

CEPHALOPODS OBSERVED FROM SUBMERSIBLES IN THE WESTERN NORTH ATLANTIC

Michael Vecchione and Clyde F. E. Roper

ABSTRACT

Records of 158 observations of cephalopods from submersibles, primarily the JOHNSON SEA-LINK, have been compiled through collaboration with several investigators. These observations include 118 videotape sequences, 58 collected specimens, and numerous shipboard photographs of live animals. At least 33 species have been observed to date; a few species have been observed repeatedly and could be good subjects for directed studies. The methods developed for in situ observation and subsequent collection of specimens with little or no damage allow descriptions of behavior, morphology, physiology, and distribution that are not possible with other methods of collecting.

*Don't try to describe the ocean if you've never seen it.
Don't ever forget that you just might wind up being wrong.*

Jimmy Buffett
"Mañana"

Ultimately, the goal of any discipline of biology is to understand organisms as they occur in nature. Students of cephalopods often find it difficult to approach this goal because of many potential sources of artifactual errors. Systematic studies suffer because external features of these soft-bodied animals are easily damaged during collection or preservation, while many morphometric characteristics are subject to gross alteration by contraction and shrinkage. Conclusions about distribution and ecology are weakened by the cephalopod's well-known abilities to avoid capture. Most published information on the behavior of deep-sea cephalopods comes either from inferences based on morphology or from short-term observations of trawl-caught specimens in aquaria. Thus, any technological development that allows a new perspective on morphology, behavior, or distribution is a welcome addition to our research capabilities.

Since common use of research submersibles began in the early 1960s, a number of observations have been made on benthic and midwater faunas. While most biological research programs using submersibles are directed toward specific habitats or faunal components, observations of cephalopods from submersibles have been largely incidental (Clark, 1990). Published accounts mention the sightings of cephalopods but, with few exceptions, little information has been gained except the locality and occasionally the depth of occurrence. Photography of cephalopods from unmanned vehicles has yielded valuable information about habitats, orientation, size, locomotion, and gross morphology (Jahn, 1971; Roper and Brundage, 1972; Percy and Beal, 1973) and, more recently, videotapes from remotely operated vehicles (ROVs) have provided data about aggregations, schooling behavior, and spawning (Vecchione and Gaston, 1985; Vecchione, 1988).

A few cephalopod biologists have made dives in submersibles, but the most interesting or spectacular sightings of cephalopods seem to occur on the dives preceding or following the teuthologists' dives. The advent of reliable, high-resolution video recorders for deep-sea use has mitigated somewhat the necessity for the presence of a cephalopod researcher aboard the submersible, although it should be emphasized that specific knowledge of the group, its systematics, morphology, and behavior, are critical to distinguish what is important from the

mundane. Furthermore, in spite of advances in video imaging, the human eye remains a superior observational instrument.

One of the earlier reports of significant observations on cephalopods was the description by Waller and Wicklund (1968) of mating and spawning by *Loligo plei* in the lights of the JOHNSON SEA-LINK, stationary on the bottom in shallow water in the Bahamas. Likewise, Milliman and Manheim (1968) made significant observations from ALVIN, documenting high concentrations of the squid *Illex illecebrosus* associated with strong daytime scattering-layer recordings (12 kHz) at 220–250 m and 490–510 m off Cape Hatteras. During studies of the deep scattering layer (DSL) in the Gulf of Mexico using DEEPSTAR 4000, Clarke (1970) observed that many fishes (lanternfishes, hatchetfishes) and squid (not identified but likely an ommastrephid species) appeared to be in an inactive or lethargic state that remained unbroken until the submersible approached very closely; only when the water around them was disturbed or the light field became intense did the animals become alert and swim away. Further, Clarke (1970) noted that squid commonly follow the descending submersible and actively feed on organisms in the DSL, particularly the "lanternfish layer." Below that, though, were deeper populations of the "same species" of squid that were completely dormant. Individuals hung motionless in the water in a "J" posture with arms and tentacles held together and folded back over the head; they would "wake up" only when strongly disturbed. We now have numerous observations that confirm this "J" posture as a common occurrence among certain ommastrephids, onychoteuthids, and enoploteuthids.

