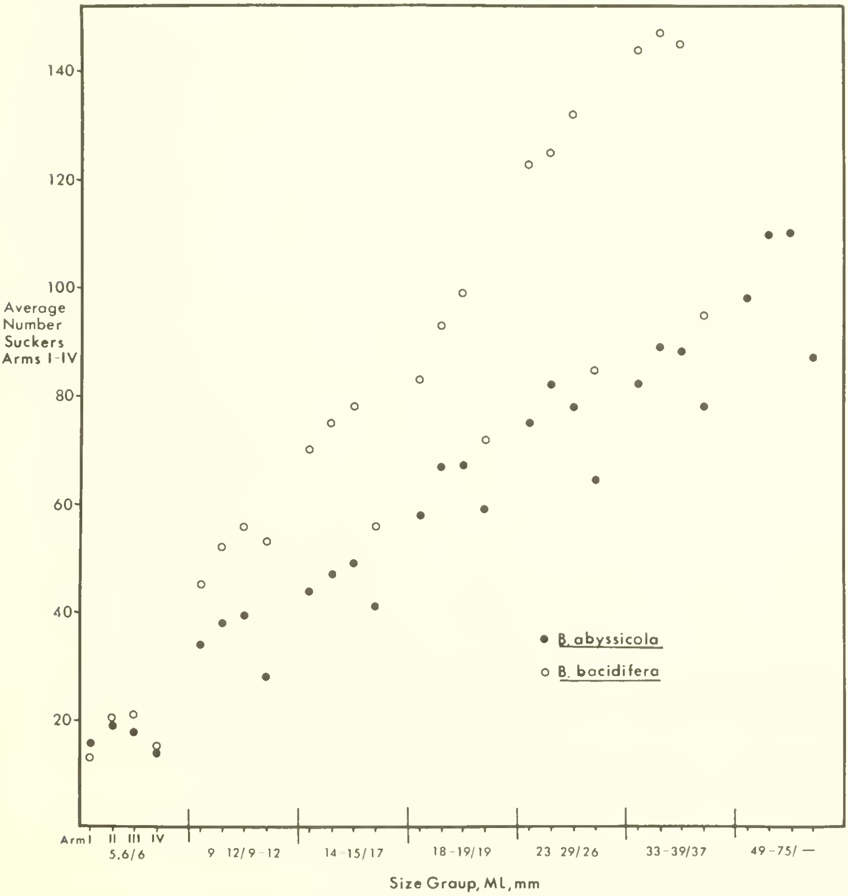


FIGURE 17.—Average number of suckers on the arms of *Bathyteuthis abyssicola* (Antarctic) and *B. bacidifera*. Size groups are divided into mantle lengths of *B. abyssicola*/*B. bacidifera*.

TABLE V.—*Comparison of numbers of arm suckers*

	B. abyssicola, Antarctic			*B. bacidifera*			
Arm	*ML size group, millimeters*	*Range*	*Average*	*ML size group, millimeters*	*Range*	*Average*	*Times greater*
I	5. 6	16		6	13		.81
II		19			20		1.05
III		18			21		1.17
IV		14			15		1.07
I	9–12	23–43	(34)	9–12	41–50	(45)	1.32
II		25–45	(38)		49–54	(52)	1.37
III		25–48	(39)		50–60	(56)	1.43
IV		20–35	(28)		40–48	(53)	1.89
I	14–15	38–50	(44)	17	70		1.59
II		44–49	(47)		75		1.59
III		41–57	(49)		78		1.59
IV		35–46	(41)		56		1.37
I	18–19	56–60	(58)	19	80–85	(83)	1.43
II		64–69	(67)		90–95	(93)	1.39
III		63–71	(67)		92–105	(99)	1.48
IV		54–63	(59)		69–75	(72)	1.22
I	23–29	57–87	(75)	26	115–130	(123)	1.64
II		60–96	(82)		120–130	(125)	1.52
III		68–91	(78)		130–133	(132)	1.69
IV		53–72	(64)		82–88	(85)	1.33
I	33–39	66–91	(82)	37	128–170	(144)	1.76
II		82–96	(89)		142–153	(147)	1.65
III		73–102	(88)		131–158	(145)	1.65
IV		68–92	(78)		90–103	(95)	1.22
I	49–75	91–101	(98)		no specimens		
II		104–120	(110)				
III		97–119	(110)				
IV		79–96	(87)				

exhibit less of a proportional increase than the other arms, but they maintain between a fourth and a third more suckers than in *abyssicola* of the same size group.

Not only is the average number of suckers greater in *bacidifera*, but the ranges of values between the two species show virtually no overlap, so that the species are quite easily separable on numbers of arm suckers alone.

In addition, the largest specimens of *abyssicola* (49–75 mm), the largest of which is two times longer in mantle length than the largest *bacidifera*, do not approach the largest known *bacidifera* in range or average of suckers; the equivalent number of suckers would be found in specimens of *bacidifera* one-half to one-third the size of the largest *abyssicola* from the Antarctic.

3. *Bathyteuthis berryi*

B. berryi was discovered after the above analysis was completed. The suckers on the arms of this species far outnumber those of *abyssicola* and *bacidifera*. The following figures for *berryi* can be compared with those in Table V:

ML, millimeters	*Arm*	*No. of suckers*
12	I–III	62–75
	IV	48
23	I–III	175–185
	IV	110
49	I–III	275
	IV	150

Gill Size

A conspicuous difference in the size of the gills is apparent between *abyssicola* from the Antarctic and *bacidifera*. *B. abyssicola* has small gills while *bacidifera* has larger, more voluminous gills. A character such as gill size, however, may be a phenotypic expression of environmental conditions rather than a genotypic difference. Antarctic and eastern Pacific equatorial waters differ considerably in environmental conditions, particularly in oxygen content, which in this context would probably most influence gill size. The oxygen content of eastern Pacific equatorial waters is significantly lower than that of Antarctic waters. In an attempt to evaluate the extent and signficance of the differences observed between *bacidifera* and Antarctic *abyssicola*, it is necessary to examine the gill dimensions of specimens of *abyssicola* from the same locality as *bacidifera* and from localities other than the Antarctic and the eastern Pacific. Although the sample sizes are not large for the Atlantic and eastern Pacific populations of *Bathyteuthis*, they do present some interesting trends.

Size of the gills may be determined by length, width, volume, and number of gill filaments. In the current study gill volume has been omitted.

1. Gill filaments

The number of gill filaments for specimens of *bacidifera* and of *abyssicola* from the Antarctic, Atlantic, and eastern Pacific is plotted against mantle length in figure 18. The plot for *abyssicola* shows an

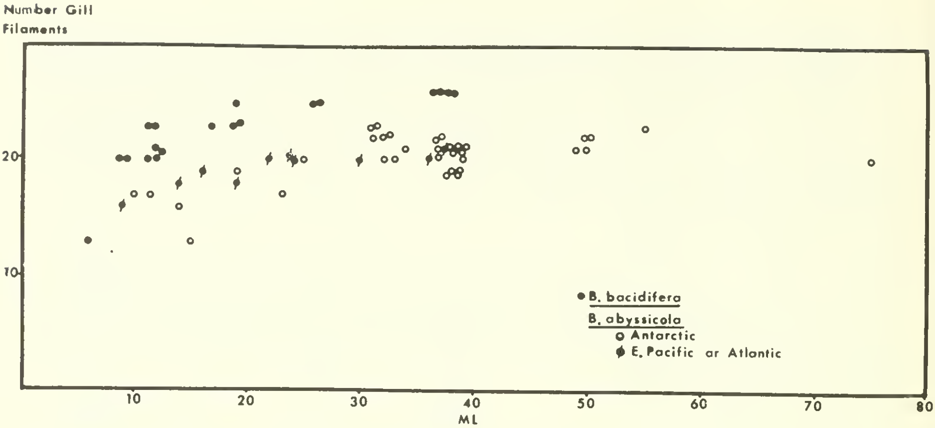


FIGURE 18.—Number of gill filaments in *Bathyteuthis bacidifera* and *B. abyssicola* plotted against mantle length.

increase in number of gill filaments up to about 30 mm ML; above 30 mm the points level off at an apparently maximum number of filaments (20–23). The three populations of *abyssicola* overlap in number of gill filaments and are not divisible into separate components.

The plot for *bacidifera* rises sharply in the first 12 mm of ML; between 17 and 37 mm the increase in numbers is gradual, rising from 23 to 26 filaments.

Specimens of *bacidifera* of 9–12 mm ML have 20–23 filaments; *abyssicola* does not attain 20 filaments until a mantle length of about 22 mm, and only two specimens had 23 filaments (31 and 55 mm ML). In any size group there is a difference of 2–3 filaments between the minimum number in *bacidifera* and the maximum in *abyssicola*. Eastern Pacfiic *abyssicola* is inseparable from other populations of this species in number of gill filaments, and no apparent overlap of values exists between the two species.

2. Gill length

Figure 19*b* shows gill length against mantle length. The points for *abyssicola* from the Antarctic fall well below those for *bacidifera*. while the points for *abyssicola* from the Atlantic and eastern Pacific lie between these values. Atlantic specimens have gills nearly the same length as Antarctic specimens, but eastern Pacific specimens have gills intermediate in length between Antarctic specimens and *bacidifera*. Figure 20*a* plots the mean of the gill length to mantle length indices of the four populations. The gills of Antarctic and Atlantic *abyssicola* are about one-third as long as the mantle and gills of eastern Pacific *abyssicola* are just over 40% as long; *B. bacidifera* has gills nearly one-half as long as the mantle.

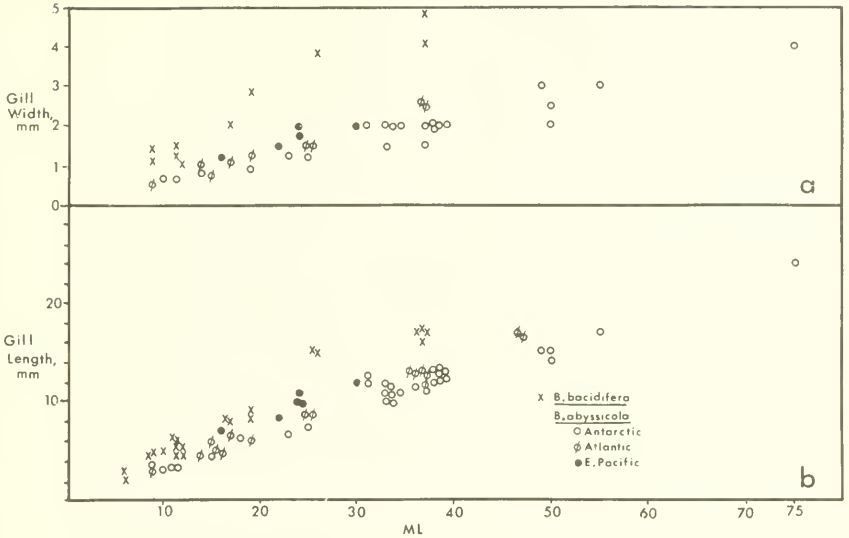


FIGURE 19.—*Bathyteuthis bacidifera* and *B. abyssicola: a*, gill width vs. mantle length; *b*, gill length vs. mantle length.

3. Gill width

The plots of gill width against mantle length (fig. 19*b*) indicate a distinct separation between the two species. The points for eastern Pacific *abyssicola* lie just above those for Antarctic specimens, but, still, these gills are distinctly narrower than those of *bacidifera.*

The means of the gill width to mantle length indices for *abyssicola*, plotted on figure 20*b*, lie between 5.5% and 7.4%, but the mean index for *bacidifera* is 12.4%. Although the gills of eastern Pacific *abyssicola* tend to be slightly wider than those of other specimens, the difference is not nearly so great as between the populations of *abyssicola* and of *bacidifera*. The gills of *bacidifera* average nearly 2.3 times wider than the gills of Antarctic *abyssicola* and 1.7 times wider than eastern Pacific *abyssicola*. Therefore, gill width is significantly greater in *bacidifera* than in *abyssicola*.

4. Gill width: gill length index

Perhaps a better expression of actual gill size is the index of gill width to gill length. Figure 20*c* plots the average values for the populations of *Bathyteuthis;* the data are summarized in Table VI. *B. bacidifera* has a mean gill-width to gill-length index that is considerably greater than that for *abyssicola*. That is, the width of any sized gill of *bacidifera* will be about one-fourth of its length, but in *abyssicola* it will be only about one-sixth of the gill length.

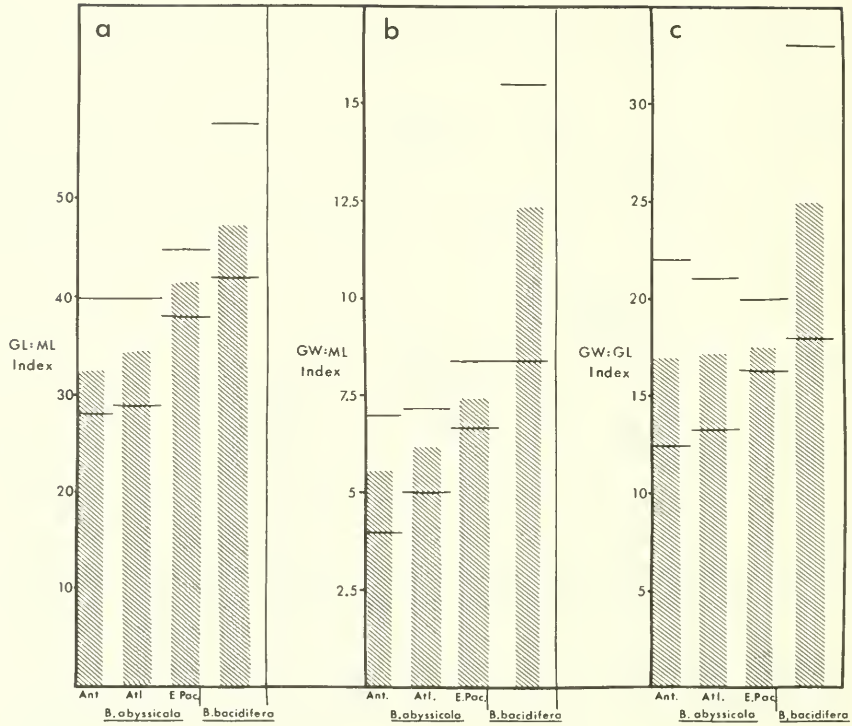


FIGURE 20.—*Bathyteuthis abyssicola* and *B. bacidifera: a*, index of gill length to mantle length; *b*, index of gill width to mantle length; *c*, index of gill length to gill width.

B. bacidifera has larger gills than *B. abyssicola*, but in one dimension (gill length) the eastern Pacific form of *abyssicola* approaches *bacidifera*. This is not totally unexpected since the Eastern Pacific Equatorial Water Mass is extremely low in oxygen content and certain species may have to adapt to the lowered oxygen concentrations (see following discussion and Ebeling and Weed, 1963; Marshall, 1960; Walters, 1961). The slight increase in gill length in eastern Pacific *abyssicola*, however, is not accompanied by an increase in number of gill filaments or a more favorable gill-width to gill-length ratio. Meristic characters might be preferred to morphometric features as being more stable and more indicative of differentiation. In this case, however, the meristic and morphometric characters combine to lead to the conclusion that the observed differences in gill size between *abyssicola* and *bacidifera* are specific and are not only a phenotypic expression of environmental conditions. Furthermore, the differences within populations of *abyssicola* are also genetic and are maintained within the geographic boundaries of the populations.

TABLE VI.—*Gill indices of the populations of* B. abyssicola *and* B. bacidifera [1]

	B. abyssicola						*B. bacidifera*	
	Antarctic		*Atlantic*		*E. Pacific*		*E. Pacific*	
Character [2]	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*
GL : ML	28–40	(32.4)	29–40	(34.4)	38–45	(41.4)	42–58	(47.5)
GW : ML	4–7	(5.5)	5–7.2	(6.2)	6.7–8.3	(7.4)	8.3–15.5	(12.4)
GW : GL	12.5–22	(16.9)	13.3–21	(17.1)	16.4–20	(17.6)	18–33	(25)

[1] The dimensions of gills from *B. berryi* 16–49 mm in ML are appended here. Gill filaments number 19–21. Indices—GL : ML=43–53 (48.6); GW : ML=7.5–15.7 (12.5); GW : GL=17–30 (25.5).

[2] GL=gill length; GW=gill width; ML=mantle length.

Significance of Gill Size

In the order Octopoda the number of gill filaments is commonly used as a taxonomic character, but in the suborder Oegopsida the size of the gills has not previously been examined for taxonomic or biological significance. Robson (1925, p. 1337) presented a study of gill size in the deep-sea Octopoda. He showed that, in general, the gills of deep-sea octopods are more or less reduced in area, in number of filaments, and by atrophy of the inner demibranch. Although Robson reached no definite conclusions, he suggested that the reduction in respiratory surface in deep-sea octopods was related to lowered metabolism in the low temperatures of the depths. Voss (1967) also considered that reduced gill area is due to reduced metabolic requirements.

Differences in gill size have been recorded for several groups of mesopelagic and bathypelagic fishes. Marshall (1960) and Walters (1961) have noted that the surface area of gills in bathypelagic fishes is much less than in mesopelagic species. Three species of the bathypelagic genus *Gonostoma* exhibit a trend toward reduction in gill surface with the shallowest living species having the greatest gill area. The suggestion for these fishes is that the deeper living species tend to have lower metabolisms and to lead less active lives. Walters considered that the bathypelagic giganturids have a metabolic level about one-third that of coastal fishes.

Ebeling and Weed (1963) reported a clinal tendency in the length of the gill filaments in three geographically distinct populations of the melamphaid fish, *Scopelogadus mizolepis*. Gill filaments on the first arch of *S. m. mizolepis* from the Sargasso Sea were short, those of *S. m. bispinosus* from the Gulf of Panama were long, and those of *S. m. mizolepis* from the Indo-Pacific and off West Africa were intermediate in length. Contrary to Marshall's findings in *Gonostoma* spp., Ebeling and Weed were unable to correlate differences in gill area in *Scopelogadus* with depth of capture. However, there was a correlation between gill size and the oxygen content in the areas where the subspecies live. Oxygen concentration in the Sargasso Sea habitat of *S. m. mizolepis* with short filaments is relatively high, ranging 3–6 ml/L, while the oxygen content of the eastern tropical Pacific habitat of *S. m. bispinosus* with long filaments is very low, from less than 0.1 to 2 ml/L; much of the 200–2000 m depth range of *S. m. bispinosus* corresponds to the oxygen minimum layer. Specimens of another melamphaid, *Poromitra megalops*, also from the oxygen-poor tropical eastern Pacific, have a greater gill surface area than do specimens from the North Atlantic. Ebeling and Weed suggested that the increase in gill surface is an adaptation toward more efficient utilization of oxygen in regions of low oxygen concentration.

An interesting parallel exists between *Scopelogadus* and *Bathyteuthis. B. bacidifera* has gills with greater dimensions and more filaments than *abyssicola.* The only specimens of *bacidifera* that are available to this study come from the eastern tropical Pacific within the boundaries of the oxygen-poor eastern Pacific Equatorial Water Mass. Oxygen concentrations were determined at each station so an accurate estimate of oxygen values at depths of capture is available (Table VII). The oxygen values range from 0.47 ml/L at 750 m to 1.47 ml/L at 1550 m, and they correspond to the midportion of the oxygen minimum layer which has its lowest values somewhat shallower (200–700 m). Large gill size in *bacidifera*, therefore, may well be an adaptation to these very low oxygen concentrations.

The various populations of *abyssicola* show differences in gill size also. *B. abyssicola* has the smallest gills in the Antarctic; it has larger gills in the eastern Pacific; it has intermediate-sized gills in the Atlantic. Oxygen content of Antarctic waters is very high, ranging from 4.0 to 5.0 ml/L in the depth range that *abyssicola* inhabits; oxygen

TABLE VII.—*Oxygen, temperature, salinity, and sigma-t values at* Bathyteuthis *stations in the eastern tropical Pacific* (circa 07° N 80° W)

Station number	*Depth, meters*	*Oxygen ml/L*	*Temperature °C*	*Salinity °/₀₀*	*Sigma-t*
D 1203 XVI	750	.48	5.92	34.56	27.27
D 1208 VIII	750	.59	5.58	34.56	27.30
D 1203 XIII	1000	.87	4.84	34.59	27.40
D 1208 XVI	1050	.96	4.70	34.58	27.41
D 1209 III	1250	1.12	4.2	34.60	27.47
D 1203 VI	1250	1.15	3.9	34.58	27.50
D 1203 XII	1250	1.21	3.8	34.61	27.51
D 1208 XIV	1550	1.47	3.35	34.60	27.56
D 1209 I	1750				

values nearer the surface and in greater depths may exceed these values. The few specimens of *abyssicola* captured in the eastern Pacific were taken in the same stations as the deeper specimens of *bacidifera* where oxygen values ranged from 1.12 ml/L to 1.47 ml/L. Oxygen concentrations in the eastern tropical Pacific do not exceed 2.0 ml/L until depths greater than 2000 m (Sverdrup et al., 1942; Wooster and Cromwell, 1958). The Atlantic specimens of *abyssicola* came from a broad range of oxygen concentrations with extremes of 2 ml/L and 6 ml/L, but generally the values were 3–5 ml/L.

The correlation between oxygen concentration and gill size in *Bathyteuthis*, as in *Scopelogadus*, prompts speculation that larger gills provide more efficient means of obtaining oxygen. The possibility may be further strengthened by the fact that when the two species of *Bathyteuthis* occur in the same area of extremely low oxygen concentrations they both possess longer, wider gills.

Relationship of *Ctenopteryx* to *Bathyteuthis*

Shortly after its description by Appelöf in 1890 *Ctenopteryx* was united with *Bathyteuthis* in the Bathyteuthidae by Pfeffer (1900). Most later authors accepted this designation (e.g., Chun, 1910; Pfeffer, 1912; Naef, 1923; Grimpe, 1922, 1925; Thiele, 1935) but generally implied that the two genera were not closely related. To emphasize the distinctiveness of the genera, Grimpe (1922) erected the subfamilies Bathyteuthinae and Ctenopteryginae. Allen (1945) felt that even subfamilial distinction was insufficient so she withdrew *Ctenopteryx* from the Bathyteuthidae and elevated it to the family Ctenopterygidae based solely on fin structure and body proportions. Allen's act constitutes the latest revision of the higher taxa that encompass *Ctenopteryx* and *Bathyteuthis*.

On the basis of the material at hand, it is necessary to reevaluate the systematic positions and relationships of these two genera.

A brief description of some taxonomic characters of *Ctenopteryx* will help to determine the degree of similarity with *Bathyteuthis*. Some of the characters compared may be only specific, but since the species of *Ctenopteryx* are poorly understood, it is advisable to use whatever characters are pertinent to this discussion.

The funnel-mantle locking apparatus is the simple, straight ridge and groove type. The funnel component is broad posteriorly and narrows anteriorly; the groove is deep and narrow. The funnel component of *Ctenopteryx* is broader posteriorly, but in general the locking apparatuses of the two genera exhibit no significant differences.

The tentacles of *Ctenopteryx* are long and slender. The tentacular stalks are naked. In proportion to the length of the tentacle, the clubs are short and unexpanded; they bear no distinct carpus, manus, or dactylus. Eight to fourteen rows of minute, closely packed suckers cover the oral surface of the club. A thin, narrow keel extends along the dorsel aboral border of the club. Protective membranes are lacking. The clubs of *Ctenopteryx* and *Bathyteuthis* are similar in basic design, but *Ctenopteryx* tends to have a few (up to four) more rows of suckers.

The connectives from the buccal membrane of *Ctenopteryx* attach to the dorsal oral edges of arms I and II and to the ventral oral edges of arms III and IV. This arrangement is in contrast to the dorsal, dorsal, ventral, dorsal arrangement in *Bathyteuthis*.

Ctenopteryx has 12–15 suckers in two rows on each of the buccal lappets. These are considerably more numerous and are slightly larger than the buccal suckers of *Bathyteuthis*.

The fins of *Ctenopteryx* are subterminal, and in adults they are nearly as long as the mantle. The fins consist of long, muscular supports connected by a thin web. In *Bathyteuthis*, too, the fins are subterminal, but they remain small and simple throughout life.

The suckers on the arms of *Ctenopteryx* originate at the bases of the arms in 1 or 2 rows. In arm pairs I–III the suckers increase to six rows on the distal half; arms IV retain two rows throughout. *Bathyteuthis* has a similar increase to four rows. The suckers on the arms are minute in both genera. Swimming keels and protective membranes are rudimentary in both genera.

Dentition on the sucker rings is usually a specific character; in *Ctenopteryx*, however, the sucker rings may be distinct at the generic level, since they lack true teeth entirely. They bear only roughly scalloped borders. *Bathyteuthis* has sucker rings that bear truncate to rounded teeth.

The funnel organ in *Ctenopteryx* is very large. The dorsal member has an inverted U- or V-shape with long, broad limbs. A distinct papilla protrudes anteriorly from the apex. In *Bathyteuthis* the dorsal member of the funnel organ is noticeably smaller, but since a great deal of intraspecific variation exists in the structure of the funnel organ, no strong significance can be placed on this difference alone.

The gladius of *Ctenopteryx* has a long, narrow rhachis that is deeply V-shaped in cross section. The narrow sides of the rhachis are straight, and the lateral edges are tapered, not rolled under. A heavy, median ridge extends the length of the gladius; the ridge tapers posteriorly along the vane and terminates just before the end of the gladius. The vane is thin, broad, and rounded. A conus is lacking, but the posterolateral edge of the vane folds under to form a shallow, cup-shaped terminus of the gladius.

In contrast, the long narrow rhachis of *Bathyteuthis* is C-shaped in cross section; its lateral edges are rolled under to form longitudinal rods, and it lacks a median ridge. The lateral rods of the rhachis taper along the vane and terminate before the end of the gladius. The vane is tissue-thin and marked with series of concentric lines. A conus is lacking in *Bathyteuthis*, too; the posterolateral edges of the vane barely turn under to form a broad, spoonlike, tissue-thin end to the gladius. Therefore, the gladii of the two genera exhibit marked differences.

The eyes of *Ctenopteryx* are huge and are directed laterally. A large, strip-photophore is located on the ventral half of the bulbus (in some species, at least). The eyes of *Bathyteuthis* are large and globular; they are directed anterolaterally. Photophores on the eye are unknown.

The muscular bridles that connect the anterior dorsal wall of the funnel to the ventral surface of the head are narrow and thin in *Ctenopteryx*. In *Bathyteuthis* the bridles are broad, thin bands embedded in the posterior depression of the funnel groove.

Some *Ctenopteryx* have a huge, median, visceral photophore. Visceral photophores are lacking in *Bathyteuthis*, but it has six simple photophores at the bases of the dorsal three pairs of arms. *Ctenopteryx* has no corresponding light organs.

The female reproductive systems show marked differences between the two genera. The oviducal glands of *Ctenopteryx* are small and inconspicuous; they are flat, round glands that lie within the visceropericardial coelom. The oviducal glands of *Bathyteuthis* are large, conspicuous, swollen structures that lie in the mantle cavity dorsolateral to the nidamental glands. The nidamental glands of both genera are similar in structure and positon. The most striking feature of *Ctenopteryx* is the possession of "accessory nidamental glands." No other oegopsid, including *Bathyteuthis*, is known to have these glands. Accessory nidamental glands are found in sepioids and myopsids. In *Ctenopteryx* the supposed accessory nidamental gland is a single, median structure that lies on the wall of the nephridial coelom anterior to the nidamental glands and ventral to the kidneys. It is flat, lobate, glandular, and unsculptured; it bears little resemblance to the paired, swollen, striated accessory nidamental glands of myopsids and sepioids.

This review of the characters of *Ctenopteryx* reveals that *Bathyteuthis* and *Ctenopteryx* share some features that may indicate relationship: simple mantle-funnel locking apparatus; short, simple club with many (8–14) rows of minute suckers; short arms with more than two rows of small suckers (4–6 except on arm IV); suckers on the buccal lappets, etc. Although differences in these characters do occur between genera, they are not necessarily of a magnitude that require separation at the familial level.

The different order of attachment of the buccal connectives to the ventral arms, however, is a major obstacle to the close relationship between *Ctenopteryx* and *Bathyteuthis*. A survey by Young and Roper (1968) pointed out that the arrangement of buccal connectives is an extremely stable character within the families of Oegopsida. The Bathyteuthidae with *Ctenopteryx* included would be the only oegopsid family that did not conform to this pattern. For this reason it is difficult to reconcile the differences in attachment of buccal connectives between *Ctenopteryx* and *Bathyteuthis*.

Although the general shape of the gladius is similar in *Ctenopteryx* and *Bathyteuthis*, some of the details of structure indicate that the similarities may be more superficial than earlier authors thought (e.g., Pfeffer, 1900; Naef, 1923). Unfortunately, no analysis of the value of the detailed structure of the gladius in showing relationships in higher taxa is available. Without such an analysis for the Oegopsida it is impossible at this time to determine how much weight to place on the observed differences between *Ctenopteryx* and *Bathyteuthis*. A priori it would seem, however, that the differences in the structure of the gladii are basic and probably of familial significance.

Naef (1923) was the first to recognize the gland in *Ctenopteryx* that he believed to be homologous with the accessory nidamental glands of sepioids and myopsids. He gave a comparison with the true accessory nidamental glands of myopsids and sepioids, and he concluded that the glands are similar in structure, except that they have become fused in *Ctenopteryx*. This may be so, but the gland that I have observed in *Ctenopteryx* bears no resemblance to the accessory nidamental glands of other decapods. It may be an entirely different structure, but further comparative studies are necessary before a final decision can be reached. In any case, the gland is lacking in *Bathyteuthis*, and the oviducal glands of the two genera are clearly dissimilar.

In summary, *Ctenopteryx* and *Bathyteuthis* share several distinctive features, one of which is unique among the Oegopsida. Other important characters, however, show sharp contrasts between the genera. The first set of characters implies that *Bathyteuthis* and *Ctenopteryx* may be related forms, but the second set precludes a very close relationship. *Bathyteuthis* and *Ctenopteryx* are sufficiently distinct to warrant their separation into separate families.

Familial Relationships of the Bathyteuthidae

Few earlier authors have attempted to establish the relationships of the Bathyteuthidae with other families of the Oegopsida. The Bathyteuthidae is usually placed in a diverse group that includes the Histioteuthidae, Brachioteuthidae, Ommastrephidae (e.g., Hoyle, 1885, 1904, etc; Pfeffer, 1900, 1912; Thiele, 1935; Voss, 1956). Chun (1910) concluded that although the buccal connectives are similar to those of the Enoploteuthidae, Histioteuthidae and Ommastrephidae, the nearest relatives of the Bathyteuthidae cannot be given and that the family occupies a truly isolated position in the Oegopsida. Naef (1916, 1921, 1921a, 1922) listed the Bathyteuthidae at the beginning of the Oegopsida next to the Myopsida. In his monograph Naef (1923) explained his reasons for considering the Bathyteuthidae primitive: primarily, the unique possession of suckers on the buccal lappets, and the 4-rowed arrangement of suckers on the arms and more than four rows on the club; secondarily, rhachis incompletely grown over by mantle muscle, fins loosely attached, neck folds weak, etc. Grimpe (1922, 1925) concurred with Naef's decision.

It is not unique for the Bathyteuthidae that familial relationships have yet to be established. Most families of the Oegopsida stand alone in spite of the valuable works of Chun (1910), Pfeffer (1912), and Naef (1923). Familial relationships seem to exist for the Enoploteuthidae and Lycoteuthidae (Voss, 1962), for Ommastrephidae and Thysanoteuthidae, and for Chiroteuthidae, Mastigoteuthidae, Promachoteuthidae, and Joubiniteuthidae (see discussions in Roper and Young, 1968; Young and Roper, 1968).

The Bathyteuthidae is a distinct family; but is it more closely related to some families than to others? Several characters are useful at the familial level in the Oegopsida and some of the more important of these have been reviewed by Young and Roper (1968) and by Roper, Young, and Voss (in press).

The funnel-mantle locking apparatus is one of the most stable familial characters in the Oegopsida, and it is the primary character that defines some families (e.g., Ommastrephidae and Thysanoteuthidae). Three types of locking apparatus exist: (1) Mantle and funnel components are separate and simple; a straight ridge on each mantle component locks into a straight, median sulcus on each funnel component. Although some variability exists among families in relative dimensions of the apparatus, most oegopsid families have the simple type. These include the Enoploteuthidae, Onychoteuthidae, Lycoteuthidae, Architeuthidae, Histioteuthidae, Octopoteuthidae, Batoteuthidae, etc. (2) Mantle and funnel components separate and complex. This category includes the inverted-T and lazy-T locks of the

Ommastrephidae and Thysanoteuthidae, the ovoid, ear-shaped locks of the Chiroteuthidae and Mastigoteuthidae, the ovoid, bowl-shaped locks of the Promachoteuthidae and Joubiniteuthidae, and the subtriangular locks of the Cycloteuthidae. (3) Mantle and funnel componets completely fused. This type is found only in the Grimalditeuthidae and Cranchiidae. The Bathyteuthidae, therefore, with its straight, simple locking apparatus, is aligned with the majority of oegopsid families and is distinct from the Ommastrephidae, Thysanoteuthidae, Chiroteuthidae, Mastigoteuthidae, Cranchiidae, etc. The sulcus of the funnel component in the Bathyteuthidae tends to become broader and shallower in the posterior part, and in this respect, the lock resembles that of the Histioteuthidae and Octopoteuthidae.

Tentacular clubs provide stable familial characters among the Oegopsida. The typical club is short, expanded and somewhat flattened; it is generally divisible into carpus, manus, and dactylus; it generally has protective membranes, swimming keels, and a 4-rowed arrangement of suckers (and/or hooks). The Ommastrephidae (except *Illex*), Thysanoteuthidae, and Lycoteuthidae are examples of the basic type. Several variations from the basic type occur. For instance, histioteuthids and gonatids have a few more rows of suckers on the manus or dactylus; architeuthids and neoteuthids have a small cluster of irregularly arranged suckers on the proximal part of the manus.

Some families have distinctive clubs that bear no resemblance to the typical club. These include the Mastigoteuthidae, Promachoteuthidae, Joubiniteuthidae, Ctenopterygidae, Brachioteuthidae, Batoteuthidae, Octopoteuthidae, and Grimalditeuthidae. The Grimalditeuthidae lack tentacles; the Octopoteuthidae lack tentacles in adults (except *Taningia*); the Brachioteuthidae have expanded clubs with the normal 3–4 rows distally, but rows of suckers that extend proximally along the tentacular stalk. The Mastigoteuthidae, Promachoteuthidae and Joubiniteuthidae have distinctive clubs that are very long and unexpanded; they bear many rows of minute, closely packed suckers. The Ctenopterygidae have short, simple clubs with about 14 rows of suckers.

The clubs of the Bathyteuthidae are unlike those of most other oegopsid families; they are relatively short, unexpanded, and undifferentiated into carpus, manus, and dactylus. They bear 8–10 rows of minute, closely packed suckers. The extreme distal tip serves as the growing end where sucker proliferation occurs. This feature is shared with the Mastigoteuthidae and Promachoteuthidae, but presently too little is known about growth of the clubs and sucker proliferation in other oegopsid families to place emphasis on this similarity. The clubs of the Bathyteuthidae weakly resemble those of the Promachoteuthidae, Mastigoteuthidae, or Joubiniteuthidae by having many rows of minute suckers, but the bathyteuthid clubs are very short and they have fewer sucker rows; in this respect they resemble the Ctenopterygidae.

The connectives of the buccal membrane attach to the oral surface of the base of each arm at either the dorsal or ventral edge. The connectives attach dorsally to arms I and II and ventrally to arms III in all oegopsids. (*Enoploteuthis dubia* Adam, 1960, is the only known exception; the connectives attach dorsally to all four pairs of arms.) The connectives to arms IV may attach dorsally or ventrally. The order of attachment is a constant feature within oegopsid families. Furthermore, families that show relationships by other characters also have the same order of attachment (e.g., Lycoteuthidae and Enoploteuthidae; Mastigoteuthidae, Chiroteuthidae, and Promachoteuthidae). The Bathyteuthidae have buccal connectives that attach dorsally to the ventral arms. This character is shared with the Enoploteuthidae, Lycoteuthidae Histioteuthidae, Psychroteuthidae, Neoteuthidae, Architeuthidae, and Ommastrephidae.

Most oegopsid families have a biserial arrangement of suckers or hooks along the arms. The Enoploteuthidae and Octopoteuthidae, which have mainly hooks, may have two to four rows of minute suckers at the arm tips. Species of Gonatidae generally have two median rows of hooks and two lateral rows of small suckers on the dorsal three pairs of arms. At the arm tips the hooks may be replaced by suckers. The ventral arms always have four rows of suckers. The tips of the arms in *Gonatopsis octopedatus* have many rows of small suckers. The Joubiniteuthidae have five to six rows of suckers along the dorsal three pairs of arms and four rows along the ventral arms. The Ctenopterygidae have five to six irregular rows. In the Bathyteuthidae the suckers originate on the bases of the arms in a biserial arrangement, then increase to three and four irregularly arranged rows. The number of rows of suckers in the Joubiniteuthidae, Ctenopterygidae and Bathyteuthidae is generally similar, but other characters weigh more heavily to preclude a close relationship. Therefore, multiple rows of suckers occur independently in a few families that are widely diverse on the basis of more stable familial characters.

The gladius in oegopsids should show relationships between higher taxa, but no comprehensive study of oegopsid gladii has appeared in the literature, and, other than the gross features, no taxonomically important characters of the gladius have been delineated. In fact, in many species the gladius remains undescribed. Still, it is possible to find general similarities between gladii of some groups. Several families have a long, thin rhachis, a reduced or absent free vane, and a conus (usually long) formed by the ventral infolding and fusion of the lateral edges of the vane. Diverse families with this type of gladius include the Chiroteuthidae, Mastigoteuthidae, Joubiniteuthidae, Batoteuthidae, Grimalditeuthidae, Brachioteuthidae, some Cranchiidae, etc. Another type of gladius, like that of the Ommastrephidae, is heavily constructed with a thick rhachis, a long, narrow (or absent) vane, and a short, heavy conus. Lycoteuthids, enoploteuthids, and histioteuthids have a type of gladius that tends to have a short free rhachis, a fairly broad, convex or hourglass-shaped vane, and an open conus. The Onychoteuthidae have a short, free rhachis, a long, narrow vane, and a long spikelike extension of the conus. The paddle-shaped bathyteuthid gladius, with its long, free rhachis, broad, thin vane, and flat, open "conus," is unmatched in simplicity of shape and structure; at the present stage of knowledge about teuthoid gladii, the bathyteuthid gladius cannot be closely associated with the pen of any other family.

One of the most distinctive features of the Bathyteuthidae is the occurrence of suckers on the buccal lappets. This feature alone sets it apart from all other oegopsid families except the Ctenopterygidae. *Ctenopteryx*, of course, was included in the Bathyteuthidae for many years as a subfamily, primarily because of this shared character. In addition, *Ctenopteryx* has supposed accessory nidamental glands, a unique organ in the Oegopsida. Some sepioids and myopsids have buccal suckers and accessory nidamentals also, and Naef regarded them as primitive characters.

The occurrence of the accessory nidamental glands in *Ctenopteryx* in conjunction with the presumed primitiveness of the buccal suckers, four rows of arm suckers, and more than four rows of club suckers, led Naef to place the Bathyteuthidae at the beginning of the Oegopsida next to the Myopsida.

The question is not settled, however, for it may be argued that some of these characters are not primitive but are adaptive. Many rows of suckers on the arms and clubs and suckers on the buccal lappets may be adaptations to particular environmental requirements or, more specifically, to certain types of food organisms. The many-rowed condition, or tendencies toward it, occurs in several diverse groups of oegopsids: on the arms of gonatids, joubiniteuthids, enoploteuthids, and octopoteuthids, and on the clubs of mastigoteuthids, promachoteuthids, joubiniteuthids, gonatids, histioteuthids, brachioteuthids, and batoteuthids. All of these groups are mesopelagic or bathypelagic or, in the case of gonatids and brachioteuthids, they are transitional forms that live closer to the surface and range down into the mesopelagic zone. An increased number of suckers on arms and tentacles would be advantageous in capturing and holding prey. Buccal lappets on an expanded buccal membrane fit neatly between the bases of the arms, and suckers on the lappets would provide an additional holding mechanism.

Finally, it is not certain that the glandular structure that Naef described in *Ctenopteryx* is the homologue of the accessory nidamental glands of sepioids and myopsids. Naef perhaps realized this, for had he been more certain he surely would have made a greater point of it.

Therefore, based on the characters presently used to indicate familial relationships, the Bathyteuthidae can be aligned with the relatively small group of families that have simple, straight locking apparatuses and buccal connectives attached to the dorsal side of arms IV. Within this group it shares a club that has (at least some) suckers in more than fours rows with the Histioteuthidae, Psychroteuthidae, Neoteuthidae and Architeuthidae; other similarities in the clubs, however, are lacking. The Bathyteuthidae and Ctenopterygidae share a number of features, e.g., suckers on the buccal lappets, more than two rows of suckers on the arms, more than four on the clubs, and simple, straight locking apparatuses, but they differ in the attachment of buccal connectives to the fourth arms. This difference is basic and probably precludes a close relationship between the two families.

PART II.

ZOOGEOGRAPHY

Review of Antarctic Ocean Oceanography

The Antarctic or Southern Ocean is unique in that it encircles a continent, Antarctica; it provides about 22% of the area of the world oceans, and its oceanographic characteristics are extremely uniform. Since the 1920s, the Southern Ocean has received the attention of oceanographers from many nations, and since the International Geophysical Year (1957–1958) studies of all aspects of the Antarctic Ocean have been intensified. Many detailed and specific works are available on the oceanographic and dynamic features of the Southern Ocean; more comprehensive accounts, upon which the following summary is based, include the studies of Deacon (1933, 1937, 1937a, 1963), Sverdrup et al. (1942), Kort (1962), Pickard (1963), and Brodie (1965).

Water Masses

The Antarctic Ocean is bounded in the south geographically by the Antarctic Continent, and in the north oceanographically by the Subtropical Convergence. The Southern Ocean comprises two major regions: the subantarctic region between the Antarctic and Subtropical Convergences and the antarctic region between the Antarctic Convergence and the Continent. The convergences are distinguished as regions of rapid increase in temperature of the surface waters in a northward direction.

The Subtropical Convergence is not so easily defined as the Antarctic Convergence; it is much more variable in position, and it is not circumglobal as is the Antarctic Convergence. The position of the Subantarctic Convergence is marked by a rapid increase in surface temperatures in the vicinity of 40°S in all oceans except the eastern Pacific. The increase is from 10° to 14° C in winter and 14° to 18° C in summer. Salinity increases from 34.3‰ to 34.9‰. The sharp changes represent the region of convergence of north-flowing subantarctic water and south-flowing subtropical water. The subantarctic region is made up of five different water masses: the warm, saline Subantarctic Surface Water, the cool, dilute Antarctic Intermediate Water, the "warm" saline Upper and Lower Deep Waters, and the cold, saline Bottom Water. These subantarctic water masses vary somewhat between oceans, but the antarctic water masses are similar throughout their extent.

The Antarctic Convergence is a major fundamental boundary zone; it is continuous all around the continent and its location between 50° and 60° south latitudes depends upon land masses, oceanographic conditions and bottom topography. Land masses that impinge from the north create a relatively narrow channel and force the convergence southward toward the Antarctic Continent. This is particularly the case south of the Australia, Tasmania, New Zealand region and between South America and the Antarctic Peninsula. Bottom topography is important to the location of the convergence. In regions approaching ridges or rises the convergence is deflected to the north; downstream of the shoal areas the convergence moves southward. The sharp bends in the convergence are imposed by such bottom features as the Pacific-Antarctic Ridge, the South Antilles Arc, and the Kerguelen and Macquarie Ridges. Position of the convergence is marked at the surface by a steep temperature gradient that ranges from 1°–3° C in winter and 3°–8° C in summer (Mackintosh, 1946). Just beneath the surface convergence zone the northward flowing Antarctic Upper Water sinks beneath the southward moving Subantarctic Surface Water. In subsurface waters Deacon (1937) considered that the convergence is coincident with the area in which warm Deep Water rises above Antarctic Bottom Water.

The water masses in the Antarctic Ocean are characterized by the temperature-salinity relationships. The Antarctic Surface Water occurs as a thin sheet of nearly homogeneous water over the entire Antarctic region; it has low temperatures, between −1.8° and 1.0° C, and low salinities, between 34.0‰ and 34.51‰. In winter the temperature is lowest and the salinity is highest due to reduced solar radiation and ice formation. The reverse conditions prevail in summer. The mixed layer extends from 50 to 200 m depending primarily upon the wind conditions over the sea surface. It is deepest near the convergence and the continent and shallowest near the divergence (ca 65°–70°S) between the east and the west wind drifts (Deacon, 1963). Over the continental shelf, particularly in the Weddell Sea and probably in the Ross Sea, the very cold, saline water (−1.95°C, 34.70‰) resulting from ice formation may extend to the bottom and contribute to the formation of bottom water (see below). Immediately beneath the surface layer is a transition zone that increases rapidly to over 2° C and gradually to over 34.5‰.

Antarctic Circumpolar Water lies below the Antarctic Surface Water and is characterized by temperatures between 0.5° and 2.0° C and salinities slightly above 34.70‰. Maximum temperatures occur at 500–600 m and maximum salinities slightly deeper at 700–1300 m. The Antarctic Circumpolar Water is an extremely uniform water mass that retains its identity entirely around the continent. Close to the continent the temperature and salinity are slightly lower, and they increase with distance from the continent. The Antarctic Circumpolar Water has the same characteristics as the Lower Deep Water that lies at about 2000 m in the subantarctic region.

Antarctic Bottom Water is characterized by extremely low temperature and relatively high salinity. This water mass is formed by the admixture of cold (−1.9° C), fairly low salinity (34.62‰) Antarctic shelf water and warmer (0.5° C), more saline (34.68‰) Antarctic Circumpolar Water that lies close to the continent. The resulting Bottom Water has a temperature around 0° and a salinity around 34.66‰; it has a high density of sigma-t=27.86. Antarctic Bottom Water is formed primarily in the Weddell Sea and it spreads northward and eastward into the Atlantic, Indian, and Pacific Oceans. In the Atlantic it is detected as far as 40°N (Wüst, 1935), and in the Indian Ocean it has been identified in the Bay of Bengal and the Arabian Sea between 10°–20°N (Kort, 1962).

Water Movements

The circulation of water masses of the Antarctic Ocean is governed by wind forces at the surface and by parameter gradients at all depths. Two types of movement occur: latitudinal, mainly from west to east in the whole circumpolar water mass, and meridional, equally from north to south and from south to north (or northeast, southeast) in stratified masses.

A narrow band of easterly winds close to the continent induces surface waters to move westward around most of the continent. This East Wind Drift of the Antarctic Surface Water involves a relatively small volume of water that moves at a slow velocity. The movement of the main mass of Antarctic waters is from west to east, driven by the strong and nearly continuous west winds that blow in the region between 40° and 60°S. The surface movement is referred to as the West Wind Drift and the entire eastward circulation is termed the Antarctic Circumpolar Current. Coincident with the boundary between the easterly and westerly wind belts is an area of divergence at the sea surface at about 65°S. In the Southern Hemisphere, wind drift deviates to the left of the direction of the wind so that easterly winds produce a southerly component and westerly winds a northerly component to the surface currents. The resulting divergence creates an upwelling of "warm," high-salinity deep water toward the surface. The northern portion mixes with Antarctic Surface Water and moves to the north and east. The southern component mixes with the cold waters adjacent to the continent and moves south and west. In winter the mixed, upwelled and surface water becomes colder and more saline due to loss of water to ice formation. This low-temperature, high-salinity water is very dense and it sinks along the continental margin; with some mixing with Deep Water, it forms Antarctic Bottom Water. As noted above, this process occurs chiefly in the Weddell Sea, but more recent information indicates that it occurs in the Ross Sea as well (Kort, 1962; Brodie, 1965; this report). Antarctic Bottom Water spreads northward and eastward along the sea floor away from the continent; it is found throughout the Antarctic Ocean; it extends beyond the Equator in the Atlantic Ocean; it is present in the southern portions of the Indian and Pacific Oceans.

The Antarctic Circumpolar Current is the result of a strong wind-driven current in the surface layers and a gradient current, due to variations in density, throughout the entire water mass (Sverdrup et al., 1942). More recent work confirms the existence of eastward movement of the Antarctic Circumpolar Current around the entire Southern Ocean. The structure of this largest current in the oceans is extremely complicated and the total flow breaks up into streams of fast-moving cores; in some places countercurrents exist (Kort, 1962). The maximum current flow is in the zone of the Antarctic Convergence. Previous mention has been made of the location of the Antarctic Convergence in relation to bottom topography. The relationship is really to the current system that in turn is responsive to bottom topography. The Coriolis effect in the Southern Hemisphere exerts a northerly bend to the current as it approaches a submarine ridge and a southerly bend as it passes the ridge. In all, five distinct ridges are crossed by the Antarctic Circumpolar Current: the South Antilles Arc, the Bouvet Island Rise, the Kerguelen Ridge, the Macquarie Ridge, and the Pacific-Antarctic Ridge. An additional influence contributes to the sharp northward displacement of the Antarctic Circumpolar Current in the South Pacific sector of the Southern Ocean over the Pacific-Antarctic Ridge: the strong anticyclonic circulation near the Ross Sea forces the major current system northward. Land masses have an effect on the Antarctic Circumpolar Current similar to that described for the Antarctic Convergence.

In the subantarctic region the current is directed from west to east, also, but only the southern portion close to the Antarctic Convergence circulates around the Southern Ocean as part of the Antarctic Circumpolar Current. In the Pacific Ocean, at least, the northern portion of the subantarctic region belongs to the current system of that ocean.

Transverse or meridional water movements are set up as a result of the convergences and divergences. The southwesterly trend of the upwelled waters mixed with surface water in the region of the Antarctic

Divergence has already been discussed. The movements of water associated with the Antarctic Convergence are even more significant and far reaching. The dynamics of the Antarctic Convergence are not fully understood. Deacon (1937) considered that the Antarctic Convergence is caused primarily by the deep water circulation. He reasoned that the cold Antarctic Surface Water is prevented from sinking in the antarctic region by the underlying warmer but highly saline, more dense Deep Water. But once the Antarctic Surface Water passes the region where the Deep Water climbs steeply toward the surface above the Antarctic Bottom Water, the surface water is no longer held up and it sinks below the warm, less dense Subantarctic Surface Water. Another view is taken by Sverdrup (1934); he suggested that the convergence is caused by the different types of circulation in the surface layers of the antarctic and subantarctic regions. The thermohaline circulation of the subantarctic region forces the warm, light surface waters to the south; the wind-driven circulation of the antarctic region drives the cold, dense surface waters to the north. When these waters meet, the more dense mass submerges.

Wyrtki (1960) concluded that in regions of strong westerlies a zone of convergence develops to the north of the axis of maximum wind force and a zone of divergence develops to the south of the axis. As the axis shifts north and south so do the convergence and divergence zones. The degree of convergence and divergence varies with the strength of the wind. Wexler (1959) similarly reasoned that the convergence is caused by meteorological factors. Whatever the underlying cause is, the result is the same.

The water that sinks at the convergence all around the Southern Ocean is characterized by a temperature of 2.2° C and a salinity of 33.80‰. As it sinks it very rapidly becomes mixed with water from above, the Subantarctic Surface Water, and from below, the Deep Water. The resulting water mass is the Antarctic Intermediate Water that spreads northward throughout the southern portions of the three oceans. In the Atlantic, where no equatorial water mass exists, the Antarctic Intermediate Water spreads to 20°N whereas in the Pacific and Indian Oceans it reaches only to about 10°S. The Antarctic Intermediate Water is characterized as a salinity-minimum core that lies between 800–1200 m between sigma-t surfaces of 27.20 and 27.40; temperatures range between 3°–7° C.

The circulation of the deep waters of the Southern Ocean is linked with the occurrence of the Deep Water masses from the Atlantic, Indian, and Pacific Oceans. In the South Atlantic the Deep Water is characterized as a core of high-salinity water flowing southward that is sandwiched between the north-flowing Antarctic Intermediate

Water and Antarctic Bottom Water. In the boundary zones the Deep Water mixes with the Intermediate and Bottom Waters so that when it reaches the high southern latitudes of the Antarctic Ocean it is somewhat diluted and cooler. Nevertheless it retains its characteristic high salinity, and this mass of saline, "warm" Deep Water rises toward the surface above the descending Antarctic Bottom Water and contributes to the formation of the Antarctic Circumpolar Water. The process in the Indian and Pacific Oceans is similar though less pronounced, and deep water in these oceans has a strong component of Atlantic Deep Water. The location of the Antarctic Convergence is marked as distinctly by the positions of the Deep and Bottom Waters as by the submergence of the Antarctic Surface Water; the isotherms and isohalines at great depths slope as steeply as those near the surface (Deacon, 1963).

The concentration of oxygen in the antarctic region is generally high and probably never goes below 3–3.5 ml/L. Around the antarctic region the oxygen minimum layer is located between 600–1200 m. In the Drake Passage the concentration is relatively low, but eastward in the Scotia and Weddell Seas the oxygen content increases and the oxygen minimum layer is shallow and has a high value. Farther eastward the concentration gradually diminishes in the minimum oxygen layer and in the Deep and Bottom Waters. In the northern subantarctic region the oxygen minimum layer lies in the Deep Water mass at around 2000 m, but it rises to shallower depths farther south. Antarctic Intermediate Water is high in oxygen content as it leaves the surface, but the oxygen concentration diminishes northward and with depth. In most areas, and particularly north of the Weddell Sea the Antarctic Intermediate Water is characterized as an oxygen maximum which overlies the oxygen minimum of the Deep Water. Antarctic Circumpolar Water generally has more oxygen than Deep Water to the north. Antarctic Bottom Water has very high oxygen concentrations because it has so recently been in contact with the surface. In the Weddell Sea, oxygen concentration may reach 7 ml/L at the surface. Bottom Water has concentrations as high as 5.5 ml/L (Sverdrup et al., 1942).

The concentrations of nutrient salts in the Antarctic Surface Waters rarely fall below the winter maxima of temperate regions (Clowes, 1938). The surface waters of the subantarctic region have less nutrients, but in deeper waters between the Antarctic Intermediate Water and the Deep Water nitrates and phosphates appear to be regenerated; this boundary layer also conforms to the oxygen minimum, so that the region probably is an area of mortality and decomposition of phytoplankton. The decomposition releases nitrates and phosphates to the southward-moving warm Deep Water, and in the antarctic region this water mass has the highest concentrations of nutrients. These rise close to the surface, particularly in the area of divergence, and are utilized by the phytoplankton during the season of productivity.

The Antarctic Ocean, therefore, is not a closed system circulating around the Antarctic Continent without renewal; it has an inseparable, dynamic association with the oceans that lie to the north, contributing Intermediate and Bottom Waters and receiving Deep Water. Not only is the volume of water in balance, but the physical properties remain stable also by external processes of cooling and heating, formation and melting of ice, evaporation and precipitation, and mixing.

Analysis of Environmental Parameters; Correlation with Distribution of *B. abyssicola* in the Antarctic Ocean

While the general features of the oceanography of the Southern Ocean are known, there is little published specific material on the details of the distribution of physicochemical parameters over the broad expanse of the Antarctic Ocean. Deacon's classic work remains the primary source of data; this is based upon a few transects across the Southern Ocean around the continent. Most of the *Discovery* transects were diagonal to the meridians, so the vertical sections of oceanographic parameters are not meridional, and often one end of a section represents conditions many miles to the east or west of the other end. Certainly the information has been valuable and much sound physical and biological work has been based on it. Attempts to determine the effects of oceanographic parameters on the distribution and biology of marine organisms, however, must be based upon data that coincide in time and space with the captures of the specimens. Variations of appreciable magnitude occur even in the stable Antarctic Ocean, and as will be pointed out in the following discussion, perhaps some earlier ideas of Antarctic oceanography will need revising.

Completely simultaneous oceanographic and capture data, of course, are extremely difficult to get, but operations aboard the *Eltanin* are such that oceanographic stations are taken within a few hours and a few miles of biological stations. In the future, biological and oceanographic station information should be available in a computer program. Oceanographic data will be summarized and plotted on vertical sections. For the present work, however, only lists of raw data were available, and I have constructed the vertical sections from them. Meridional sections were constructed along 25°, 35°, 55°, 65° 75°, 115°, 130°, and 160° west longitudes, and latitudinal sections along 60° south latitude from 25° to 160° west longitude. The vertical sections present temperature, salinity, density (sigma-t) and oxygen values from the surface to 3000 m. Details of the isotherms and isohalines have not been plotted in the upper few hundred meters, because they have no direct influence on the distribution of *B. abyssicola.* The locations of captures of *B. abyssicola* have been plotted on the sections. Each section will be discussed in relation to the oceanographic features and the distribution of *B. abyssicola.* The location of the capture points represents the most probable depth of capture by the open Isaacs-Kidd Midwater Trawl. Specimens could have been captured shallower or deeper, but the indicated depths are probably accurate (see discussion and calculations of depth of capture). The values for all plotted captures may not correspond exactly to the "simultaneous" oceanographic values. Some variation with season may exist even at depths below 500 m, especially in the convergence zone where the steep isotherms may move north and south with seasonal changes. Also, many captures were not made along the exact longitudes that are represented in the sections. The locations of lines of equal values vary with longitude, sometimes quite sharply. Therefore capture points have not been plotted in cases where the "simultaneous" capture values vary significantly from the values on the sections.

25° West Longitude; 55° to 63° South Latitudes

The sections from 25°W (figs. 21, 22) extend northward from the northeastern part of the Weddell Sea and pass east of the South Sandwich Islands. The temperature section (fig. 21) locates the Antarctic Convergence between 57° and 58°S during the fall and early winter. The influence of the frigid Weddell Sea water is evident in the entire section. South of the convergence, the Surface Water is 0° C and below 63°S the water at all depths is around 0° C or colder; the 0° isotherm lies at about 2400 m at 57°S and rises to 1500 m at 63°S. Water with the character of Antarctic Bottom Water extends from these levels to the bottom. The presence of the southward flowing Deep Water is indicated by the 0.5° isotherm that rises steeply from below 2000 m at 54°S and forms a layer of "warm" water in the Antarctic Circumpolar Water mass between 200 and 1000 m from 58° to 63°S. In other areas around the Southern Ocean the corresponding isotherm at these levels and latitudes is around 2.0° C, so the influence of the Weddell Sea is apparent. The 1° isotherm rises steeply from below 1500 m at about 54°S to about 400 m at 57°S, then it bends sharply northward under the influence of the cold surface layer. A small core of 1° C water lies between 59° and 60°30′S at 200–600 m. Water of 1.5° C occurs only north of the convergence zone and is represented in the section by a nearly vertical isotherm around 55°S.

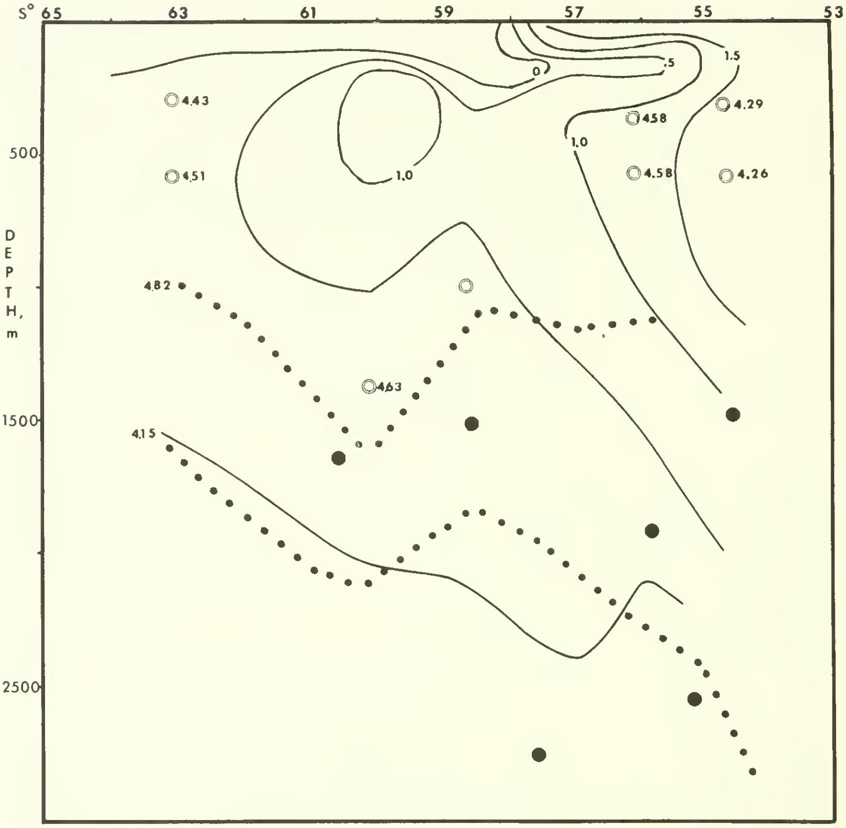


FIGURE 21.—Vertical section, 25°W, 55°–63°S; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola*.

The salinity section (fig. 22) in general shows low salinities throughout the region. The 34.70‰ isohaline extends as a thin tongue to about 60°30′S at 600 m; at 57°S it is located between 650 and 1050 m and encloses a thin tongue of high salinity water of 34.73‰–34.74‰. Below 1100 m at 57°S and at all depths south of 61°S the salinity is below 34.70‰; the deeper water is Antarctic Bottom Water of about 34.66‰ which flows northward and eastward into the major oceans.

The density is uniformly high below the Surface Water and increases rapidly from sigma-t=27.50 to 27.82 (fig. 22); below 750–1000 m and in the south the density is very high, above 27.85, due to the extremely cold water.

Oxygen concentrations are quite high along the entire section (fig. 21); minimum values south of the convergence range from 4.43 ml/L to 4.81 ml/L. The layer of minimum oxygen in the south is from 300 to

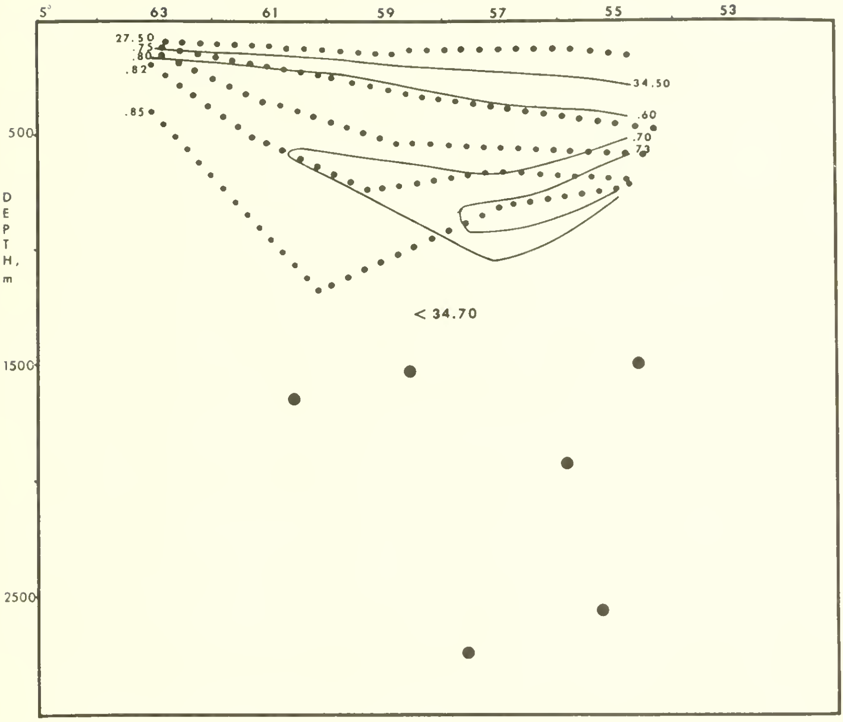


Figure 22.—Vertical section, 25°W, 55°–63°S; salinity°/oo, sigma-t. Capture points of *Bathyteuthis abyssicola.*

600 m and at 58°30′S it dips to about 1000 m, although the value is quite high. South of the convergence below 1000 m the oxygen concentration is always above 4.80 ml/L and increases with depth to well over 5.25 ml/L. North of the convergence the lowest concentrations are 4.26–4.29 ml/L; the minimum layer lies at 350–600 m.

Eltanin Cruise 8 was the only cruise to work the waters covered by the 25°W sections. During that cruise twenty-five 3-meter IKMT tows were made below 500 m in depths normally inhabited by *B. abyssicola.* Of these, six tows were successful in capturing this species. These captures, made between 22° and 29°W, are plotted on the 25°W sections. Four captures, with five specimens, were taken between 1490 and 1922 m; two specimens were taken in nets that fished below 2500 m: one larva at 2562 m and one adult at 2743 m. These two specimens probably were taken somewhat shallower. All captures were made in water of less than 1° C: one between 0.5° and 1° C, three between 0° and 0.5° C and two below 0° C. All captures were in salinities less than 34.70‰, in densities greater than sigma-t = 27.85, and in oxygen concentrations from 4.75 ml/L to well above 5.20 ml/L in water beneath the oxygen minimum layer. The specimens were taken in the Antarctic Circumpolar Water mass.

35° West Longitude; 46° to 62° South Latitudes

The sections along 35°W cross the eastern end of the South Antilles Arc (where the water shoals to less than 3000 m) and pass east of South Georgia. A prominent feature of the temperature section (fig. 23) is the relatively far northern position of the Antarctic Convergence in the vicinity of 48°S. The northern location of the Antarctic Convergence is due primarily to the bottom topography: as the Antarctic Circumpolar Current (which has its greatest flow along the Antarctic Convergence) flows eastward against the South Antilles Arc it is deflected to the left by the Coriolis force; after the current passes over the ridge it bends toward the south again. The data are winter values. At all depths south of 60°S the water temperature is less than 0.5° C; the 0.5° isotherm descends sharply to the bottom between 60° and 56°S.

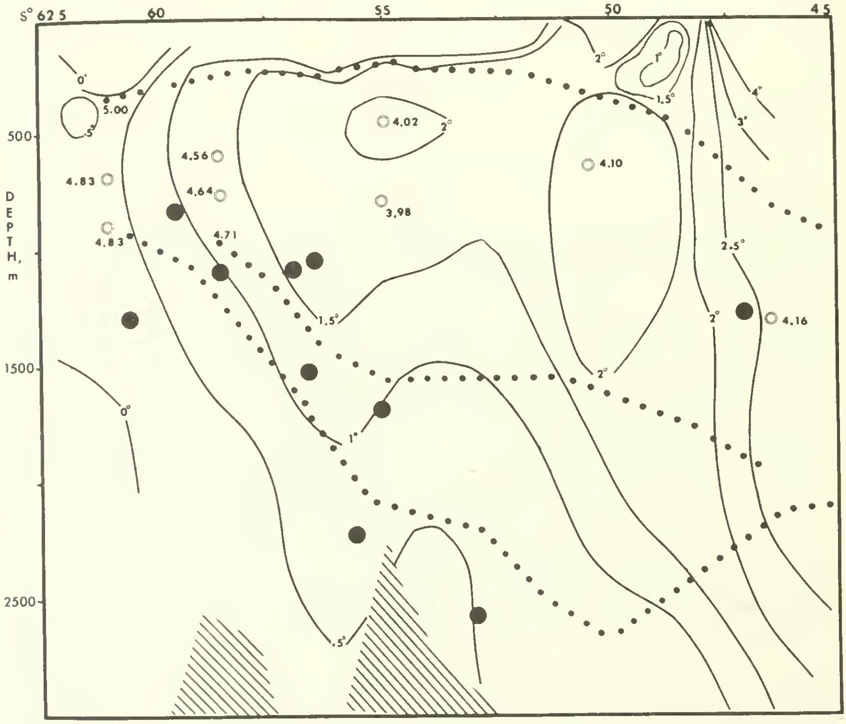


Figure 23.—Vertical section, 35°W, 46°–62°S; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola.*

The major portion of the Antarctic Circumpolar Water is between 0.5° and 2° C. The 1.5° isotherm penetrates to 58°S as an 800–1000 meter thick layer between depths of 250 and 1300 m; north of 52°S the isotherm dips sharply into Deep Water. The 2° isotherm ascends vertically (in the section) from over 2500 m to the surface in the convergence zone. Two cores of 2° C and slightly warmer water occur between 48°30′ and 51°30′S and between 53°30′ and 56°S; the larger, more northerly core exists between 400 and 1500 m and the smaller core occupies a thin layer between 350 and 600 m. In summer the northern core, and perhaps the southern core, merges with the 2° isotherm so that continuous 2° C water extends farther southward than in winter.

The salinity section (fig. 24) shows the submergence of low salinity Surface Water between 48° and 50°S. The isohalines through 34.60‰ originate in shallow water in the south; they gradually descend northward until, beneath the convergence, they dip more sharply into deeper water. At 46°S the 34.60‰ isohaline lies at 1500 m. South of 60°S all salinities are below 34.70‰. The major portion of the section shows a complexity of isohalines outlined by the 34.70‰ line. This envelops the

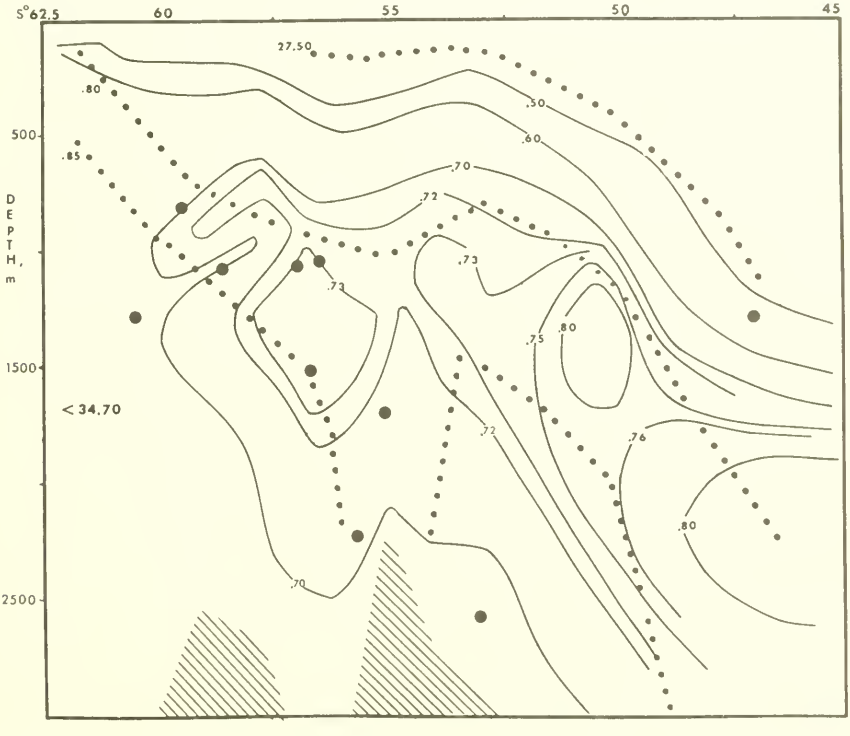


Figure 24.—Vertical section, 35°W, 46°–62°S; salinity°/₀₀, sigma-t. Capture points of *Bathyteuthis abyssicola*.

waters from about 600 to over 2500 m and represents a large segment of Antarctic Circumpolar Water. The high salinity tongue penetrates from the north and represents the southern limits of the highly saline North Atlantic Deep Water. Salinities greater than 34.80‰ penetrate the antarctic region 2000–2500 m under the convergence at the surface as far as about 48°S. South of this zone the saline water ascends to shallower depths and becomes somewhat dilute southward. The 34.72‰ isohaline is continuous nearly to 60°S; the 34.73‰ isohaline is continuous to 54°30′S and a core of 34.73‰ water occurs at 1000–1750 m between 55° and 58°S. This high salinity water of Atlantic origin remains as a constant feature of the Antarctic Circumpolar Water mass and is evident even in sections from the eastern Pacific. The 25°W salinity section does not extend very far north, but the tongue of high salinity water at 500–1000 m is the southern edge of the salinity core that is so prominent in the 35°W section.

The plot of sigma-t values (fig. 24) shows high densities in deeper waters coincident with the high salinities and low temperatures. Most of the Antarctic Circumpolar Water mass has densities greater than sigma-t=27.80.

The distribution of oxygen along 35°W (fig. 23) reveals the oxygen minimum layer at 600–800 m in the antarctic region. Minimum values range from 3.98 ml/L to 4.83 ml/L with the higher values located around 55°S. The minimum value just north of the convergence is 4.16 ml/L and it is located at a depth of 800 m. Concentrations increase gradually with depth below the layer of oxygen minimum.

Eltanin Cruises 9 and 12 covered the area included in the sections for 35°W. During Cruise 9 twenty 3-meter IKMT tows were made in the region under discussion, but five of these were at depths shallower than 500 m where *B. abyssicola* generally is not found. Eight of the remaining tows captured *B. abyssicola.* Many IKMT tows in the right depth range were taken during Cruise 12 but specimens from only two tows have been received. Both of these samples contained *B. abyssicola.* The ten captures, taken between 31° and 38°W, are plotted on the 35°W oceanographic sections. Eight captures of 12 specimens were made between 55° and 60°30′S. Six captures of these were made where the water temperature ranged from just under 1° C to just over 1.5° C in depths from 800–1700 m. Three tows were taken in water around 0.5° C; the specimen at 60°30′S could not have come from a temperature greater than 0.5° C (the "simultaneous" temperature for that location and depth, 1281 m, was 0.17° C); the other specimens in this temperature were taken in water close to the 0.5° isotherm. The simultaneous temperature for the deepest specimen is 0.65° C, and for the capture at 2214 m (two specimens) it is 0.34° C. The 2214 m capture was made at 37°57′W where a tongue of cold water below 0.5° C ascends to a shallower depth; this accounts for the slight discrepency in the location of the plot. The single specimen that was taken at 47°S came from a water temperature of about 2.5° C.

In relation to salinity nearly all the captures are associated with the high salinity segment of the Antarctic Circumpolar Water. Seven captures were in 34.70‰ or greater; three were in 34.73‰. The southernmost specimen came from water of 34.69‰. If the deepest specimen actually came from 2575 m it was taken in 34.69‰ also; if it came from a few hundred meters shallower it was in salinities over 34.70‰. The northernmost specimen was captured in 34.56‰.

Seven of the captures were made at a density of sigma-t=27.80–27.85, two from greater than 27.85, and one, the northernmost, from 27.60.

All captures lie within or below the layer of minimum oxygen. The southernmost capture was made in an oxygen concentration greater than 5 ml/L. The remaining eight captures in the antarctic region were taken in oxygen concentrations of about 4.60 ml/L; five of these were taken along the 4.83 ml/L line that descends northward. The shallowest capture was 810 m in the oxygen minimum and the deepest 2575 m near the oxygen maximum. The specimen at 47°S was taken in the oxygen minimum at a value of 4.16 ml/L.

In summary, the majority of captures was made at temperatures between 1° and 1.5° C, at salinities at or near the maximum (34.70‰–34.73‰), at high densities greater than sigma-t=27.80, and at moderate oxygen concentrations below the oxygen minimum layer.

55° West Longitude; 52° to 62° South Latitudes

The sections along 55°W lie in the eastern end of the Drake Passage and extend from just north of Elephant Island to just east of the Falkland Islands. The oceanographic data were collected during midsummer during *Eltanin* Cruise 6. Unfortunately there must have been some wide gaps between Nansen bottles because the data tabulated in Friedman (1964) are rather scattered. This means that a certain amount of interpolation has been necessary in constructing the sections and in determining the simultaneous values for the captures. Jacobs (pers. comm.) has warned that some of the early *Eltanin* oceanographic data may not be too reliable.

The temperature section (fig. 25) locates the Antarctic Convergence between 58° and 59°S. The relatively warm Subantarctic Surface and Upper Waters to the north of the convergence represent the Falkland Current which bends northward in this region. The 2.5° isotherm descends from the convergence zone and, after a reverse trend at 56°S, it drops to 1500 m where it levels off to the north. The 2° isotherm

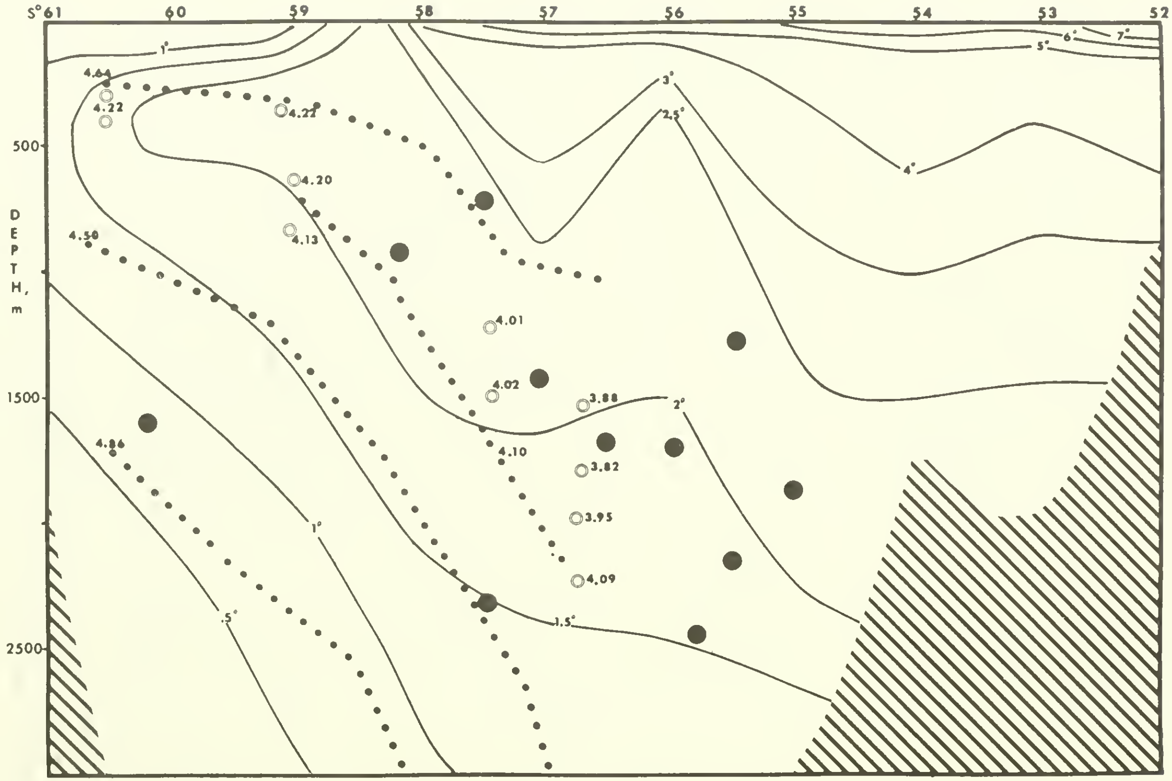


FIGURE 25.—Vertical section, 55°W, 52°–61°S; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola.*

protrudes to beyond 60°S at 300–500 m then descends northward and ends against the Falkland Rise at 2400 m. Below the 2° isotherm the water cools gradually toward the bottom.

The salinity section also shows the influence of the Falkland Current in the subantarctic region (fig. 26). The isohalines that originate near the surface in 59°–61°S descend northward and meet the Falkland Rise at increasing depths. The 34.60‰ isohaline runs at a diagonal from near the surface at 61°S to 1700 m against the Falkland Rise. The high-salinity core typical of Antarctic Circumpolar Water is present as a large segment of 34.72‰ that occupies the layer between 500 and 1500 m at 60°30′S and between 2200 and 2800 m at about 55° to 57°S. In this region there can be no entry of Deep Water directly from the north because of the broad expanse of the Patagonian continental shelf off eastern South America. A small tongue or core of higher salinity water up to 34.74‰ occurs in 600–1500 m at 59°–61°S.

The density of the water in the 55°W section remains low to considerable depths particularly along the northern edge of the section (fig. 26). Sigma-t values of 27.75 are encountered on the bottom at 2500 m in the north at 55°S, while the same density is found at 350 m at 60°30′S. Higher densities occur in association with the salinity maximum layer and the diminishing temperatures.

The isopleths for oxygen concentration descend steeply toward the north in the major portion of the Antarctic Circumpolar Water mass (fig. 25). The oxygen minimum of 4.22 ml/L lies between 300 and 400 m at 60°30′S. Northward the oxygen concentration decreases in value and location of the minimum increases in depth. At about 56°40′S the minimum value is 3.82 ml/L, and the layer of minimum values is located between 1500 and 2000 m.

The captures that are plotted on the sections were all made between 50° and 59°W during Cruise 6. Twenty 3-meter IKMT tows were made in depths greater than 500 m and twelve of these were successful in capturing *B. abyssicola.* Most of the unsuccessful tows were at depths of less than 1000 m north of the convergence zone where the temperature is generally over 3° C. Six of the captures were made at temperatures between about 1.5° and 2° C in depths between 1650 and 2440 m; these six tows produced 39 specimens. The shallow captures plotted at about 57°30′ and 58°S are shown in water that is slightly warmer than the "simultaneous" temperature at time of capture. The two specimens at 914 m came from 1.94° C, and the one specimen at 713 m came from 2.11° C. The three remaining captures in the 2° to 2.5° C layer had simultaneous temperatures from 2.09° to 2.23° C; 27 specimens were taken in these three tows. The plot at 60°11′S represents a single specimen that had a simultaneous temperature of about 1.4° C, so it is plotted in water a little too cold.

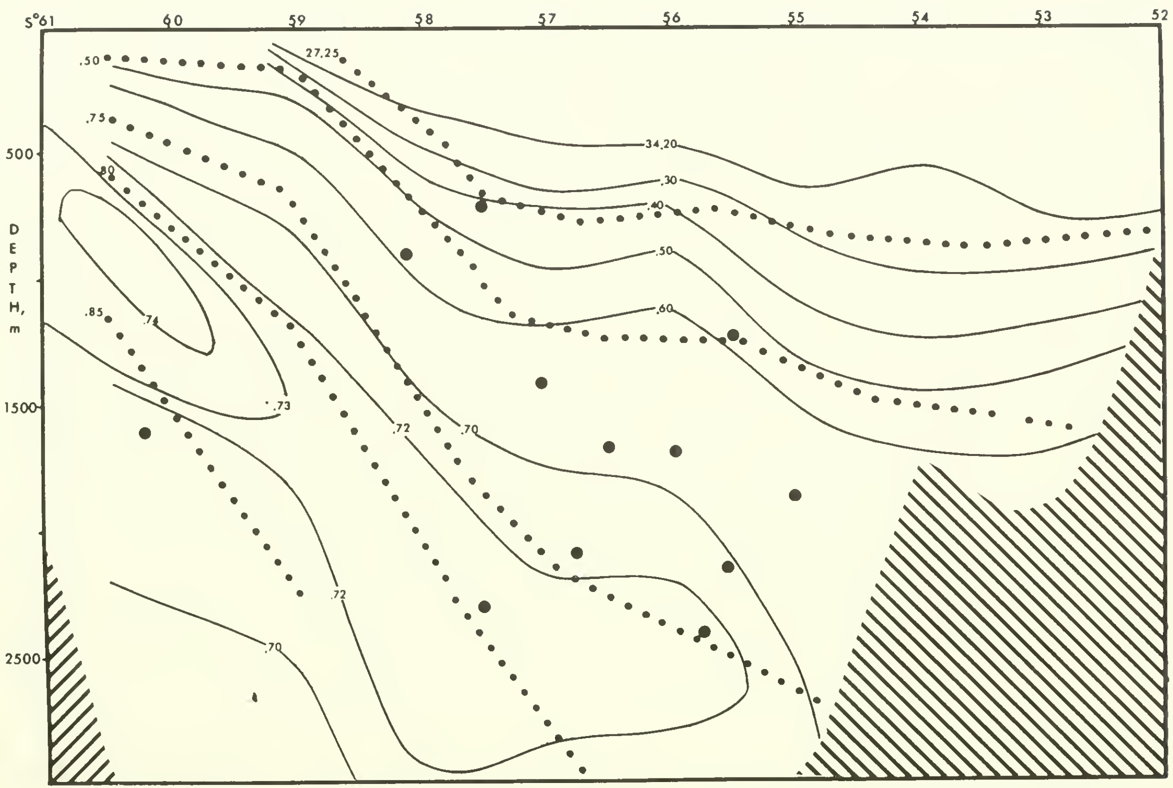


FIGURE 26.—Vertical section, 55°W, 52°–61°S; salinity°/oo, sigma-t. Capture points of *Bathyteuthis abyssicola*.

The distribution of captures on the salinity section shows that most of the points lie below the 34.60‰ isohaline. The three points on or shallower than this line actually had simultaneous salinities greater than 34.64‰. So all captures are in the high salinity range of Antarctic Circumpolar Water. The salinity values for the three shallowest specimens probably are not accurate and the plots of the sigma-t values are too low. All captures were made in densities greater than about sigma-t=27.60.

Where oxygen data are available the plots of captures generally fall within the low to middle range of values, between about 3.80 ml/L and 4.20 ml/L. Two captures were made at high values between 4.80 ml/L and 5.50 ml/L.

To summarize, the captures plotted on the 55°W sections were made mainly at temperatures beween 1.5° and 2.25°, at high salinities close to the maximum, at fairly high densities, and at low to moderate oxygen concentrations.

65° West Longitude; 56° to 63° South Latitudes

The sections along 65°W extend across the Drake Passage from the South Shetland Islands to Tierra del Fuego. The oceanographic data were taken in late winter during *Eltanin* Cruise 4. The Antarctic Convergence is located on the temperature section between 58° and 59°S (fig. 27). The Subantarctic Surface Water north of the convergence represents the beginning of the Falkland Current. Cores of "warm" water (2.5°–4° C) pass along the edge of the South American continental shelf; the bottom of the 2.5° isotherm is located at about 1700 m. The 2° isotherm is at the surface in the convergence zone; below the surface at 250–400 m it passes southward past 61° S, descends to about 800 m, then turns sharply northward forming a long tongue of 2° C water that protrudes to the south. It slopes gradually northward from 1000 m at 59° S to about 1800 m on the bottom at 56°30′S. Below 61°S the water is below 2° C at all depths. Beneath the 2° isotherm the water shows gradual cooling to temperatures less than 0.5° C toward the bottom.

The salinity section shows a well-stratified salinity structure across the Drake Passage (fig. 28). The isohalines originate close to the surface at 63°S, but they get progressively deeper toward the north. The 34.60‰ isohaline originates on the section in about 250–300 m at 63°S and slopes down to about 1300 m at 56°30′ S. A well-defined core of high salinity occurs at depths of 1100 to 2100 m between 57° and 62° S; values in the core are 34.73‰ to 34.74‰. At 62°S a small core of 34.74‰ water lies between 600–1000 m. Below the salinity maximum the isohaline for 34.72‰ crosses the Passage between 2000 and 2500 m with a dip to 2900 m at 58°S.

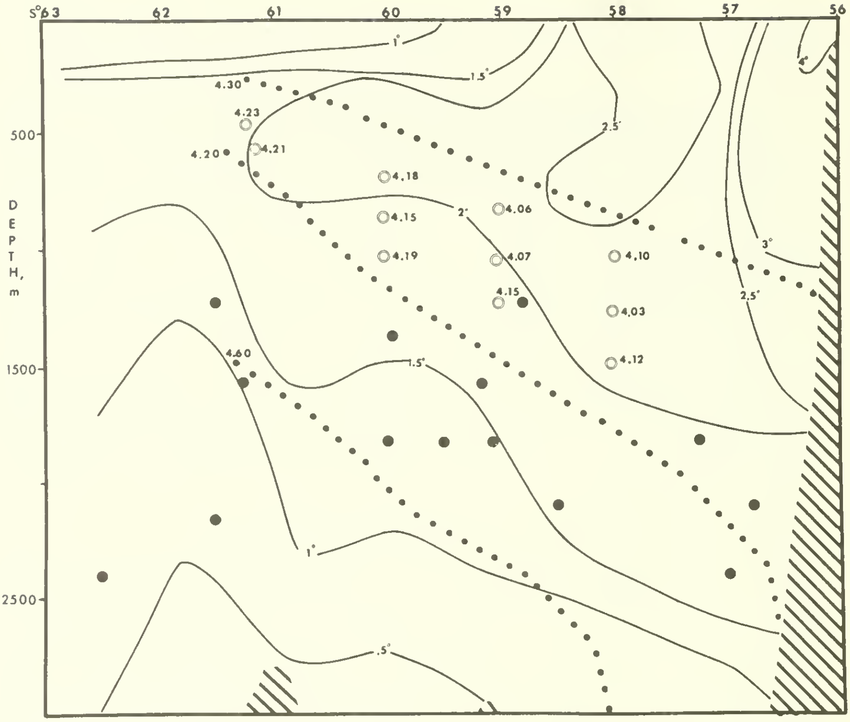


FIGURE 27.—Vertical section, 65°W, 56°–63°S; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola.*

Isopycnics across the Drake Passage in general follow the isohaline contours (fig. 28). The denser water occurs at shallower depths on the southern side of the Passage. A sigma-t of 27.75 occurs at 350 m at about 63°S; at 56°30′S the same value is encountered at nearly 2500 m.

Isopleths of oxygen concentration also lie deeper along the South American continental shelf than along the southern edge of the Drake Passage (fig. 27). At 61°10′S the oxygen minimum occurs at a depth of 500 m with values of 4.21 ml/L to 4.23 ml/L. At 58°S the minimum oxygen layer lies between 1000 and 1500 m with values of 4.03 ml/L to 4.12 ml/L. Below the minimum layer the oxygen concentration increases slightly with depth to values just under 5.0 ml/L.

The fourteen captures that are plotted on the sections represent successful tows between 60°W and 70°W during *Eltanin* Cruises 4 and 5. During Cruise 4, fourteen tows were made at depths greater than 500 m and ten of these were successful in catching *B. abyssicola;* the four unsuccessful tows were in less than 1000 m (two from

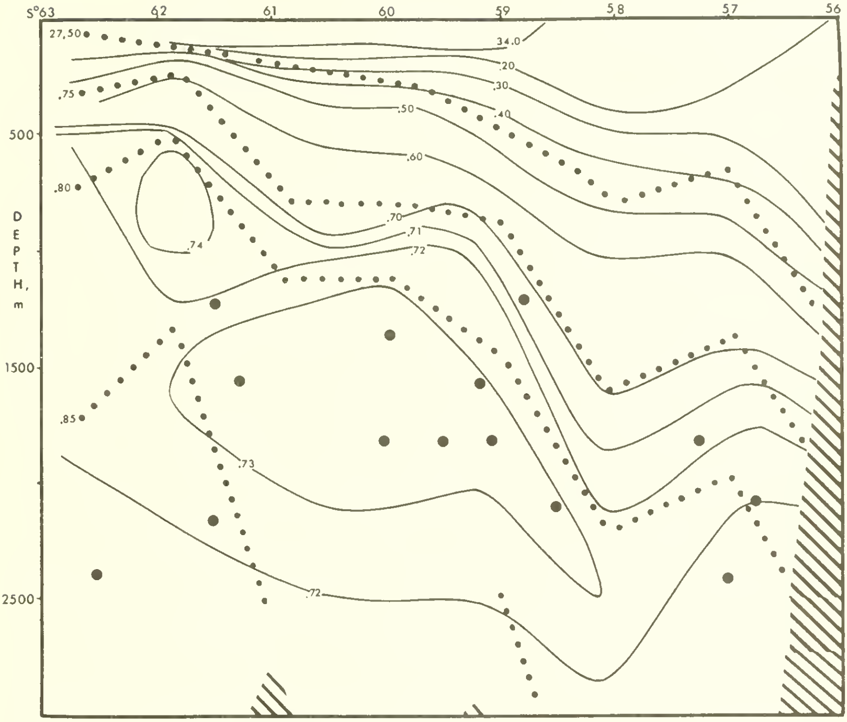


FIGURE 28.—Vertical section, 65°W, 56°–63°S; salinity°/₀₀, sigma-t. Capture points of *Bathyteuthis abyssicola.*

900 m and two from 600 m) while the successful tows were from 1200 to 2400 m. Seven tows were made during Cruise 5 in the region covered by the section for 65°W. The five successful tows were made between 1300 m and 2400 m and the unsuccessful tows were from 800 m and 2500 m. All capture-plots on the temperature section lie below the 2° isotherm; seven captures lie between 1.5° and 2° C, five between 1° and 1.5° C and two between 0.5° and 1.0° C. Most of the plots coincide with the simultaneous temperature values. Three tows caught exceptionally large numbers of *B. abyssicola* (10, 12, and 20 specimens) at depths of 1556, 1370, and 2100 m; these plots lie close to the 1.5° isotherm. The remaining tows took 29 specimens. Of the six unsuccessful tows, five were made at less than 1000 m in the subantarctic region or in the antarctic region where the temperature was warmer than 2° C.