Barham (1970) reported that nearly 100% of myctophid fishes observed during the day, primarily between 350–260 m, were vertically oriented, lethargic, and immobile, while at night in the upper 100 m only 31% were lethargic, compared with 68% below 100 m. We have found similar lethargy, vertical orientation, and escape reactions in some species of cephalopods. Several observations of squids were made from DEEPSTAR 4000 during descent in waters off southern California, but squid numbers were meager in comparison with the abundance of fishes and no behavioral activity was noted (Pickwell et al., 1970). Early color photographs of deep-sea squids presented by Church (1971) include a *Gonatus* in the "J" posture at 1,000 m, a vertically oriented *Galiteuthis* at 1,166 m and a curled-up *Histioteuthis* at 666 m; all photos were taken from DEEPSTAR 4000 off southern California. Observations of a cirrate octopod were made from ALVIN by R. Ballard, who filmed it swimming by use of its large fins, not by jet propulsion (Aldred et al., 1983). Color photos of cirrate octopods in situ have been published by Nesis (1987). Gutsal (1989) reported data from submersibles on distribution and behavior of the cuttlefish *Sepia pharaonis* in shallow water during fishery investigations in the Arabian Sea. Other investigations have been noted in Soviet literature (Moiseev, 1986). Saunders (1990) used a deep-water camera attached to a baited trap for a survey of *Nautilus* in the Admiralty Islands.

Occasionally, net-captured deep-sea squid have survived fortuitously in ship-board aquaria long enough for casual observations to be made. Among those reported in the literature are the following: Verany (1851) on bioluminescence in *Histioteuthis*; Chun (1903) on bioluminescence in *Lycoteuthis diadema*; Clarke (1962) on respiratory and swimming movements in *Cranchia scabra*; Pereyra (1965) on medusoid swimming by *Opisthoteuthis californiana*; Denton et al. (1969) on buoyancy and orientation in cranchiids, including *Helicocranchia*; Dilly (1972) on balling behavior by *Teuthowenia megalops*; Young (1972) on the spherical posture of *Cranchia scabra*; Denton and Gilpin-Brown (1973) on vertical orientation in *Mastigoteuthis*; Clarke, in Dilly et al. (1977) on orientation by *Mas-*

tigoteuthis; McSweeney (1978) on locomotion and orientation in *Galiteuthis glacialis*; and Macalaster (1981) on coloration and swimming in *Bathypolypus arcticus*.

Experimental studies on living deep-sea cephalopods became possible only when techniques were developed for gentle capture and for shipboard simulation of the diurnally fluctuating mesopelagic habitat. This enabled a series of studies on living cephalopods to be conducted in Hawaiian waters under the leadership of R. E. Young, primarily on various aspects of bioluminescence (Young and Roper, 1976; 1977; Young et al., 1979a; 1979b; 1980; 1982; Young and Mencher, 1980).

Marine biologists understand that observations made on captive higher marine organisms in aquaria are subject to qualification due to possible effects of containment. The degree to which captivity affects behavior varies greatly depending on the species being studied and the milieu of the experimental situation. Placing an observer in a container that is then introduced into the natural habitat of the deep sea may help to reduce the effects of observational constraints and to enhance the goal of understanding organisms in nature.

Thus, research submersibles, both manned and unmanned, provide an opportunity for a novel perspective on cephalopods. We have begun to compile a collection of observations on cephalopods made by numerous investigators using submersibles. This collection includes in situ videotapes and photographs, collected specimens, and shipboard observations and photographs of live animals. We report here the observations from the western North Atlantic, including the Gulf of Mexico and Caribbean Sea.