The capture-plots on the salinity section all fall below the 34.70‰ isohaline; only three are at less than 34.72‰ and seven are at greater than 34.73‰ in the maximum salinity core. All captures are plotted at densities greater than sigma-t=27.75, and eleven captures are located at densities greater than sigma-t=27.80. One capture lies within the zone of oxygen minimum and the rest lie deeper than the layer of minimum oxygen, mostly at values between 4.25 ml/L and 4.60 ml/L.

In summary, the major portion of the captures (and specimens) came from water characterized by temperatures between 1° and 2° C, by salinities in the maximum range, by high densities, and by moderate oxygen values below the oxygen minimum layer.

75° West Longitude; 34° to 67° South Latitudes

The 75°W sections extend from 67°S in the Bellingshausen Sea to 34°S off Valparaiso, Chile. The sections transect the western end of the Drake Passage and extend northward in the Peru Current. The temperature section (fig. 29) shows the Antarctic Convergence as a series of vertical isotherms between 59° and 60°S. The 2.5° C isotherm drops steeply from the convergence zone to 1500 m, tapers to 2000 m at 55°S, and extends northward in the Peru Current between 2100 m and 2250 m. North of 52°S the 3° and 4° isotherms remain at about 1250 m and 800 m respectively, and south of this latitude they rise to the surface in the convergence zone. The 2° isotherm outlines a long wedge of water that protrudes southward from the convergence at depths between 350 m and 750 m; it reaches just beyond 66°S before it turns northward gradually increasing in depth to about 2500 m at 55°S. In the Peru Current the 2° isotherm lies at about 2200 m. The 1.5° and 1° isotherms extend from the surface south of the convergence to depths greater than 3000 m at 59° to 62°S. A large portion of the Antarctic Circumpolar Water in this region is between 1.5° and 2.5° C.

The salinity section (fig. 30) shows the isohalines descending irregularly from near the surface at 67°S to middle depths in the Peru Current. The slopes of the isohalines are steepest under the zone of the convergence. The 34.60‰ isohaline drops from 300 m at 67°S to 2000 m at 55°S, then passes northward at about 1800 m. The large core of maximum salinity of 34.72‰ envelops two smaller cores of 34.73‰ and 34.74‰. The salinity maximum lies between 1000 m and 2500 m and is shallowest in the southern portion (62° to 65°-30′S) and deepest in the northern segment (62° to 59°S).

The density is uniformly high at depths of maximum salinity values and low temperature values (fig. 30). The isopleth of sigma-t=27.75 nearly parallels the 34.70‰ isohaline and the 2° isotherm. The distribution of oxygen (fig. 29) shows a decrease in concentration toward the north at equal depths. The oxygen minimum value at 65°S is 4.20 ml/L at 600 m and the layer of low oxygen concentration is roughly 500–1000 m. At 62°S the lowest value is 4.05 ml/L

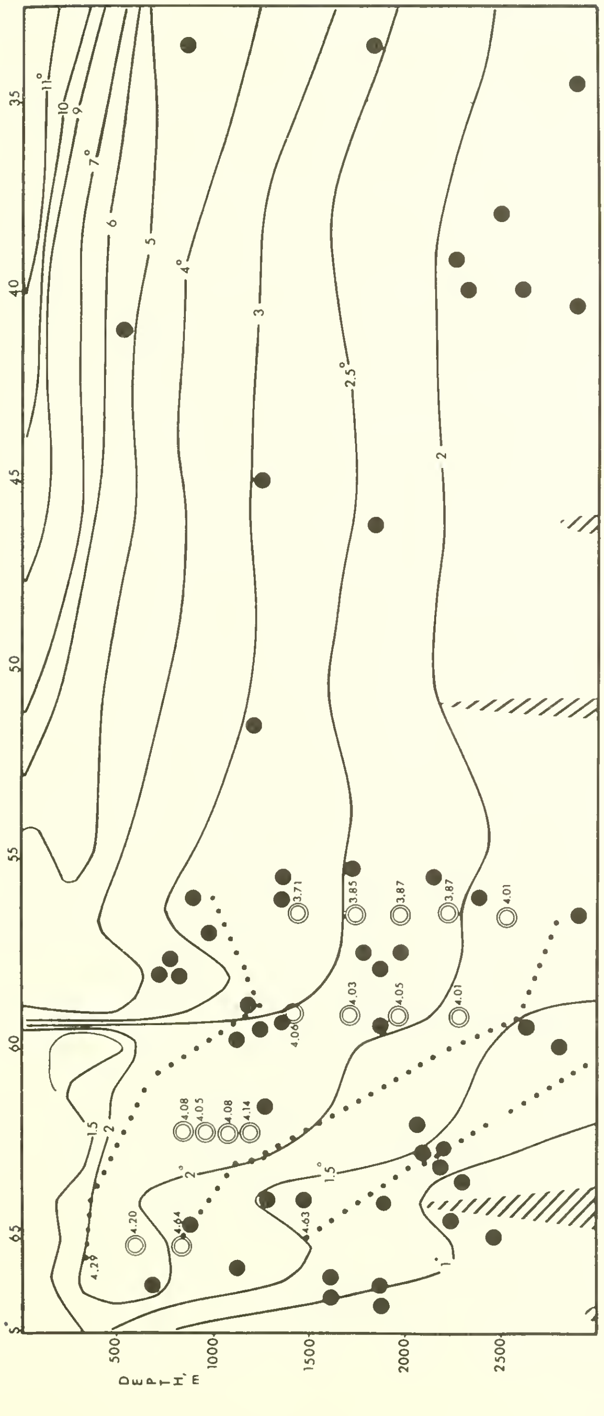


FIGURE 29.—Vertical section, 75°W, 34°–67°S; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola*.

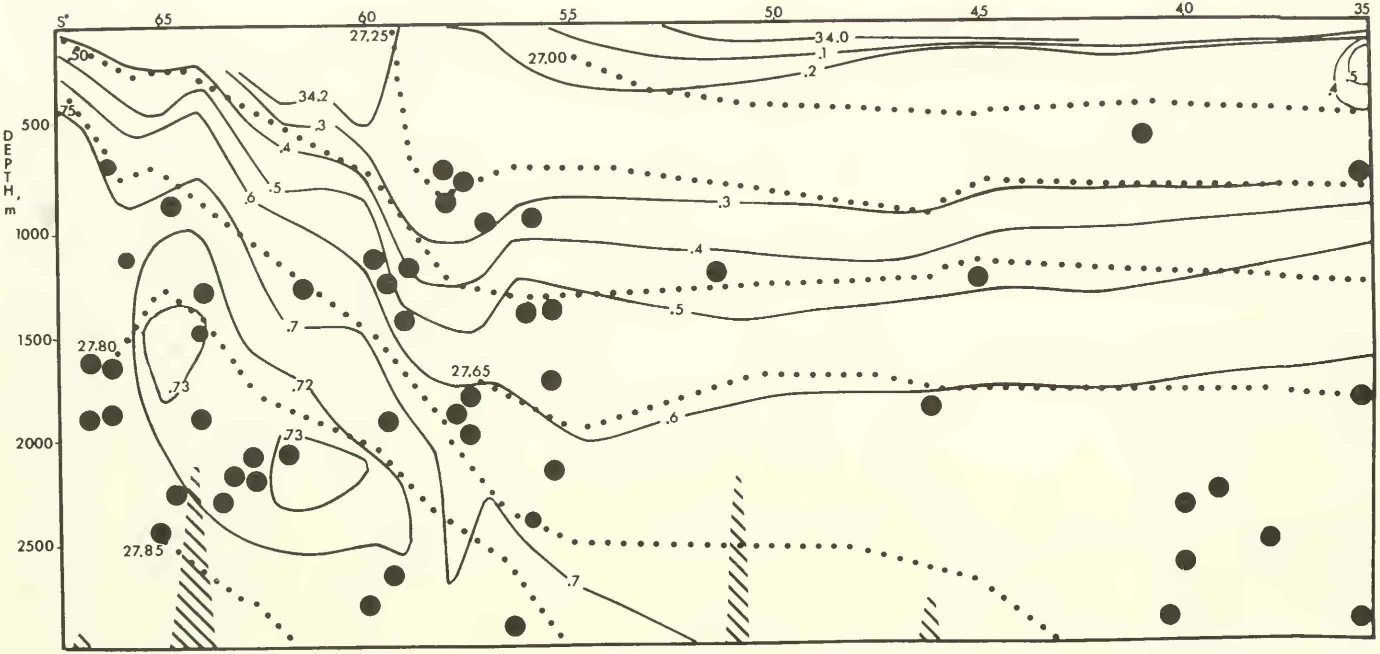


FIGURE 30.—Vertical section, 75°W, 34°–67°S; salinity°/₀₀, sigma-t. Capture points of *Bathyteuthis abyssicola.*

at 950 m and the layer of low concentration is between 750 and 1500 m. Beneath the convergence the minimum oxygen value is 4.01 ml/L at 2250 m and low concentrations extend from 1250 to 2600 m. The oxygen minimum ascends to 1450 m at 56°S where the value is 3.71 ml/L, and the layer of low concentration lies between 1250 and 2700 m.

The 51 captures plotted on the 75°W sections were taken during several *Eltanin* cruises that worked between 70° and 95°W; most captures came from between 70° and 85°W. Cruise 10 accounted for 25 of the captures and the remaining catches were divided among Cruises 4, 5, 9, 11, 13, and 15.

Twenty-nine tows that where made at depths greater than 500 m in the same region were not successful in capturing *B. abyssicola:* twenty-one of these were fished at depths between 500 and 1000 m, three were made at depths greater than 3000 m, only three were from the range of maximum abundance and two were from transitional depths. Therefore, it can be concluded that nets set to fish in the depth range between 1000 and 2500 m (maximum abundance range between about 1200 and 2250 m) will have a 90% probability of catching *B. abyssicola.*

The plots of captures in the Circumpolar Water Mass look fairly even between 700 m and 2500 m. South of 55°S a number of captures was made around the 1° and 1.5° isotherms; five captures were just below the 1° isotherm, ten captures were between the 1° and 1.5° isotherms and five captures were between the 1.5° and 2° isotherms (three were very close to the 1.5° C line). A cluster of successful captures lies at 2000–2500 m between 62° and 65°S; these seven tows took 31 specimens. The fifteen tows at temperatures below 1.5° C took 64 specimens, well above the average. Three tows are plotted below 2500 m; these possibly came from somewhat shallower depths where *B. abyssicola* is more abundant, perhaps from around 2000–2250 m.

Eleven points lie between 2° and 2.5° C. Two of the captures from shallower water above the 2.5° isotherm had simultaneous temperatures below 2.5° C; they came from longitudes where the 2.5° isotherm lies at a shallower depth than at 75°W or where the convergence is a few miles farther north. The shallowest capture in this temperature range (2°–2.5° C) was just under 700 m at 66°S where the 2° isotherm lies closer to the surface; the simultaneous temperature was 2.08° C. The catch was comprised of seven specimens 39–61 mm in ML. The three captures clustered around the 2.5° isotherm at 1100–1200 m between 59° and 60°S in the convergence zone took ten specimens—seven larvae and three juveniles.

Four captures were made between 2.5° and 3° C at 55° to 57°S; there were four juveniles and two adults (at 1400 m only). Two captures were made between 3° and 4° C with simultaneous temperatures of 3.10° and 3.88° C; they contained two larvae and one juvenile. In the subantarctic waters above the 2.5° isotherm and south of 55°S the five captures in less than 1000 m took six specimens, five of them juveniles. The one adult, however, had a simultaneous temperature of 2.2° C, while the simultaneous temperatures of its two closest neighbors were 3.10° and 3.88° C. Except for that one specimen, adults were not taken until a depth of 1400 m, and then two of the four specimens from the two tows were juveniles. Therefore, in the convergence zone the eight shallowest captures (725 m to 1250 m) were comprised of larvae and juveniles of *Bathyteuthis* with the exception of one specimen.

The capture points in the Peru Current north of 55°S are widely scattered but give useful information. The four captures taken in waters shallower than the 2.5° isotherm that lies between 1600 m and 1750 m comprised a total of 21 specimens; only three of these were as large as 21 mm in mantle length. Of these three, one was a juvenile male, one was a maturing male and one was a mature male. The remaining 18 specimens ranged from 6 to 19 mm. The tow at 1850 m at 33°S was close to the 2.5° isotherm and contained two maturing females of 28 and 29 mm, three juveniles between 13 and 18 mm, and one larva of 9 mm. The seven deeper tows, six of them below the 2° isotherm, captured many adults; of the 27 specimens 20 were maturing or ripe adults.

Water movements along the eastern boundary of the Peru Current are extremely complex and the entire region is marked by periodic upwellings. It is possible that the shallow catches in the Peru Current represent specimens that were borne upward in upwelled water masses.

Seven tows are plotted below 2500 m. The occurrence of *B. abyssicola* at these depths is uncommon, but when the proper conditions prevail it lives at those depths. All seven captures were made at temperatures between 1.4° and 1.8° C. A later section shows that *B. abyssicola* probably does not often exceed 2500 m in depth and that specimens recorded from great depths probably come from slightly shallower in the zone of abundance that ends at about 2250 m. This may apply particularly to the populations in the Antarctic where *B. abyssicola* is so abundant. At least the adults in the six deep captures between about 35° to 40°S in the Peru Current probably came from close to the depths plotted, because the temperature at those depths corresponds to the temperatures where *B. abyssicola* is most abundant in the antarctic region. Perhaps the few juveniles caught in these tows came from shallower depths because only small specimens were captured in less than 1800 m in the Peru Current.

The examination of the distribution of capture-plots with temperature reveals that the majority of captures, including the greatest number of specimens, was taken below the 2.5° isotherm. All these captures were deeper than 1000 m except for two tows in the south where the 1.5° to 2° C water rises to shallow depths. North of the convergence in water above 2.5° C eight of eleven tows contained only larvae or juveniles (26 specimens). The other three tows captured ten specimens, six of which were larvae and juveniles. No adults were taken in water warmer than 2.5° C in less than 1250 m.; the four adults occurred at 1400–1830 m.

The plot of captures on the salinity section reveals that catches were made at a variety of salinities (fig. 30). In the Antarctic Circumpolar Water Mass 21 captures were made in the layer of maximum salinity of greater than 34.70‰; nine of these were in the maximum salinity core of greater than 34.72‰. Six captures were between 34.60‰–34.70‰, and three in less than 34.30‰. In the Peru Current sector four successful tows were at salinities between 34.30‰–34.50‰. The remaining eight tows in this region were in the layer of maximum salinity, which in Pacific Deep Water has values greater than 34.60‰ but less than 34.70‰.

Distribution of the plots of captures with density in the Antarctic Circumpolar Water Mass corresponds with the maximum salinity and low temperatures. Twenty-three captures were made at sigma-t values of 27.75 to 25.85. Only six captures were at less than 27.50; these were in water less than 1000 m deep just north of the convergence where the salinities are relatively low and the temperatures relatively high. In the Peru Current the two shallowest tows were at sigma-t values of less than 27.25, the two intermediate tows were around 27.50, and the remaining tows were at high densities greater than 27.65.

The pattern of distribution in relation to oxygen concentration is difficult to assess. In the Antarctic Circumpolar Water Mass south of 55°S most of the captures are at or below the oxygen minimum layer, the values of which decrease northward; south of 60°S the simultaneous oxygen concentrations range from 4.00 ml/L to 4.90 ml/L and north of 60°S the values below the minimum range from 3.71 ml/L to 4.40 ml/L. Captures occur shallower than the oxygen minimum layer only north of 60°S where, in the convergence zone, at least, the minimum oxygen layer dips to over 2000 m. Only the few shallow captures, containing mostly juveniles and larvae, occur at concentrations greater than 5.00 ml/L. No oxygen data are available for the deeper waters of the Peru Current, but, if the oxygen distribution there is similar to that farther west in the Pacific, it is reasonable to assume that the captures below 1800 m occur in and below the oxygen minimum layer.

To summarize, the majority of captures (and the great majority of specimens) was taken in waters characterized by temperatures less than 2.5° C, salinities greater than 34.60‰ (salinity maximums), densities above sigma-t=27.65, and oxygen concentrations of 3.80 ml/L to 4.80 ml/L. The relatively few captures in waters of high temperature and low salinity contained almost exclusively larval and juvenile specimens. By far the greatest number of captures and specimens came from the deep waters (below 1000 m) of the Antarctic Circumpolar Water Mass. Just north of the Antarctic Convergence the location of captures in less than 1000 m corresponds to the Antarctic Intermediate Water Mass. The plots in the Peru Current shallower than 1250 m are also located in Antarctic Intermediate Water. All of the tows in Antarctic Intermediate Water were comprised mostly of larvae and juveniles of *B. abyssicola.* Captures deeper than 1800 m in the Peru Current were made in the Upper Pacific Deep Water Mass.

115° West Longitude; 55° to 70° South Latitudes

The sections of oceanographic parameters for 115°W transect the central region of the Pacific Antarctic Basin from 70°S to 55°S. The temperature section locates the Antarctic Convergence between 63° and 64°S (fig. 31). The southerly position of the convergence at this longitude is the result of the southward bend imparted to the Antarctic Current as it flows down the slope of the Pacific Antarctic Ridge that lies to the west.

South of 64°S the water is cold at all depths. The 2° isotherm that lies at the surface in the convergence zone (ca. 60°30′S) swings sharply northward below the surface so that between 100 m and 300 m a tongue of water less than 2° C penetrates as far as 50°30′S. From there the 2° isotherm swings southward with increasing depth and reaches its southernmost penetration in 900–1000 m at 64°S before again passing northward with gradually increasing depth. The southward tongue of the 2° isotherm is much less developed than at 75°W where it penetrates beyond 66°S at depths between 300 and 800 m. The 2.5° isotherm lies at 1350 m at 55°S and ascends to the surface in the convergence zone. The 1.5° isotherm lies at 700 m at 70°S and it descends evenly northward and lies at 2950 m at 55°S.

The isohalines that lie in less than 500 m at 70°S gradually descend and become more widely spaced in lower latitudes (fig. 32). The 34.50‰ isohaline lies at 200 m at 70°S and descends to 1200 m at 55°S.

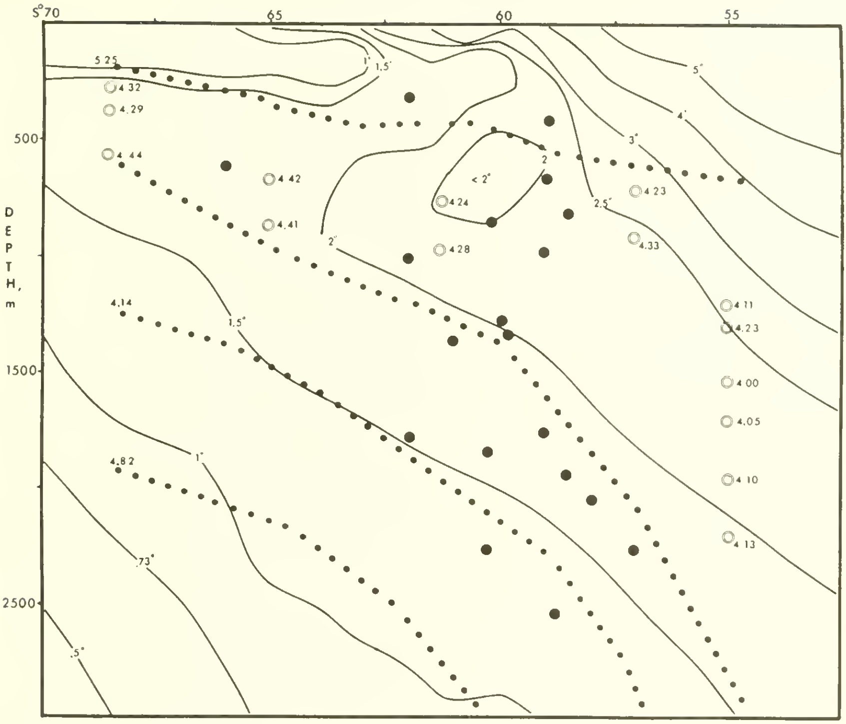


FIGURE 31.—Vertical section, 115°W, 55°–70°S; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola.*

A huge area of high salinity water, characteristic of the Antarctic Circumpolar Water Mass, lies below the 34.70‰ isohaline that transects the 115°W section from 400 m in the south to 2000 m in the north. The large diagonally oriented core of maximum salinity is outlined by the 34.73‰ isohaline that encloses two secondary cores of 34.74‰: a small, shallow core to the south and a large, deep core to the north.

The plot for density shows that the sigma-t value of 27.75 very closely parallels the 34.70‰ isohaline (fig. 32). The sigma-t=27.82 line lies about 500 m below this.

Minimum oxygen values of 4.29 ml/L occur at 400 m at 68°30′S; between 65°S and 57°S the oxygen minimum values (4.23–4.41 ml/L) occur between 900 and 700 m (fig. 31). At 55°S the oxygen minimum drops to 4.00 ml/L at 1500 m, and there is a broad layer of low oxygen values. Oxygen concentration increases gradually with depth and isopleths slope into deeper water as they pass northward.

Nineteen captures are plotted on the 115°W sections. Ten were taken during Cruise 15, six during Cruise 19, and one each from

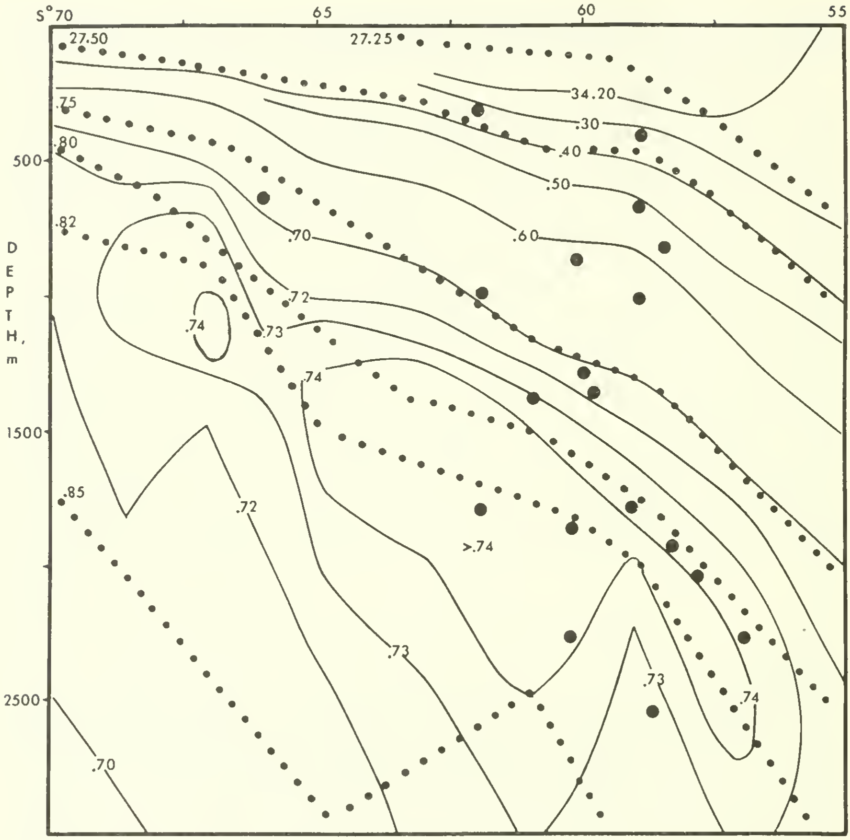


FIGURE 32.—Vertical section, 115°W, 55°–70°S; salinity°/₀₀, sigma-t. Capture points of *Bathyteuthis abyssicola.*

Cruises 11, 13, and 18. The plots range from 98°W to 120°W. In the same area only six tows were unsuccessful in the normal depth range of *B. abyssicola*: three were in less than 1000 m, two were in over 2500 m, and one was in 1600 m.

All plots on the temperature section fall within the ranges of the simultaneous temperatures. Two tows with nine specimens were taken below the 1.5° C isotherm. Ten captures were made in the 1.5° C to 2° C range. The eight deeper tows (1350–2200 m) took 56 specimens, an average of seven specimens per tow. The two shallow tows took one specimen each in 625 and 325 m. The remaining seven captures were made in water of 2° C to less than 2.5° C. The three captures from 1000–1300 m contained 16 specimens; the four tows between 425 and 875 m captured five specimens, all juveniles. The tows at 325 and 425 m represent the shallowest captures that are recorded for *B. abyssicola* in the Antarctic; each had one specimen and was in water between 1.5°–2.5° C.

Four captures on the salinity section were in salinities less than 34.60‰. Of the remaining 15 tows 13 were at or greater than 34.70‰ and 9 of these were in the layer of maximum salinity, 34.73–34.74‰. Five captures were in densities less than sigma-t=27.75; the other 14 were between 27.75 and 27.85, corresponding to the high salinity and low temperature. The two shallowest captures were in high oxygen concentrations (greater than 5.00 ml/L), while the rest were in or below the oxygen minimum layer at concentrations that ranged from 4.25 to 4.75 ml/L.

In summary, all captures of *B. abyssicola* were made in temperatures from just below 1.5° C to less than 2.5° C. Between 1000–2500 m, 13 tows captured 81 specimens in water slightly warmer than 2° C to slightly cooler than 1.5° C. Six tows shallower than 900 m captured only seven specimens in temperatures greater than 1.5° C and less than 2.5° C. Nine tows with 55 specimens were in the core of high salinity (34.73‰ and 34.74‰). Only four tows, with one specimen each, were below the 34.60‰ isohaline. Most tows and specimens were in high densities (above sigma-t=27.75) and in minimum to moderate oxygen concentrations (4.25 ml/L to 4.75 ml/L). All of the captures are within the Antarctic Circumpolar Water Mass.

130° West Longitude; 50° to 66° South Latitudes

The sections for 130°W transect the western-central Pacific-Antarctic Basin in the south and the Pacific-Antarctic Ridge in the north. The oceanographic data were collected during Austral midwinter and the Antarctic Convergence is located between 57°30′ and 58°30′S. The area is on the down-slope eastern side of the Pacific-Antarctic Ridge where the main stream of the Antarctic Circumpolar Current is deflected southward.

The temperature section reveals a relatively uncomplicated temperature structure (fig. 33). The steepest isotherm is the 2° C isotherm that ascends from 2750 m at 50°S to the surface at 59°30′S. The 2° isotherm exhibits no pronounced southward extension as it does farther east; it rises nearly vertically from 1000 m to the convergence zone at the surface. Water between 1.5° and 2° C protrudes well to the south (66°30′S) as a broad tongue between 250 and 1150 m. The 2.5° isotherm slopes from the surface in the convergence zone to 1800 m at 50°S.

The salinity section is dominated by the large segment of high-salinity water that lies below the 34.70‰ isohaline (fig. 34). This line lies at 500 m at 65°30′S and descends in a moderate slope to 1600 m at 55°S.

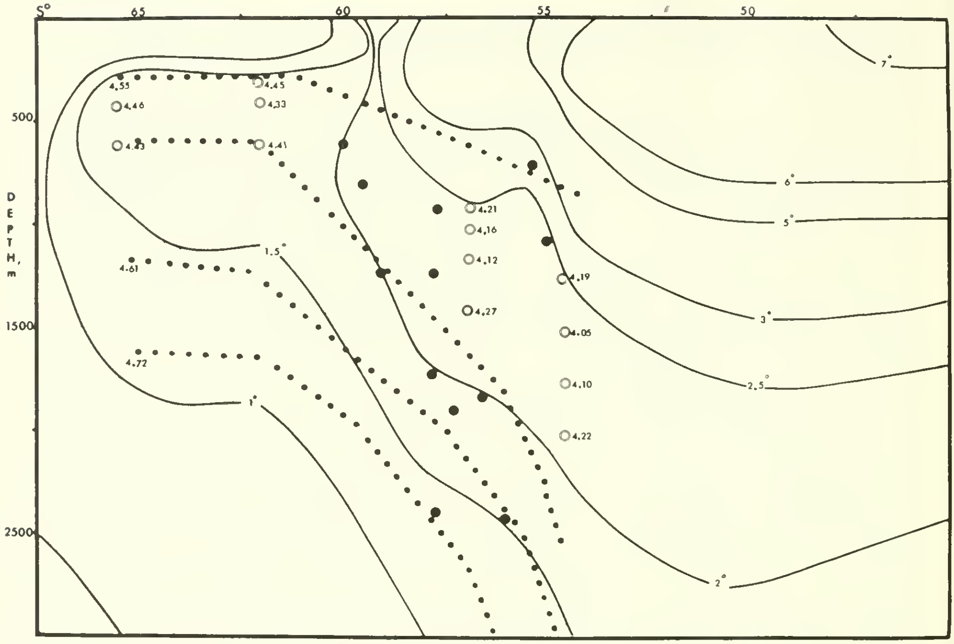


Figure 33.—Vertical section, 130°W, 50°–66°S; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola*.

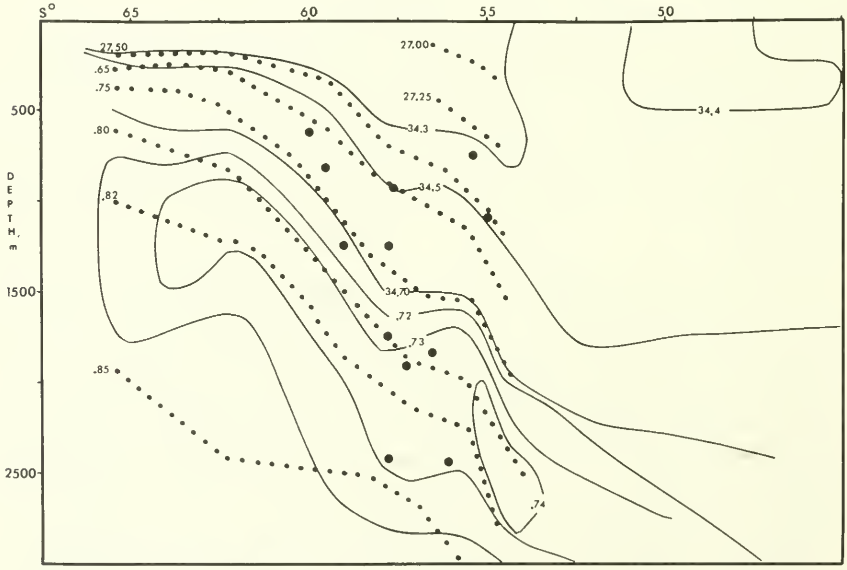


Figure 34.—Vertical section, 130°W, 50°–66°S; salinity°/oo, sigma-t. Capture points of *Bathyteuthis abyssicola*.

The thick layer of the salinity maximum, with salinities of 34.72‰ to 34.73‰, occupies the depths between 750 m and 1800 m in the south and 1600 m to 2800 m at 55°S. A tongue of 34.74‰ water protrudes from the Pacific Deep Water to the north and terminates at 55°30′S in 2000–2500 m. The lines of equal density slope to deeper water toward lower latitudes; the sigma-t=27.75 line nearly parallels the 34.70‰ isohaline. Minimum oxygen concentrations of 4.43 ml/L to 4.33 ml/L occur between 600 and 450 m between 65°30′ and 62°S. Then the oxygen minimum layer descends gradually to 1500 m at 55°S with a value of 4.05 ml/L. Isopleths of oxygen concentration also descend from south to north.

Twelve tows that were successful in catching *B. abyssicola* between 120° and 145°W are plotted on the sections. The captures were made during Cruises 13, 14, and 15. The plots on the temperature section for the most part correspond well with the simultaneous temperatures. Two deep tows (2400 m) that captured nine specimens lie at or just below the 1.5° isotherm. The three tows in 1700–1900 m at 57°–58°S occur beneath the 2° isotherm. All but one of the remaining tows lie between the 2° and 2.5° C isotherms. The temperature plots for the two tows near 35°S do not correspond with the simultaneous temperatures. The tow at 705 m had a simultaneous temperature of 2.16° C and the capture at 1080 m had a simultaneous temperature of 2.96° C. The five tows between 625 and 1080 m captured thirteen specimens; twelve of them were larvae and juveniles. The two tows at 1250 m, just above the 2° isotherm between 57°30′ and 59°S, captured 40 specimens, and the five tows below the 2° isotherm caught 28 specimens. Seven unsuccessful tows were made in the region under discussion: four between 500–600 m, two between 1000–1100 m, and one at 2300 m.

On the salinity section nine captures occur below the 34.60‰ isohaline; four of these are in the layer of maximum salinity. The shallow tow around 55°S is plotted in relatively low salinity just under 34.40‰, but its simultaneous salinity is 34.68‰. Six shallow tows are in densities below sigma-t=27.75, and the remaining six tows are above that value, five of them between 27.80–27.85. All specimens were taken at oxygen concentrations between 4.05 ml/L and 4.75 ml/L and most were between 4.20 ml/L and 4.50 ml/L. All but one were in or below the oxygen minimum layer.

In summary, only one tow was successful in water warmer than 2.5°C, and most captures were made within 0.5° C of the 2° isotherm. The shallowest tows contain primarily larval and juvenile specimens. Only two tows were in less than 34.60‰ salinity, and six tows were above 34.70‰. A range of densities is occupied by the plots, but most are above sigma-t=27.60. Most specimens were located in or below the oxygen minimum layer. Again, the captures and specimens plotted on this section are situated in the Antarctic Circumpolar Water Mass.

160° West Longitude; 48° to 65° South Latitudes

The sections along the 160° west meridian transect the Pacific Anarctic Ridge in the south and extend into the southern region of the South Pacific Basin. Between 61°30′ and 63°30′S the Pacific Antarctic Ridge rises above 3000 m and at 62°19′S it crests at 2317 m.

The temperature section shows the location of the Antarctic Convergence close to 57°S (fig. 35). The 2.5° C isotherm descends nearly vertically from the surface in the convergence zone to about 1000 m where it levels off briefly; then it slopes evenly to 1750 m at 50°S. Above the 2.5° isotherm the warmer Upper Subantarctic Water extends to the Antarctic Convergence. The 2° isotherm drops vertically from the convergence to 300 m before turning sharply southward; it envelops a great tongue of water between 2°–2.5°. At 58°S the layer enclosed by the 2° isotherm is over 1200 m thick. The 2° isotherm makes it southernmost penetration to just beyond 62°30′S between 450 and 700 m. Then it slopes into deeper water as it passes northward, and it lies at 2500 m at 50°S. Only a narrow band of water exists between the 1.5° and 2° isotherms.

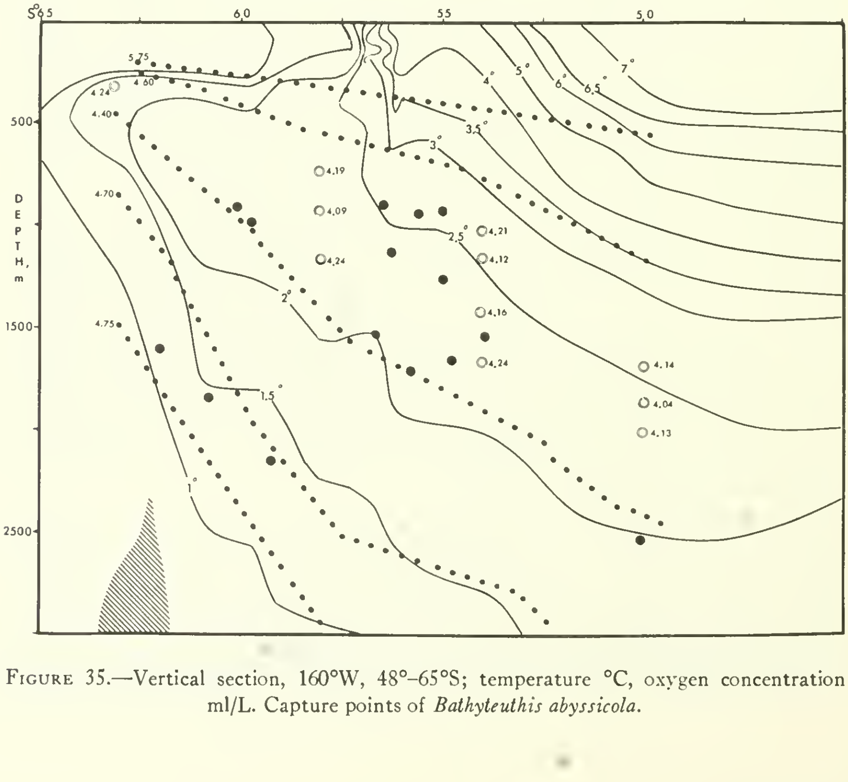


FIGURE 35.—Vertical section, 160°W, 48°–65°S; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola*.

The isohalines plotted on the salinity section slope gradually deeper as they extend northward (fig. 36). The 34.50‰ isohaline occurs at 250 m at 63°S, and it descends to 1500 m at 50°S. The 34.70‰ isohaline that lies just above the salinity maximum lies at 350 m at 63°S and drops to 2200 m at 50°S. The very large segment of the salinity maximum that is outlined by the 34.72‰ isohaline appears below 2250 m at 50°S. Long ascending tongues of high salinity water penetrate southward from the Pacific Deep Water Mass. The 34.74‰ tongue terminates at about 62°30′S in 1000 m. From 55°S to 61°S the maximum salinity layer above 34.72‰ is 1500 m thick.

The isopycnics closely parallel the isohalines; the line for sigma-t = 27.75 follows the isohalines for 34.70‰ and 34.72‰. Oxygen concentrations at a given depth decrease northward. The lines of equal oxygen slope steeply below the oxygen minimum layer. An oxygen minimum of 4.24 ml/L is located at 300 m at 63°S while the minimum value of 4.04 ml/L is in 1850 m at 50°S.

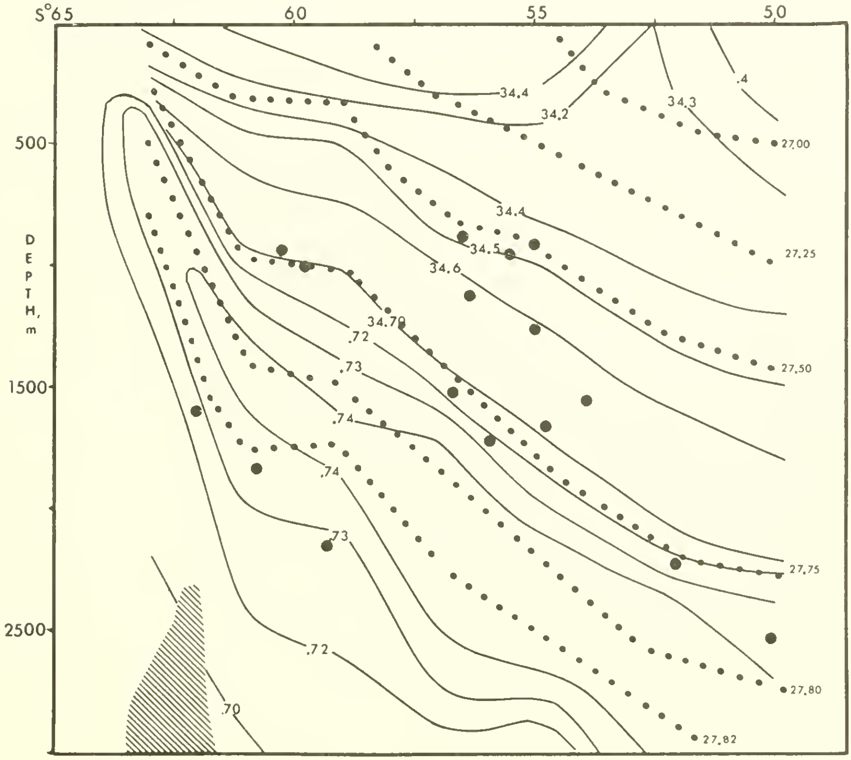


FIGURE 36.—Vertical section, 160°W, 48°–65°S; salinity°/₀₀, sigma-t. Capture points of *Bathyteuthis abyssicola.*

During *Eltanin* Cruises 14 and 15 sixteen successful captures of *B. abyssicola* were made between 145°W and 170°W. Three captures were made in the 1° to 1.5° C band at depths from 1600 m to 2150 m at 59° to 62°S. Three successful captures were made in the 1.5°–2° C water: one with two juvenile specimens at 60°S in 900 m; one with one specimen (not plotted) had a simutaneous temperature of 1.66° C and was taken in 1550 m at about 57°S; and one with a single specimen from 2525 m at 50°S. Seven captures are plotted in the 2° to 2.5° C segment, but the capture from 900 m at 56°30′S had a simultaneous temperature of 2.27° C. The two remaining capture plots are around 925 m at about 55°S. Both tows were made at 150°W and had simultaneous temperatures of 2.26°–2.28° C. Evidently the 2.5° isotherm is a few hundred meters shallower 10° of longitude to the east of the section. So, actually no specimens were taken in temperatures greater than 2.5° C.

Ten unsuccessful tows were made in the region included in the 160°W section. Seven fished at less than 1000 m, and one each at 1700 m, 1950 m, and 2700 m.

Of the sixteen captures plotted on the salinity section, nine are at salinities greater than 34.70‰ and seven are from just below 34.50‰ to over 34.60‰. A gap appears to be present in the layer of maximum salinity, but in fact, across the whole region, only one tow (unsuccessful) was made to the depths of the salinity maximum. Therefore, it is a false gap.

All captures are at densities greater than sigma-t=27.50. The tows were all taken in oxygen concentrations ranging from about 4.10 ml/L to 4.70 ml/L, but most were associated with the lower end of the range, below 4.40 ml/L at or below the oxygen minimum layer.

In summary, all captures of *B. abyssicola* were made in a 1° C temperature range from just below 1.5° to just below 2.5° C; all captures were at densities greater than sigma-t=27.50, mostly 27.50–27.75; most tows were in salinities higher than 34.60‰; most captures were from the zone of low or minimum oxygen concentration.

60° South Latitude; 20° to 160° West Longitudes

The vertical sections along 60°S latitude reveals some interesting features of Antarctic oceanography. The eastern portion of the temperature section is characterized by the extremely low temperatures that reflect the influence of the frigid Weddell Sea (fig. 37). The temperature at all depths is less than 1° C, and mostly lower than 0.5° C; below about 2000 m and above 250 m the temperature is less than 0° C. At 50°W a steep vertical isothermal pattern marks the western limit of the influence of the Weddell Sea, and the entire structure of the temperature regime is altered. Temperature increases rapidly from

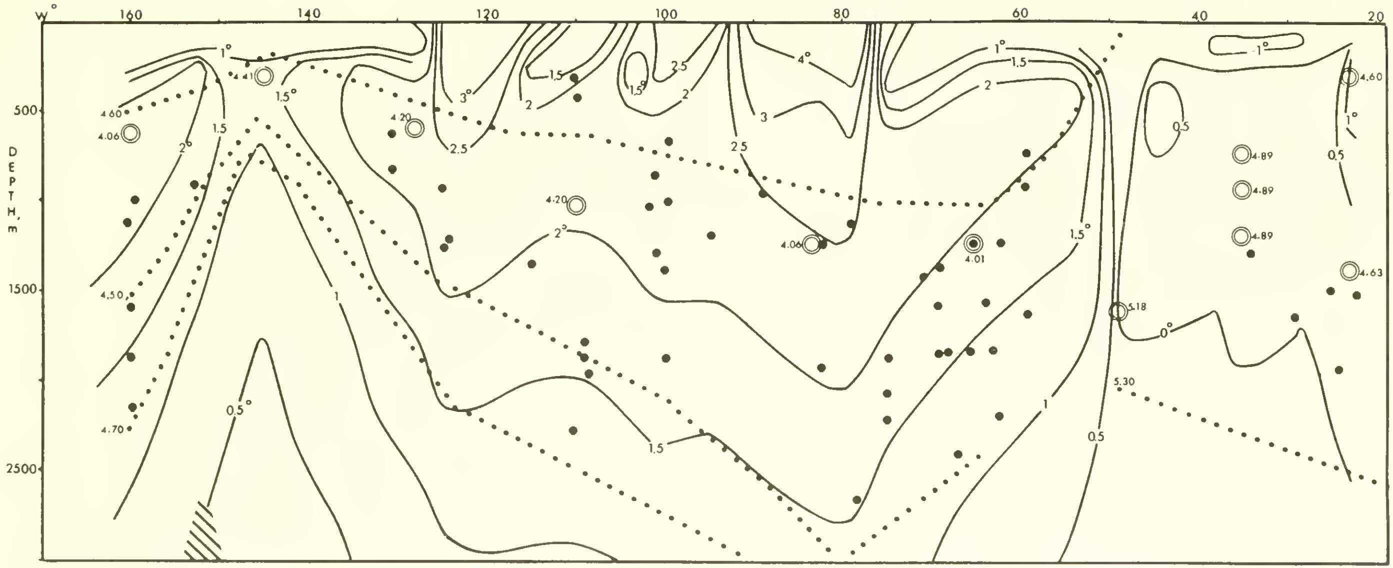


FIGURE 37.—Vertical section, 60°S, 20°–160°W; temperature °C, oxygen concentration ml/L. Capture points of *Bathyteuthis abyssicola*.

0° to 1.5° C in depths less than 2000 m within a few degrees of longitude.