MATERIALS AND METHODS

The majority of our material has come from our participation in G. R. Harbison's Direct Study of Midwater Communities (DSMC) project. This ongoing project to observe and to collect megaplankton and nekton at mesopelagic and upper-bathypelagic depths has used the JOHNSON SEA-LINK I and II manned submersibles for several years. Although most of the dive time has been spent at depths of 457-914 m, shallower observations, made while descending, also have been included. Because of safety requirements for the submersibles, dive locations have been limited to areas where the bottom is about 914 m deep or less. Usually, the dive protocol has included one daytime and one nighttime dive per day, each of about 4-h duration.

Dive logs include date, time, latitude, longitude, records of temperature through the water column during descent, depth (and usually temperature) of each observation, videotape recordings, and the gear used to collect specimens. Collection gear includes (1) a conical net with a mouth opening of 1 m fitted with an internal lip to prevent escape, 5 mm mesh netting, and a suction device in the cod-end leading to a rotating series of holding containers; (2) a "critter-gitter" suction device with a plexiglass funnel at the intake and a rotating series of holding containers at the discharge end; and (3) a bank of large-bore plexiglass traps with rotating covers on each end. Cephalopods have been collected with all gear types. The ability to collect specimens is often very important for confirming identifications. Shipboard observations and photographs of live specimens have been made in vertical and horizontal chilled-seawater aquaria, usually in darkened, refrigerated rooms. This protocol has been followed during two cruises to the Northwest Providence Channel in the Bahamas, and one cruise each off New England and Key West.

Other observations presented here come from a variety of sources at various locations and depths. Several investigations by personnel from Harbor Branch Oceanographic Institution have supplied us with material. These include Grant Gilmore's study of deep rockfaces and dropoffs, John Miller's work on benthic animals, Edie Widder's investigation of oceanic bioluminescence, and Marsh Youngbluth's study of water-column processes. Additionally, James Tyler of the Smithsonian Institution collected cephalopods while sampling ichthyoplankton attracted to the lights of the stationary JOHNSON SEA-LINK. Eugenie Clarke of the University of Maryland provided a videotape of a cirrate octopod seen from DSRV ALVIN during a study of deep-sea sharks. The NOAA National Undersea Research Centers at the Universities of North Carolina and Connecticut have sent material from several benthic studies, listed below in the Acknowledgments section. Finally, unpublished observations on adult cephalopods are included from a dive series in which the distribution of juvenile *Loligo* was described by Vecchione and Gaston (1985).

In the presentation that follows, an observation refers to a single encounter with a cephalopod. Such an encounter may result in photographs, one or more videotape sequences, a collected specimen, a reliable description in the dive log, or any combination of these; all would be counted as a single observation. In a few cases, a single observation includes more than one cephalopod, e.g., a school of *Lolliguncula brevis* videotaped in turbid water, but these cases are exceptions. A general discussion of overall impressions and patterns follows the list of observations.

OBSERVATIONS

So far, we have a data base of about 158 observations of cephalopods from the western North Atlantic, Caribbean Sea and Gulf of Mexico, including 58 specimens collected in nearly perfect condition. At least 33 species have been observed to date. Some species have been observed repeatedly and could be effective targets for directed studies using submersibles. This paper is a preliminary presentation of part of a large data base that is growing rapidly as new material accumulates from a variety of sources.

Observations are briefly summarized below for each species seen to date in the western North Atlantic. The following abbreviations are used: obs., total number of observations; vid., number of in situ videotaped sequences; coll., number of specimens collected; ML, size range (mantle length in mm) of specimens collected; depth, depth range of observations (m); temp., water temperature range at observation depths (°C). In some cases, depth or temperature were not recorded and therefore do not appear below.

SEPIOLIDAE. *Stoloteuthis leucoptera* (Verrill, 1878): 3 obs., 2 vid., 2 coll., ML = 17-19, depth = 244-407, temp. = 6.2-8.3.

PICKFORDIATEUTHIDAE. *Pickfordiateuthis* n. sp.: 2 obs., 2 vid., 2 coll., ML = 24-25, depth = 113, temp. = 23.8.

LOLIGINIDAE. *Loligo plei* Blainville, 1823: 2 obs., 2 vid., 0 coll. *Loligo* sp.: 5 obs., 2 vid., 4 coll., ML = 13-46, depth = 59-128. *Lolliguncula brevis* (Blainville, 1823): 11 obs., 11 vid., 0 coll., depth = 15-507.