In surface waters the temperature remains below 1° C as far as 72° W. Between 72°W and 75°W there is a rapid increase in surface temperature to 4° C that marks the location of the Antarctic Convergence as it passes north of 60°S just before entering the Drake Passage. The 1.5° isotherm descends from the surface at 74°W to about 500 m, then it rises somewhat and extends eastward at 200 m to 52°W. The 0.5° and 1.0° isotherms descend below 3000 m between 50°W and 60°W. The 1.5° isotherm ascends very gradually west of 79°W but remains below 2000 m until 125°W where it begins a steep ascent toward the surface; at 143°W the 1.5° isotherm is located in 350–400 m, but it swings sharply to the east under a layer of cold surface water and does not reach the surface until 127°W. The 2.0° isotherm nearly parallels the 1.5° isotherm 400–700 m above it. The upper waters (500–700 m) between 75°W and 125°W are characterized by four cores that represent northward tongues of cold water or southward tongues of warm water that meander across the 60°S latitude. The largest tongue lies between 75° and 92°W where the 2.5° isotherm dips briefly to 1300 m. The Antarctic Convergence is again seen between 125° and 128°W where it passes southward across 60°S latitude after flowing off the Pacific-Antarctic Ridge to the west. A wedge of very cold water extends northward west of the convergence. The narrowest part of this cold water lies between 142° and 150°W at 300–500 m where the warmest water is located between the 1° isotherms that lie at 200 m and between 700–1000 m. The peak of cold water spreads out with depth so that temperatures less than 1° C are found at 2500 m between 128° and 160°W; the 0.5° isotherm rises to a peak at 1750 m at 145°W. This mass of cold water has its origin in the Ross Sea, and it serves as a cold wedge that slices across the Circumpolar Water Mass. Warmer water (1.5°–2° C) is encountered again to the west of 150° W.

The distribution of salinity along 60°S also demonstrates the meridional displacement of water (fig. 38). Low salinity water of less than 34.70‰ from the Weddell Sea occupies the entire portion of the section between 20° and 50°W. The 34.70‰ isohaline rises vertically from 3000 m to 700 m at 51°W; westward it descends to 2150 m beneath the convergence zone at 79°W. It slopes gradually shallower in a series of humps farther to the west until it reaches 250 m between 140° and 150° W beyond which the 34.70‰ isohaline slopes into deeper water. Sections of the salinity maximum lie below 1250 m between 65° and 130°W. The wedge of lower salinity water from the Ross Sea forces the maximum salinity layer into the upper water level between 350 m and 750 m at 138°W to 150°W.

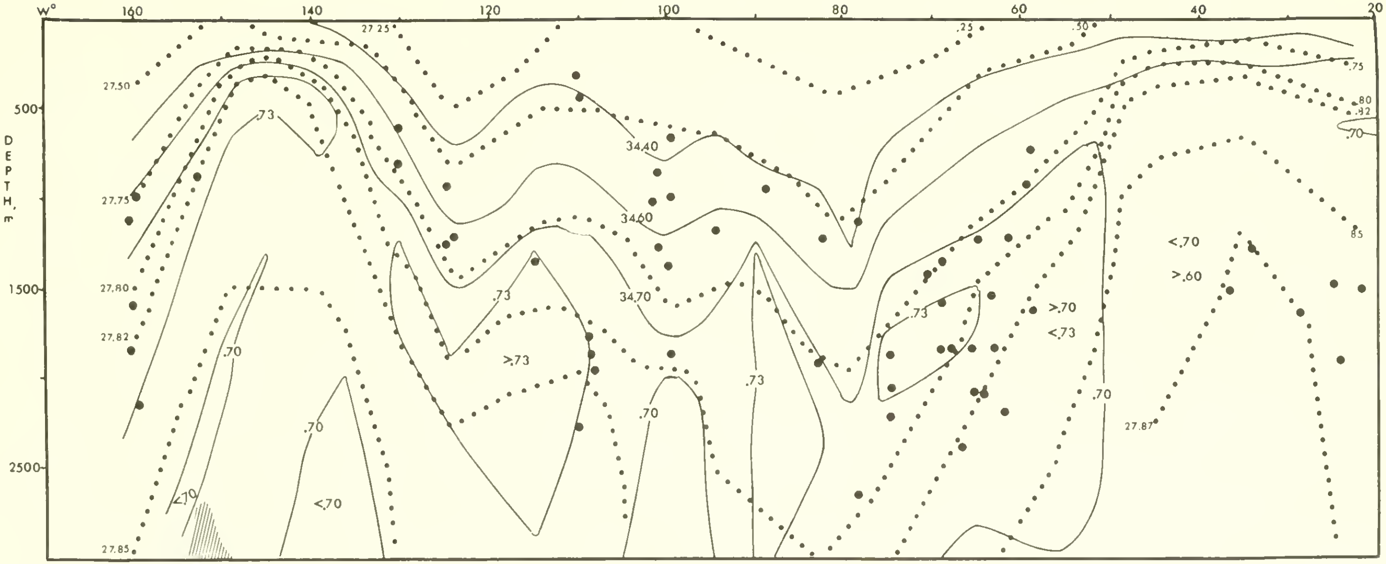


Figure 38.—Vertical section, 60°S, 20°–160°W; salinity°/oo, sigma-t. Capture points of *Bathyteuthis abyssicola*.

The isopycnic distributions closely parallel the isohalines on the section (fig. 38). The sigma-t value of 27.75 nearly parallels the 34.70‰ isohaline from 50° to 160°W. Water of high density from the Ross and Weddell Seas is evident in the western and eastern regions of the section. The oxygen content of waters between 20°W and 50°W is very high with minimum values ranging from 4.63 ml/L to 5.18 ml/L (fig. 37). The oxygen minimum layer lies between 1000 and 1600 m; a shallow layer of minimum oxygen concentration in this area is located at 200–250 m. At 65°W the oxygen minimum of 4.01 ml/L is at 1250 m; westward the oxygen minimum values gradually increase and the depths at which they are found decrease until at 145°W the minimum of 4.4 ml/L is located at 300 m. By 160°W the oxygen values are again low, about 4.06 ml/L at 650 m. The same value at 65°W lies at 1600 m. Isopleths of oxygen concentrations ascend to shallow depths in the areas influenced by the outflow of the Weddell and Ross Seas.

The vertical sections along 60°S complement the meridional sections and give a broad picture of oceanographic features. The captures that have been plotted on the 60°S sections come from that latitude and from latitudes 2° to 3° north and south if a similar arrangement of isotherms exists at the proper depths. For example, if a capture were made at 57°S 100°W in 2000 m between the 1.5° and 2° C isotherms it would be plotted because the same conditions exist on the 60°S section. The points of capture on the temperature section are concentrated between the 1.5° and 2.5° isotherms. All points at less than 1000 m represent juvenile or larval specimens. The shallowest points at 110°W remain in a cold water tongue that passes northward between two cores of warmer water. In relation with salinity the points of captures are generally associated with the layer of high salinity above 34.70‰; all except a few shallow specimens occur in salinities greater than 34.60‰. Distribution of captures with density follow sigma-t values greater than 27.50, mostly 27.75 to 27.82. The plots of captures generally follow the oxygen minimum layer or deeper; only a few specimens are above the zone of minimum oxygen.

Summary of Distribution With Oceanographic Parameters

Since captures from areas as broad as 25° of longitude are plotted on each vertical section and since there is appreciable variation in the distribution of oceanographic parameters with locality, it is necessary to bring together the data presented in the vertical sections. The information is summarized using the simultaneous or in situ oceanographic data taken at the oceanographic station closest in time and space to each biological station.

Figures 39 to 42 present the frequencies of occurrences of *B. abyssicola* at in situ values of oceanographic parameters. Table VIII gives the numbers and percents of captures and individuals taken at simultaneous oceanographic values.

Figure 39 is a histogram of the frequency of occurrence of captures and individuals at 0.5° C increments. A gradually increasing number of tows caught a greatly increasing number of specimens as the temperatures increase from 0° to 2.5° C. A sudden drop-off in numbers occurs in waters warmer than 2.5°. Of the successful tows 28% captured 37% of the total number of individuals at temperatures between 2.0° and 2.49° C (Table VIII). Another 28% of the tows caught 32% of the population between 1.50° and 1.99° C. Therefore, in the 1° range between 1.5° and 2.49° C, 56% of the captures accounted for 69% of the individuals. Between 1.0° and 2.49° C, 85% of the population was captured by 75% of the tows.

The histogram for salinity shows a very low number of catches and individuals below 34.60‰ (fig. 40). The 34.60–34.69‰ and the 34.70–34.79‰ columns have been subdivided for a more detailed breakdown of salinity frequencies. The first of these columns represents 34% of the population with 28% of the tows and the second 52% of the population in 55% of the tows. Of the captured population 82% of the individuals came from salinities between 34.64 and 34.75‰ and 52% from 34.70 and 34.75‰. The sudden drop-off above 34.75‰ is not due to exclusion of *B. abyssicola* from higher salinity waters; the salinity at the depths where this species occurs in the Antarctic very seldom, if

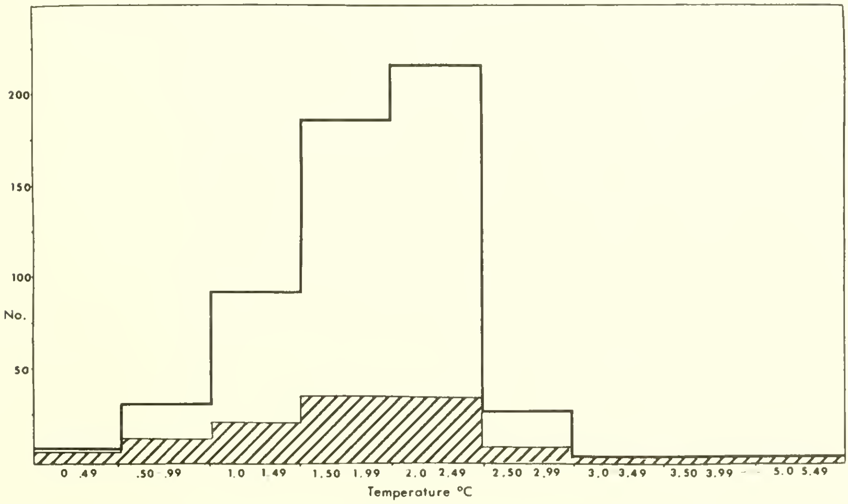


FIGURE 39.—Frequency of captures and individuals of *Bathyteuthis abyssicola* at temperature increments in the Antarctic Ocean. Hatched area is number of captures (n = 136); clear area is number of individuals (n = 591).

ever, exceeds 34.75‰. Therefore, the Antarctic population of *B. abyssicola* occurs very prominently in the layer of maximum salinity.

The greatest frequency of tows and individuals occurs on the density histogram between sigma-t=27.70 and 27.85 (fig. 41). Forty-two percent of the individuals, taken by 43% of the tows, occupy 27.80 to 27.85 and 29%, from 18% of the tows, occupy 27.70 to 27.74. Eighty-three percent of the individuals were captured in high densities greater than sigma-t=27.70.

The histogram for oxygen (O_2) concentration shows two peaks of abundance (fig. 42). The first peak occurs at the 4.00–4.14 ml/L increment where 14% of the total captures accounted for 24% of the specimens. The second peak lies at the two increments between 4.45 ml/L

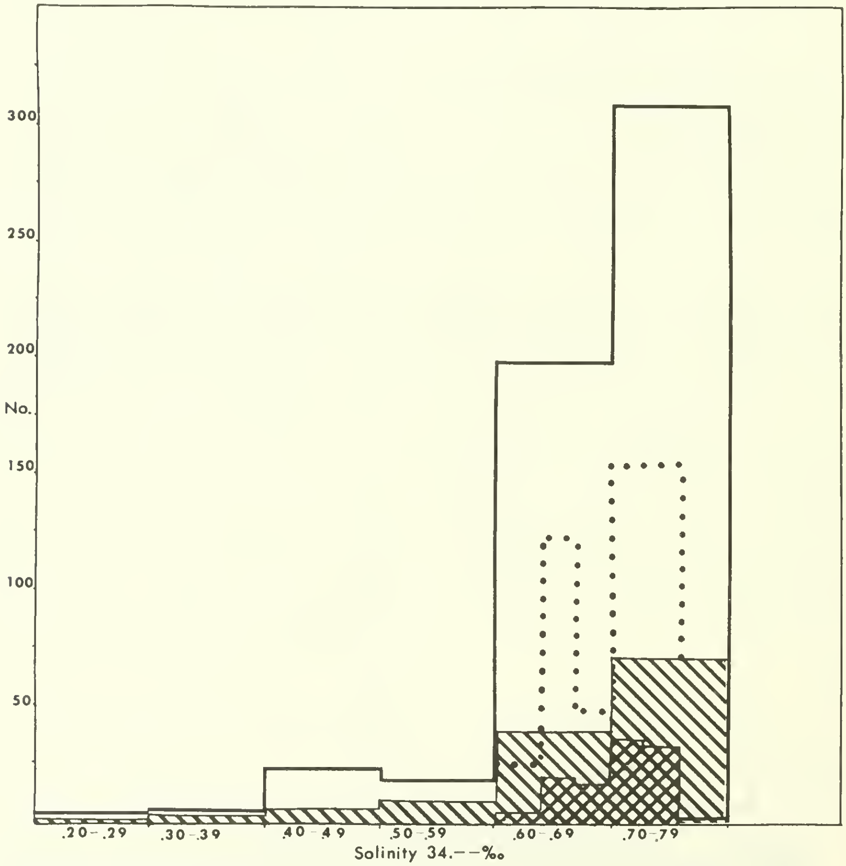


FIGURE 40.—Frequency of captures and individuals of *Bathyteuthis abyssicola* at salinity increments in the Antarctic Ocean. Hatched area is number of captures (n=136); clear area is number of individuals (n=591); crosshatch and dots are breakdown of captures and individuals by .03°/oo.

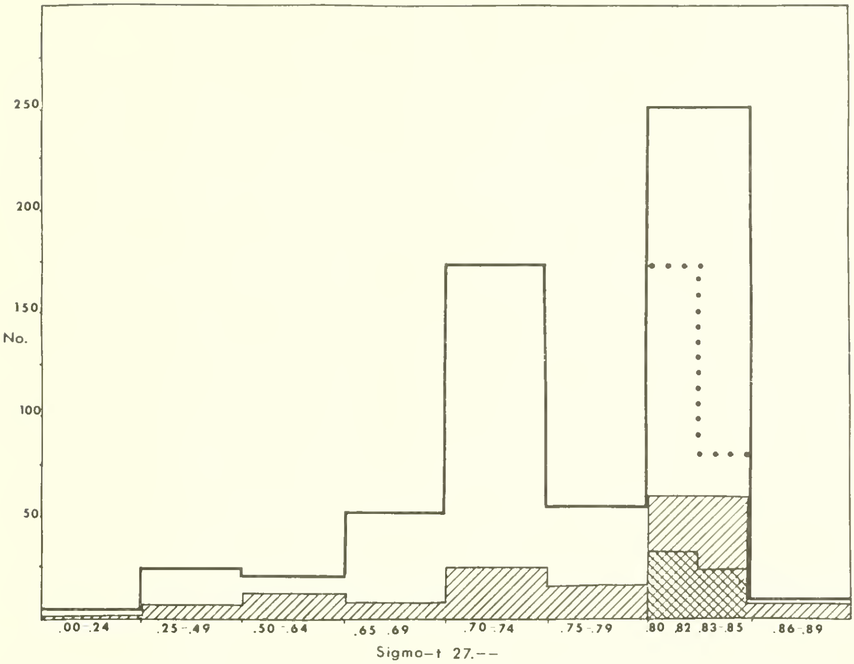


FIGURE 41.—Frequency of captures and individuals of *Bathyteuthis abyssicola* at density increments in the Antarctic Ocean. Hatched area is number of captures (n=136); clear area is number of individuals (n=591); crosshatch and dots are breakdown of captures and individuals by .02 units.

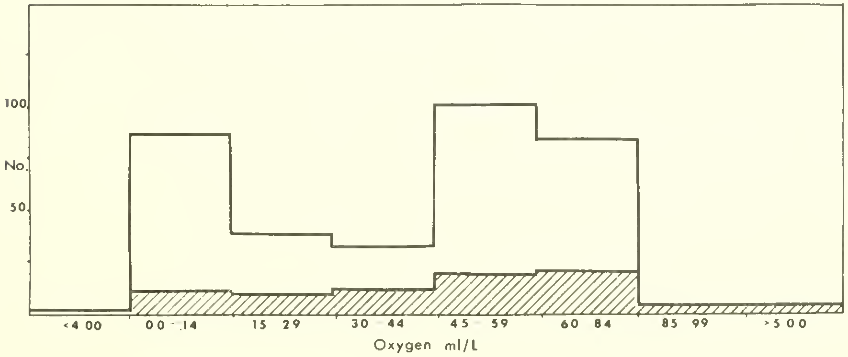


FIGURE 42.—Frequency of captures and individuals of *Bathyteuthis abyssicola* at oxygen concentrations in the Antarctic Ocean. Hatched area is number of captures (n=88); clear area is number of individuals (n=360).

TABLE VIII.—*Occurrence of* B. abyssicola *at simultaneous temperature, salinity, density, and oxygen values in the Antarctic Ocean. For temperature, salinity, and density there are 136 captures and 591 individuals; for oxygen there are 88 captures and 360 individuals*

Temperature, ° C	0°–.49°	.50°–.99°	1.0°–1.49°	[1.50°–1.99°	2.0°–2.49°]	2.50°–2.99°	3.0°–3.49°	3.50°–3.99°	4.0°–5.00°
Number of captures	7	15	24	38	9	2	2	1	1
% of total captures	5.2	11	17.6	28	6.6	1.5	1.5	.8	.8
				35					
Number of individuals	9	33	95	188	217	29	2	2	3
% of total individuals	1.5	5.6	16	32	37	4.9	.3	.3	.5
				69					

Salinity, 34.xx°/₀₀	.20–.29	.30–.39	.40–.49	.50–.59	.60–.63	.64–.66	.67–.69	[.70–.72	.73–.75]	>.75
Number of captures	2	4	6	9	3	18	17	38	36	1
% of total captures	1.5	3	4.4	6.6	2.3	13	13	28	27	.8
								55		
Number of individuals	5	5	23	18	25	122	49	153	153	1
% of total individuals	1	1	4	3	4.2	21	8.4	26	26	.2
								52		

Density, sigma-t=27.xx	.00–.24	.25–.49	.50–.64	.65–.69	[.70–.74	.75–.79	.80–.82	.83–.85]	>.85
Number of captures	2	7	12	7	25	16	33	26	8
% of total captures	1.5	5.2	9	5.2	18	12	24	19	6
Number of individuals	5	25	21	52	173	55	171	79	10
% of total individuals	.9	4.2	3.6	8.8	29	9.3	29	13	1.7
					80				

Oxygen, 4.xx ml/L	4.00	.00–.14	.15–.29	.30–.44	[.45–.59	.60–.84]	.85–.99	>5.00
Number of captures	1	12	11	13	20	21	5	5
% of total captures	1.1	14	13	15	23	24	5.7	5.7
Number of individuals	1	88	40	34	102	85	5	5
% of total individuals	3	24	11	9.7	28	24	1.4	1.4
					52			

and 4.84 ml/L. In the 4.45–4.59 ml/L group 23% of the tows took 28% of the specimens while in the 4.60–4.84 ml/L group 24% of the tows captured 24% of the individuals. A sudden drop-off occurs at concentrations higher than 4.85 ml/L; in the two increments 11.4% of the total successful tows took only 2.8% of the specimens. Tows that were taken at these concentrations were either in very shallow or very deep water, above and below the range of abundance of *B. abyssicola.* The peaks reflect in part, at least, the geographic positions of the captures. The high O_2 concentrations (above 4.70 ml/L) tend to come from the Atlantic sector; middle values generally come from the eastern Pacific, Drake Passage, and Peru Current region; captures at low concentrations come mostly from west of 120°W. Of course, values through the whole range of concentrations may be found in nearly every area, but they may not be at optimum depths or temperatures for *B. abyssicola.* The species is distributed primarily in low to medium O_2 concentrations (4.00 to 4.85 ml/L) in or below the O_2 minimum layer in the Antarctic, but O_2 content is not the primary factor in governing the distribution of *B. abyssicola*, because, where other factors are favorable (e.g., temperature, depth, salinity), specimens have been taken in very high or very low O_2 concentrations. This is especially true in the Atlantic sector of the Antarctic where the O_2 concentration is high at all depths. In other sectors of the Antarctic the very high O_2 concentrations are encountered only at relatively shallow depths; *B. abyssicola* has been taken occasionally at these depths where it is out of its normal temperature range as well.

The capture-plots on the vertical sections and the frequency distributions of oceanographic parameters together delineate the physicochemical conditions under which *Bathyteuthis abyssicola* exists in the Antarctic Ocean.

Geographic Distribution in Relation to Water Masses

An understanding of the three-dimensional distribution of pelagic marine organisms requires the correlation of both horizontal plots of geographic range and vertical plots of relationships of bathymetric range with water masses. Ebeling (1962) has summarized previous works that attempted to delimit animal distributions by the physicochemical and biological parameters of the environment.

Very little has been done with the distributions of cephalopods, particularly the oceanic forms. Bruun (1943) presented the geographical and vertical distribution of *Spirula spirula* but made no attempt to correlate distribution with parameters of water masses. In a later work based on *Galathea* material, Bruun (1955) reevaluated his previous decisions about the vertical range of *S. spirula;* he concluded that the lower limit of distribution of this species is governed by the 10° isotherm that generally lies at 400 m (more or less) over the geographic range of *Spirula*. Bruun's earlier work had set the depth limit of *Spirula* at 1750 m. Thore (1949) examined the distributions of the *Dana* pelagic octopods, particularly of *Japetella diaphana*. The vertical distributions were determined principally by Bruun's method of statistical analysis of depths of captures; the distribution of *J. diapuana* was defined by parameters of temperature, salinity, and productivity. Pickford (1946) was the first to study the distribution of a marine animal in relation to the T-S characteristics of water masses; she plotted the distribution of *Vampyroteuthis infernalis* on T-S diagrams and determined that density is the common factor governing the distribution of this species.

Most workers (e.g., Haffner, 1952; Bieri, 1959) have plotted only the points of capture on T-S diagrams, but Sund (1961, 1964), Ebeling (1962), and Ebeling and Weed (1963) have constructed T-S curves for each capture (over the determined vertical range of each species) and have plotted these in the water mass envelopes. This method more precisely defines the water column and the water mass in which the species were captured. Backus, Mead, Haedrich, and Ebeling (1965), using a different approach, have presented a statistical method of determining faunal boundaries between or within water masses.

A large amount of material from a number of locations plus concurrent oceanographic and capture data are needed to determine properly the distribution of a species in relation to the physicochemical parameters of its environment. These requirements are easily met for *Bathyteuthis abyssicola* from the Antarctic Ocean, but for this species from the Atlantic and eastern Pacific and for *B. bacidifera* the data are less complete. Nevertheless, it is possible to make some fairly definitive statements concerning the distribution of *Bathyteuthis*.

Antarctic Ocean

Figure 43 is the T-S capture diagram for specimens taken by the *Eltanin* in Antarctic waters. Capture points rather than capture curves are used because of the uniform nature of the water masses in the Antarctic region. The vertical component of the plot represents Antarctic Circumpolar Water of high salinity and low temperature and Lower Deep Water of the same characteristics and at greater depths. Most of the points plotted below 1°C are from the Atlantic sector of the Antarctic Circumpolar Water Mass while the points above 1°C are from the Pacific sector and the Drake Passage. Five of the deepest captures from the Peru Current, representing Deep Water, are also included in the vertical component of the plot. The area where

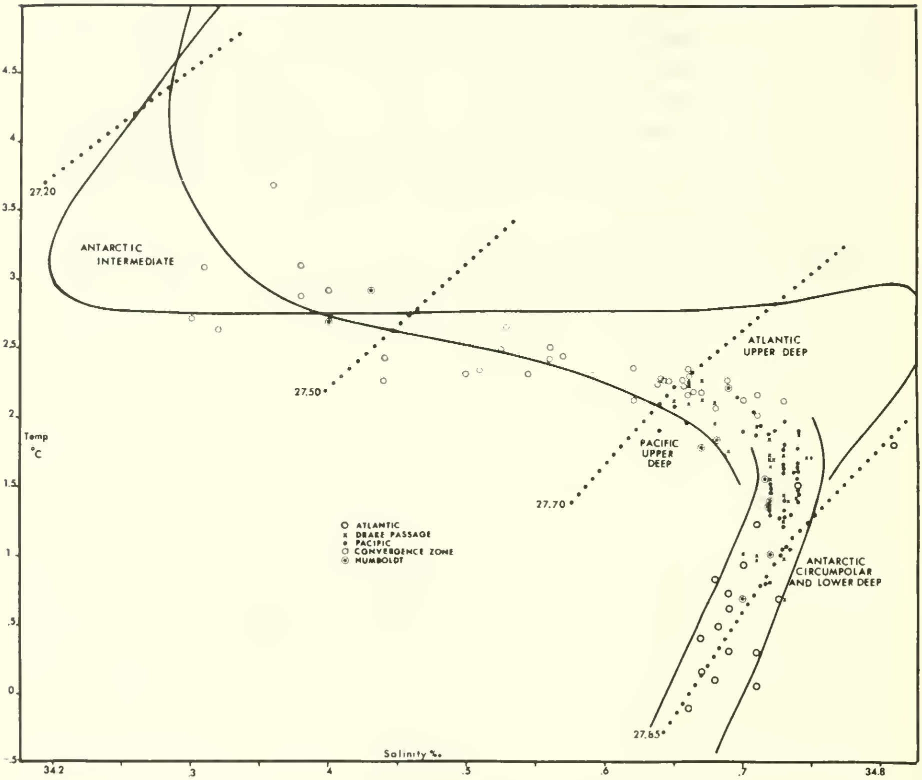


FIGURE 43.—T-S capture diagram of *Bathyteuthis abyssicola* in the Antarctic Ocean. See text for details.

the plot bends sharply toward lower salinity (below 34.70‰) is classified as Upper Deep Water (Sverdrup et al., 1942), but the points actually represent captures made in the waters underlying the Antarctic Convergence zone; the water in this section of the plot is considered to be constituted primarily of Circumpolar Water in transition with the Deep Water that underlies the Subantarctic Upper Water. The three captures from the Peru Current represent Pacific Upper Deep Water, and the single capture at a very high salinity (34.80‰) corresponds to the Atlantic Upper Deep Water. Water between salinities of about 34.60‰–34.40‰ comes from below the convergence zone (at the surface) and represents the mixture of water masses that occurs in this transitional region. The plots at the lower salinities and higher temperatures lie in the Antarctic Intermediate Water. The great majority of captures and specimens comes from Circumpolar Water of maximum salinity and relatively high temperatures (1.25°–2°C) and from Circumpolar-Transitional water at lower salinity (around 34.65‰) and slightly higher temperature (2°–2.35°C).

Although there are some areas in the Antarctic waters studied to date where *B. abyssicola* is more abundant than in other areas, it is reasonable to assert that this species is circumpolar in distribution; when the remaining portion of the Antarctic Ocean is explored (the eastern half), probably no signficant changes will be required in the distributional pattern as it is now understood.

The easternmost record of *B. abyssicola* in Antarctic waters is Hoyle's type specimen from 46°16′S 48°27′E between Prince Edward and the Crozet Islands. No further captures are recorded across the Indian or southwestern Pacific-Antarctic Waters until the area of operation of the *Eltanin* southeast of New Zealand. The southernmost location for *B. abyssicola* is recorded by Hoyle (1912) at 71°22′S 18°15′W off Coates Land. *Eltanin* specimens were taken a little beyond 66°S in the Bellingshausen Sea during Cruise 13. Future cruises of *Eltanin* into higher latitudes should disclose the southern limit of distribution of *Bathyteuthis abyssicola*. The limit will correspond, in part, to water that shoals above 1500–2000 m. Presumably this species inhabits the bathypelagic zone of the entire circumpolar ocean.

Eastern Pacific Ocean

The T-S capture diagram (fig. 44) for *Bathyteuthis* in the eastern Pacific Ocean along South and Central America reveals that the genus occurs in two distinct water masses. Captures of *B. abyssicola* that were made in the Peru Current between about 33° and 51°S fall along the T-S values of Antarctic Intermediate Water; the points at the greater depths (2000–3000 m) overlap with Pacific Upper Deep Water. The locations of captures of *B. bacidifera* and *B. abyssicola* in the eastern tropical Pacific are plotted in figure 45 where they lie in the Pacific Equatorial Water Mass. This relatively warm, saline water mass attains its characteristics by in situ advective mixing. In the area of the captures off Central America the thermocline is shallow and a pod of nutrient-rich deep water ascends to the euphotic zone and is responsible for the region's high productivity. The T-S capture plots for both species are clustered in the 700–1750 m section of the Pacific Equatorial Water Mass envelope where the temperature ranges from 3°–6° C and the salinity ranges from 34.55–34.65‰. Records from the literature include Hoyle's (1904) in the Bay of Panama and Robson's (1948) around Cocos and Galapagos Islands.

The *Dana* and *Eltanin* specimens and Robson's (1948) records are plotted on the vertical sections of hydrographic parameters (figs. 46–49). One of Robson's specimens, a larva, was taken at 550 m where

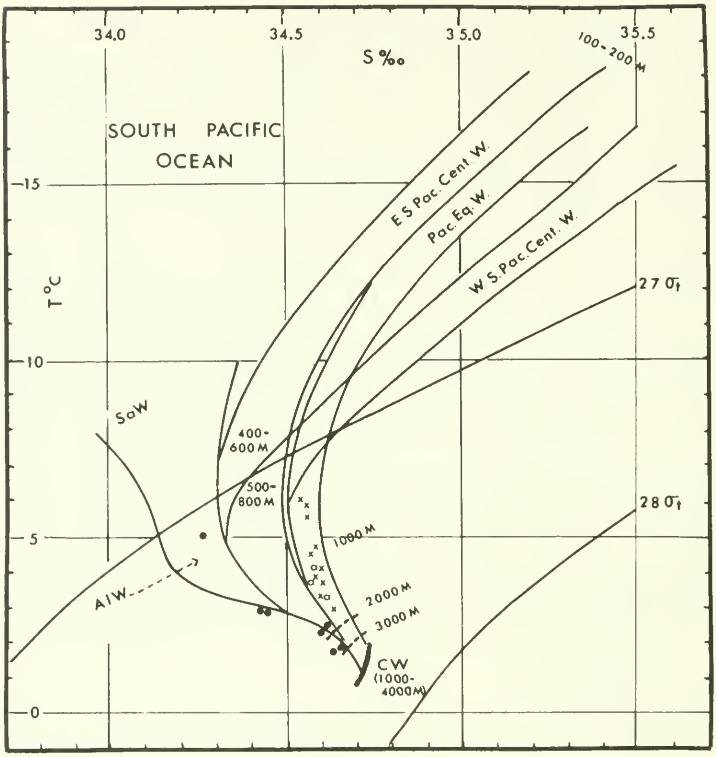


Figure 44.—T-S capture diagram of *Bathyteuthis* in the eastern South Pacific Ocean. In Pacific Equatorial Water *Bathyteuthis bacidifera* is marked by "x" and *B. abyssicola* by "a"; *B. abyssicola* in Intermediate Water is marked by a dot.

the temperature is generally between 7° and 8° C; four captures, including the holotype of *B. bacidifera*, were made at 700–750 m close to the 6° isotherm. All remaining captures were made in water colder than 5° C, the majority between 4° to 5° C (fig. 46). Vertical sections from the type locality of *B. bacidifera* are plotted in figure 49. Oxygen concentrations in the eastern tropical Pacific are very low with minimum values of less than 0.5 ml/L occurring in the upper layers. The plot of captures against oxygen concentration (fig. 47) shows that the two species occur below the minimum concentrations that range from about 0.5 ml/L to 2.0 ml/L. The effect of these low concentrations is discussed elsewhere. The distribution of the two species of *Bathyteuthis* in relation to phosphate concentration coincides with the region of PO_4 maximum (fig. 48). The plots all occur at concentrations greater than 2.75 microgram atoms/liter. Phosphates are quickly diminished in the upper waters where high productivity takes place.

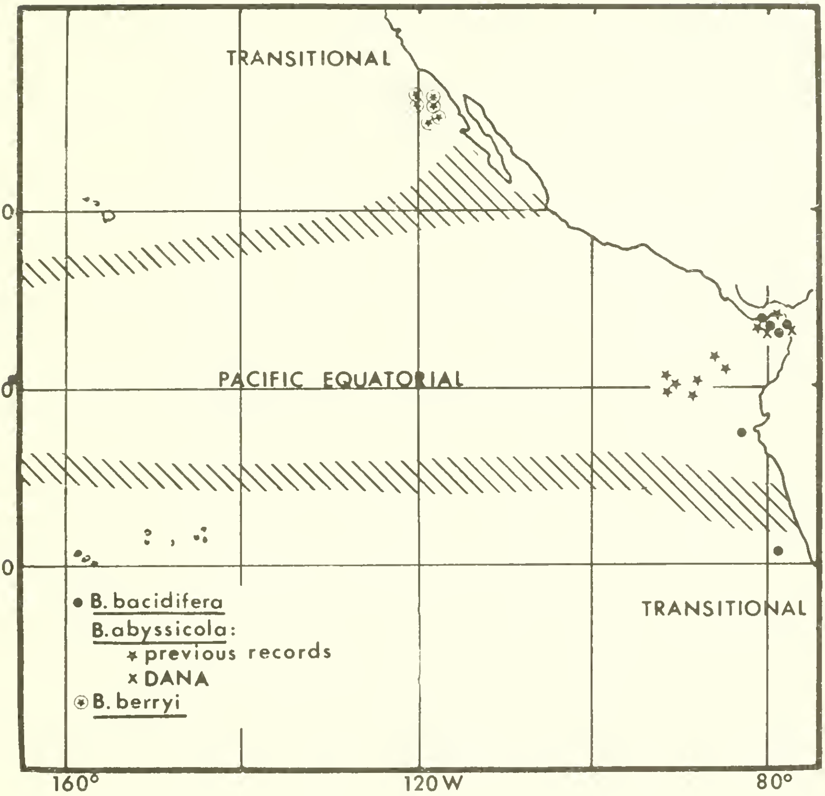


Figure 45.—Distribution of *Bathyteuthis abyssicola*, *B. bacidifera*, and *B. berryi* in the tropical eastern Pacific Ocean.

Although presently there are no specimens to substantiate it, both species of *Bathyteuthis* may be expected to range farther westward in the Pacific Equatorial Water Mass borne by the deeper components of the North and South Equatorial Currents.

Bathyteuthis is presently unknown throughout the remainder of the vast Pacific waters. Whether species will be found to inhabit the various Pacific water masses is difficult to predict; *Bathyteuthis* is rare in salinities lower than 34.50‰. It may be excluded from the eastern and western North Pacific Central Water Masses and the North Pacific Intermediate Water Mass because these masses have salinities lower than 34.50‰. Perhaps *Bathyteuthis* occurs at least in the cooler, more saline waters of the southern eastern and western South Pacific Central Water Masses. Because *Bathyteuthis* is so widespread in the Antarctic, Atlantic, and to a lesser extent the Indian and eastern Pacific Oceans, in a variety of water masses, it would seem that a species should occur

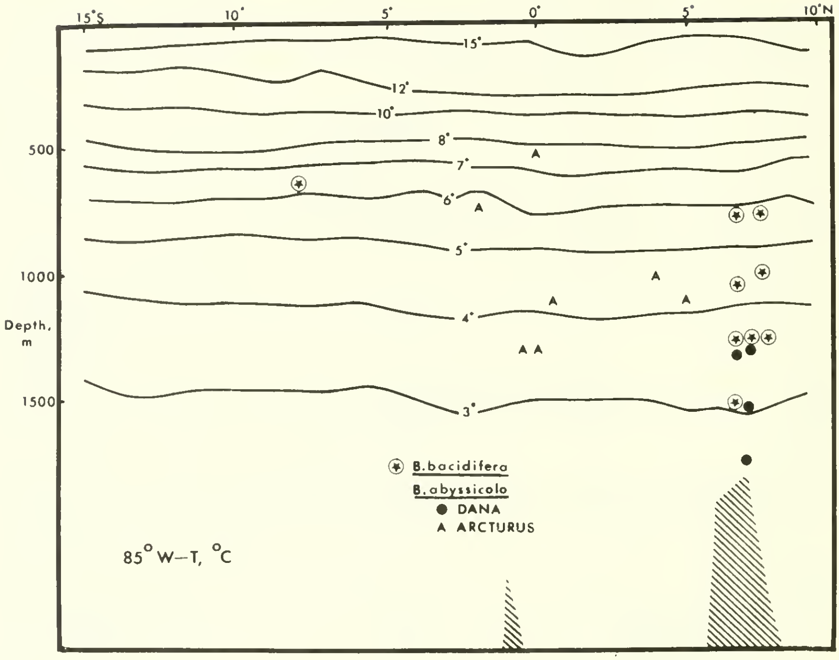


Figure 46.—Vertical section, 85°W; temperature °C. Capture points of *Bathyteuthis abyssicola* and *B. bacidifera* in the eastern Pacific. (Physical data in figures 46–49 from Wooster and Cromwell, 1958.)

in the rest of the Pacific also. The diverse water masses in which *Bathyteuthis* has been found, however, all have salinities higher than 34.50‰ in the temperature range of *Bathyteuthis* (except in some of the Antarctic Intermediate Water); the salinities of the Pacific water masses (except Pacific Equatorial and Transitional) are all lower than 34.50‰ at temperatures below 8° C. Possibly factors other than those of the physicochemical environment combine to limit the distributions of *Bathyteuthis*.

Atlantic Ocean

The distribution chart shows that *B. abyssicola* has been captured at widely scattered points throughout the Atlantic Ocean (fig. 50). The species is common in the eastern South Atlantic where exploratory fishing has been relatively light. The *Dana* made a number of captures during her northward passage; the *Pillsbury* caught several specimens during two cruises to the Gulf of Guinea; and the *Chain* has made two captures in the region. On the other hand, exploratory fishing has been very heavy in the western Atlantic, the Gulf of Mexico, and the Caribbean Sea, but *B. abyssicola* has been collected

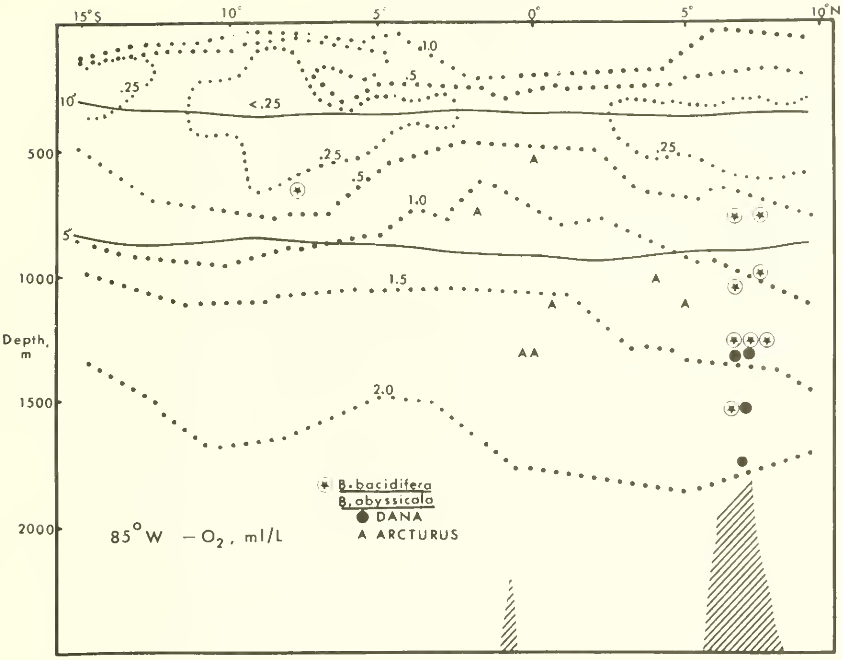


FIGURE 47.—Vertical section, 85°W; oxygen ml/L. Capture points of *Bathyteuthis abyssicola* and *B. bacidifera* in the eastern Pacific.

only a few times. The IMS collections contain only one specimen from the Gulf of Mexico, which has been very thoroughly fished by the *Oregon*, and two specimens from the northern Florida Current. The Straits of Florida have been fished extensively by *Gerda*, but no *B. abyssicola* have been taken. The *Dana*, *Gerda*, and recently, the *Pillsbury* and other vessels have worked the Caribbean Sea but this species has not been among the captures. Woods Hole vessels and the *Dana* and *Pillsbury* have extensively explored the western North Atlantic and Sargasso Sea, yet only one capture of *B. abyssicola* is recorded. Some specimens have been taken off northeastern America across the North Atlantic in the region traversed by the Gulf Stream. Only four larvae of *B. abyssicola* have been reported from the eastern North Atlantic (Massy, 1916; Joubin, 1920, 1924), an area that has been subjected to very extensive exploratory fishing.

The rarity of *B. abyssicola* from the Gulf and Caribbean may be related to the relatively shallow sill depths that enclose the Caribbean and Mexican Basins, though more information is needed before definite conclusions can be made. Along the Antilles Arc from the Windward Islands to South America the sill depth is less than 1000 m except

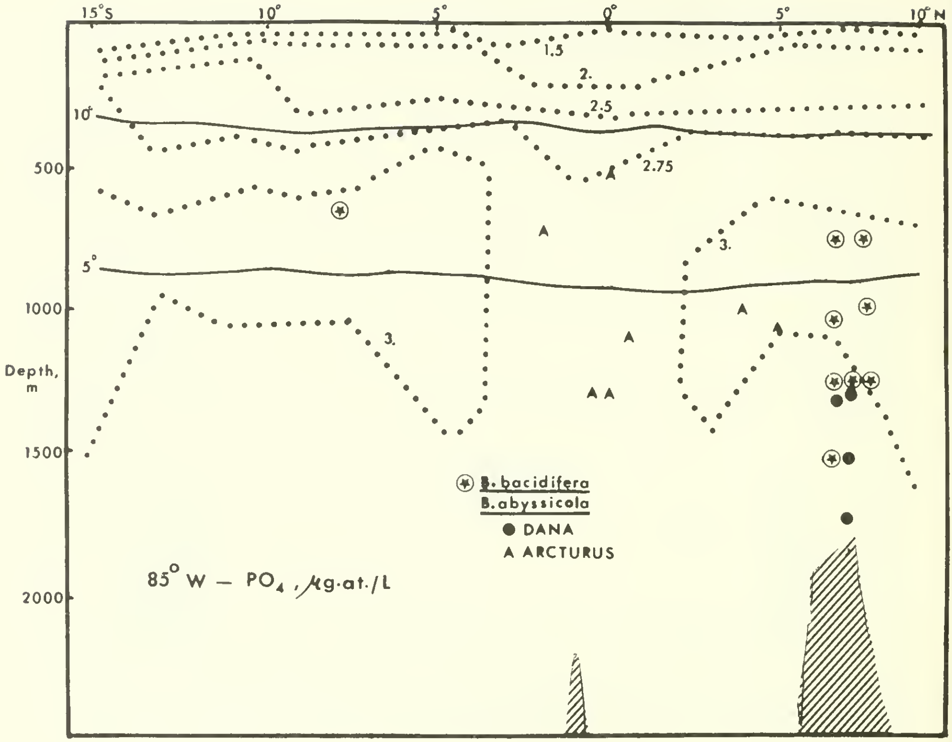


Figure 48.—Vertical section, 85°W; phosphate, microgram atoms/L. Capture points of *Bathyteuthis abyssicola* and *B. bacidifera* in the eastern Pacific.

between Dominica and Martinique where a narrow channel drops to less than 1500 m. The deepest portals into the Caribbean are the Windward Passage between Cuba and Hispaniola and the Anegada and Jungfern Passages between the Virgin and Windward Islands, and the Virgin Islands and St. Croix Island. The sill depth of these passages does not exceed 1600 m. Similarly the sill across the Yucatan Channel into the Mexican Basin is about 1600 m; the portal into the Straits of Florida has a sill depth of 800 m. The water that flows through the Caribbean is a mixture of North and South Atlantic Water Masses. The surface waters are composed of western North Atlantic (Sargasso Sea) water in a ratio of 3–4 to 1 over South Atlantic waters; slightly deeper, the ratio falls to 2 to 1 (Sverdrup et al., 1942). Antarctic Intermediate Water and Upper Deep Water flow in over the sills; the deep water of the Caribbean is renewed from the North Atlantic through the Windward and the Anegada and Jungfern Passages. Below 500–1000 m the temperature and salinity conditions

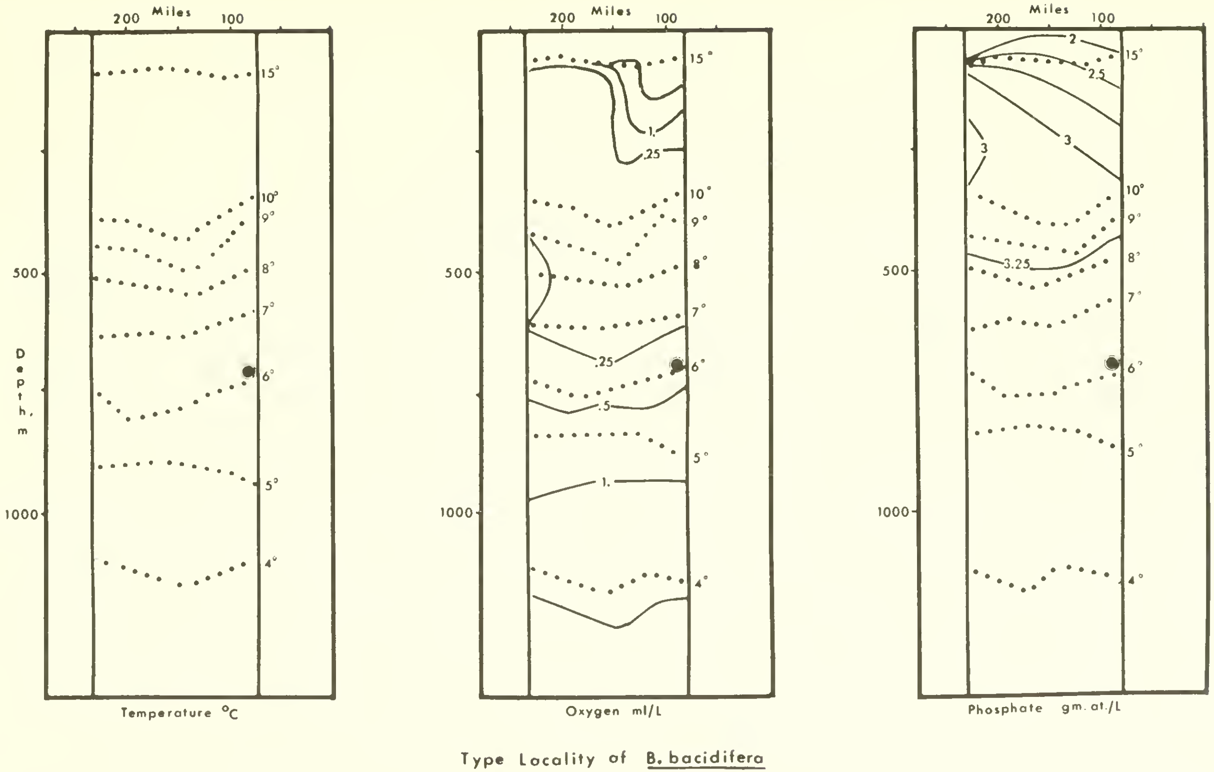
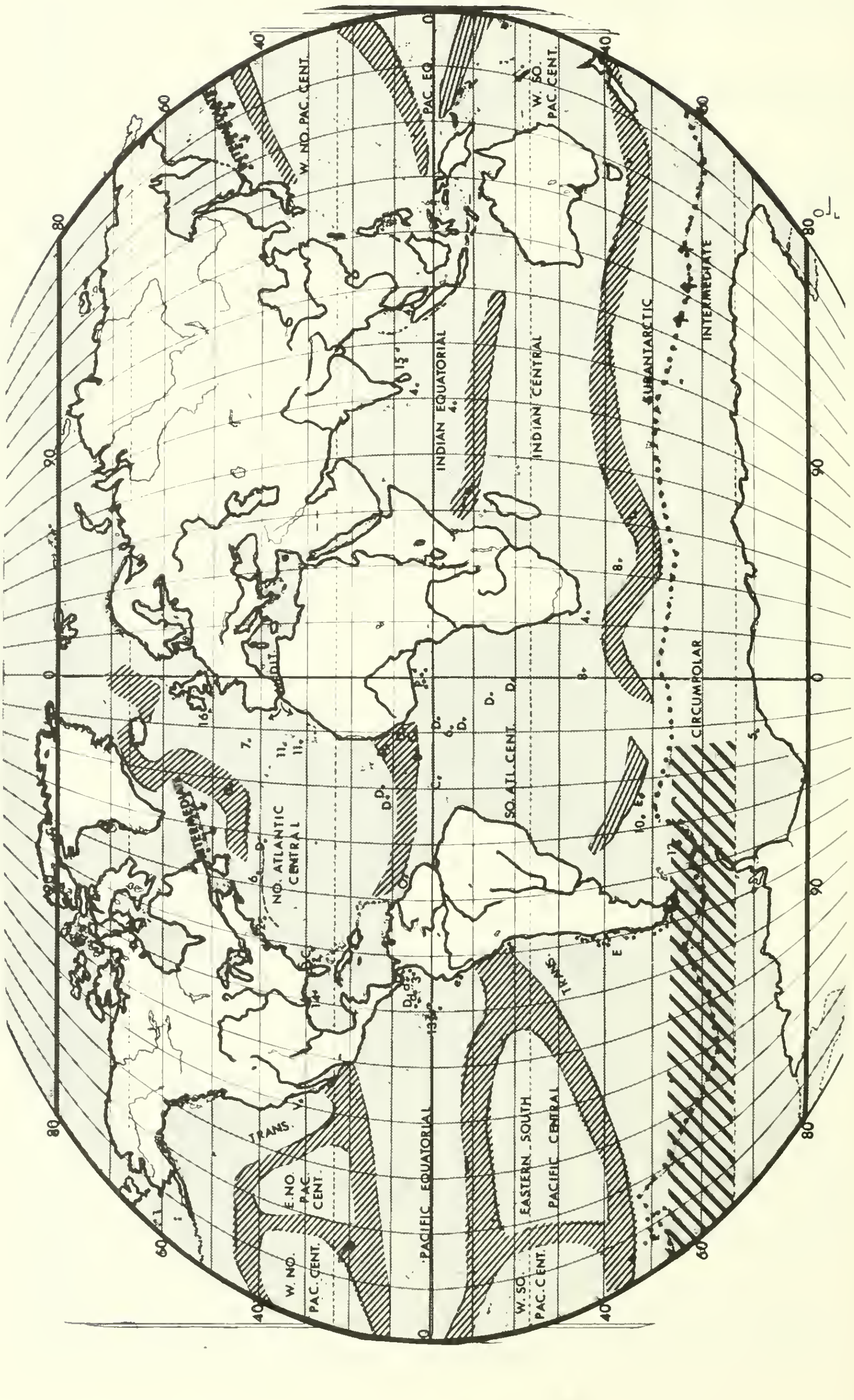


FIGURE 49.—Vertical sections, 80°–82°W; temperature °C, oxygen ml/L, and phosphate microgram atoms/L. Capture point of the holotype of *Bathyteuthis bacidifera* in the eastern Pacific. Latitudes 8°–11°S; top numbers indicate miles offshore (from Wooster and Cromwell, 1958).