LYCOTEUTHIDAE. *Selenoteuthis scintillans* Voss, 1959: 1 obs., 0 vid., 1 coll., ML = 29, depth = 671.

ENOPLOTEUTHIDAE. *Abralia redfieldi* Voss, 1955: 2 obs., 0 vid., 2 coll., ML = 20-36, depth = 91-100. *A. veranyi* Rüppell, 1844: 4 obs., 2 vid., 4 coll., ML = 40-43, depth = 588-732, temp. = 12.5-12.9. ?*Abralia* sp.: 3 obs., 0 vid., 3 coll., ML = 9-10, depth = 139. *Enoploteuthis leptura* (Leach, 1817): 3 obs., 1 vid., 3 coll., ML = 66-94, depth = 725-762, temp. = 9.7-9.8.

ONYCHOTEUTHIDAE. *Onychoteuthis* cf. *banksii* (Leach, 1817): 2 obs., 0 vid., 2 coll., ML = 29-52, depth = 671-893, temp. = 11.7. *Onychoteuthis* n. sp.: 1 obs., 1 vid., 1 coll., ML = 45, depth = 754.

HISTIOTEUTHIDAE. *Histioteuthis corona* (Voss and Voss, 1962): 1 obs., 1 vid., 1 coll., ML = 13, depth = 610, temp. = 12.2. *H. hoylei* Goodrich, 1896 (= *H. dofleini* Pfeffer, 1912): 1 obs., 1 vid., 0 coll., depth = 789, temp. = 8.4. *Histioteuthis* sp.: 2 obs., 2 vid., 0 coll., depth = 888.

NEOTEUTHIDAE. *Neoteuthis thieli* Naef, 1921: 1 obs., 0 vid., 1 coll., ML = 14, depth = 448, temp. = 15.9.

OMMASTREPHIDAE. *Ille illecebrosus* (LeSueur, 1821): 29 obs., 29 vid., 2 coll., ML = 205, depth = 326-882. *Ommastrephes barramii* (LeSueur, 1821): 1 obs., 1 vid., 1 coll., ML = 66, depth = 757, temp. = 9.8. ?*O. caroli* Furtado, 1887: 8 obs., 0 vid., 0 coll., depth = 305-838, temp. = 6.7-18.2. *Ornithoteuthis antillarum* Adam, 1957: 19 obs., 13 vid., 11 coll., ML = 90-153, depth = 100-893, temp. = 7.4-15.0. *Hyaloteuthis pelagica* (Bosc, 1802): 2 obs., 2 vid., 0 coll., depth = 509-686. unid. ommastrephids: 9 obs., 9 vid., 0 coll., depth = 58-780.

Table 1. Observations of cephalopods from various geographic areas (numbers followed by "*" indicate schools of squid)

Area	Species	Observations
New England	<i>Teuthowenia megalops</i>	4
	<i>Stoloteuthis leucoptera</i>	3
	<i>Mastigoteuthis hjorti</i>	1
	uncertain identifications	4
Key West	<i>Ornithoteuthis antillarum</i>	2
	<i>Illex illecebrosus</i>	1
	<i>Onychoteuthis cf. banksii</i>	1
	<i>Onychoteuthis</i> sp.	1
	<i>Mastigoteuthis hjorti</i>	1
	<i>Vampyroteuthis infernalis</i>	1
Lesser Antilles	<i>Opisthoteuthis agassizii</i>	1
	<i>Illex illecebrosus</i>	5 (+2 paralarvae)
	<i>Abralia redfieldi</i>	2 (+3 paralarvae)
	<i>Loligo</i> sp.	3
	<i>Ornithoteuthis antillarum</i>	1
Louisiana/Texas slope	<i>Opisthoteuthis agassizii</i>	1
	<i>Illex illecebrosus</i>	14
Louisiana shelf	<i>Ornithoteuthis antillarum</i>	1
	<i>Lolliguncula brevis</i>	9*
North Carolina/South Carolina slope	<i>Loligo plei</i>	2
	<i>Illex illecebrosus</i>	6
Cape Hatteras slope	<i>Illex illecebrosus</i>	2*
	unid. octopodids	2
	<i>Pholidoteuthis adami</i>	1
	unid. cirrate	1

CHIROTEUTHIDAE. *Chiroteuthis veranyi* (Ferussac, 1835): 4 obs., 1 vid., 2 coll., ML = 40-56, depth = 732-740.