W. NO. PAC. CENT.
PAC. EQ.
W. SO. PAC. CENT.
INDIAN EQUATORIAL
INDIAN CENTRAL
SUBANTARCTIC
INTERMEDIATE
CIRCUMPOLAR
NO. ATLANTIC CENTRAL
INTERMEDIATE
SO. ATL. CENT.
TRANS.
E. NO. PAC. CENT.
W. NO. PAC. CENT.
PACIFIC EQUATORIAL
EASTERN SOUTH PACIFIC CENTRAL
TRANS.
W. SO. PAC. CENT.
40
60
80
90
0

are favorable for *Bathyteuthis:* less than 6°–7° C with an average salinity of 34.98‰. Since *B. abyssicola* has been taken in the eastern Atlantic in less than 1000 m on several occasions it seems likely that it could easily enter the Caribbean and Mexican Basins over the sills. In addition, it seems possible that a resident population of this species could exist in Caribbean and Gulf waters, because the Panama portal was probably open to deep-water communication between Atlantic and Pacific bathypelagic populations until the Upper Cretaceous (Schuchert, 1935). With the presence of seemingly adequate temperature and salinity conditions, other factors must exist to limit occurrence of *B. abyssicola* in the Gulf and Caribbean waters.

The T-S capture diagram for the Atlantic Ocean (fig. 51) shows that *B. abyssicola* occurs in both North and South Atlantic Central Water Masses. Only four captures are plotted in the North Atlantic Central Water. Two captures, consisting of two larvae, were made in the North Central Atlantic between about 40° and 47°N at 1500 m where the temperature is just below 3° C and the salinity is about 34.90‰; the remaining two captures, also consisting of 2 larvae, came from 1500 m in the southern limits of the North Atlantic Central Water Mass where the temperature is above 3° C and the salinity is above 34.95‰, due to the outflow of saline Mediterranean Water. The plots of the captures between 1300–1800 m in the South Atlantic Central Water overlap with those from the North Atlantic where oceanographic conditions are similar. Deeper tows (over 2000 m) from the South Atlantic also partly overlap with similar conditions in the North Atlantic. The deepest tows from around 3000 m lie in the zone

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FIGURE 50.—Geographical distribution of *Bathyteuthis.* Numbers indicate previous records of *Bathyteuthis abyssicola* (Table 1). The hatching in the western sector of the Antarctic Ocean represents *Bathyteuthis abyssicola* captured by the *Eltanin.*

1 = Hoyle, 1885
2 = Verrill, 1885
3 = Hoyle, 1904
4 = Chun, 1910
5 = Hoyle, 1912
6 = Pfeffer, 1912
7 = Joubin, 1920
8 = Thiele, 1921
9 = Robson, 1921
10 = Odhner, 1923
11 = Joubin, 1924
12 = Robson, 1932
13 = Robson, 1948
14 = Voss, 1956
15 = Massy, 1916a
16 = Massy, 1916, 1928

E = *B. abyssicola—Eltanin*
e = *B. bacidifera—Eltanin*
D = *B. abyssicola—Dana*
d = *B. bacidifera—Dana*
P = *B. abyssicola—Pillsbury*
c = *B. abyssicola—Chain*
o = *B. abyssicola—Oregon*
PE = *B. abyssicola—Pelican*
s = *B. abyssicola—Silver Bay*
v = *B. berryi—Velero*

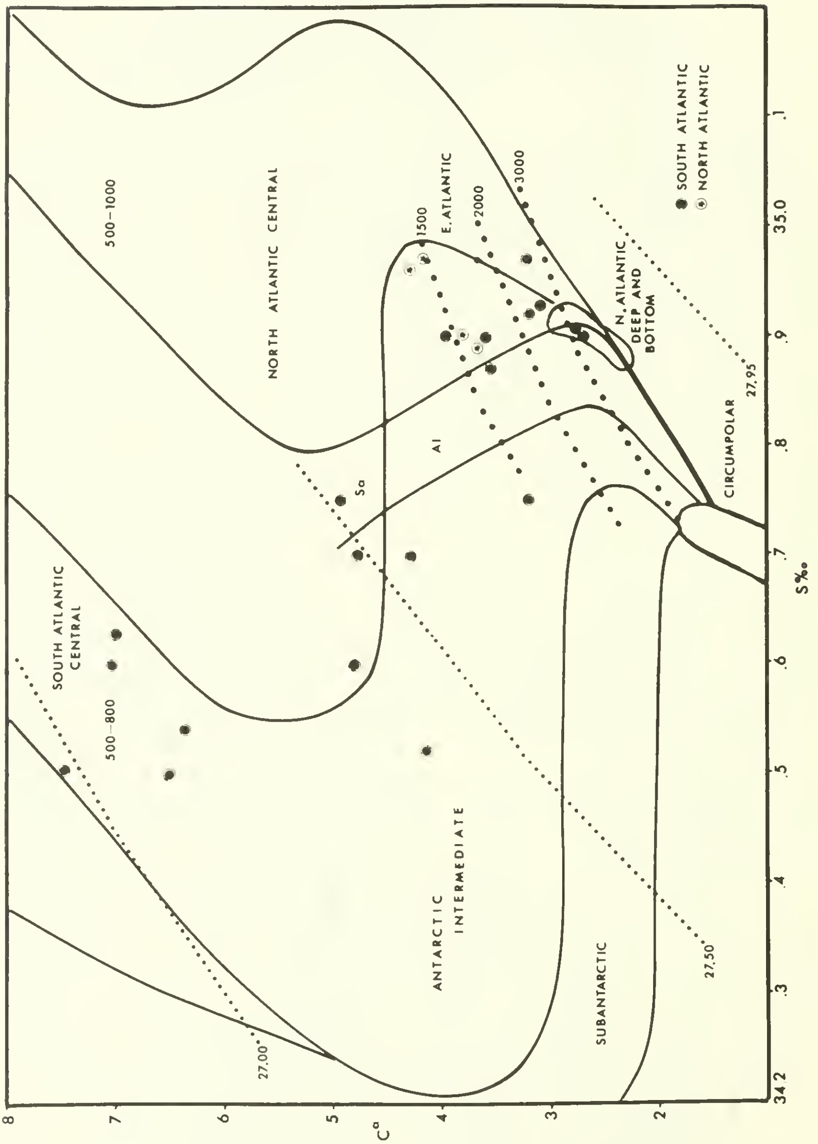
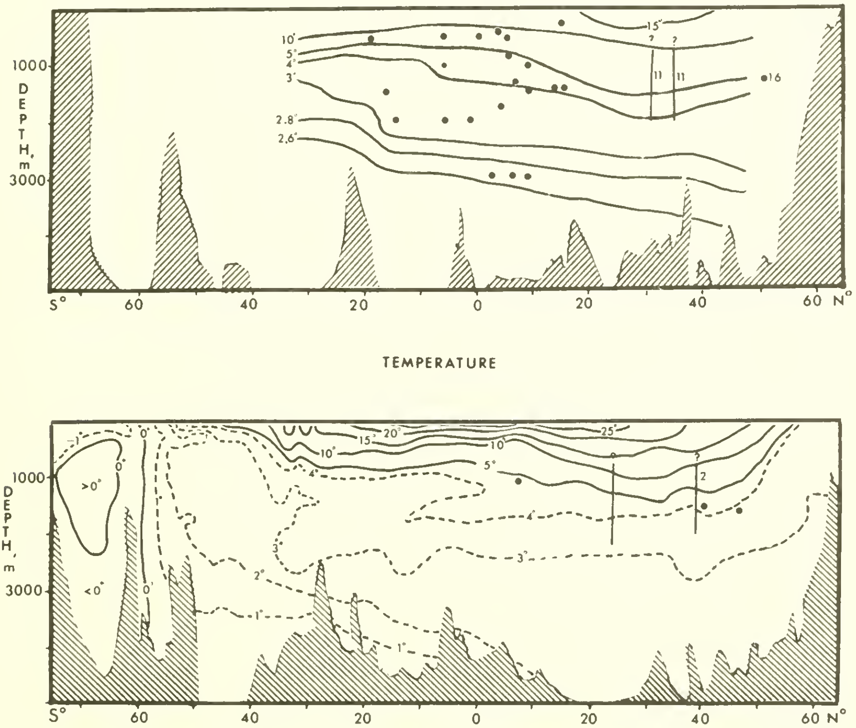


FIGURE 51.—T-S capture diagram for *Bathyteuthis abyssicola* in the Atlantic Ocean.

of overlap between South Atlantic Central Water and North Atlantic Deep Water that has a low temperature and a relatively high salinity. Captures that were made around 1000 m in the South Atlantic Central Water come from the Antarctic Intermediate Water that penetrates well northward at these depths. The shallow captures fall within the South Atlantic Central Water Mass envelope where the temperature is high (6°–7.5° C) and the salinity is relatively low (34.50–34.65‰).

The plots of the captures on vertical sections constructed for the eastern and western Atlantic show the location of *B. abyssicola* in relation to temperature, salinity, and oxygen concentration (figs. 52–59). Only one juvenile specimen was taken in the eastern Atlantic at a temperature above 10°; the remaining captures were in less than 10° water and most of these were below the 5° isotherm (figs. 52–54A). The distribution with salinity shows that *B. abyssicola* tends to occur in waters where the salinity is above 34.50‰ but below 35.00‰ (figs. 55, 56, and 54B); in the North and South Atlantic Central Water Masses the values correspond principally to Antarctic Intermediate



FIGURES 52–53.—Capture points of *Bathyteuthis abyssicola*. Temperature °C. 52 (top).—Vertical section, eastern Atlantic. (Modified from Fuglister, 1960.) 53 (bottom).—Vertical section, western Atlantic. (Figures 53–59 after Wüst, 1935.)

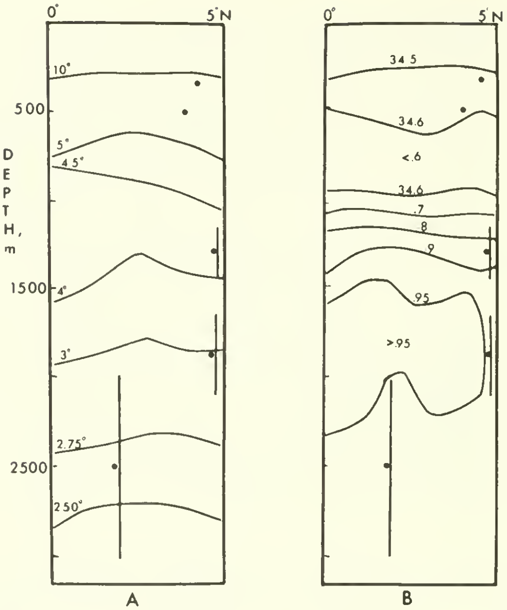


FIGURE 54.—Vertical sections, Gulf of Guinea: A, temperature °C; B, salinity°/oo. Capture points of *Bathyteuthis abyssicola.*

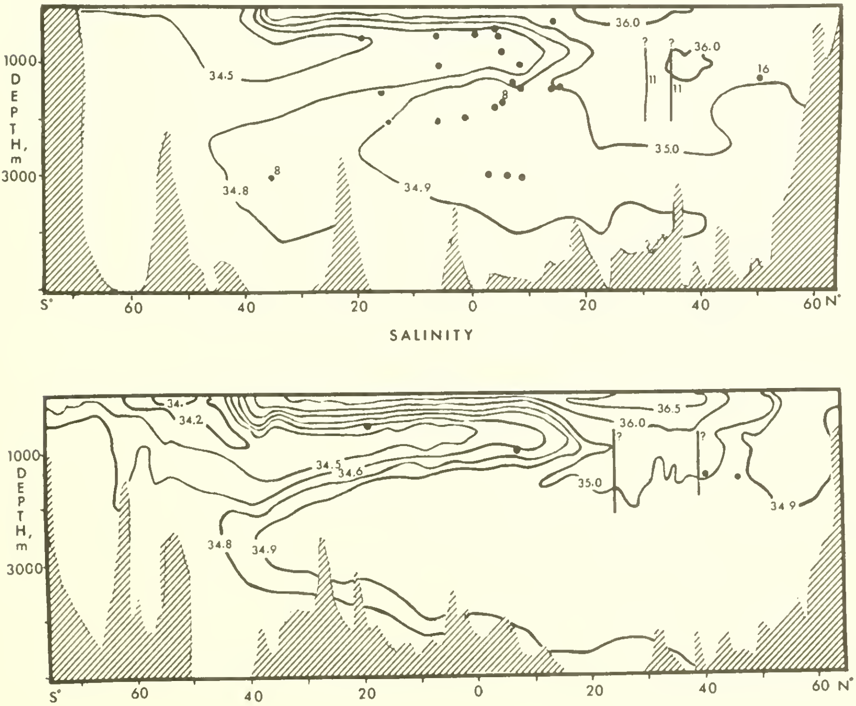
Water and North Atlantic Upper Deep Water (fig. 51). The few captures that come from the western Atlantic were made at relatively high oxygen concentrations (3.5–6 ml/L) below the oxygen minimum layer. In the eastern Atlantic the oxygen minimum values are 1 to 2 ml/L lower than in the western North Atlantic; several captures were made in the oxygen minimum layer and the remainder were below the minimum at concentrations ranging from 3.5 ml/L to greater than 5.0 ml/L (figs. 57, 58). Capture points have been plotted on a vertical section of PO_4 concentration through the central Atlantic (fig. 59); the plots are clustered in the layers of phosphate maxima between 20°S and 15°N. Most points lie in the maximum values of 1.5–2.0 microgram atoms/liter. Deeper specimens in the South Atlantic and the North Atlantic specimens occur at values below 1.0 microgram atoms/liter.

Mediterranean Sea

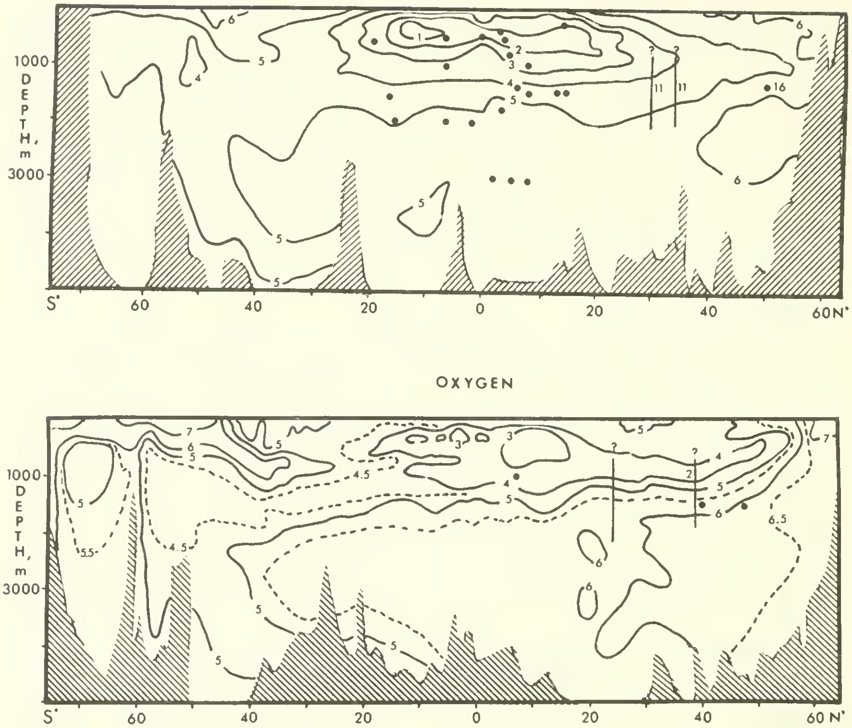
B. abyssicola is excluded from the Mediterranean Sea by a number of factors: the depth of the sill across the Straits of Gibraltar is only 320 m; the strong current that flows out over the sill into the Atlantic consists of water of 13° C and of greater than 37.00‰; within the Mediterranean Basin the temperature, even in the deep water masses, remains at 13° and the salinity in deep water approaches 38.40‰ (Sverdrup et al., 1942). Captures of *Bathyteuthis* in less than 500 m are rare (these are usually associated with areas of upwelling) and it seems unlikely that *B. abyssicola* could buck the strong outflow-current over the sill. Even if it were able to negotiate the Straits, it would be subjected to temperatures and salinities much greater than those at which it normally lives. Pfeffer's (1912) and Joubin's (1920) reports of *B. abyssicola* from the Mediterranean have been shown to be misidentifications (see Historical Résumé); present information about the ecology of the species further confirms the conclusion that these authors were in error.

Indian Ocean

Although no specimens of *Bathyteuthis* from the Indian Ocean have been available for this study, several records do exist. Chun's specimens, with the exception of one from off South Africa, all come from the Indian Ocean: southwest of Ceylon, north of the Chagos Archipelago, and northwest of Sumatra in the Malacca Straits. Massy (1916) recorded two specimens from east of Ceylon in the southern Bay of Bengal. One location of the specimens of *B. abyssicola* recorded by Thiele (1921) lies below 40°S at the far western end of the Indian Ocean. The holotype of *B. abyssicola* Hoyle (1885) was taken in the



FIGURES 55–56.—Capture points of *Bathyteuthis abyssicola*. Salinity°/oo. 55 (top).—Vertical section, eastern Atlantic. 56 (bottom).—Vertical section, western Atlantic.



Figures 57–58.—Capture points of *Bathyteuthis abyssicola.* Oxygen concentration ml/L. 57 (top). Vertical section, eastern Atlantic. 58 (bottom).—Vertical section, western Atlantic.

southern limits of the Indian Ocean between Prince Edward and the Crozet Islands. The last two records are considered to lie within the influence of the subantarctic waters of the Southern Ocean and not in an Indian Ocean water mass.

Chun's specimen from the Chagos region probably is *B. bacidifera*, but the rest of his specimens are apparently *B. abyssicola*. The specimen of *B. bacidifera* was taken at about 2000 m in the transition zone between the Indian Central Water Mass and the Indian Equatorial Water Mass. Oceanographic data from Tressler (1963) indicate that at 2000 m the temperature is about 3° C and the salinity is about 34.77‰ giving a sigma-t value of 27.75. The oxygen concentration below the oxygen minimum layer is 2.75 ml/L; in the north the minimum layer has values lower than 1.00 ml/L. Chun's specimens of *B. abyssicola* from south of Ceylon at 4°N also were taken in a net that had fished at 2000 m; temperature and salinity values are the same as for the Chagos specimen and the oxygen concentration is slightly lower, 2.50 ml/L. Massy's shallowest specimen (870 m) was taken at a temperature between 7°–8° C and a salinity between 34.90‰ and

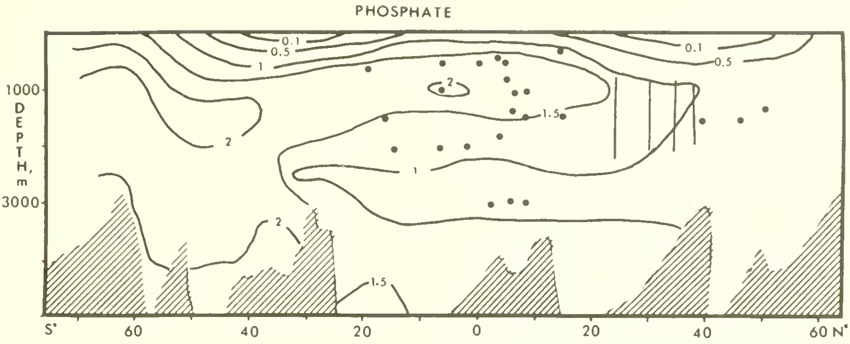


FIGURE 59.—Vertical section, central Atlantic; phosphate concentration, microgram atoms/L. Capture points of *Bathyteuthis abyssicola*.

35.00‰. The oxygen concentration at that depth is less than 1.0 ml/L. Massy's specimen from deep water was taken between 2°–3° C and around 34.80‰. The oxygen concentration was around 3.0 ml/L. The specimen from the Straits of Malacca probably comes from water of about 6° C, above 34.70‰, and below 2.0 ml/L. The salinity in the western Straits of Malacca is too low for the last specimen to be considered as coming from the Indian Equatorial Water Mass, but all other specimens come from this water mass that is characterized by relatively high salinities (34.80–35.20‰), higher than those of the Indian Central Water. The possible influence of waters of low oxygen concentration has been discussed previously.

According to observations made by the *Ob*, Antarctic Intermediate Water may penetrate as far as the Arabian Sea and Bay of Bengal at 10°–20°N (Kort, 1962), but Tressler's (1963, p. 14) salinity section and the section prepared by Fell (Ph.D. dissertation, 1967) do not bear this out; these works indicate the Antarctic Intermediate Water loses its identity in the region of 10°–15°S.

When pelagic material becomes available from the Indian Ocean Expedition, a clearer picture of the distribution of *Bathyteuthis* in the Indian Ocean may emerge. Barring other factors it would not be surprising to find *Bathyteuthis* in the Indian Ocean Central Water Mass where the temperature is cool enough (below about 7° C) and the salinity high enough (above 34.50‰); it also may be found in the Antarctic Intermediate Water that has salinities around 34.70 to 34.75‰.

Biological Factors Governing Distribution

The physicochemical factors in waters inhabited by *Bathyteuthis* have been discussed in detail. It is concluded that, although the species of *Bathyteuthis* appear to occur in particular water masses and within certain limits of oceanographic conditions, no single conservative or nonconservative oceanographic parameter constitutes a limiting factor to distribution. Instead, the combination of physicochemical factors unites with biological factors to control the distribution of *Bathyteuthis*.

The biological factors that have been shown to influence the distribution of bathypelagic animals are the rate of organic production, food supply, and the availability of certain dissolved metabolites. Bruun (1957, p. 651) emphasized that it is not depth that determines the supply of food available to deep-sea animals, but that it is the proximity to land and the productivity at the surface. Furthermore, disjunct distributions of many deep-sea forms are related to surface productivity (Bruun, 1956). Food that reaches deep-living animals is a reflection of the abundance and nature of the plankton at the surface that in turn are regulated by local oceanographic conditions that supply varying amounts of inorganic materials (Moore, 1958, p. 134). Based on his own work on melamphaids and on the work of previous authors, Ebeling (1962, p. 143) suggested that the "segregation of populations into regions of greater or lesser productivity intensifies their genetic isolation." Therefore, areas of greatly disproportionate productivity in the oceans result in faunas that are distinct in composition and abundance.

Primary productivity and resulting food supply are greatest in areas where nutrients that have accumulated in the depths replenish the euphotic zone; replenishment is greatest in regions of upwelling and vertical mixing and close to runoff from land. Intense upwellings occur along the eastern boundaries of the oceans against the continents; areas of divergence of oceanic water masses also produce upwellings. Therefore, boreal and eastern equatorial waters are highly productive where the shallow, unstable thermocline allows vertical replenishment of nutrients; the central water masses are relatively sterile because the deep, stable, thermocline prevents vertical mixing. A layer of minimum oxygen concentrations due to the oxidation of dead organisms builds up below the surface layer in regions of high productivity.

The chart of organic production in the world oceans (fig. 60) is reconstructed from Ebeling (1962) based on the report of Fleming and Laevastu (1956) and others. It agrees well with the findings of Nielsen (1954) and Nielsen and Jensen (1957). The most prominent areas of high productivity lie in the boreal regions of the world. The great Southern Ocean forms a broad belt of highly productive water that extends around the Antarctic Continent. The boreal waters of the North Atlantic have a high organic production; the Norwegian Sea is one of the most highly productive areas of the world oceans. Another

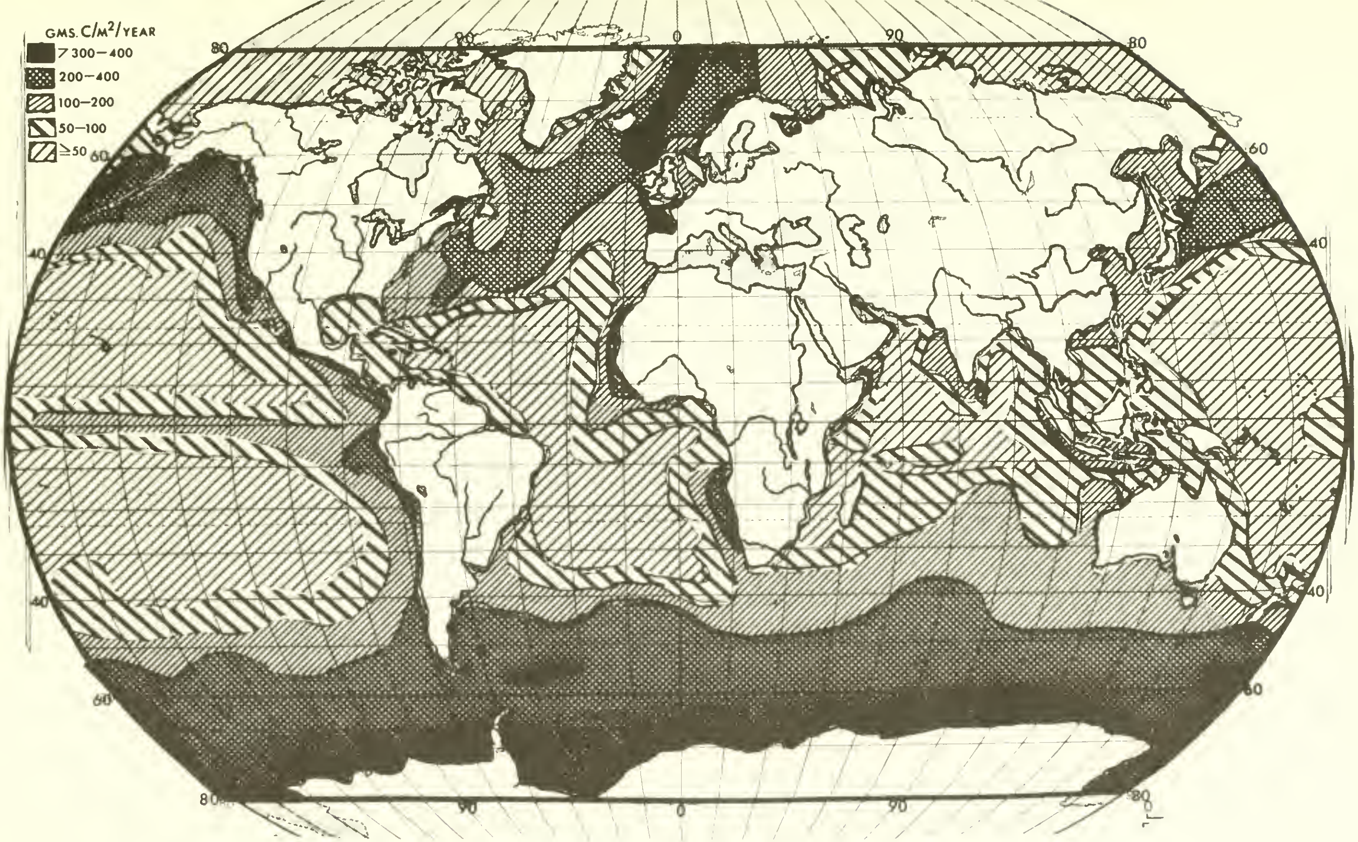


Figure 60.—Annual organic production in the oceans; estimate in grams of carbon fixed per square meter of sea surface per year. (From Ebeling, 1962; Fleming and Laevastu, 1956.)

broad belt of productive water extends across the North Pacific in cold-temperate and boreal regions; parts of the Bering Sea equal the Norwegian Sea in organic production. The Sargasso Sea, which constitutes much of the North Atlantic Central Water Mass, has the lowest values of productivity. South Atlantic Central Water, Indian Central Water, and North and South Pacific Central Water are also low in organic production (Nielsen and Jensen, 1957). Vertical mixing and strong upwelling along the western coasts of the American and African Continents result in greater production than in western and central regions of the Atlantic and Pacific. The Benguela Current that flows northward along southwest Africa has areas of intense upwelling and high productivity, and in this way it is analogous with the Peru Current off western South America (Hart and Currie, 1960). Recent explorations in the Gulf of Guinea and along the south coast of West Africa by the Institute of Marine Sciences (Miami) and the Bureau of Commercial Fisheries leave little doubt that these waters are considerably more productive than has previously been thought. Therefore the shading on the chart in this area underestimates actual productivity. The eastern Pacific equatorial waters are highly productive, and a belt of relatively high production extends westward along the equator and attenuates between 160° and 180°W. A similar, though less pronounced, westward extension of productive waters occurs in the eastern tropical Atlantic, although it is bisected by a tongue of low-productivity water borne eastward by the Equatorial Countercurrent (Nielsen and Jensen, 1957). Moderate to high productivity occurs around the near-shore waters of the Indian Ocean and in a narrow band along the divergence between the South Equatorial Current and the Equatorial Countercurrent at 8°–10°S.

A positive relationship between productivity and distribution of *Bathyteuthis* is apparent when the locations of captures (fig. 50) are compared with the chart of organic production (fig. 60). The correspondence in the Antarctic Ocean is expected, but nearly every other capture of *Bathyteuthis* throughout the eastern Pacific, the Atlantic, and the Indian Oceans, as well, comes from a region of highly productive waters. This is especially so along the west coast of South America, in the Gulf of Panama, off southern California, in the North Atlantic, and off West Africa.

The captures in the midequatorial Atlantic, off northeastern South America, in the Gulf of Mexico, off the southeastern U.S., and in the Indian Ocean are in areas of moderate productivity. No captures are available from the regions of lowest productivity; the rarity of *Bathyteuthis* in the western Atlantic and Gulf of Mexico and its apparent absence from the Caribbean Sea and Central North Atlantic may well be attributed to the low to minimum productivity of these regions. This condition would account for the discrepancies between the poor success of the extensive exploratory fishing efforts in the West Atlantic and the high success of the small exploratory fishing effort in the East Atlantic, especially in the tropical region. Moreover, this may be an example of the exclusion of a species from an area that has the proper physicochemical oceanographic conditions (e.g., the Caribbean) but lacks proper biological conditions.

The comments in the preceding oceanographic section concerning distribution in the water masses that presently are not known to contain *Bathyteuthis* are also applicable to the discussion of distribution with productivity. *Bathyteuthis* may be expected to inhabit the oceanic regions that combine the optimal oceanographic conditions and high productivity. In addition, *Bathyteuthis* may well occur in regions where more influential factors, e.g., productivity and temperature, are optimal and outweigh suboptimal conditions of less important factors. For instance, *Bathyteuthis* may occur in North Pacific Intermediate Water where the salinity generally is below the normal range (34.5‰) but temperatures are within range and productivity is high. Areas of low or minimum productivity, e.g., the Central Water masses, also generally do not have oceanographic conditions that are suitable for *Bathyteuthis*. Conditions within the acceptable range for *Bathyteuthis* are met in some transitional areas (e.g., bordering the southern Central Water masses of the three oceans) where productivity is moderate. Otherwise, it appears that *Bathyteuthis* does not occur in regions of poor organic production regardless of the physicochemical properties.

Each water mass has diagnostic biological characteristics (e.g., in organic production and faunal composition) as well as unique temperature-salinity characteristics. The T-S relationships, and other physicochemical phenomena such as current systems, vertical mixing, enrichment of surface waters with nutrient salts, and insolation, may characterize or index the resultant biological elements or productivity and food supply that are the primary limiting factors. Ebeling (1962) and Marshall (1963) have emphasized that these biological factors have significance as isolating mechanisms in the deep-sea fauna.

Ebeling found that distributions of species of *Melamphaes* generally follow the water masses and that when they depart from this it is to follow the contours of productivity. Moreover, four species that occur in Central Water masses of low food supply are dwarf species, while seven species found in productive waters are giants. And within one species, *Melamphaes janae*, which has a disjunct distribution, the adults in the eastern Pacific are considerably larger than adults in the

Indian Central where productivity and food supply are lower. Also, the bathypelagic fish faunas of the productive subantarctic, subarctic, transitional, and eastern equatorial regions exhibit a high degree of endemism; these faunas do not overlap into the sterile Central Water masses.

In his review of speciation of deep-sea fishes, Marshall (1963, p. 189) concluded that

> earlier colonizers lived in more productive parts of the ocean: in those parts most resembling the environments of their shallow-water ancestors, which were probably fishes from subtropical and tropical regions. These more favorable parts would be the waters over the upper reaches of the continental slope and those in equatorial oceanic regions. The least productive parts of the tropical ocean, particularly those underlying the great central gyres, would have been colonized last.

Concerning the colonization of temperate and polar waters, Marshall (1963, p. 191) stated that the temperature barriers are less imposing than the great contrast between growing and dormant seasons that exist in higher, and particularly polar, latitudes. Bathypelagic species that inhabit open ocean regions in the tropics must be adapted to the uniformity and stability of continuous growing seasons; their metabolic and reproductive rhythms would be unsuited to the unstable, cyclic productivity of the high latitudes. But, great upwellings occur along eastern boundaries of warm oceans, and the ". . . dominant physical features of upwelling regions is their irregularity even under normal conditions and this is paralleled with a constantly changing biological picture" (Hart and Currie, 1960, p. 285). Therefore, the productive, though fluctuating, conditions of upwelling regions offer an environment somewhat similar to that of higher latitudes. Species existing in upwelling regions may be preadapted to the fluctuating conditions of temperate and cold waters; such species could be the colonizers of the high-latitude waters (Marshall, 1963, p. 191).

A more detailed analysis of the zoogeography of *Bathyteuthis* in the light of the preceding discussion must await more extensive material from the Atlantic, Pacific, and Indian Oceans. The information presently available, however, suggests that the physicochemical and biological environmental conditions enumerated above (particularly organic production), acting as integrated isolating mechanisms, have molded the distributional patterns exhibited by the populations of *B. abyssicola* and *B. bacidifera*. If we assume that bathypelagic cephalopods emerged and dispersed in a manner similar to some other invertebrates and to deep-sea fishes, then the ancestors of the species of *Bathyteuthis* could have arisen in the warm, productive seas. *B. abyssicola* has perhaps taken advantage of possible preadaptation to fluctuating conditions and has dispersed to the productive regions of higher latitudes and has differentiated into distinct geographic populations. The more restricted *B. bacidifera*, on the other hand, apparently does not share this degree of adaptability and is limited to equatorial waters of the eastern Pacific Ocean (and possibly the Indian Ocean).

Summary of Distribution With Physicochemical and Biological Factors

B. abyssicola inhabits several different water masses and is capable of crossing water-mass boundaries particularly to follow zones of high productivity. Within particular water masses, however (e.g., Antarctic Circumpolar, Pacific Equatorial, and Atlantic Central). *B. abyssicola* exhibits geographical populations. *B. bacidifera* on the

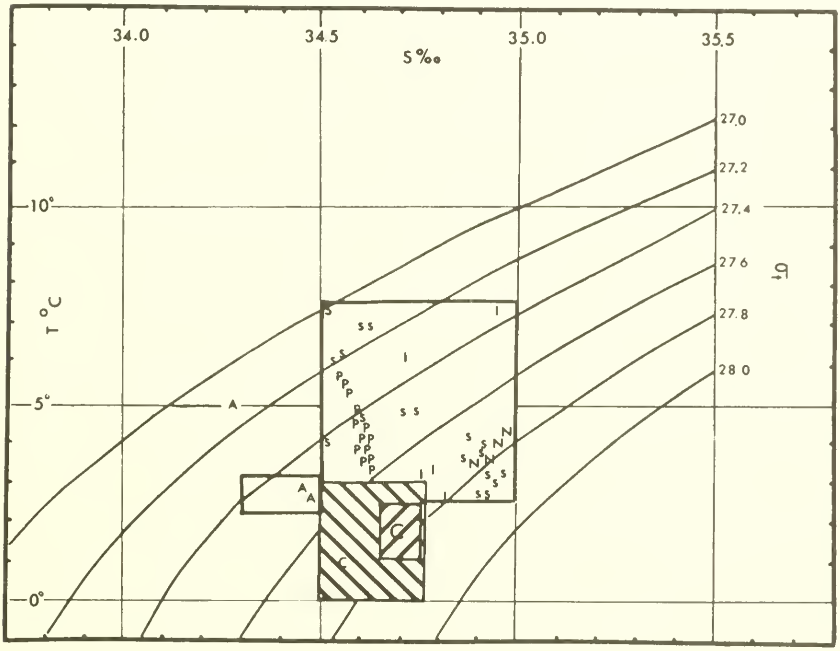


FIGURE 61.—Summary of T-S-density relationship of *Bathyteuthis* captures in the Antarctic, Atlantic, Pacific, and Indian Oceans. The boxes outline areas of occurrence. Abbreviations as follows:

I, Indian Ocean
N, North Atlantic Ocean
S, South Atlantic Ocean
P, Pacific Equatorial Water
A, Antarctic Intermediate (Pacific)
C, Circumpolar Water Mass (majority of captures)
c, Circumpolar Water Mass (few captures)

other hand, appears to be restricted to the Equatorial Water Masses of the Pacific and possibly the Indian Ocean; no equatorial water mass occurs in the Atlantic, and despite heavy exploratory fishing efforts in equatorial regions, no specimens of this species have been captured.

Wherever *Bathyteuthis* is found, it occurs within waters of relatively high productivity that have similar oceanographic characteristics. Figure 61 presents the T-S-density relationships of *Bathyteuthis* captures from Antarctic, Pacific, Atlantic, and Indian Oceans. In the Antarctic the great majority of captures (small box) falls between 1° to 2.5° C, 34.65‰ to 34.75‰, and sigma-t=27.70 to 27.85. The few remaining Antarctic captures (large box) range from 0° to 3° C, 34.30‰ to 34.75‰, and sigma-t=27.20 to 27.90. In the Pacific Equatorial Waters (P) the captures were made between 3° to 6° C, 34.55‰ to 34.65‰, and sigma-t=27.25 to 27.55. In the Atlantic (N, S) most captures came from conditions between 2.5° to 4.5° C, 34.85‰ to 34.97‰, and sigma-t=27.70 to 27.87. Other scattered captures from shallower South Atlantic Central Water (S) range from 4° to 7.5° C, 34.50‰ to 34.75‰, and sigma-t=27.00 to 27.50. The few captures in the Indian Ocean (I) range from 2.5° to 7.5° C, above 34.70‰ to 34.95‰, and sigma-t=27.30 to 27.80. *B. abyssicola* occurs over a broad range of oxygen concentrations from about 1.50 ml/L to greater than 5.25 ml/L, while *B. bacidifera* occurs in lower concentrations from less than 0.50 ml/L to about 2.75 ml/L. In either case, specimens occur in or, most often, below the oxygen minimum layer.

Finally, *Bathyteuthis* is most closely associated with areas where high productivity takes place in the surface layers (fig. 60). Captures come from the layer of maximum or high phosphate concentrations. The high productivity, of course, is responsible for the oxygen minimum layer.

In conclusion the species of *Bathyteuthis* may be considered stenothermic (1°–5° (–7°) C), stenohaline (34.50‰–34.95‰), stenopycnic (sigma-t=27.00–27.20–27.90), and euryaerobic (1.5–5.25 ml/L). (*B. bacidifera* is oligoaerobic (0.5–2.75 ml/L)). They are true bathypelagic cephalopods that seldom approach within 1000 m of the bottom (usually more than 2000 m) or within 500 m of the surface. Specimens that occur in less than 750 m are generally juveniles or larvae and are in waters that have suitable temperature and salinity values (because of high latitude locations or areas of upwelling).

But, above all, the limiting factor that has the greatest effect upon the distribution of *Bathyteuthis* is organic productivity.

Vertical and Regional Distribution

Calculation of Maximum Depth of Capture and Vertical Range

The shallowest depth of the vertical range of a species is easily defined by the shallowest tows that took specimens, when an adequate number of samples have been taken. The depths where most of the population lives are indicated by the frequency of captures and numbers of specimens at particular depth increments. The lower limit of the vertical range of deep-sea, pelagic species is extremely difficult to establish with open nets because of the possibility (or probability) that the specimens in deep tows were captured while the nets were being set or retrieved. Often the lower limit of a species is set near the depth below which a sudden, sharp decline occurs in numbers of captures and specimens. Frequently, however, no sharp break exists and in general this approach is unsatisfactory.

Bruun (1943, p. 21) devised a method for determining the vertical range of *Spirula spirula* taken during the *Dana* expeditions. First he calculated the number of *Spirula* that were caught during a standardized tow (S–200 hours) in the depth-layers (in terms of meters of wire out) where *Spirula* appeared to be abundant. To determine if the specimens that were taken in nets fished at depths greater than the zone of abundance actually came from those depths, Bruun first calculated the number of *Spirula* that would be expected to be caught during the time that the deep-fishing nets passed through the layer of abundance; then he compared this figure with the actual catch per standard tow. When the actual catch was smaller than the number that would be expected while the net passed through the zone of abundance, the specimens probably were not taken at the set-depth but at shallower depths while the net was being set or, more likely, hauled. Pickford (1946) and Thore (1949) used the same method for determining the vertical distributions of *Vampyroteuthis* and pelagic octopods.

Since the specimens of *B. abyssicola* taken on *Eltanin* have been captured in open 3-meter Isaacs-Kidd Midwater Trawl nets, some of which fished at depths in excess of 3000 m, a means of determining actual depths of capture and true vertical range must be applied. More than one hundred 3-meter IKMT tows (and numerous 1-meter IKMT tows) were made at depths of less than 500 m during the cruises currently being studied (through Cruise 15); no specimens of *B. abyssicola* have been taken in these tows. This is a good indication that the species does not normally occur shallower than 500 m in the Antarctic. (A survey of captures through Cruise 24 has revealed that a total of only three tows shallower than 500 m have captured *B. abyssicola.*

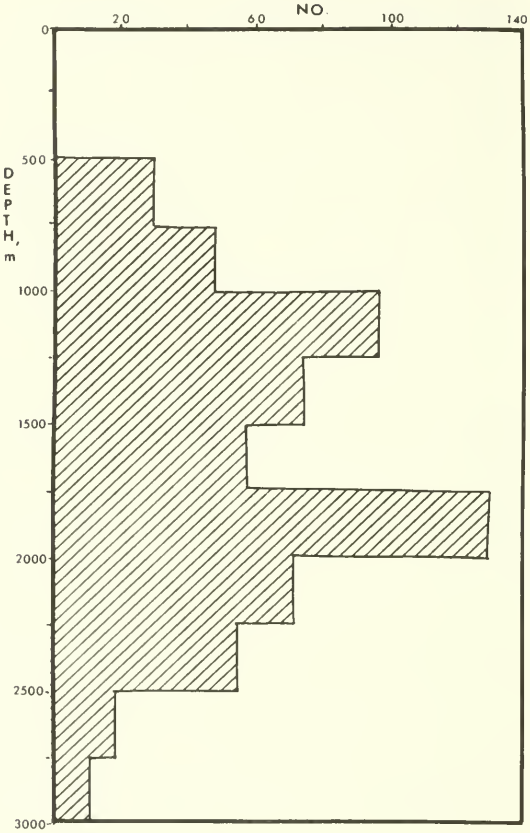


FIGURE 62.—Vertical distribution by 250-meter increments of total sample population of Antarctic *Bathyteuthis abyssicola* captured by standardized 2-hour tows.

These were taken under very unusual oceanographic conditions, apparently during a period of extreme upwelling at the localities—see below.)

The major block of specimens comes from 500–2500 m. Only a few individuals have been taken from 2500–3000 m (fig. 62). The following calculations are designed to indicate if the few specimens from tows that fished below 2500 m actually were captured in these depths.

Total number of 2-hour tows taken between 500–2500 m=215

Total number of specimens captured between 500–2500 m=565

Therefore, average number of specimens captured per 2-hour tow between 500–2500 m=2.63

Total number of 2-hour tows taken between 2500–3000 m=21

Total number of specimens captured between 2500–3000 m=33

Therefore, average number of specimens captured between 2500–3000 m=1.57

In the overall productive layer (500–2500 m) 21 two-hour tows would have been expected to catch 21×2.63 specimens = 55 specimens. The actual catch (33 specimens) in the 2500–3000 m layer was only 60% of the expected.

Further, to determine if the specimens were captured in the deep layer or in the productive layer while the nets were set and hauled through it, the factor of time must also be considered: the average time required for a tow below 2500 m is 5.3 hours, with two hours spent towing at depth and 3.3 hours spent setting and hauling. Thus, it requires 3.3 hours to cover 5000 m (2500 down, 2500 up) giving an average set-haul rate of 1500 m per hour. Since no *B. abyssicola* are caught in the upper 500 m (1000 m up and down), about 0.7 hours can be subtracted from the travel time leaving $3.3 - 0.7 = 2.6$ hours during which the net is in the productive zone between 500 and 2500 m. (Another approach: the net has to pass through 4000 m of productive zone ($2500 - 500 = 2000$; $2000 \times 2 = 4000$) which requires $4000 \div 1500$ or 2.6 hours.) If the average catch is 2.63 specimens per two-hour tow in the productive area, then 3.42 specimens would be expected to be caught in 2.6 hours while the net passed down and up through the zone of abundance ($2.6 \times 2.63 = 6.85$; $6.85 \div 2 = 3.42$). Since only 1.57 specimens were captured per two-hour tow below 2500 m, probably no specimens were captured below 2500 m, i.e., *B. abyssicola* does not normally live below 2500 m.

Since the 2250–2500 m zone shows some fall-off in the graph (fig. 62), the same method can be applied to the tows taken below 2250 m in an effort to determine if the lower limit of distribution is shallower than 2500 m:

Total number of 2-hour tows between 500–2250 m = 196
Total number of specimens captured between 500–2250 m = 510
Average number of specimens captured per 2-hour tow between 500–2250 m = 2.60
Total number of 2-hour tows below 2250 m = 40
Total number of 2-hour tows between 2250–2500 m = 19
Total number of specimens captured below 2250 = 86
Total number of specimens captured between 2250–2500 m = 53
In the layer below 2250 m forty 2-hour tows averaged 2.15 specimens per tow.
In the layer between 2250 and 2500 m nineteen 2-hour tows averaged 2.79 specimens per tow.
In the productive layer 40 tows would be expected to catch 104 specimens ($40 \times 2.60 = 104$). The actual catch was 86 or 82% of the expected catch.
In the productive layer 19 tows would be expected to catch $19 \times 2.60 = 49.4$ specimens. The actual catch was 53 or 9% greater.

Again the time factor of the nets passing through the productive layer should be taken into consideration. The same times required for the below-2500 m calculation also apply to the below-2250 m calculation. The nets have to pass through 3500 m of productive zone (2250−500=1750; 1750×2=3500 m). This requires 2.3 hours. Therefore, 2.99 specimens would be expected to be caught while the nets were traversing the zone where *B. abyssicola* is abundant. This figure is greater than those representing the total catches below 2250 m and also the limited zone of 2250–2500 m, although the latter catch approaches the theoretical figure. Taken as a total unit below 2250 m, 2.15 specimens may be sufficiently fewer than the theoretical 2.99 specimens to indicate that *B. abyssicola* does not live in numbers below 2250 m. On the other hand, the 2.70 specimens value for the zone 2250–2500 m may approach too closely the 2.99 value to be significant for establishing the lower limit of vertical distribution of *B. abyssicola* within this zone. With the sources of error inherent in any system using open nets, this is as far as the calculations should be pursued.

A more conservative and perhaps more accurate approach can be taken by assuming the IKMT captures specimens only while being hauled and not while being set. The IKMT probably does not filter a large volume of water while being set because the rate of pay-out of cable may be nearly as great as the speed of the vessel; water may pass through the net at only one or two knots. This would be sufficient speed to capture the lethargic and less mobile forms, while allowing the more active or more perceptive animals to escape. Based on the morphology of *B. abyssicola* and on observations of living specimens, it is clear that this animal is not an extremely rapid, active swimmer; neither is it completely lethargic and immobile. Possibly, some specimens may be captured even at the low filtering speed during the setting of the net. Therefore, the following calculations represent minimum values. The assumption that the IKMT fishes only while being hauled will give greater significance to the few specimens taken in the deeper tows by reducing by ½ the number of specimens which are assumed to be captured in the productive levels during set and retrieval of the trawl. At depths greater than 2500 m the time spent fishing in the shallower productive zone would be 1.3 hours instead of 2.6 hours, during which time 1.71 specimens would be expected to be captured. Since 1.57 specimens per 2-hour tow were captured below 2500 meters this value probably still does not indicate that *B. abyssicola* regularly lives below 2500 m.

The result is different when considering the zone below 2250 m and especially the block between 2250 and 2500 m. Assuming that the net fishes only during haul-in, the catch would amount to 1.5 specimens. Since all tows below 2250 m averaged 2.15 specimens, it is possible that 0.65 specimens could actually be captured below 2250 meters. In the restricted zone between 2250 and 2500 m the average was 2.79 specimens per 2-hour tow. Therefore this zone may account for 1.29 specimens per tow.

These different approaches to the determination of the deeper levels of distribution lead to the conclusion that *B. abyssicola* does not occur in appreciable numbers below 2500 m and that the lower range of occurrence for this species is in the region of 2250–2500 m. A closer estimation than this is not warranted because of the nature of the sampling gear and the variability involved in determining depth of capture primarily from wire angle.

A further test of the method is to examine the individual tows taken below 2500 m where an apparently large number was captured. For each tow the number of specimens is calculated that would be expected during the time it took to pass through the productive layer.

Four tows that fished below 2500 m caught an apparently large number of specimens:

Eltanin *station number*	*Actual number specimens captured*	*Number hours in productive zone*	*Average No. specimens expected per 2 hrs.*	*Number expected in productive zone*
1323	4	2. 3	2. 63	3. 1
1288	4	3. 3	2. 63	4. 3
867	7	3. 5	2. 63	4. 6
782	6	5. 0	2. 63	7. 2

The two tows that caught more specimens than would be expected should be compared with other IKMT tows taken in the same area at the same time. In the immediate vicinity of station 1323 four IKMT tows to the productive zone produced 6, 9, 11, and 15 specimens, all well above the average. This is an area of high concentration of *B. abyssicola*, and it indicates that the estimated catch here is too low and that most (or all) of the four specimens from 1323 were taken above 2500 m.

With station 867 the picture is not quite so clear because other tows taken within the immediate area were all made at less than 1300 m where relatively few specimens would be expected. Station 858, taken at the same longitude and 2° farther south, was the closest tow that fished at a depth where *B. abyssicola* is abundant, and it caught twelve specimens, considerably more than the average. Therefore, it is probable in this case, too, that apparently high numbers taken below 2500 m were actually taken in the shallower zone of abundance.

Figure 62 gives the total number of specimens captured by standard 2-hour tows with depth. The bulk of the population occurs between 1000–2500 m. (A slight decline in numbers occurs between 1500–

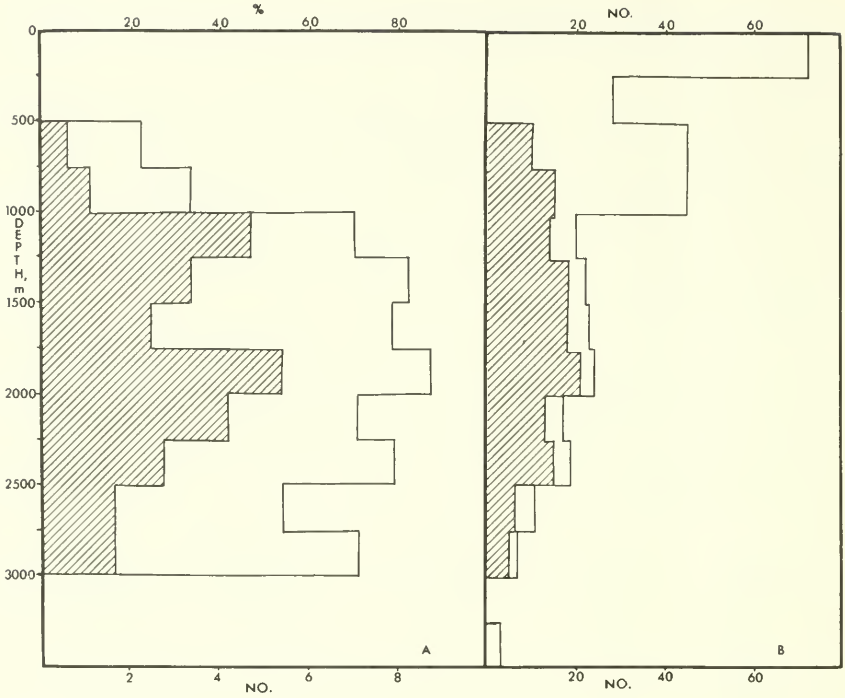


Figure 63.—Antarctic. a, Average number of specimens captured per tow for total tows (hatched area) and percentage of successful tows (clear area) by 250-meter increments. b, Total number of 3-meter IKMT tows (clear area) and number of successful tows (hatched area) by 250-meter increments.

1750 m.) Figure 63a gives the average number of specimens captured per total tows grouped by 250 m intervals. The average catch, as well as the total catch, drops off between 1500–1750 m then reaches a peak at 1750–2000 m. The percent of successful tows taken at each depth increment is also plotted on the graph. The plot generally follows the plot for captures; that is, the greater the catch and the greater the average per tow, then the greater the number of successful tows (or vice versa). Even the tows below 2500 m were relatively successful, undoubtedly because they passed through the thick layer of abundance. Figure 63b shows the relationship between total number of tows at each depth interval and the number of successful tows. A great number of tows was made between the surface and 1000 m, but only a few below 500 m caught *B. abyssicola.* Fewer tows were made below 1000 m but they were considerably more successful (also compare with figure 63a for percent of successful tows).

Vertical Distribution by Size

The sizes (ML) of 563 specimens of *B. abyssicola* are plotted against depth of capture in figure 64. The plot shows a tendency for the smaller specimens to be located at shallower depths and the larger specimens to be concentrated at greater depths. Although no sharp break occurs on the overall chart, the division between the shallow and deep concentrations lies at about 30 mm ML. This length also corresponds with the size above which all males are fully mature and all females are either well advanced in maturity or are fully ripe. The following discussion determines the degree to which the size-segments of the sample population are concentrated at difference depths.

Thirty-six percent (204 specimens) of the total population is composed of specimens less than 30 mm in ML; the remaining specimens range from 30 mm to 75 mm in ML. Eighty-three percent (167 specimens) of the small specimens was captured between 500 and 2000 m; 111 of these (55% of the small population) came from 500–1300 m. The major concentration, representing 46.3% of the small population (94 specimens), lies between 800 m and 1300 m; 40 specimens (20%) range between 500 m and 1000 m, and 8.4% lie between 500 m and 750 m. Thirty-six specimens (17%) come from nets that fished below 2000 m; the points are scattered and it is probable that the bulk of these came from the shallower tows, perhaps from the zone of concentration (800–1300 m) or from a possible secondary concentration at 1700–2000 m. If the specimens below about 2000 m were proportionally redistributed according to the calculations below they would lie within the layer of abundance.

The greatest proportion (72.5%) of the individuals in the segment of the population above 30 mm was captured below 1500 m; 51% of the large population is concentrated between 1650 m and 2200 m, with 13% below 2200 m. The remaining 27.5% of the large population is distributed between 625 m and 1500 m in the following proportions: 3.3% between 625–750 m; 9% between 625–1000 m; 18.6% between 1000–1500 m. The graph (fig. 64) shows some specimens plotted below 2500 m; but the calculations made in the preceding section indicate that few *B. abyssicola* live below 2500 m; therefore, the specimens deeper than 2500 m should be proportionally redistributed in the layer of abundance between 1650 m and 2500 m (see calculations below). Between 1500 and 2200 m are 187 specimens that range from 30 mm to 50 mm in ML; this group represents 52% of the large population and 33% of the total population.

Tables IX–XI summarize the distributions of specimens in the sample population by size at the various depth increments. A total of 490 specimens lies between 1000 m and 2500 m; these account for

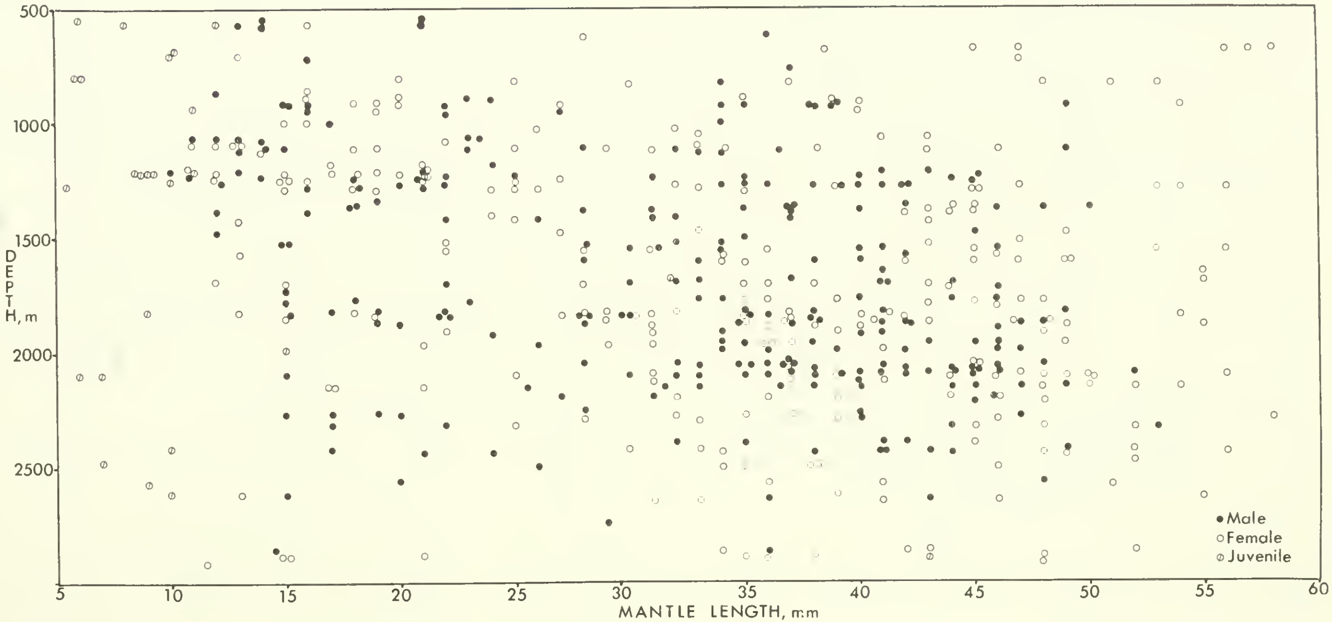


FIGURE 64.—Vertical distribution of Antarctic *Bathyteuthis abyssicola* by size (mantle length). Points are plotted at recorded depths and not at corrected depths of capture; most of those below 2500 meters could be redistributed in the shallower zone of abundance (see text). The large specimens at depths of less than 750 meters were taken in only two tows under unusual conditions (see text).

Table IX.—*Bathymetric distribution of the total sample population by size group; 563 specimens of* B. abyssicola *from the Antarctic Ocean*

Depth, meters	*Total number of specimens*	*Percent of total population*	*Less than 30 mm; number and percent of total population*	*Greater than 30 mm; number and percent of total population*
500–750	29	5.1	17=3%	12=2.1%
750–1000	44	7.8	24=4.2	20=3.6
1000–1300	112	20.0	70=12.4	42=7.6
1000–1500	150	26.6	83=14.7	67=11.9
1500–2000	169	30.0	43=7.6	126=22.4
2000–2500	171	30.4	36=6.4	135=24.0
	563		36%	64%

Table X.—*Bathymetric distribution of greater than 30 mm ML size group; 360 specimens*

Depth, meters	*Number of specimens*	*Percent*
625–750	12	3.3
625–1000	32	8.9
1000–1500	67	18.6
625–1500	99	27.5
1500–1650	30	8.3
1650–2200	184	51.1
2200–2500	47	13.1

Table XI.—*Bathymetric distribution of less than 30 mm ML size group; 203 specimens*

Depth, meters	*Number of specimens*	*Percent*
500–750	17	8.4
500–1000	41	20
500–1300	111	55
800–1000	24	11.8
800–1300	94	46.3
1000–1300	70	34.5
1000–1500	83	41
1500–2000	43	21
2000–2500	36	17.7

87% of the total sample population of *B. abyssicola*. The distribution is fairly even by 500 m increments. Of the total population 60.4% (340 specimens) occurs between 1500 and 2500 m; of this segment 77% (261 specimens) are greater than 30 mm in ML and only 23% (79 specimens) are smaller than 30 mm ML. Only 13% of the total population occurs between 500–1000 m, over half of which are individuals smaller than 30 mm ML.

These data confirm that small *B. abyssicola* tend to live at shallower levels than larger specimens. Furthermore, an examination of all tows shallower than 750 m shows that 7 of the 8 specimens greater than 30 mm were taken in one tow and the remaining specimen was taken in an adjacent tow. These two unusual captures (1133 and 1137) were made south of 66°S in the area of upwelling along the Antarctic Divergence. Of the 11 specimens below 30 mm ML taken in less than 750 m 10 are larvae and juveniles 21 mm ML or smaller. Nine of these were taken in two tows in the Peru Current; the other two came from tows in the convergence zone. Another tow that captured 6 specimens above 30 mm fished at depths that varied from 823–1300 m; these have been plotted at the shallower depth but could just have easily come from 1300 m; this tow (812) also came from a southern locality, 64° 45′S, where upwelling occurs. One other shallow tow (1383) to 914 m accounts for 10 more of the shallow specimens above 30 mm mantle length; this station was located at 55°S 149°W in the tongue of frigid water that extends northeastward from the Ross Sea, possibly an area of strong vertical movement. Therefore, all except 6 specimens larger than 30 mm that were captured in less than 1000 m came from a few tows that fished in areas of unusual conditions, particularly upwellings. Further, the great majority of tows in less than 1000 m caught only small specimens or mostly small specimens with only one or two larger individuals.

The calculations in the previous section indicate that *B. abyssicola* probably does not live below 2500 m. Therefore, the 35 specimens that came from nets that fished at depths greater than 2500 m may have come from the shallower depths, presumably from the zone of abundance.

A method for the proportional redistribution of the deepest living specimens has been devised. The size group above 30 mm had 23 specimens captured deeper than 2500 m. It is assumed that they were distributed in the 2000–2500 m zone in numbers proportional to the plotted distribution; 112 specimens are plotted in the zone: 65% (73) from 2000–2200 m, and 35% (39) from 2200–2500 m. Therefore, about two-thirds (or 15) of the specimens from below 2500 m can be added to the 2000–2200 m zone, bringing the total number of specimens in that zone to 88 and in the overall zone of abundance (1650–2200 m) to 184, a 4% increase.

Specimens in the less than 30 mm size group are evenly distributed in the 2000–2500 m range; 12 specimens are plotted below 2500 m. (Actually, specimens below 2000 m are relatively sparse and it is possible that that depth is the lower limit of vertical range for small specimens.) It might be tempting to redistribute all the small specimens from greater than 2000 m into less than 2000 m, but it is safer for the present to redistribute only those from greater than 2500 m.

Since no real clustering occurs between 2000 and 2500 m, the 12 specimens from greater depths can be divided evenly through the zone, giving an additional 2.4 specimens to each 100 m increment. Therefore, the number of specimens in the 2000–2200 m range is increased by 4.8 (or 5) to 15 and in the 1650 to 2200 m overall zone of abundance to 50. The total of both size groups for the 1650–2200 m layer is 234 specimens or 41.6% of the total population; 78.7% of this number are greater than 30 mm ML and 21.3% are less than 30 mm ML. These represent 33% and 8.9% of the total population respectively.

Depth of Capture in Relation to Depth of Ocean

Several of the earlier specimens of *B. abyssicola*, including the holotype taken by the *Challenger*, were captured in bottom trawls. This, and the "peculiar structure" of *B. abyssicola*, led Hoyle (1885, p. 272; 1886, p. 169) to conclude that this species was a bottom dwelling form that collects "nutritive matters from an oozy bottom." Subsequent captures in vertically hauled plankton nets, however, soon left little doubt that *Bathyteuthis* is a pelagic squid.

A scatter diagram (fig. 65) was constructed to determine if any relationship exists between the depth of the sea and the depths inhabited by *B. abyssicola*. The pattern shows in general that with greater ocean

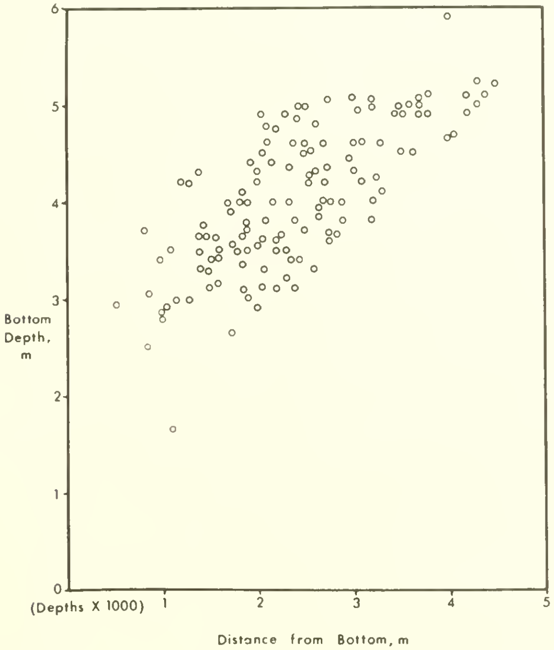


FIGURE 65.—Relationship between ocean depth and the distance from the bottom of captures of *Bathyteuthis abyssicola* in the Antarctic Ocean.

depths the captures were made farther from the bottom, which indicates that this species inhabits a particular zone in the sea in relation to the surface and not to the bottom.

The points along the left and upper edges of the scatter diagram beginning at 500 m above the bottom and 3000 m depth represent the maximum depths of capture for *B. abyssicola.* The points on the right and lower edges of the scattergram represent shallowest captures. Most captures were made in water between 3000 and 5000 m deep, and most ranged from 1400 to 3800 m above the bottom.

Only one capture occurred where the bottom was less than 2500 m deep: the tow was made 1100 m above the bottom at a bottom depth of 1650 m along the edge of the Peru Current off southern Chile. The bottom descends very steeply in that area, and possibly the capture was made over deeper water a short distance from the point of the sounding or the specimen was carried inshore by currents.

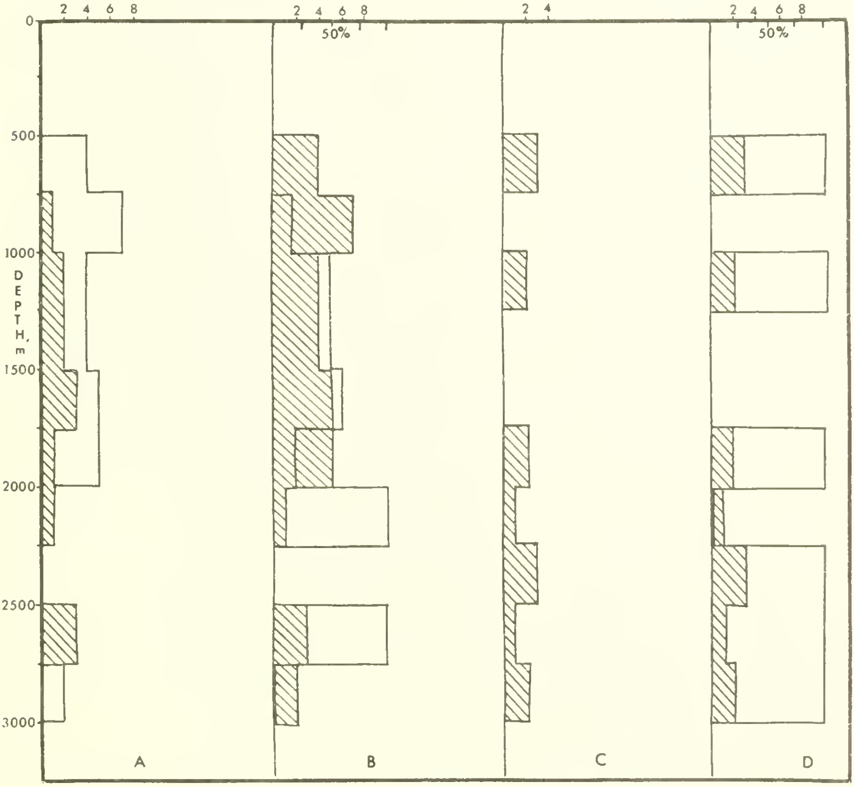
Two factors must be considered. Because of the possibility of the midwater trawl fouling, it is generally not set to fish close to the bottom, so the indication that *B. abyssicola* does not often occur closer than about 1000 m from the bottom may merely be a reflection of cautious trawling techniques. In addition, tows deeper than 3000 m are rare from the *Eltanin* because they require such a long time to complete.

The chart of geographical distribution of *Bathyteuthis* (fig. 50) shows that captures are generally made well offshore over deep water. Captures that are plotted relatively close to shore are in areas where the bottom drops off steeply, e.g., along the western coasts of continents (South and Central America, West Africa, Southern California). If *B. abyssicola* is found inshore in shallow water it is probably because currents have swept it out of its normal deep habitat. This is undoubtedly the case with the single specimens taken by the *Pelican II* and the *Silver Bay* in the northern Straits of Florida. In regard to the Straits of Florida another possibility exists. Some evidence indicates that specimens of normally deep-living species in the Caribbean and Atlantic are forced up into the relatively shallower water over the 800 m sill between Florida and the Bahama Banks. In any case, *B. abyssicola* normally is not associated with the bottom in any direct way.

Aspects of Regional Distribution and Relative Abundance

1. Regional Occurrence

Bathyteuthis abyssicola is common throughout the Antarctic, but is not equally abundant in all areas. Furthermore, within particular areas its abundance is dependent upon its proximity to the Antarctic Convergence Zone. Table XII gives a breakdown of successful tows and average catch by areas; Table XIII gives the number and percent of successful tows at various depths by area. Figures 66 through 68 are graphic representations of the data. The plots of distribution on the vertical sections along selected meridians also illustrate the points of the discussion (figs. 21 to 36). The term Antarctic Convergence is used in this section to refer to a general area of the ocean that underlies the Antarctic Convergence Zone and is not used in the restricted sense in reference to the oceanographic phenomenon at a point on the surface. "Total tows" refers to all the tows made at depths greater than 500 m, because 100 3-meter IKMT tows were made at depths of less than 500 m throughout the Antarctic during the period covered by this study, and not a single specimen of *B. abyssicola* was captured. (Three exceptions have occurred since Cruise 19 and these are discussed elsewhere.)



FIGURES 66.—A, C, Total number of 3-meter IKMT tows (clear area) and number of successful tows (hatched area) at 250-meter depth increments in the Atlantic sector of the Antarctic Ocean (A) and in the Peru Current (C). B, D, Percentages (clear area) of total number of 3-meter IKMT tows (hatched area) that caught *Bathyteuthis abyssicola* at 250-meter increments in the Atlantic sector of the Antarctic Ocean (B) and in the Peru Current (D).

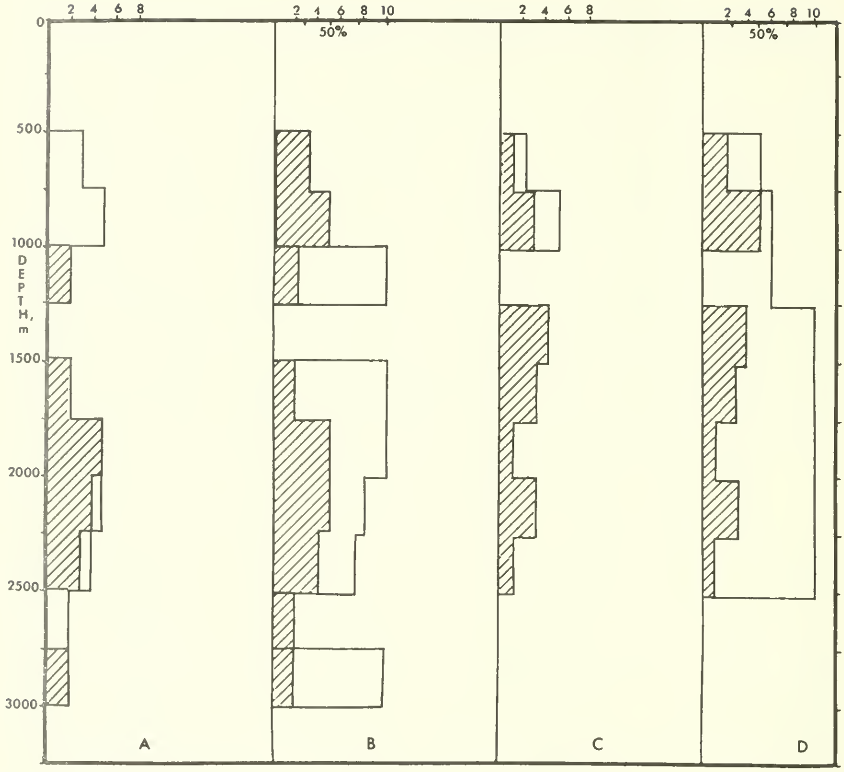


Figure 67.—A, C, Total number of 3-meter IKMT tows (clear area) and number of successful tows (hatched area) at 250-meter increments in the Drake Passage (A) and Drake Passage Convergence (C). B, D. Percentages (clear area) of total number of 3-meter IKMT tows (hatched area) that captured *Bathyteuthis abyssicola* at 250-meter increments in the Drake Passage (B) and Drake Passage Convergence (D).

In the Atlantic sector of the Antarctic Ocean 12 successful tows were made from a total of 34 tows; the tows, 35.2% successful, averaged 0.82 specimens per total tow. Under the Convergence Zone only three tows were attempted; all were successful and averaged 1.67 specimens per tow (Table XII). Only 1 of 11 tows between 500–1000 m in the Atlantic sector was successful, while 4 of the 8 tows between 1000–1500 m were successful. The few deeper tows attained 100% success in the 2000–2250 m range, but this was offset by the unproductive shallow tows (Table XIII, fig. 66A, B). The combined success of Atlantic tows was 40%.

In the Drake Passage 16 (55%) of the 29 tows were successful in catching *B. abyssicola* for an average of 1.65 specimens per total tow. Fifteen of eighteen tows (83.5%) in the Drake Passage Convergence

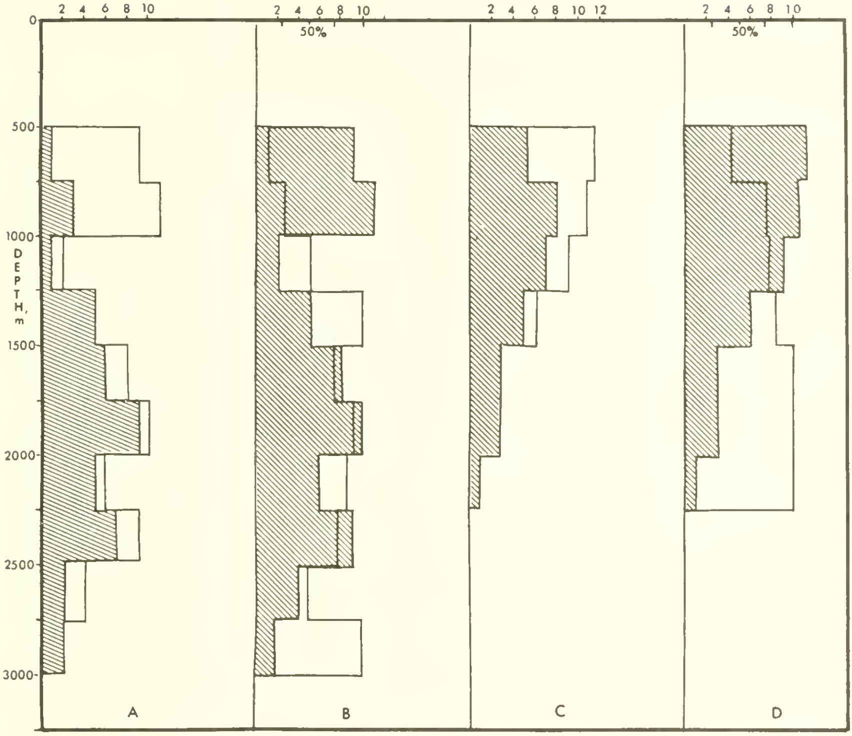


FIGURE 68.—A, C, Total number of 3-meter IKMT tows (clear area) and number of successful tows (hatched area) at 250-meter increments in the South Pacific (A) and South Pacific Convergence (C) regions of the Antarctic Ocean. B, D, Percentages (clear area) of the total number of 3-meter IKMT tows (hatched area) that captured *Bathyteuthis abyssicola* at 250-meter increments in the South Pacific (B) and South Pacific Convergence (D) regions of the Antarctic Ocean.

were successful and averaged 4.85 specimens per total tow, a considerable increase over the area to the south. In the Drake Passage no captures were made in eight tows to less than 1000 m, whereas four of seven tows at the same depths in the Drake Passage Convergence caught *B. abyssicola.* No tows were made between 1000–1250 m in the Drake Passage Convergence, but every tow (12) below 1250 m was successful; success was slightly less complete below 1250 m in the Drake Passage (figs. 67A–D). Therefore, in the convergence zone the tows were more successful and caught more specimens. The combined success of the two Drake Passage areas was 66%.

The South Pacific region produced 42 successful catches (65.6%) from 64 tows. The average catch was 3.28 specimens per total tow. Forty-three tows in the South Pacific Convergence yielded 30 successes or 69.8% of the total for the region, only slightly higher than in the

TABLE XII.—*Number of successful 3 m IKMT tows and average catch of* B. abyssicola *in different regions of the Antarctic Ocean*

Area	*Number successful tows*	*Number unsuccessful tows*	*Total tows*	*Percent successful*	*Total specimens from 2-hr. tows*	*Average number/ successful tow*	*Average number/ total tows*
S Atlantic (Scotia Sea)	12	22	34	35.2	28	2.34	0.82
Atlantic Convergence	3	–	3	100.0	5	1.67	1.67
Drake Passage	16	13	29	55.0	48	3.0	1.65
Drake Passage Convergence	15	3	18	83.5	87	5.8	4.85
South Pacific	42	22	64	65.6	203	4.78	3.28
South Pacific Convergence	30	13	43	69.8	151	5.04	3.52
Humboldt (Peru Current)	12	1	13	92	57	4.75	4.38
N of Atlantic Conv.	1	6	7	14.3	2	2.00	0.29
N of Pacific Conv.	3	5	8	60	17	2.66	2.12

TABLE XIII.—*Percentage of successful 3 m IKMT tows at 250 m increments in different regions of the Antarctic Ocean*

*Depth, meters	DP		DPC		SP		SPC		SA		H		NCA		NCP	
	s	u	s	u	s	u	s	u	s	u	s	u	s	u	s	u
500–750	0	3	1	1	1	8	5	7	0	4	3	0	0	4	0	1
	0		50		11		42		0		100		0		0	
751–1000	0	5	3	2	3	8	8	3	1	6	0	0	0	0	0	0
	0		60		27		73		17		–		–		50	
1001–1250	2	0	0	0	1	1	7	2	2	2	2	0	0	0	0	0
	100		–		50		78		50		100		–		–	
1251–1500	0	0	4	0	5	0	5	1	2	2	0	0	2	1	0	0
	–		100		100		84		50		–		67		–	
1501–1750	2	0	3	0	6	2	3	0	3	2	0	0	0	1	0	0
	100		100		75		100		60		–		0		–	
1751–2000	5	0	1	0	9	1	3	0	1	4	2	0	0	0	0	0
	100		100		90		100		20		100		–		–	
2001–2250	4	1	3	0	5	1	1	0	1	0	0	1	0	0	1	1
	80		100		84		100		100		0		–		50	
2251–2500	3	1	1	0	7	2	0	0	0	0	3	0	0	0	0	1
	75		100		78		–		–		100		–		0	
2501–2750	0	2	0	0	2	2	0	0	3	0	1	0	0	0	1	1
	0		–		50		–		100		100		–		50	
2750–3000	2	2	0	0	2	0	0	0	0	2	2	0	0	0	0	0
	100		–		100		–		0		100		–		–	

*The figures in the upper row of each increment represent the number of successful (s) and unsuccessful (u) tows; the lower figure is the percent of success. DP = Drake Passage; DPC = Drake Passage Convergence; SP = South Pacific; SPC = South Pacific Convergence; SA = South Atlantic; H = Humboldt Current; NCA = North of Atlantic Convergence; NCP = North of Pacific Convergence.

region to the south. The average catch, 3.52 specimens per total tow, was also only slightly higher. The major differences are seen in the distribution of successful catches with depth; in the South Pacific tows between 500–1250 m were less successful than tows to the same depths in the South Pacific Convergence (fig. 68A–D). Below 1250 m the percentage of success was generally quite high. So each region in the South Pacific had nearly equal success in averaging about the same catch, although the values for the convergence region were slightly higher. The two areas had 68% success of the total tows.

Thirteen tows were made in the Humboldt (Peru) Current, and twelve of them (92%) succeeded in capturing *B. abyssicola*. The 12 tows produced 57 specimens for an average of 4.38 specimens per total tow. All depths to which tows were made yielded 100% success except the 2000–2250 m zone where the sole unsuccessful tow was made (fig. 66C, D). The number of tows in the region of the Peru Current is not large, but the degree of success attained and the number of specimens captured excels the performance of tows in the regions of the Southern Ocean.

In summary, the Drake Passage and the South Pacific regions had about the same overall success of captures (66–67%) but the distribution of successful catches and number of specimens between regions was disproportionate: 83.5% successful with 4.85 specimens per total tow for the Drake Passage Convergence versus 55% and only 1.65 specimens per total tow for the Drake Passage. The South Pacific and South Pacific Convergence regions both yielded many successful tows (65.6–69.8%) that averaged 3.28 to 3.52 specimens per total tow. The Atlantic sector was not fruitful in comparison; only 40% of the tows were successful. All tows (3) in the convergence zone were successful, but they averaged only 1.67 specimens per tow. A meager 35.2% of the tows in the Scotia Sea region produced a scant 0.82 specimens per total tow.

Therefore, up to a 6-fold difference in abundance of *B. abyssicola* exists between different areas of the Antarctic. The Drake Passage Convergence and the Peru Current are the areas of peak abundance followed by the nearly equal South Pacific regions. The Drake Passage and the Atlantic Convergence regions yield about the same low average catch. (The data for the Atlantic Convergence are so few that the picture may change if more material becomes available.) The Scotia Sea, in relation to other areas, is nearly a desert for *B. abyssicola*.

2. Influence of a Few Exceptional Tows

During the *Eltanin* cruises under discussion (3–6; 8–10; 13–15; see Appendix) a total of 236 3-meter IKMT tows was made below 500 m in the depth range of *B. abyssicola*; of these, 134 (57%) were successful in capturing this species (100 tows shallower than 500 m were entirely unsuccessful). The captures averaged 2.5 specimens per total 2-hour tow, and they ranged from 1 to 24 specimens per tow. Several tows caught large numbers of *B. abyssicola;* these have a pronounced effect on the overall catch figures. Sixteen 2-hour tows that caught 9 or more specimens captured a total of 210 specimens. This means that 11.8% of the 134 successful 2-hour tows accounted for 35.2% of the total sample. All but two of these stations were located in regions of the Antarctic Convergence. The specimens are grouped at the peaks of occurrence on the vertical distribution chart, and, in fact, they are responsible for these peaks. Only one capture was in less than 1000 m (914 m) and only two were deeper than 2100 m (2150 m, 2269 m). Table XIV compares the total number of specimens captured at depth intervals with the number taken in exceptionally successful tows and indicates the influence of these tows on the distribution of the total sample population. The major effect of the exceptional tows is apparent when they are deleted from the curve of the bathymetric distribution. This results in the smoothing out of the curve so that the peaks of abundance shift from sharp, bimodal peaks at 1000–1500 m and 1750–2250 m to a single major peak at the 1750–2000 m range with very slight secondary peaks above and below this depth increment (fig. 69). The large number of specimens from relatively few tows does not mean that the concept of the vertical distribution of the total population has to be altered; instead it indicates that *B. abyssicola* has a patchy distribution, both horizontally and vertically with peaks of abundance located under the region of the Antarctic Convergence.

TABLE XIV.—*The influence of exceptionally successful tows on the total sampte population*

Depth, meters	*A* *Total number specimens/2-hour tow*	*B* *Number specimens from tows with >9 specimens*	*C* *Percent of total*	*D* *A minus B*
500–750	30	0	0	30
750–1000	51	13	25.5	38
1000–1250	97	68	70.2	29
1250–1500	75	27	36.0	48
1500–1750	58	0	0	58
1750–2000	129	58	44.9	71
2000–2250	72	35	48.6	37
2250–2500	53	9	17.0	44
2500–2750	19	0	0	19
2750–3000	14	0	0	14

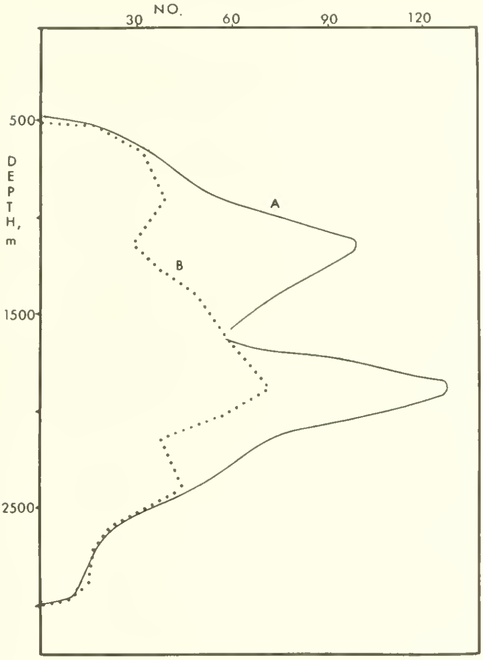


FIGURE 69.—Influence on curve of vertical distribution of 16 tows that caught 9 or more specimens. A, curve for total sample population; B, curve exclusive of the 16 exceptional tows. Antarctic.

3. Seasonal Abundance

Although seasonal data are incomplete, there is some indication of seasonal fluctuation in the abundance of *B. abyssicola.* Of the 16 tows that captured more than 9 specimens (totaling 210 specimens), 12 were taken during October, November, and December (5, 5, and 2 tows respectively), 3 were taken in August and September, and 1 was taken in July (well north of the convergence) (Table XV). No such large captures were taken between April and July. Furthermore, a breakdown of successful to unsuccessful tows by months indicates that more tows were successful during the austral late spring and early summer months. During October, November, and December there were 74 successful tows and 40 unsuccessful tows, a success rate of 65% or nearly 2 to 1. During August and September there were 34 successful tows and 22 unsuccessful tows, for 60% success, or 1.5 to 1. In April through July there were 20 successful and 27 unsuccessful tows for a success rate of 42% or 0.74 to 1. These winter values, however, may be more a factor of locality than of season, because one cruise is primarily responsible for the reverse of the successful to unsuccessful ratio. Cruise 8 took place during April and May

TABLE XV.—*Seasonal and regional occurrence of the 16 tows that caught 9 or more specimens per 2-hour tow*

Elt. Sta. Number	*Month*	*Number specimens*	*Depth, meters*	*In Convergence region*
99	VII	10	1210	No
1201	VIII	20	1120	Yes
1262	VIII	14	1230	Yes
1269	IX	24	1248	Yes
248	X	12	1370	Yes
1287	X	9	2269	No
1324	X	15	1958	Yes
1327	X	9	2060	Yes
1328	X	11	1775	Yes
846	XI	12	1866	Yes
847	XI	9	1991	Yes
858	XI	12	2099	Yes
1364	XI	11	1848	Yes
1383	XI	13	914	Yes
354	XII	14	2150	Yes
382	XII	15	1280	Yes

in the Scotia Sea region with the poor success to unsuccessful ratio of 6 to 20 or only 23% successful. This region has been shown to be sparsely populated with *B. abyssicola*, so the low success may be related to area. On the other hand, Cruise 9 covered the same general area in August and September and it scored an 8:7 success ratio (53%), still fairly low in comparison with other areas, but it may indicate an increase in abundance during the austral spring. Unfortunately, no further data are available for this region. The remaining winter tows were made in the Drake Passage and the South Pacific and these amounted to 14 successful tows and 7 unsuccessful tows for a 66% success rate, equally as successful as spring and summer tows.