MASTIGOTEUTHIDAE. *Mastigoteuthis hjorti* Chun, 1913: 2 obs., 1 vid., 1 coll., ML = 50, depth = 902. *M. magna* Joubin, 1913: 2 obs., 1 vid., 1 coll., ML = 30, depth = 841-882, temp. = 7.4-8.4.

CRANCHIIDAE. *Taonius pavo* (LeSueur, 1821): 4 obs., 4 vid., 1 coll., ML = 140, depth = 834-862, temp. = 7.5-8.8. *Megalocranchia oceanica* (Voss, 1960): 2 obs., 2 vid., 2 coll., ML = 42-65, depth = 813-881, temp. = 7.8-8.0. ?*Megalocranchia* sp.: 1 obs., 0 vid., 0 coll., depth = 914. *Teuthowenia megalops* (Prosch, 1847): 4 obs., 4 vid., 2 coll., ML = 137-145, depth = 716-781, temp. = 4.9-5.2.

UNID. SQUIDS: 12 obs., 12 vid., 0 coll., depth = 97-862, temp. 4.7-25.5.

VAMPYROTEUTHIDAE. *Vampyroteuthis infernalis* Chun, 1903: 1 obs., 0 vid., 1 coll., ML = 10, depth = 823.

CIRROTEUTHIDAE OR STRAUROTEUTHIDAE. unid. cirrates: 3 obs., 3 vid., 0 coll., depth = 854-2,743.

Table 2. Observations of cephalopods during two autumn cruises in the Northwest Providence Channel, Bahamas

Species	Cruise		Total
	1988	1989	
<i>Ornithoteuthis antillarum</i>	10	3	13
<i>Ommastrephes cf. caroli</i>	8		8
<i>Abralia veranyi</i>	1	3	4
<i>Enoplateuthis leptura</i>	2	1	3
<i>Taonius pavo</i>	2	1	3
<i>Hyaloteuthis pelagica</i>	2		2
<i>Mastigoteuthis magna</i>	2		2
<i>Pickfordiateuthis n. sp.</i>	2		2
<i>Megalocranchia oceanica</i>	1	1	2
<i>Neoteuthis thieli</i>	1		1
<i>Chiroteuthis veranyi</i>	1		1
<i>Ommastrephes bartramii</i>	1		1
<i>Onychoteuthis sp.</i>	1		1
<i>Selenoteuthis scintillans</i>	1		1
<i>Vitreledonella richardi</i>	1		1
<i>Histioteuthis corona</i>		1	1
<i>Histioteuthis hoylei</i>		1	1
<i>Opisthoteuthis agassizi</i>		1	1
uncertain identifications	7	4	11

OPISTHOTEUTHIDAE. *Opisthoteuthis agassizii* Verrill, 1883: 3 obs., 2 vid., 3 coll., depth = 581-905, temp. = 6.6.

VITRELEDONELLIDAE. *Vitreledonella richardi* Joubin, 1918: 1 obs., 1 vid., 1 coll., ML = ca.74, depth = 874, temp. = 8.0.

OCTOPODIDAE. *Octopus defilippi* Verany, 1851: 3 obs., 3 vid., 3 coll., ML = 10-15, depth = 60. ?*Octopus sp.*: 1 obs., 1 vid., 0 coll., depth = 79. ?*Benthoctopus piscatorum* (Verrill, 1879): 1 obs., 1 vid., 0 coll., depth = 518. ?*Bathypolypus arcticus* (Prosch, 1847): 1 obs., 1 vid., 0 coll., depth = 615.

ALLOPOSIDAE. *Alloposus mollis* Verrill, 1880: 1 obs., 0 vid., 1 coll., ML = ca. 36, depth = 634.

A summary of the observations from various geographic areas gives an indication of which species may be expected to be seen most often in those areas (Table 1), although this method of compiling observations does not permit quantitative estimates of abundance. Comparison of observations during two cruises to the same area of the Bahamas during autumn of consecutive years shows that variability can be expected (Table 2), but the species most frequently observed was the same on both cruises, *Ornithoteuthis antillarum*, a fast-swimming species of ommastrephid rarely caught by trawling. Furthermore, 5 species, out of a total of 18, were seen on both cruises. One of us (M.V.) participated in the 1988 Bahamas cruise and the second half of the 1989 cruise. The number of observations of cephalopods was substantially higher when a cephalopod specialist was aboard than during the first half of the 1989 cruise, when investigators interested in other groups made observations for us.

So far, we have recognized two undescribed species among the specimens collected. We also have obtained rare species in excellent condition, such as juvenile *Neoteuthis*. We have found morphological structures that previously have not been noted, such as rows of chromatophore-free spots along the arms and mantle of *Opisthoteuthis* and the tail morphology of the "Doratopsis" stage of *Chiroteuthis*. Furthermore, behaviors not previously described have been seen repeatedly.

For example, all cranchiid species observed so far hold their arms and tentacles in a tight, straight bundle above the head (Figs. 1, 2). The submersible crews refer to cranchiids as "cockatoo squids" because they frequently are sighted in this posture that resembles a crested cockatoo. We also have been able to confirm or to deny previously published speculation about functional morphology, such as the use of the "tentacular sheaths" on the ventral arms of chiroteuthids. Detailed descriptions of these species, structures, and behaviors, and a discussion of their implications are not within the scope of this paper. Rather, we intend this paper to be an introduction to the utility of submersibles in the study of cephalopod systematics and ecology.

DISCUSSION

A comprehensive analysis and interpretation of behavior, postures, chromatophore patterns, etc., is beyond the scope of this paper but is planned for the future. Several important factors, however, can be highlighted as a result of the current presentation.

The observations collected from a large number of submersible dives conducted over a broad geographic range in the western North Atlantic verify that it is now feasible to engage in directed studies from submersibles on selected species of cephalopods. For example, multiple sightings of *Illex illecebrosus*, *Ornithoteuthis antillarum*, and *Teuthowenia megalops* indicate that these species are abundant in some areas and readily observable in situ. *Illex illecebrosus* has been seen in many areas in both pelagic and benthic habitats. As this species is an extremely important fishery resource, about which little biology is understood, submersibles could be used as an aid in studying its areal and diel vertical distribution, predatory behavior, and possible spawning sites.

Taxonomic specialists will certainly concur with our assertion that observers in submersibles form specific mental search images that essentially delineate and limit what they notice. Consequently, a non-specialist is less effective than a specialist in observing an unfamiliar group. Of course exceptions occur, especially when a particularly large, spectacular, or unusual individual, such as a cirrate octopod (Fig. 4) or cockatoo cranchiid (Figs. 1, 2), is observed. Similarly, interactions between groups (e.g., predation, Fig. 3) attract attention. Fortunately, specialists in other groups generally are willing to look for cephalopods once they have been shown what may be of value. Nevertheless, we consider it extremely important that a cephalopod specialist be aboard during submersible cruises whenever possible. In this way we will be able to concentrate on the specific and critical observations that are so important to our understanding of the biology and behavior of these animals.

The ability to capture specimens is very important for confirming identifications and for accurate determination of specimen size. For example, the squid in a deep-water photograph identified as *Octopoteuthis* by Roeleveld et al. (1989) probably was actually a rossiin sepiolid. Collection of the specimen would have eliminated this taxonomic problem.