It appears then that *B. abyssicola* can be caught with about the same frequency of success in most regions of the Antarctic during most of the year. But the data suggest that more individuals are present during the austral spring and summer or at least that they tend to congregate in patches in the region of the convergence. This suggests a correlation with the spring-summer peak of high organic productivity in the surface waters of the Antarctic Ocean.

No evidence exists to suggest that there are significant differences in the size of *B. abyssicola* over the seasons. Specimens of all sizes and all stages of maturity have been taken throughout the year; often specimens that range from larvae through juvenile and maturing stages, to ripe and spent individuals occur in the same trawl-haul. Few tows that catch more than 2 or 3 specimens have all individuals of the same size or stage of maturity, unless they are shallow tows which tend to have predominantly larvae and juveniles. The 16 tows that caught more than 9 specimens per 2-hour tow had the following composition in order from greatest to least abundance: five tows had ripe, maturing, juvenile, and spent stages that ranged in size from 14–56 mm ML; three tows had ripe, maturing, and spent individuals 25–56 mm ML; five tows had nearly equal numbers of juvenile, maturing, and ripe specimens 14–48 mm ML; two tows had ripe and maturing specimens 26–54 mm ML of which the ripe were 2½ times more numerous; one tow had even numbers of juvenile and larval specimens that ranged from 8–21 mm ML.

4. Size-Frequency Distribution

The composition of the sample population from the Antarctic by size is represented in the frequency distribution histograms (figs. 70 and 71). The standard for size, mantle length, has been plotted in 3 mm increments for 598 individuals for the total sample population (fig. 70) and 287 males and 284 females for the plot by sex (fig. 71). The plots for the populations are moderately skewed. Few small lar-

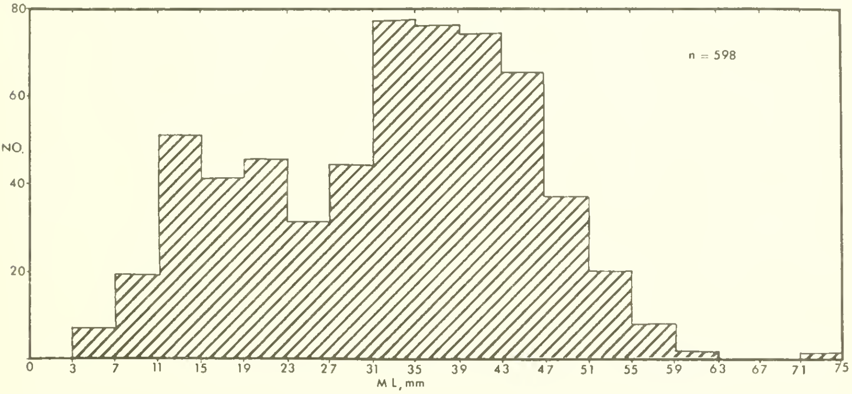


Figure 70.—Size-frequency distribution of total sample population of *Bathyteuthis abyssicola* from the Antarctic Ocean; n = 598.

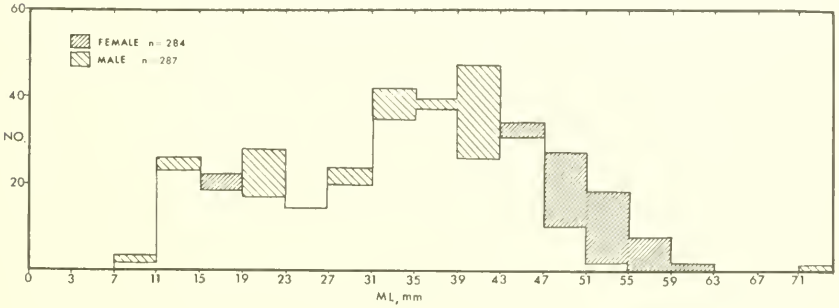


Figure 71.—Size-frequency distribution of males (n = 287) and females (n = 284) of *Bathyteuthis abyssicola* from the Antarctic Ocean.

vae are present in the 4–11 mm size range, but the plot for larger larvae and juveniles (12–23 mm) constitutes a secondary peak in the curve, with a large number of individuals in the 12–15 mm category. The slight depression between 24–31 mm represents individuals in the maturing stage. Most males, particularly by 28–31 mm, are ripe, but females are only in the beginning of the maturing stage. The major peak in the sample population is composed of individuals from 32–47 mm in ML; in this range all the males are ripe and the females are maturing and ripe. At about 48 mm the population, composed of ripe males and ripe and spent females, decreases rapidly in numbers. Therefore, the portion of the sample population that occurs with the greatest frequency has individuals that are near or in the spawning conditions.

Although the sex ratio of males to females in the overall population is 1:1, some marked differences occur within certain size groups. In general, there are a few more males than females in the juvenile and maturing stages up to the 28–31 mm category. There are several more males than females in the 32–39 mm group where all the males are ripe and the females are maturing or ripe. A large difference occurs in the 40–43 mm increment where there are 47 males and 26 females; i.e., only 36% of the specimens in this category are females. A sudden reversal of the predominance of males occurs above the 40–43 mm increment. Only a few more females than males exist in the 44–47 mm class, but above that the males drop off sharply in numbers so that in the 48–51 mm and 52–55 mm categories males represent only 27% and 10% of the specimens. The 56–59 mm and 60–63 mm size groups contain only females; no specimens occur between 64 and 75 mm, but the largest *B. abyssicola* recorded is a male of 75 mm mantle length.

Such a preponderance of females over males in the larger sizes is curious. Apparently, males do not generally grow as large as females, although the single "giant" specimen at least partially contradicts this conclusion. Males mature early and some may have fully developed spermatophores and packed Needham's sacs at about 25 mm mantle length. All males above 28–30 mm are fully ripe. On the other hand, females generally are not ripe until about 40 mm and often not until 45–48 mm.

Size differences between the sexes of other adult squid have been noted, primarily in loliginids (review in Roper, 1965). Adam (1952) noted that the males of *Illex illecebrosus coindetii* were smaller than the females, and this is borne out in IMS specimens from the Gulf of Guinea. We have also observed, though not tabulated, that males of *Ommastrephes pteropus* tend to be smaller than females; none of the numerous large specimens are males. Garcia-Tello (pers. comm.) of the Estacion Biologia Marina in Monte Mar, Chile, informs me that the same phenomenon exists in the Humboldt squid, *Dosidicus gigas*. Finally, our observations on *Architeuthis*, as sparse as they are, indicate that the males mature at a much smaller size than the females, and apparently they do not attain the larger size of the females. All of these species are oceanic forms that live mostly in the upper water layers. Until now information on size differences between sexes in deep-sea forms has been entirely lacking.

A priori it would seem that once the males of the forms mentioned have fully developed spermatophores packed in Needham's sac, no biological necessity would exist for attaining a larger size, so long as small size did not render the males incompatible with the larger females.

Another presently unempirical possibility is that large males of *B. abyssicola* are able to escape the net, while females, all fully ripe at the larger size, are unable to avoid capture. *B. abyssicola*, however, is generally a poor swimmer; it is not equipped for rapid motion, and it is difficult to imagine that even the "sleek" males could be significantly more agile than the females to avoid being captured.

5. Comparison of Antarctic and Gulf of Guinea Tows

A rough estimate of the relative abundance of *Bathyteuthis* in different parts of its range can be made by comparing trawl-catches between two different regions. Midwater trawl tows were made during the two cruises of the R/V *Pillsbury* to the Gulf of Guinea; this material gives the only available information that can be used to compare with the *Eltanin* tows. Unfortunately, no vessel has conducted a survey that adequately compares with the program on the *Eltanin*. Therefore, the data from the *Pillsbury* are offered only as a preliminary indication of relative abundance.

Table XVI is a summary of tows and catches made by the *Pillsbury* in the Gulf of Guinea and the *Eltanin* in the Antarctic. In brief, the *Pillsbury* tows that were set at depths (300 to 3000 m) where *B. abyssicola* might be caught were 17% successful; in the Antarctic 52% of the tows in the same depth range was successful. This figure includes 28 tows in less than 500 m where *B. abyssicola* normally does not occur in Antarctic waters. The captures in the Gulf of Guinea averaged 0.21 specimens per total tows, while those in the Antarctic averaged 2.3 specimens per total tows. (The difference is even greater if the 300–500 m column is omitted.) Again, the *Pillsbury* data are meager in comparison with the *Eltanin* data, but they reflect relative numbers of *B. abyssicola* in Antarctic and Guinean waters. *Eltanin* tows were three times more successful than *Pillsbury* tows and they captured 10 times the number of specimens. This may be a reasonable estimate because, although no data from other vessels are available, a great amount

TABLE XVI.—*Summary of 3-meter IKMT tows made by R/V* Pillsbury *and USNS* Eltanin

Depth Range	*300–500*	*500–1000*	*1000–1500*	*1500–2000*	*2000–2500*	*2500–3000*	*Total*	
Pillsbury:								
Total tows	11	10	4	1	1	2	29	
No. successful	2	0	1	1	0	1	5	
% successful	18	0	25	100	0	50	17	
No. specimens	2	0	1	1	0	2	6	
Average/tow	0.18	0	0.25	1	0	1	0.21	
Eltanin:								
Total tows	28	90	44	47	36	18	263	*235
No. successful	0	25	32	39	28	12	136	136
% successful	0	28	73	80	78	66	52	58
No. specimens	0	81	172	187	125	33	598	598
Average/tow	0	0.90	3.9	4.0	3.5	1.8	2.3	2.6

*Data exclusive of the 300–500 m range where *B. abyssicola* is not represented.

of exploratory fishing with midwater trawls has been conducted in the Atlantic Ocean, and the records of *Bathyteuthis* are disproportionately small. The IMS Museum houses the collections of *Gerda*, *Pillsbury*, *Oregon*, *Dana*, etc., representing thousands of tows, and only a few specimens of *B. abyssicola* are among them. Furthermore, I have searched the collections of pelagic material at Woods Hole Oceanographic Institute, at the Museum of Comparative Zoology, and at the U.S. National Museum and have found only one or two specimens. The conclusion is that *B. abyssicola* is not abundant in the Atlantic; it is found mostly in regions of relatively high productivity (e.g., eastern tropical waters).

Comparisons With Other Species; Abundance and Distribution

Bathyteuthis abyssicola is the most abundant cephalopod that has been taken during the *Eltanin* cruises. Nearly 600 specimens are represented in the material studied through Cruise 15. The species is so common in midwater tows that personnel returning from cruises show little enthusiasm about having caught so many specimens and about having been able to observe these bathypelagic animals alive in aquaria. This discussion considers the three species that follow *B. abyssicola* in abundance.

1. *Crystalloteuthis glacialis* Chun, 1906

Crystalloteuthis glacialis has been reported only three times in the literature: originally by Chun (1906), in Chun's *Valdivia* monograph

(1910), and finally by Dell (1959). Dell gives the distribution of the species in the Antarctic as between 40°E and 143°E in 750–1710 m. The geographic range is now extended in Antarctic water throughout the range covered by the *Eltanin* from about 25°W to 160°W, and it undoubtedly extends throughout the entire Circumpolar Water Mass.

Through Cruise 15 a total of 349 specimens of *C. glacialis* was taken, 231 by 3-meter IKMT and the remainder by other gear, principally the 1-meter IKMT. It is second to *B. abyssicola* in abundance in Antarctic waters. Table XVIII gives the breakdown of captures by 250 m depth increments. A total of 598 specimens of *B. abyssicola* was captured during the same period, mostly by 3-meter IKMTs (Table XVII). Therefore, in total numbers, *B. abyssicola* is about 1.7 times more common than *C. glacialis*, and in midwater trawl-hauls it is about 2.5 times more abundant.

TABLE XVII.—*The composition of the sample population of* Bathyteuthis abyssicola *Hoyle, 1885, by 250 m increments; success of trawl hauls and average catches*

Depth captured, meters	*Number specimens/ 2-hr. tow*	*Total number tows*	*Number successful*	*Number unsuccessful*	*Average number specimens/ successful tow*	*Percent successful*	*Average number specimens/ total tows*
0–250	–	72	–	72	–	–	–
251–500	–	28	–	28	–	–	–
501–750	30	45	10	35	3.0	22.2	0.6
751–1000	51	45	15	30	3.4	33.3	1.1
1001–1250	97	20	14	6	6.9	70.0	4.7
1251–1500	75	22	18	4	4.2	82.0	3.4
1501–1750	58	23	18	5	3.2	74.8	2.5
1751–2000	129	24	21	3	6.1	87.5	5.4
2001–2250	72	17	13	4	5.5	71.5	4.2
2251–2500	53	19	14	4	3.7	78.9	2.7
2501–2750	19	11	6	5	3.2	54.5	1.7
2751–3000	14	7	6	2	2.4	71.4	1.7
3001–3250	–	–	–	–	–	–	–
3251–3500	–	3	–	3	–	–	–
	598	336	134				

Vertical distribution is plotted on the graph (fig. 72) and presented in Table XVIII. The bulk of the sample population is concentrated between 500 and 1000 m where about 57% of the specimens occur. Nearly 69% live between 250 m and 1250 m. Below 1000 m a sharp decrease in number exists and about an equal number of specimens occurs in the remaining depth increments, making it difficult to establish the lower depth limit. It could be as deep as 2000–2500 m, but probably the limit is much shallower, perhaps around 1000–1500 m

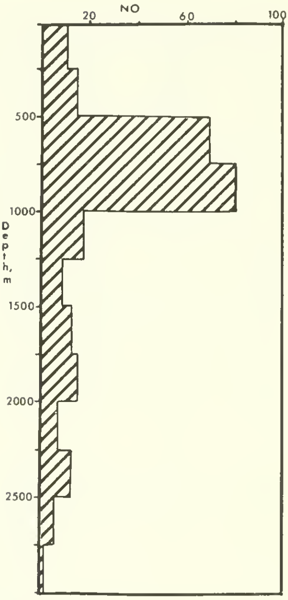


FIGURE 72.—Vertical distribution by 250-meter increments of the total sample population of *Crystalloteuthis glacialis* Chun, 1906. Antarctic.

just below the sharp decrease in catch. The average number of specimens per tow for the total tows ranges from a minimum of 0.14 at the shallowest and deepest depth intervals to maximums of 1.58 and 1.78 in the 500–1000 m increments.

Although considerable overlap exists in the vertical ranges of *C. glacialis* and *B. abyssicola*, the zones of maximum abundance are distinct, the former species between 500–1000 m and the latter between 1000–2250 m. *B. abyssicola*, however, is associated with *C. glacialis* more than with any other pelagic Antarctic cephalopod. The two species frequently are caught in the same tow, but these generally are tows that have fished deeper than 1000–1500 m into the zone of abundance of *B. abyssicola.*

Perhaps the most distinctive feature of the distribution of *C. glacialis* is that it is strictly limited in its northward extent by the location of the Antarctic Convergence. This is truly an Antarctic squid that is found extremely rarely north of the convergence, and then only as a straggler. It is found in the convergence zone but especially south of the convergence in the Circumpolar Water Mass. The details of the distribution must await a more thorough analysis, but at least the boundaries are clear. In fact, *C. glacialis* can be used as an indicator species; aboard *Eltanin* the location of the Antarctic Convergence can

TABLE XVIII.—*The composition of the sample population of* Crystalloteuthis **glacialis** *Chun, 1906, by 250 m increments; success of trawl hauls and average catches*

Depth captured, meters	*Number specimens/ 2-hour tow*	*Actual number of specimens*	*Total number tows*	*Number successful*	*Number unsuccessful*	*Average number specimens/ successful tow*	*Percent successful*	*Average number specimens/ total tows*	*Percent of total 2-hour population*
0–250	10	6	72	3	69	3.3	4.2	0.14	3.8
251–500	15	15	28	10	18	1.5	36.7	0.54	5.8
501–750	71	61	45	19	26	3.7	42.2	1.58	27.3
751–1000	80	71	45	17	28	5.2	37.8	1.78	30.8
1001–1250	19	14	20	7	13	2.7	35.0	0.95	7.3
1251–1500	9	9	22	5	17	1.8	22.7	0.41	3.5
1501–1750	14	17	23	5	18	2.8	21.7	0.61	5.4
1751–2000	15	12	24	9	15	1.7	37.6	0.62	5.8
2001–2250	8	8	17	2	15	4.0	11.8	0.47	3.1
2251–2500	13	13	19	8	11	1.6	42.0	0.68	5.0
2501–2750	5	4	11	4	7	1.2	36.4	0.45	1.9
2751–3000	1	1	7	1	6	1.0	14.3	0.14	0.4
	260	231	336	90	246				

TABLE XIX.—*The composition of the sample population of* Brachioteuthis picta *Chun, 1910, by 250 m increments; success of trawl hauls and average catches*

Depth captured, meters	*Number specimens/ 2-hour tow*	*Actual number of specimens*	*Total number tows*	*Number successful*	*Number unsuccessful*	*Average number specimens/ successful tow*	*Percent successful*	*Average number specimens/ total tows*	*Percent of total 2-hour population*
0–250	82	80	72	17	55	4.8	23.6	1.14	41.0
251–500	22	21	28	9	19	2.4	32.0	0.79	11.0
501–750	21	18	45	12	33	1.8	26.7	0.47	11.0
751–1000	34	29	45	15	30	2.3	33.3	0.76	17.0
1001–1250	7	7	20	5	15	1.4	25.0	0.35	3.5
1251–1500	6	6	22	5	17	1.2	22.7	0.27	3.0
1501–1750	10	10	23	6	17	1.8	26.0	0.43	5.0
1751–2000	10	8	24	5	19	2.0	20.8	0.42	5.0
2001–2250	5	4	17	2	15	2.5	8.5	0.29	2.5
2251–2500	1	1	19	1	18	1.0	5.2	0.05	0.5
2501–2750	–	–	11	–	11	–	–	–	–
2751–3000	1	2	7	1	6	1.0	–	–	–
	199	186		78					

be determined by the presence or absence of this species in the IKMT tows.

While both the vertical and horizontal ranges of these two species overlap to a certain extent, *C. glacialis*, truly an Antarctic species, is more limited and apparently is unable to survive in the conditions that exist in the subantarctic regions. *B. abyssicola*, on the other hand, may occur together with *C. glacialis*, but it possesses far greater flexibity in its tolerance to different oceanographic conditions and is much more broadly distributed.

2. *Brachioteuthis picta* Chun, 1910

Next in abundance is *Brachioteuthis picta* Chun, 1910, represented by 190 specimens (Table XIX, fig. 73). Specimens of *Bathyteuthis abyssicola* taken during the same period were 3.1 times more abundant than *Brachioteuthis picta.* The vertical ranges of the two species overlap slightly between 500–1000 m. In *Brachioteuthis picta* 41% of the population inhabits the upper 250 m and 28% lives between 500–1000 m; 80% lives between the surface and 1000 m. A rapid decrease in numbers occurs below 1000 m, and the remaining 20% of the sample population is spread evenly between 1000 and 2250 m. Undoubtedly

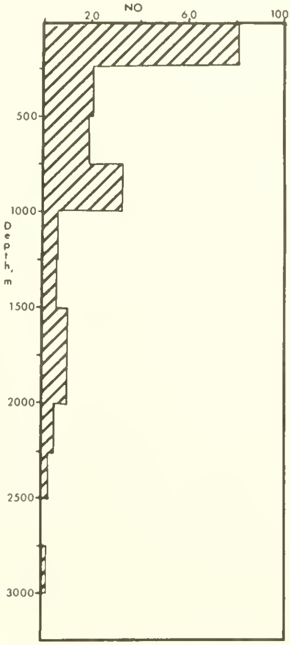


FIGURE 73.—Vertical distribution by 250-meter increments of the total sample population of *Brachioteuthis picta* Chun, 1910. Antarctic.

TABLE XX.—*The composition of the sample population of* Gonatus antarcticus *Lönnberg, 1897, by 250 m increments; success of trawl hauls and average catches*

Depth captured, meters	*Number specimens/ 2-hour tow*	*Actual number of specimens*	*Total number tows*	*Number successful*	*Number unsuccessful*	*Average number specimens/ successful tow*	*Percent successful*	*Average number specimens/ total tows*	*Percent of total 2-hour population*
0–250	77	81	72	5	67	15.4	6.9	1.1	55.0
251–500	4	4	28	2	26	2.0	7.7	0.14	2.9
501–750	8	8	45	4	41	2.0	8.9	0.18	5.7
751–1000	30	30	45	3	42	10.0	6.7	0.66	21.4
1001–1250	1	1	20	1	19	1.0	5.0	0.05	0.7
1251–1500	6	6	22	2	20	3.0	9.1	0.30	4.3
1501–1750	2	1	23	1	22	2.0	4.3	0.09	1.4
1751–2000	3	2	24	2	22	1.5	8.3	0.12	2.3
2001–2250	6	6	17	2	15	3.0	11.7	0.35	4.3
2251–2500	–	–	19	–	19	–	–	–	–
2501–2750	3	2	11	2	9	1.5	18.2	0.33	2.3
2751–3000	–	–	7	–	7	–	–	–	-
	140	141		24					

many of these were captured while the nets were passing through the shallow layer of abundance, and the lower limit for *Brachioteuthis picta* is probably much shallower than 2250 m, perhaps around 1000 m.

3. *Gonatus antarcticus* Lönnberg, 1897

The only other pelagic cephalopod that has been caught in the Southern Ocean in any quantity is *Gonatus antarcticus* Lönnberg, 1897. A total of 141 specimens was captured during the same period that 598 specimens of *B. abyssicola* were taken. Therefore, the relative abundance for specimens captured by all means is 4.2 specimens of *B. abyssicola* to each *Gonatus antarcticus. G. antarcticus* is primarily a shallow living form (Table XX, fig. 74); 55% of the sample population was taken in the upper 250 m; 30% was distributed between 250-1000 m. The sharp drop-off in catches between the 750–1000 m level and the 1000–1250 m level from 21.4% to 0.7% indicate that *G. antarcticus* does not normally live deeper than 1000 m and that the captures below that depth probably were made in the shallow zone of abundance.

It seems curious that the most abundant cephalopod in the Antarctic Ocean is a bathypelagic species that apparently outnumbers its closest rival nearly 2 to 1. The three most common species besides *B. abyssicola*

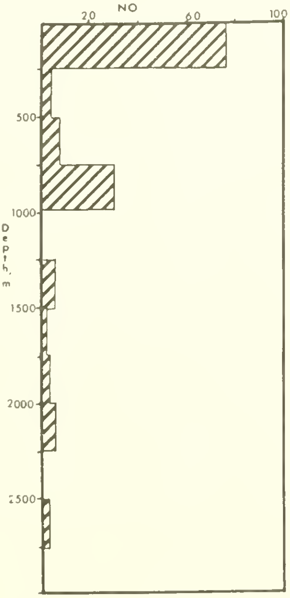


FIGURE 74.—Vertical distribution by 250-meter increments of the total sample population of *Gonatus antarcticus* Lönnberg, 1897. Antarctic.

are all relatively shallow-living forms that have 70% to 85% of their numbers in less than 1000 m; only 13% of all *B. abyssicola* captured occur in less than 1000 m. Taken together the three common shallower living species outnumber *B. abyssicola* by 13%. Assuming that the trawling gear is mutually selective, the implication is that the shallow end of the vertical range of *B. abyssicola* overlaps with the deeper parts of the ranges of *Crystallotheuthis glacialis*, *Brachioteuthis picta*, and *Gonatus antarcticus*, and that *B. abyssicola* replaces these three species in the greater depths.

Approximately 15 additional species of squid of the suborder Oegopsida were collected in Antarctic waters through Cruise 15 and their numbers total less than 250 specimens. The most common of these, *Alluroteuthis antarcticus* Odhner, 1923, is represented by 69 specimens. Deeper dwelling forms, e.g., species of *Mastigoteuthis*, *Chiroteuthis*, and *Histioteuthis*, are represented by fewer than two dozen specimens each.

Therefore, the dominance of *Bathyteuthis abyssicola* in the total known Antarctic cephalopod fauna, as well as among the bathypelagic inhabitants, is undisputed. It is a striking example of a species that occurs in small to moderate numbers over a broad geographical range but is so successfully adapted to a particular environment that it is the dominant species.

Summary and Conclusions

1. A historical résumé traces the systematics and distributional records of *Bathyteuthis abyssicola* Hoyle, 1885.
2. The name *B. abyssicola* Hoyle, 1885, is shown to have priority over *Benthoteuthis megalops* Verrill, 1885.
3. A redescription of *B. abyssicola* from the type region, the Antarctic Ocean, is presented; the species is illustrated in detail.
4. A study of morphometric features demonstrates the growth characteristics of *B. abyssicola.*
5. Two additional species of *Bathyteuthis*, *B. bacidifera* and *B. berryi*, are presented and illustrated from the eastern Pacific Ocean.
6. The taxonomic and morphometric characteristics of the species of *Bathyteuthis* are compared.
7. Distinct geographical variation exists between populations of *B. abyssicola* from the Antarctic, eastern Pacific, and Atlantic Oceans.
8. Characters that vary geographically include the number of suckers on the buccal lappets, the number of suckers on the arms, and the size of the gills.
9. Gill sizes are shown to be related to the oxygen content of the environment; large gills may be a mechanism for more efficient respiration in areas of low-oxygen availability; e.g., in the eastern tropical Pacific.
10. The relationship between *Bathyteuthis* and *Ctenopteryx* is examined and the family Ctenopterygidae is reinstated.
11. The familial relationships of the Bathyteuthidae to other groups of oegopsids are surveyed; the family exhibits no close relationships and holds a distinctive position within the Oegopsida.
12. The oceanographic features of the Antarctic Ocean are reviewed.
13. An analysis of the physicochemical parameters of the Antarctic Ocean (temperature, salinity, oxygen, and density) is presented on vertical sections along meridians 25°, 35°, 55°, 65°, 75°, 115°, 130°, 160° west and along 60° south latitude between 25° and 160° west.
14. The distribution of *B. abyssicola* in relation to these parameters in the Antarctic Ocean is analyzed.
15. The geographical distribution of *B. abyssicola* in relation to water masses in the oceans of the world is analyzed.

16. The three-dimensional distribution of *Bathyteuthis* is governed in part by physicochemical characteristics, but the primary limiting factor in the distribution of this bathypelagic species is a biological phenomenon: organic productivity. High organic production accounts for the abundance of specimens from the Southern Ocean, Peru Current, Gulf of Panama, eastern Atlantic, etc.
17. The vertical range of *B. abyssicola* in the Antarctic Ocean is determined to extend from 500 to 2500 m with a peak of abundance between 1000 and 2250 m.
18. Larvae and juveniles tend to live at shallower depths than adults. The occurrence of adults in the shallower end of the range is generally related to unusual oceanographic conditions, e.g., upwelling along the Antarctic Divergence.
19. *B. abyssicola*, a true bathypelagic squid, lives at least 1000 m above the ocean floor.
20. Although *B. abyssicola* occurs throughout the Antarctic Ocean it is not equally abundant in each region; its relative abundance is greatest in the Drake Passage Convergence, the southern Peru Current, the South Pacific and the South Pacific Convergence regions and least in the South Atlantic (Scotia Sea) region.
21. The relatively few tows that caught exceptional numbers of *B. abyssicola* were made during the austral spring and summer seasons in the convergence zones.
22. The size-frequency composition of the sample population consists of a major peak at 31 to 47 mm mantle length and a secondary peak at 11 to 23 mm ML.
23. The sex ratio of the total population is about 1:1, but males predominate below 43 mm ML and females greatly predominate above 47 mm ML.
24. A comparison of 3-meter IKMT catches reveals that tows in the Antarctic were three times more successful and caught ten times the number of *B. abyssicola* than tows in the Gulf of Guinea.
25. *B. abyssicola* is the most common pelagic cephalopod captured in Antarctic waters; the vertical ranges and the relative abundance of the three next most common species of oegopsids are compared with those of *B. abyssicola*. The ranges of these species overlap between 500–1000 m, but *B. abyssicola* replaces them at greater depths.

References

ABEL, O.

1916. Paläobiologie der Cephalopoden aus der Gruppe der Dibranchiaten. Gustav Fischer, Jena. 281 pp.

ADAM, W.

1952. Cephalopodes. Résult. Sci. Expéd. Oceanogr. Belge dans les eaux côtières Africaines de l'Atlantique Sud, vol. 3, fasc. 3, pp. 1–142.

1960. Cephalopoda from the Gulf of Aqaba. Contributions to the Knowledge of the Red Sea, no. 16. Bull. Sea Fish. Res. Station, Haifa, no. 26, pp. 1–27.

ALLAN, J.

1945. Planktonic cephalopod larvae from the eastern Australian coast. Rec. Australian Mus., vol. 21, no. 6, pp. 317–350.

BACKUS, R. H., MEAD, G. W., HAEDRICH, R. L., and EBELING, A. W.

1965. The mesopelagic fishes collected during Cruise 17 of the R/V *Chain*, with a method for analyzing faunal transects. Bull. Mus. Comp. Zool., Harvard, vol. 134, no. 5, pp. 139–158.

BAKER, A. deC.

1954. The circumpolar continuity of Antarctic plankton species. *Discovery* Rep., vol. 22, pp. 201–218.

BEEBE, W.

1926. The *Arcturus* Oceanographic Expedition. Zoologica, vol. 8, no. 1, pp. 1–45.

BERRY, S. S.

1912. Some necessary changes in cephalopod nomenclature. Science, vol. 36, no. 932, pp. 643–646.

1917. Cephalopoda. Australian Antarctic Exped. 1911–1914. Sci. Rep., ser. C. vol. 4, no 2, pp. 1–39.

BIERI, R.

1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnol. and Oceanogr., vol. 4, no. 1, pp. 1–28.

BRINTON, E.

1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., vol. 8, no. 1, pp. 51–270.

BRODIE, J. W.

1965. Oceanography. *In* Hatherton, T., ed., Antarctica. F. A. Praeger, New York, pp. 101–127.

BRUUN, A. F.

1943. The biology of *Spirula spirula* (L.). *Dana* Rep., no. 24, 46 pp.

1955. New light on the biology of *Spirula*, a mesopelagic cephalopod. Essays in the natural sciences in honor of Captain Allen Hancock, pp. 61–72. Univ. Southern California Press, Los Angeles.

1956. The abyssal fauna; its ecology, distribution and origin. Nature, vol. 177, pp. 1105–1108.

1957. Deep Sea and abyssal depths. Mem. Geol. Soc. America 67, vol. 1, pp. 641–672.

BULLETIN HYDROGRAPHIQUE

1932. Bulletin Hydrographique pour l'année 1931 publié par le bureau du Conseil service hydrographique. Conseil permanent international pour l'exploration de la Mer. Bull. Hydrogr., Copenhagen, 1932, pp. 46, 98–99, 108–109.

BULLIS, H. R., JR., and THOMPSON, J. R.

1965. Collections by the exploratory fishing vessels *Oregon*, *Silver Bay*, *Combat*, and *Pelican* made during 1956–1960 in the southwestern North Atlantic. Spec. Sci. Rep. U.S. Fish Wildl. Serv.—Fish. 510, 130 pp.

CARCELLES, A. R.

1953. Catalogo de la Malacofauna Antarctica Argentina. Anales del Museo Nahuel Huapi, vol. 3, pp. 155–250.

CHUN, C.

1903. Ueber Leuchtorgane und Augen von Tiefsee-Cephalopoden. Verhand. Deutschen zool. Ges., vol. 13, pp. 67–91.

1906. System der Cranchien. Zool. Anz., vol. 31, pp. 82–86.

1910. Die Cephalopoden. I. Teil: Oegopsida. Wiss. Ergebn. Deutschen Tiefsee-Exped. *Valdivia*, vol. 18, no. 1, pp. 1–410.

CLARKE, A. H., JR.

1962. Annotated list and bibliography of the abyssal marine mollusks of the world. Bull. Nat. Mus. Canada 181, 114 pp.

CLARKE, M. R.

1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol., vol. 4, pp. 91–300.

CLOWES, A. J.

1933. Influence of the Pacific on circulation in the southwest Atlantic Oceans. Nature, vol. 131, pp. 189–191.

1938. Phosphate and silicate in the Southern Ocean. *Discovery* Rep., vol. 19, pp. 1–120.

DEACON, G. E. R.

1933. A general account of the hydrology of the Southern Ocean. *Discovery* Rep., vol. 7, pp. 171–238.

1937. The hydrology of the Southern Ocean. *Discovery* Rep., vol. 15, pp. 1–214.

1937a. Note on the dynamics of the Southern Ocean. *Discovery* Rep., vol. 15, pp. 125–152.

1963. The Southern Ocean. *In* Hill, M. N., ed., The Sea, vol. 2. John Wiley & Sons, N.Y., pp. 1–554.

DEFANT, A.

1961. Physical oceanography. Pergamon Press, London, vol. 1, 729 pp.; vol. 2, 598 pp.

DELL, R. K.

1959. Cephalopoda. Rep. British Australian New Zealand Antarctic Exped., ser. B., vol. 8, no. 4, pp 89–106, figs 1–10.

EBELING, A. W.

1962. Melamphaidae I. Systematics and zoogeography of the species in the bathypelagic fish genus *Malamphaes* Gunther. *Dana* Rep., no. 58, 164 pp.

EBELING, A. W., and WEED, W. H., III

1963. Melamphaidae III. Systematics and distribution of the species in the bathypelagic fish genus *Scopelogadus* Vaillant. *Dana* Rep., no. 60, 58 pp.

EWING, M., and HEEZEN, B. C.

1956. Some problems of Antarctic submarine geology. Geophys. Monogr., vol. 1, pp. 75–81.

FAGER, E. W., and MCGOWEN, J. A.

1963. Zooplankton species groups in the North Pacific. Science, vol. 140, no. 3566, pp. 453–460.

FELL, J. W.

1965. Bionomics and physiological taxonomy of marine occurring yeasts. Ph. D. Dissertation, University of Miami (unpublished).

1967. Distribution of yeasts in the Indian Ocean. Bull. Mar. Sci., vol. 17, no. 2, pp. 454–470.

FLEMING, R. H., and LAEVASTU, T.

1956. The influence of hydrographic conditions on the behavior of fish. FAO Fish. Bull., vol. 9, no. 4, pp. 181–196.

FRASER, F. C.

1936. On the development and distribution of young stages of the krill (*Euphausia superba*). *Discovery* Rep., vol. 14, pp. 1–192.

FRIEDMAN, S. B.

1964. Physical oceanographic data obtained during *Eltanin* Cruises 4, 5, and 6 in the Drake Passage along the Chilean Coast and in the Bramsfield Strait, June 1962–January 1963. Tech. Rep. No. CU–1–64, NSF GA–27, Lamont Geological Observatory, 55 pp.

FUGLISTER, F. C.

1960. Atlantic Ocean atlas of temperature and salinity profiles and data from the International Geophysical Year of 1957–1958. Woods Hole Oceanogr. Inst. Atlas Series, vol. 1, pp. 1–209.

GOODRICH, E. S.

1892. Note on a large squid (*Ommastrephes pteropus* Stp.). Journ. Mar. Biol. Assoc. United Kingdom, vol. 2, pp. 314–321.

GRIMPE, G.

1922. Systemtische Übersicht der europäischen Cephalopoden. Sber. Naturf. Ges. Leipzig, vols. 45–48, pp. 36–52.

1925. Zur Kenntnis der Cephalopoden-fauna der Nordsee. Wiss. Meeresuntersuch., vol. 16, no. 3, pp. 1–124.

GUNTHER, E. R.

1936. A report on the oceanographical investigations in the Peru Coastal Current. *Discovery* Rep., vol. 13, pp. 107–276.

HAFFNER, R. E.

1952. Zoögeography of the bathypelagic fish, *Chauliodus*. Syst. Zool., vol. 1, no. 3, pp. 113–133.

HARDY, A. C., and GUNTHER, E. R.

1935. The plankton of the South Georgia whaling grounds and adjacent waters. *Discovery* Rep., vol. 11, pp. 1–456.

HART, T. J.

1934. On the phytoplankton of the southwest Atlantic and the Bellingshausen Sea, 1929–1931. *Discovery* Rep., vol. 8, pp. 1–268.

HART, T. J., and CURRIE, R. L.

1960. The Benguela Current. *Discovery* Rep., vol. 31, pp. 123–298.

HOLYE, W. E.

1885. Narrative of the Voyage of the *Challenger* Expedition. The Cephalopoda. Rep. Voy. *Challenger*, vol. 1, part 1, pp. 269–274.

1885a. Diagnosis of new species of Cephalopoda collected during the cruise of HMS *Challenger*. II. The Decapoda. Ann. Mag. Nat. Hist., ser. 5, vol. 16, pp. 181–203.

1885b. Preliminary report on the Cephalopoda collected during the cruise of HMS *Challenger*. II. The Decapoda. Proc. Roy. Soc. Edinburgh, vol 13, no. 120, pp. 281–310.

1886. Report on the Cephalopoda collected by HMS *Challenger* during the years 1873–1876. Rep. Voy. *Challenger*, Zool., vol. 16, no. 44, pp. 1–246, 33 pls.

1886a. A catalogue of recent Cephalopoda. Proc. Roy. Phys. Soc. Edinburgh, vol. 9, pp. 205–267.

1886b. On the existence of Cephalopoda in the deep sea. Rep. British Assoc. Biol., 1886, p. 1064.

1904. Reports on the Cephalopoda. Reports on the dredging operations . . . . *Albatross*. Bull. Mus. Comp. Zool., Harvard., vol. 43, no. 1, pp. 1–71, 12 pls.

1904a. A diagnostic key to the genera of recent dibranchiate Cephalopoda. Mem. Proc. Manchester Liter. Philos. Soc., vol. 48, no. 21, pp. 1–20.

1909. A catalogue of recent Cephalopoda. Second Supplement, 1897–1906. Proc. Roy. Phys. Soc. Edinburgh, vol. 17, no. 6, pp. 254–299.

1910. A list of the generic names of dibranchiate Cephalopoda with their type species. Abh. Senckenb. Naturforsch. Ges., vol. 32, pp. 407–413.

1912. The Cephalopoda of the Scottish National Antarctic Expedition. Trans. Roy. Soc. Edinburgh, vol. 48, no. 2, pp. 272–283.

Jacobs, S. S.

1965. Physical and chemical oceanographic observations in the southern oceans. USNS *Eltanin* Cruises 7–15, 1963–1964. Tech. Rep. No. 1–CU–1–65, NSF GA–194, Lamont Geological Observatory, 321 pp.

Jacobsen, J. P.

1916. Contribution to the hydrography of the Atlantic. Research from the M/S *Margrethe* 1913. Medd. Komm. Havundersøg., Kbh. (Hydrogr.), vol. 2, no. 5, pp. 1–24.

Jespersen, P., and Taning, A. V.

1934. Introduction to the reports from the Carlsberg Foundation's Oceanographical Expedition around the world 1928–30. *Dana* Rep., no. 1, pp. 1–30.

Johnson, C. W.

1934. List of marine Mollusca of the Atlantic coast from Labrador to Texas. Proc. Boston Soc. Nat. Hist., vol. 40, no. 1, pp. 1–204.

Joubin, L.

1912. Sur les Céphalopodes capturés en 1911 par S.A.S. le Prince de Monaco. Compt. Rend. Acad. Sci., Paris, vol. 154, pp. 395–397.

1920. Céphalopodes provenant des Campagnes de la *Princesse-Alice* (1898–1910). (3 e Série.) Résult. Camp. Sci. Monaco, vol. 54, pp. 1–113, 14 pls.

1924. Contribution a l'etude des Céphalopodes de l'Atlantique Nord. (4 e Série.) Résult. Camp. Sci. Monaco, vol. 67, pp. 1–95, 16 pls.

Keala, B. A. L.

1965. Table of Sigma-t with intervals of 0.1 for temperature and salinity. Spec. Sci. Rep. U.S. Fish Wildl. Serv.—Fish. 506, pp. 1–186.

Kort, V. G.

1962. The Antarctic Ocean. Scient. Amer., vol. 207, no. 3, pp. 113–128.

MACKINTOSH, N. A.

1934. Distribution of the macroplankton in the Atlantic sector of the Antarctic. *Discovery* Rep., vol. 9, pp. 65–160.

1937. The seasonal circulation of the Antarctic macroplankton. *Discovery* Rep., vol. 16, pp. 365–412.

1946. The Antarctic Convergence and the distribution of surface temperatures in Antarctic waters. *Discovery* Rep., vol. 23, pp. 179–212.

MARR, J. W. S.

1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery* Rep., vol. 32, pp. 33–464.

MARSHALL, N. B.

1954. Aspects of deep-sea biology. Hutchinson, London, 380 pp.

1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. *Discovery* Rep., vol. 31, pp. 1–122.

1963. Diversity, distribution, and speciation of deep-sea fishes. *In* Speciation in the Sea. Systematics Association, Publ. no. 5, pp. 181–195.

MASSY, A. L.

1916. Notes on the Cephalopoda of the Irish Atlantic Slope. Ann. Mag. Nat. Hist., ser. 8, vol. 18. pp. 1–114.

1916a. The Cephalopoda of the Indian Museum. Rec. Indian Mus., vol. 12, part 5, no. 16, pp. 185–247.

1928. The Cephalopoda of the Irish Coast. Proc. Roy. Irish Acad. (B), vol. 38, no. 2, pp. 25–37.

MAYR, E., LINSLEY, E. G., and USINGER, R. L.

1953. Methods and Principles of Systematic Zoology. McGraw-Hill, New York, 336 pp.

McGOWEN, J. A.

1960. The relationship of the distribution of the planktonic worm *Poecobius meseres* Heath to the water masses of the North Pacific. Deep-sea Research, vol. 6, no. 2, pp. 125–139.

MENZIES, R. J.

1964. Improved techniques for benthic trawling of depths greater than 2000 meters. *In* Biology of the Antarctic seas. Antarctic Research Series, vol. 1, pp. 93–109.

MOORE, H. B.

1958. Marine Ecology. John Wiley & Sons, New York, 493 pp.

NAEF, A.

1916. Systematische Uebersicht der mediterranean Cephalopoden. Pubbl. Sta. Zool. Napoli, vol. 1, pp. 11–19.

1921. Das System der dibranchiaten Cephalopoden und die mediterranen Arten derselben. Mitt. Zool. Sta. Neapel, vol. 22, pp. 527–542.

1921a. Die Cephalopoden. Fauna u. Flora Neapel, Monograph 35, vol. 1, part 1, no. 1, pp. 1–148, 62 figs, 37 pls.

1922. Die Fossilen Tintenfische. Gustav Fischer, Jena, 322 pp.

1923. Die Cephalopoden. Systematik. Fauna u. Flora Neapel, Monograph 35, vol. 1, part 1, no. 2, pp. ii–xiv, 149–863, 473 figs.

NIELSEN, E. S.

1954. On organic production in the oceans. Journ. Cons., vol. 19, no. 3, pp. 309–328.

NIELSEN, E. S., and JENSEN, A.

1957. Primary ocean production, the autotrophic production of organic matter in the oceans. *Galathea* Rep., vol. 1, pp. 49–136.

ODHNER, NILS HJ.

1923. Die Cephalopoden. Further Zool. Results Swedish Antarctic Exped., vol. 1, pp. 1–7.

PFEFFER, G.

1900. Synopsis der oegopsiden Cephalopoden. Mitt. hamburgischen Zool. Mus., vol. 17, pp. 147–198.

1912. Die Cephalopoden der Plankton-Expedition. Ergebn. Atlantic Plankton-Exped., vol. 2, pp. i–xxi, 1–815, Atlas 48 plates.

PICKARD, G. L.

1963. Descriptive physical oceanography. Pergamon Press, London. 199 pp.

PICKFORD, G. E.

1946. *Vampyroteuthis infernalis* Chun, an archaic dibranchiate cephalopod. I. Natural history and distribution. *Dana* Rep., no. 29, pp. 1–40.

1949. The distribution of the eggs of *Vampyroteuthis infernalis* Chun. Journ. Mar. Res., vol. 8, no. 1, pp. 73–83.

POWELL, A. W. B.

1951. Antarctic and subantarctic Mollusca. Pelycepoda and Gastropoda. *Discovery* Rep., vol. 26, pp. 47–196.

1960. Antarctic and subantarctic Mollusca. Rec. Auckland (New Zealand) Mus., vol. 5, nos. 3–4, pp. 117–193.

RICHARD, J.

1934. Liste générale des stations des campagnes scientifiques du Prince Albert de Monaco. Résult. Camp. Sci. Monaco, vol. 89, pp. 1–472.

ROBSON, G. C.

1921. No. XI. On the Cephalopoda obtained by the Percy Sladen Trust Expedition to the Indian Ocean in 1905. Trans. Linnean Soc. London (Zool.), vol. 17, no. 4, pp. 429–442.

1925. The deep-sea Octopoda. Proc. Zool. Soc. London, 1925, pp. 1323–1356.

1930. Cephalopoda. I. Octopoda. *Discovery* Rep., vol. 2, pp. 371–402.

1932. Monograph of Recent Cephalopoda. Part II. The Octopoda (excluding the Octopodinae). British Museum (Nat. Hist.) : London, pp. 1–359.

1932a. Notes on the Cephalopoda. No. 17. On the male of *Benthoteuthis*. Ann. Mag. Nat. Hist., ser. 10, vol. 10, no. 58, pp. 375–378.

1948. The Cephalopoda Decapoda of the *Arcturus* Oceanographic Expedition, 1925. Zoologica, vol. 33, no. 3, pp. 115–132.

ROPER, C. F. E.