Because in situ studies of deep-sea cephalopods are in their infancy, it is necessary to examine studies of other groups for examples of the full range of potential for these methods. Not only do in situ observations from submersibles provide an important adjunct to information gained from traditional trawling techniques, they also provide perspectives on behavior, distribution, abundance, morphological/taxonomic characters, and functional morphology that never could derive from these traditional methods. Knowledge about gelatinous megaplankton has

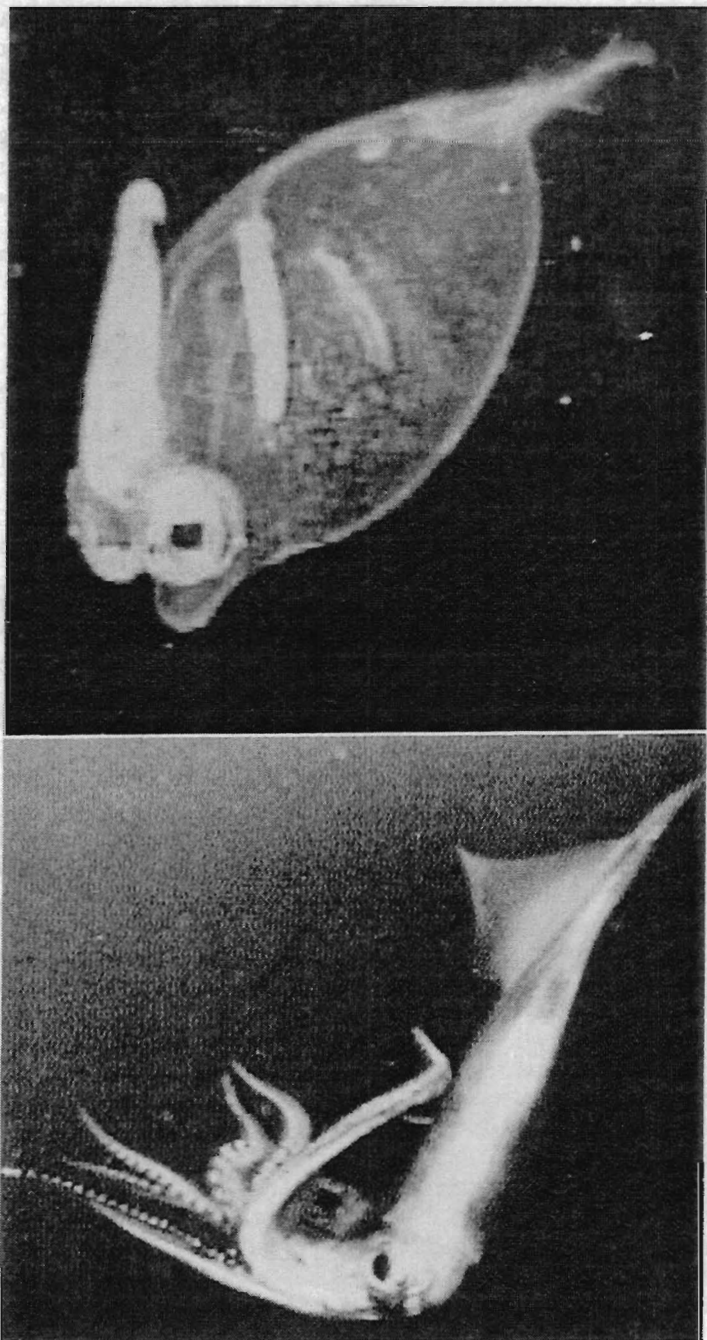
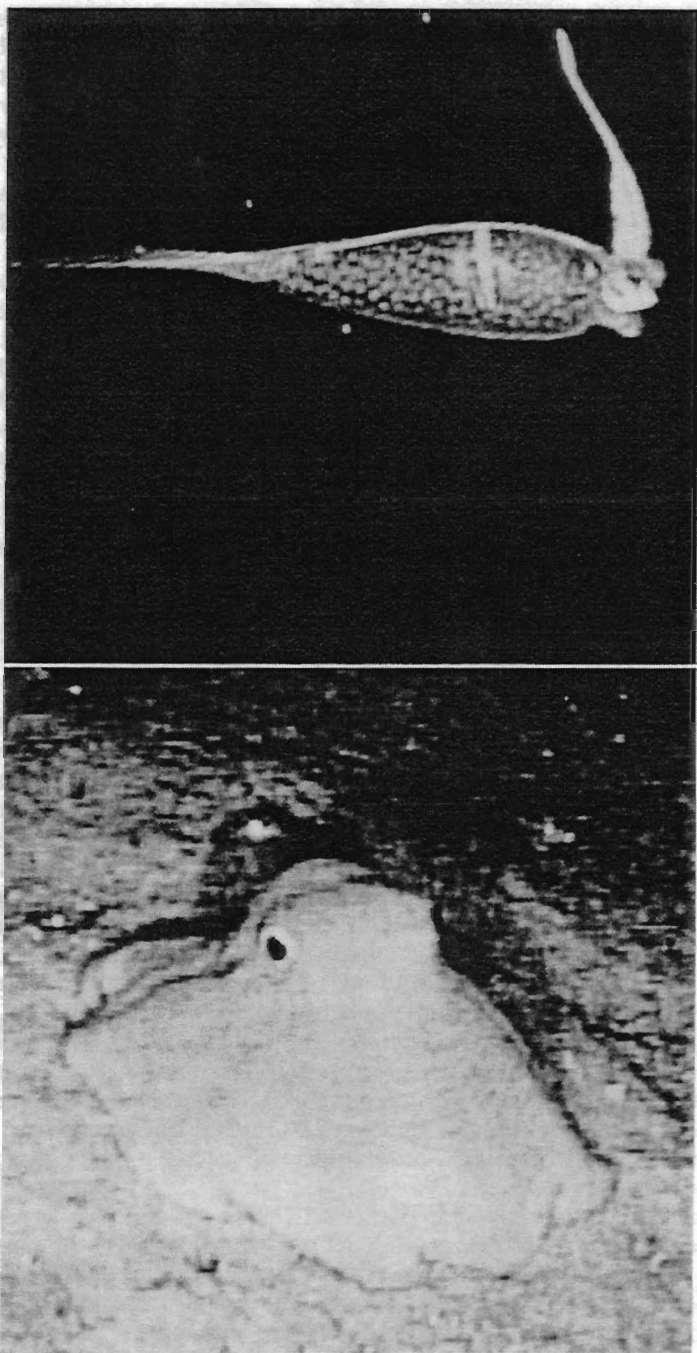