1965. A note on egg deposition by *Doryteuthis plei* (Blainville, 1823) and its comparison with other North American loliginid squids. Bull. Mar. Sci., vol. 15, no. 3, pp. 589–598.

1966. A study of the genus *Enoploteuthis* (Cephalopoda : Oegopsida) in the Atlantic Ocean with a redescription of the type species, *E. leptura* (Leach, 1817). *Dana* Rep., no. 66, pp. 1–46.

1968. Preliminary descriptions of two new species of the bathypelagic squid *Bathyteuthis* (Cephalopoda: Oegopsida). Proc. Biol. Soc. Wash., vol. 81, pp. 261–272, 7 pls.

Roper, C. F. E., and Young, R. E.

1968. The Promachoteuthidae (Cephalopoda: Oegopsida). I. A reevaluation of its systematic position based on new material from the Antarctic and adjacent waters. Antarctic Research Series, vol. 11, pp. 203–214, 3 pls.

Roper, C. F. E., Young, R. E., and Voss, G. L.

in press. An illustrated key to the families of the order Teuthoidea (Cephalopoda). Smithsonian Contr. Zool., 13.

Savage, J. M., and Caldwell, M. C.

1965. Studies in Antarctic Oceanology. Biological stations occupied by the USNS *Eltanin:* Data Summary, Cruises 1–13. Univ. Southern California, pp. i–vii, 1–87.

Savage, J. M., and Geiger, S. R.

1965. Studies in Antarctic Oceanology. Biological stations occupied by the USNS *Eltanin:* A synoptic atlas. Univ. Southern California, pp. 1–3, 76 pls.

Schmidt, J.

1919. Stations in the Atlantic, etc., 1911–15, with two charts and introductory remarks. Medd. Komm. Havundersøg. Kbh. (Fisk.), vol. 5, no. 7, pp. 1–27.

1929. Introduction to the oceanographical reports including a list of the stations and hydrographical observations. Oceanogr. Rep. *Dana* Exped. 1920–22, no. 1, 87 pp.

Schuchert, C.

1935. Historical geology of the Antillean-Caribbean region. John Wiley & Sons, pp. 1–811.

Simpson, G. G., Rowe, A., and Lewontin, R. C.

1960. Quantitative zoology. Harcourt, Brace and Co., New York, 440 pp.

Sund, P. N.

1961. Some features of the autecology and distributions of the Chaetognatha in the eastern tropical Pacific. Bull. Inter-American Trop. Tuna Comm., vol. 5, no. 4, pp. 305–340.

1964. The chaetognaths of the waters of the Peru region. Bull. Inter-American Trop. Tuna Comm., vol. 9, no. 3, pp. 113–216.

Sverdrup, H. U.

1934. Wie entsteht die Antarktische Konvergenz? Ann. Hydrogr. Mar. Meteor., 1934, pp. 315–317.

Sverdrup, H. U., Johnson, M. W., and Fleming, R. H.

1942. The oceans, their physics, chemistry, and general biology. Prentice-Hall, New York, 1087 pp.

Tåning, A. V.

1944. List of supplementary pelagic stations in the Pacific Ocean and the Atlantic. *Dana* Rep., no. 26, pp. 1–15.

Tanner, Z. L.

1885. Report on the work of the U.S. Fish Commission steamer *Albatross* for the year ending December 31, 1884. Rep. U.S. Comm. Fish., 1884, part 12, pp. 1–114.

Tebble, N.

1960. The distribution of pelagic polychaetes in the South Atlantic Ocean. *Discovery* Rep., vol. 30, pp. 161–300.

TEE-VAN, J.

1926. The *Arcturus:* Equipment and operation. Zoologica, vol. 8, no. 1, pp. 47–106.

THIELE, J.

1921. Die Cephalopoden der Deutschen Südpolar-Expedition. Deutsche Sudpol. Exped. (1901–1903) 16, Zool., vol. 8, pp. 433–466.

1935. Handbuch der systematischen Weichtierkunde. Vol. 2, part 3, pp. 779–1022.

THOMSEN, H.

1937. Hydrographical observations made during the *Dana* Expedition 1928–30. *Dana* Rep., no. 12, pp. 1–46.

THORE, S.

1949. Investigations on the *Dana* Octopoda. Part I. Bolitaenidae, Amphitretidae, Vitreledonellidae, and Alloposidae. *Dana* Rep., no. 33, pp. 1–85.

TRESSLER, W. L.

1963. Oceanographic stations taken in the Indian Ocean by USCGC *Eastwind* (WAGB–279) in 1961. Tech. Rep. U.S. Navy Oceanogr. Office 141, pp. 1–84.

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1966. Studies in Antarctic Oceanology. Biological stations occupied by the USNS *Eltanin:* Data summary, Cruises 14–16 and 18–19. Univ. Southern California, pp. i–iv, 1–31, 15 charts.

1965. Studies in Antarctic oceanology. USNS *Eltanin* Antarctic Cruise Tracks. Cruises 4–13, July 1962–July 1964. Univ. Southern California, 10 charts.

VERRILL, A. E.

1885. Third catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species with notes on others previously recorded. Trans. Connecticut Acad., vol. 6, part 2, pp. 395–452.

VOSS, G. L.

1956. A review of the cephalopods of the Gulf of Mexico. Bull. Mar. Sci. Gulf and Caribbean, vol. 6, no. 2, pp. 85–178.

1962. A monograph of the Cephalopoda of the North Atlantic. I. The Family Lycoteuthidae. Bull. Mar. Sci. Gulf and Caribbean, vol. 12, no. 2, pp. 264–305.

1963. Cephalopods of the Philippine Islands. U.S. Nat. Mus. Bull. 234, 180 pp.

1967. The biology and bathymetric distribution of deep sea cephalopods. Stud. Trop. Oceanogr. Miami, no. 5, pp. 511–535.

WALTERS, V.

1961. A contribution to the biology of the Giganturidae, with description of a new genus and species. Bull. Mus. Comp. Zool., Harvard, vol. 125, pp. 297–319.

WEXLER, H.

1959. The Antarctic Convergence—or Divergence? *In* Bolin, B., ed., The atmosphere and the sea in motion. Rockefeller Inst. Press, New York.

WOOSTER, W. S., and CROMWELL, T.
1958. An oceanographic description of eastern tropical Pacific. Bull. Scripps Inst. Oceanogr., vol. 7, no. 3, pp. 169–282, 36 profiles.

WÜST, G.
1935. Die Stratosphäre. Wiss. Ergebn. deutsches atlantischen Exped. *Meteor*, vol. 6, no. 1, pp. 1–288.

WYRTKI, K.
1960. The Antarctic Circumpolar Current and the Antarctic Polar Front. Deutschen hydrogr. Z., vol. 13, no. 4, pp. 153–174.

YOUNG, R. E., and ROPER, C. F. E.
1968. The Batoteuthidae, a new family of squid (Cephalopoda; Oegopsida) from Antarctic waters. Antarctic Research Series, vol. 11, pp. 185–202, 6 pls.

Appendix

After the manuscript had been completed, a portion of the missing specimens was found and sent to me. With the exception of one lot of three specimens from Cruise 10, these specimens were all captured during Cruise 11 which took place from mid-December 1963 to mid-February 1964; the *Eltanin* worked southward approximately along 115°W to 70°S, eastward to 90°W, then northward. All specimens were taken south of 55°S.

During Cruise 11 a total of 40 tows was made below 500 m; of these 33 were successful in catching 110 specimens of *B. abyssicola.* (Two captures with one specimen each were available earlier and were also included in the original discussion.) Of the seven unsuccessful tows, six fished shallower than 1000 m. The captures were made in water temperatures that ranged from about 0.5° C to less than 2.5° C, with the majority between 1° and 2° C. Also, the captures were taken in waters that had salinities above 34.70‰, oxygen concentrations above 4.00 ml/L, and sigma-t values above 27.50. Therefore, these additional specimens occurred within the ranges of values already determined in the original study material.

The addition of the material from Cruise 11 only slightly alters the earlier results. The tows during Cruise 11 had a success-of-capture rate of 83%; this increases the combined success rate in the South Pacific and South Pacific Convergence regions from 67% to 72%. The average number of specimens per total tow was slightly less than 3, while the previous value was slightly more than 3.

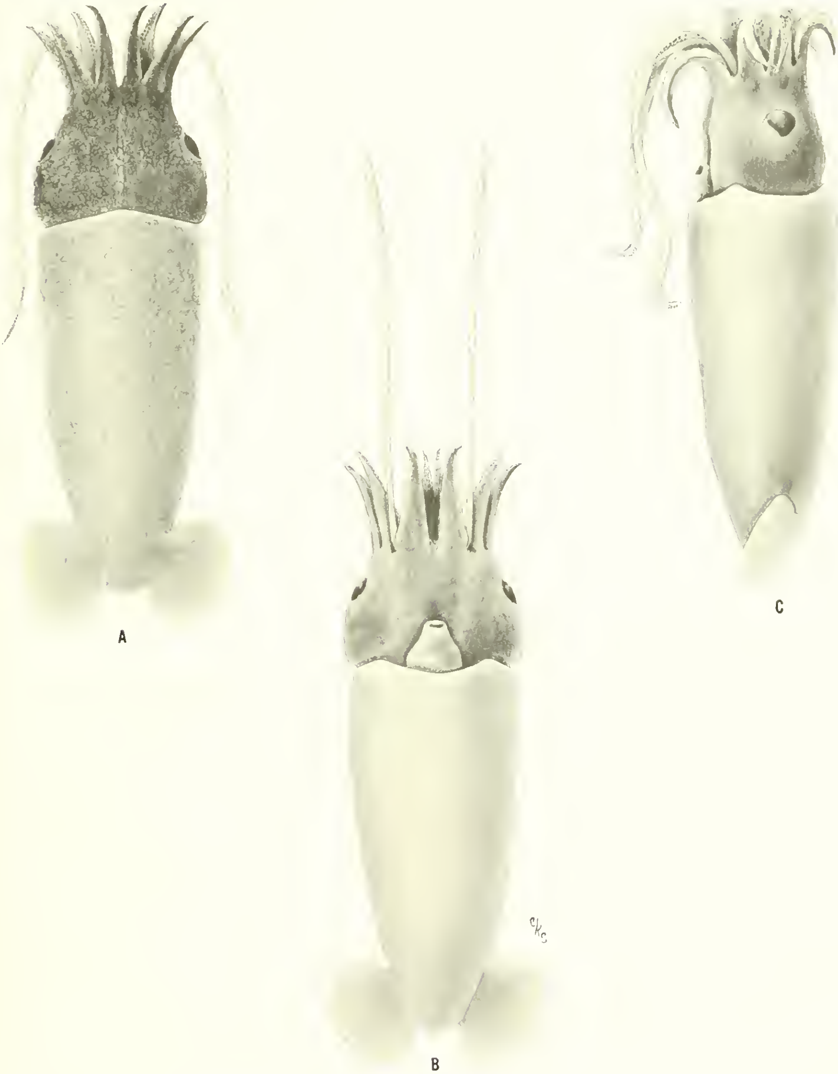
All captures were made in late December and throughout January. Two tows made exceptional catches of 13 and 25 specimens (30 December and 10 January); one was in the convergence zone and the other was slightly to the north but in water with the same characteristics as those in the convergence zone. The high rate of success of tows and the two exceptional catches add support to the suggestion made above that the abundance of *B. abyssicola* in Antarctic waters is greater during the austral spring and summer months.

Eleven of the specimens were greater than 50 mm ML (range 50–61 mm ML); only 3 (27%) of these were males (50–54 mm ML). This is about the same relationship between numbers of large males and large females that was described above.

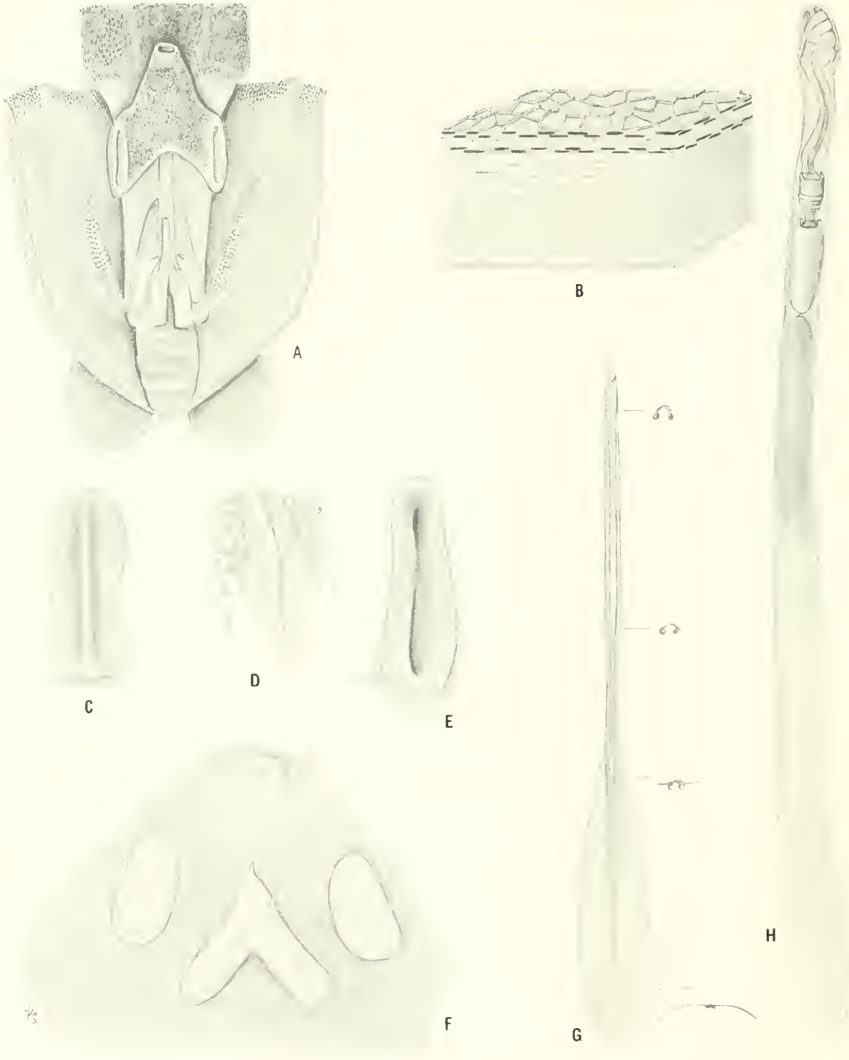
The additional specimens that are now available, therefore, are in close agreement with and further support the conclusions that were reached previously.

Additional Material

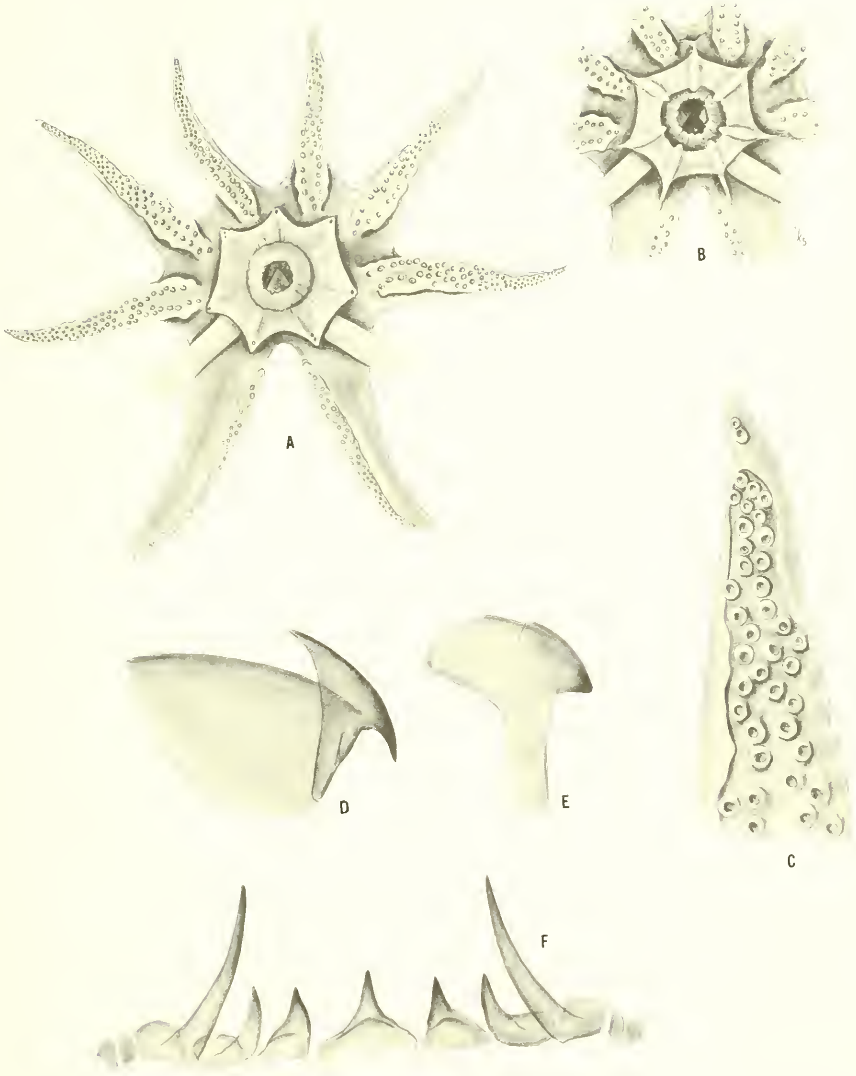
Eltanin *station number*	*Number of specimens*	*Size range mm ML*	*Estimated depth of capture, m*
849	3	16–17	1080
882	6	19–50	1554–1830
883	13	17–45	1605–1812
886	5	27–49	1903
888	4	21–44	2290
889	4	22–51	3660
892	8	24–47	490
895	3	25–48	2315
898	5	38–46	2824
900	1	24	874
901	1	51	3477
903	1	24	1169
904	1	42	2932
906	25	22–54	1185
912	1	45	3312
914	6	33–48	1116
915	3	41–56	2059
918	2	28–51	1885
919	1	28	1050
920	1	47	2196
933	1	34	1812
934	1	55	2489
936	1	45	1880
940	1	36	1049
941	2	43–46	1900
943	1	19	888
944	1	39	3029
946	2	45–50	1711
947	1	61	2690
950	2	41–46	3020
952	1	27	1848
953	3	39–52	3020



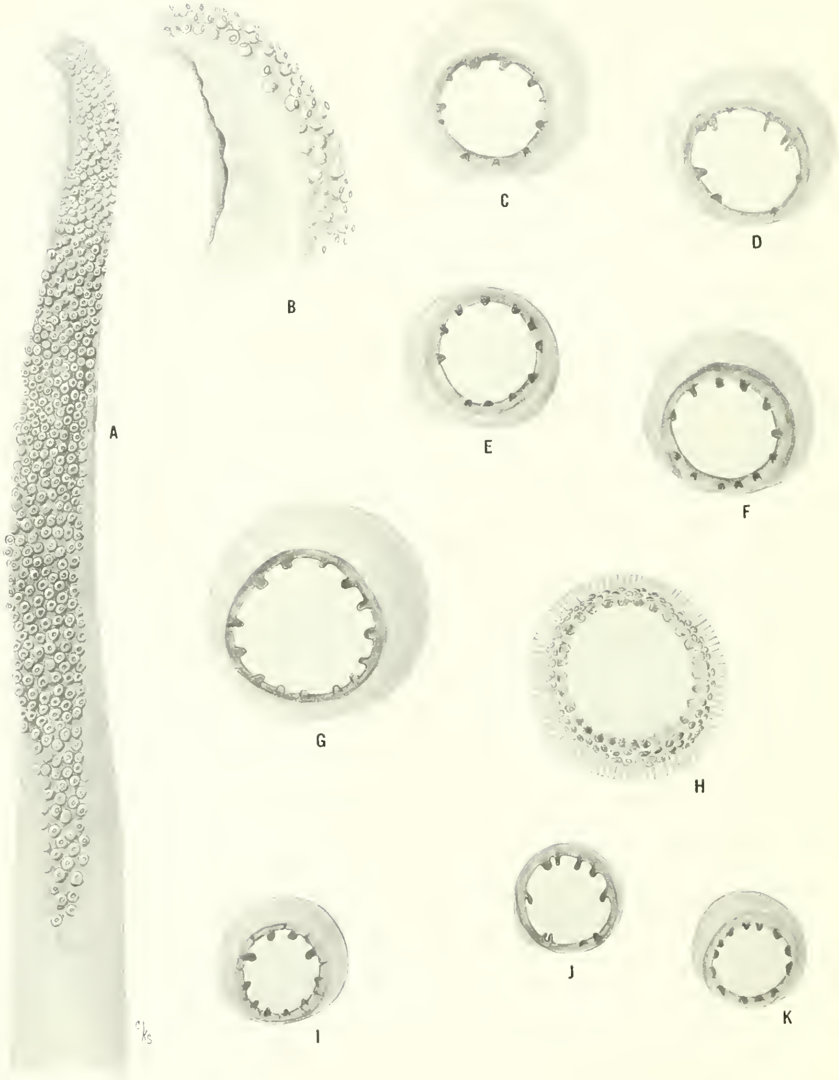
Bathyteuthis abyssicola, female, 56 mm ML, Elt. 345: A, Dorsal view; B, ventral view; C, lateral view.



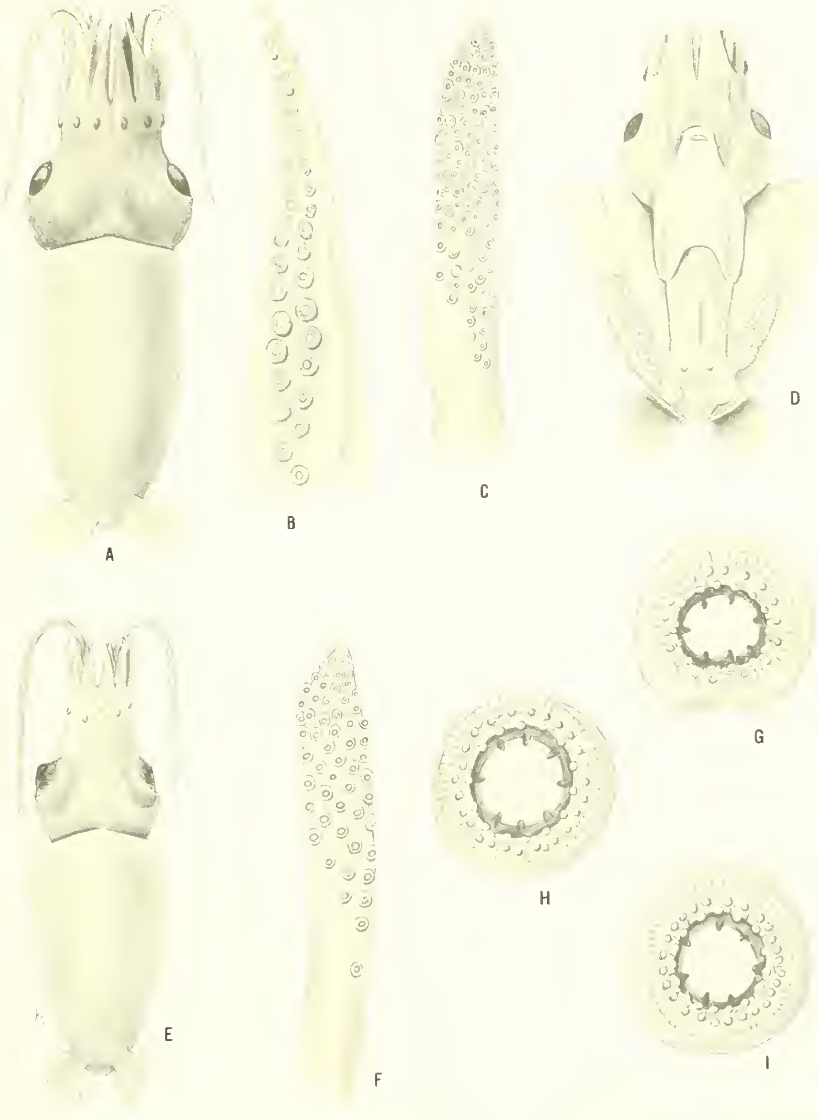
Bathyteuthis abyssicola, A–G, female, 57 mm ML, Elt. 354; H, male: A, Open mantle cavity; B, section of integumentary layers and muscle of mantle; C, nuchal cartilage; D, mantle component of locking apparatus; E, funnel component of locking apparatus; F, funnel organ and funnel valve; G, gladius; H, spermatophore.



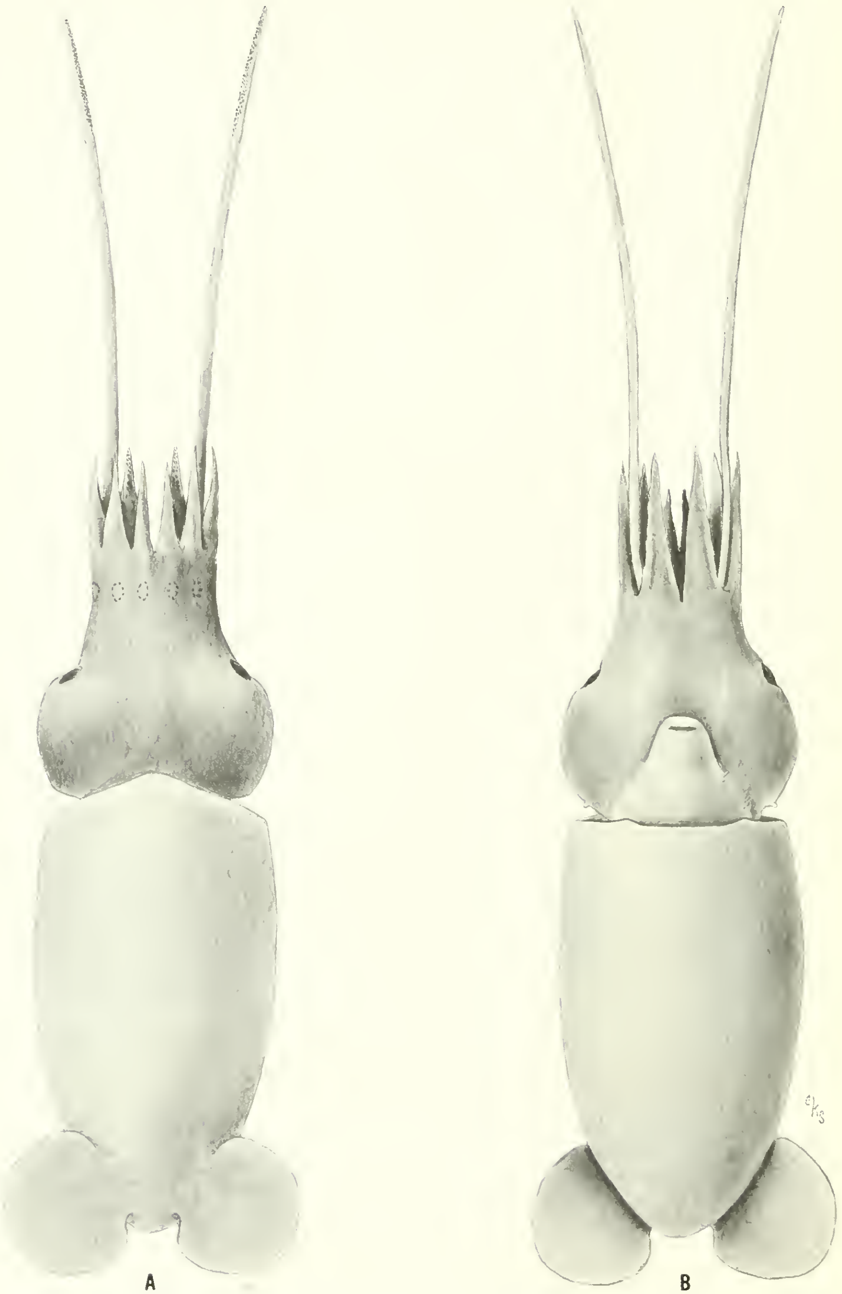
Bathyteuthis abyssicola, A–C, female, 57 mm ML, Elt. 354; D–F, 50 mm ML: A, Brachial crown with buccal membrane expanded; B, brachial crown showing connectives of the buccal membrane; C, distal tip of left Arm IV; D, upper beak; E, lower beak; F, radula.



Bathyteuthis abyssicola, A–B, 57 mm ML, Elt. 354; C, E–I, K, 38 mm ML, Elt. 274; D, J, 28 mm ML, Elt. 1201: A, Tentacular club, left; B, distal tip of club. C–G, Inner sucker rings: C–D, Arm I; E, Arm II; F, Arm III; G, Arm IV. H, Outer sucker ring, Arm IV; I, buccal sucker ring; J–K, club sucker rings.

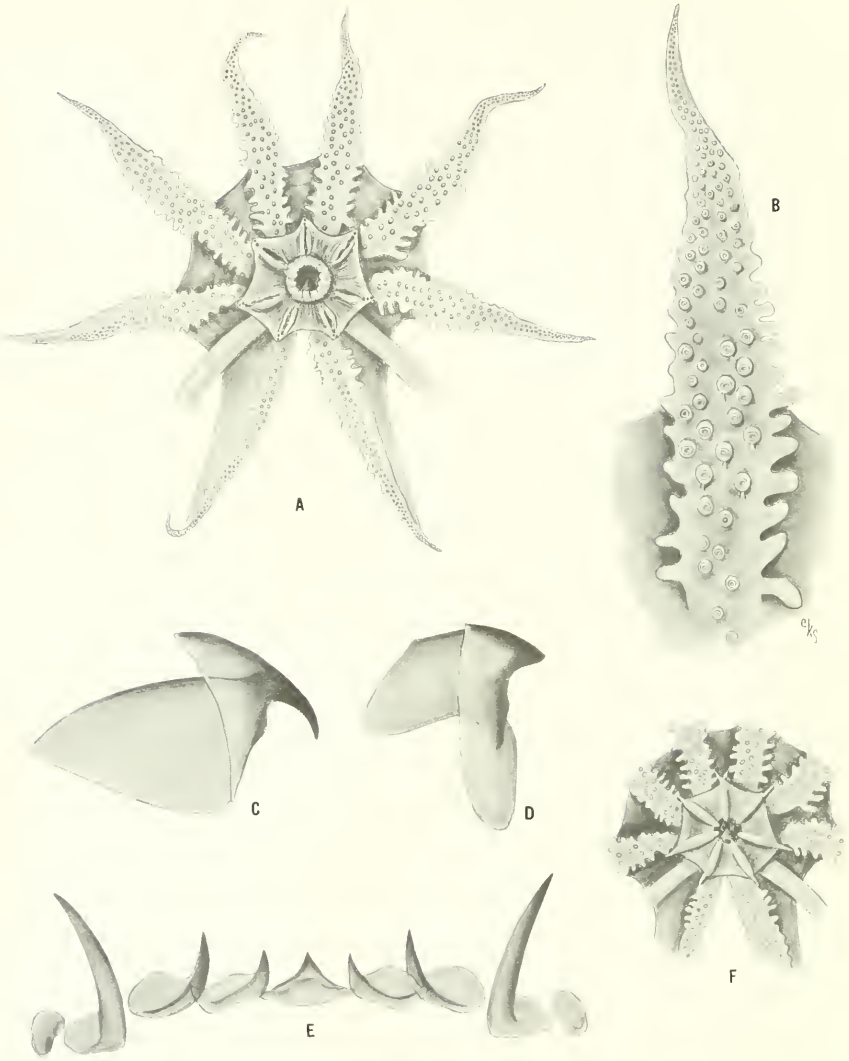


Bathyteuthis abyssicola, larvae, A–D, G, 12 mm ML; E–F, 6 mm ML; H, 16 mm ML; I, 29 mm ML: A, Dorsal view; B, Arm I, left; C, tentacular club, left; D, open mantle cavity; E, dorsal view; F, tentacular club, left; G–I, sucker rings.

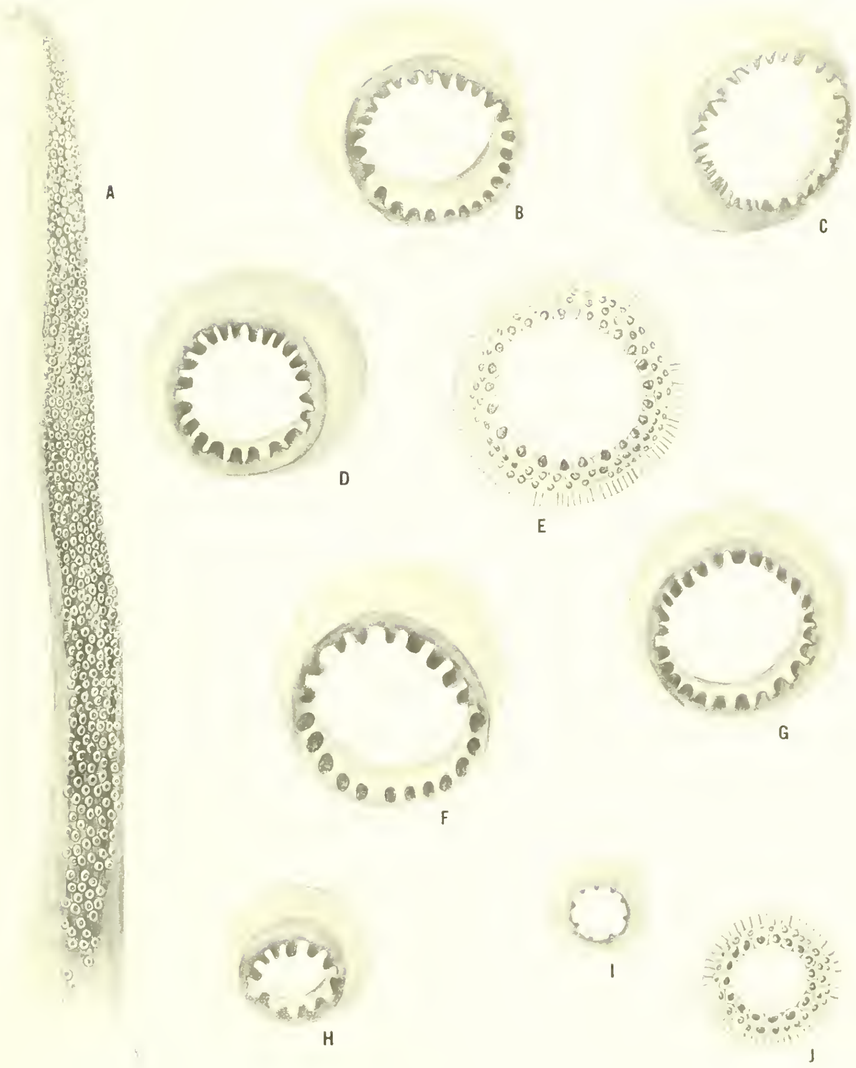


Bathyteuthis bacidifera, holotype, female, 37 mm ML, Elt. 34: A, Dorsal view; B, ventral view.

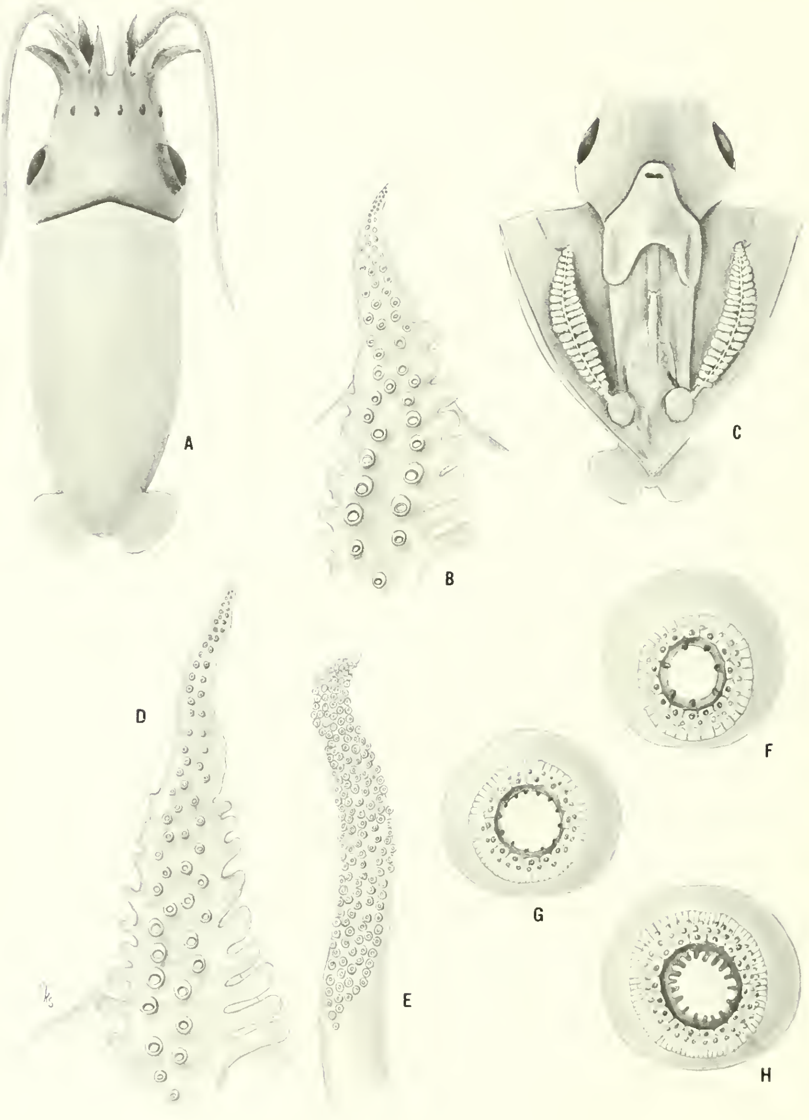
Bathyteuthis bacidifera, A, paratype, and B-F, holotype, females, 37 mm ML, Elt. 34; G, paratype, female, 34 mm ML, Elt. 54: A, Open mantle cavity; B, funnel component of locking apparatus; C, mantle component of locking apparatus; D, nuchal cartilage; E, funnel organ and valve; F, pore of funnel groove; G, gladius.



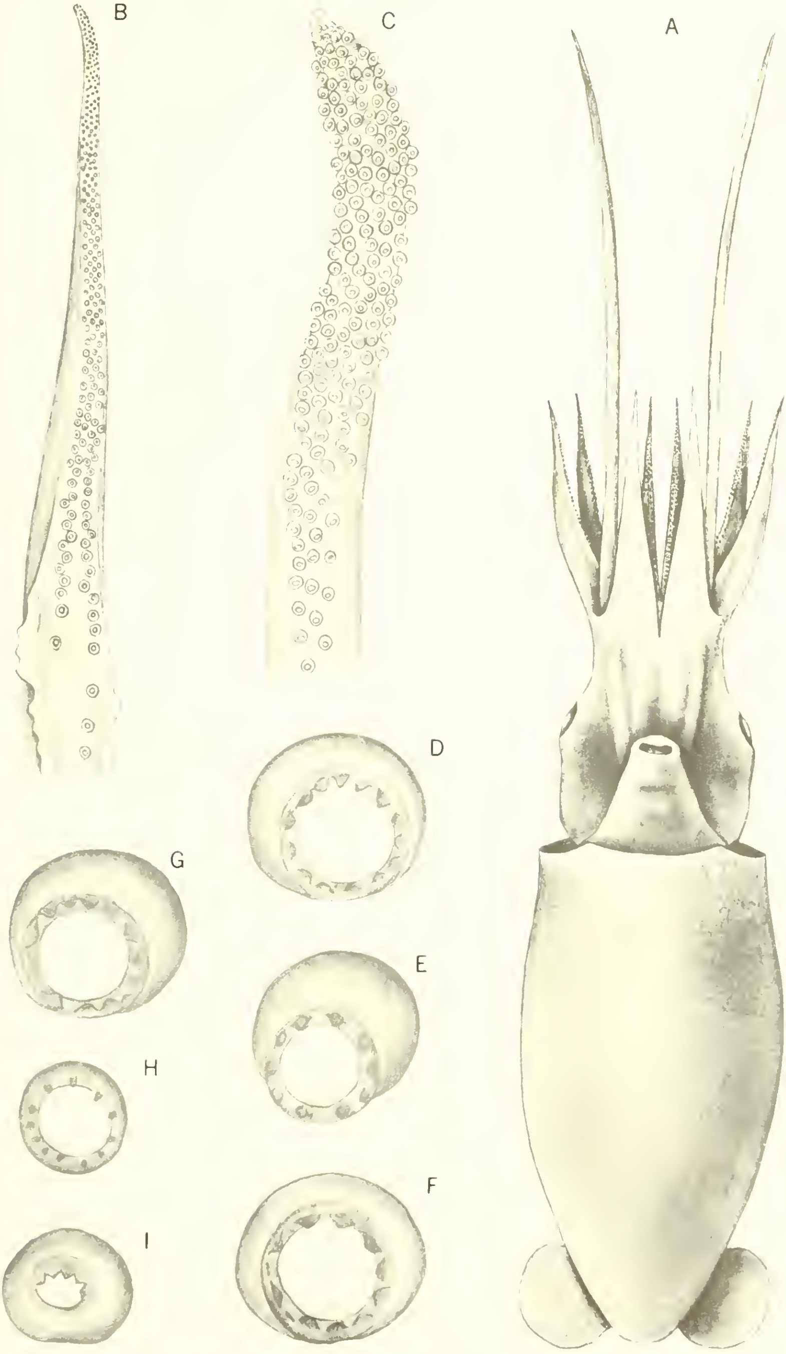
Bathyteuthis bacidifera, A, B, F, holotype, and C, D, E, paratype, females, 37 mm ML, Elt. 34: A, Brachial crown with buccal membrane expanded; B, right Arm I; C, upper beak; D, lower beak; E, radula; F, brachial crown showing connectives of the buccal membrane.



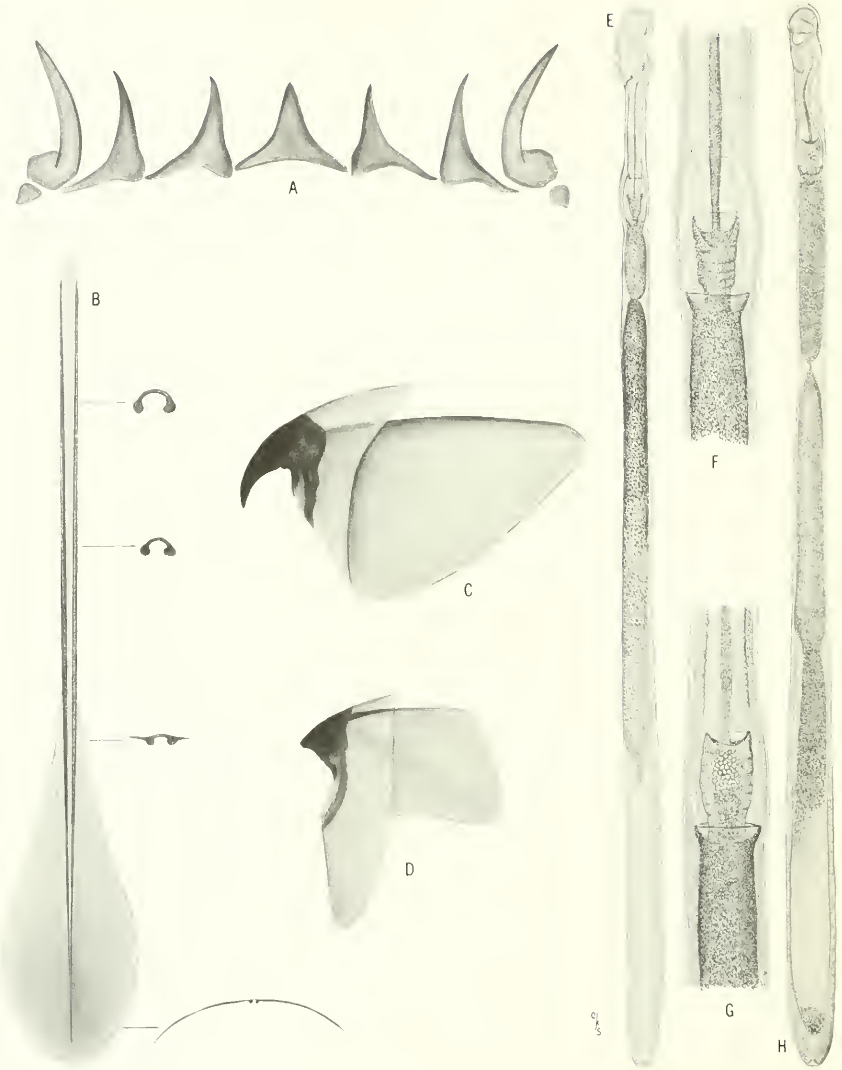
Bathyteuthis bacidifera, holotype, female, 37 mm ML, Elt. 34: A, Tentacular club; B, C, inner sucker rings, Arm I; D, E, inner and outer sucker rings, Arm II; F, inner sucker ring, Arm III; G, inner sucker ring, Arm IV; H, buccal sucker ring; I, J, inner and outer sucker rings, left tentacular club.



Bathyteuthis bacidifera, juvenile and larval specimens: A, Dorsal view, male, 11.5 mm ML, D 1208 VI; B, left Arm I, D 1208 VI; C, open mantle cavity, D 1208 VI; D, left Arm I, male, 17 mm ML, D 1208 VIII; E, tentacular club; F, sucker from left Arm I, male, 11.5 mm ML, D 1208 VI; G, sucker from left Arm I, male, 17 mm ML, D 1208 VIII; H, sucker from left Arm I, female, 26 mm ML, D 1208 XIV.



Bathyteuthis berryi, holotype, A, B, D–H, male, 49 mm ML, *Velero* 8714, and a paratype, C, I, juvenile, 19 mm ML, *Velero* 10976. A, Ventral view; B, Arm I; C, tentacular club; D–G, inner sucker rings from Arms I–IV; H, buccal sucker ring; I, inner sucker ring from tentacular club.



Bathyteuthis berryi, A–F, holotype, male, 49 mm ML, *Velero* 8714: A, Radula; B, gladius; C, upper beak; D, lower beak; E, spermatophore; F, enlarged section of spermatophore. *B. bacidifera*, G–H, paratype, male, 28 mm ML, *Pillsbury* 510: G, Spermatophore; H, enlarged section of spermatophore.

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