Figure 1 (upper). *Teuthowenia megalops* in the "cockatoo" posture. The animal rotates (head up, horizontal, or head down) with the spindle-shaped digestive gland as the fulcrum. The digestive gland is kept vertical regardless of the orientation of the mantle and head. JOHNSON SEA-LINK (JSL) I dive 2141; 4 August 1987; New England; depth = 789 m; temp. = 4.8°C; specimen collected (USNM 816889); DML = 137 mm. This and subsequent figures are prints made from videotapes recorded in situ and have been selected merely as representative examples.

Figure 3 (lower). *Ornithoteuthis antillarum* in a modified "J" posture, feeding on a *Gonostoma elongata* (fish identified by J. Craddock, Woods Hole Oceanographic Institution). In the "J" posture,



the arms and tentacles are curled above the head, slightly splayed. JSL II dive 1000; 1 November 1984; Bahamas; depth = 684 m; temp. = 10.7°C.

Figure 2 (upper). *Taonius pavo* in the cockatoo posture. JSL II dive 1685; 10 October 1988; Bahamas; depth = 853 m; temp. = 8.8°C; specimen collected (USNM 81712); DML = 140 mm.

Figure 4 (lower). *Opisthoteuthis agassizii* on the bottom. Shortly after this frame, the animal swam away beating its fins and using the arms and web for medusoid swimming. JSL II dive 1746; 25 April 1989; St. Vincent I.; depth = 586 m; temp. = 6.6°C; specimen collected (HBOM 068:00086).

advanced remarkably through use of submersibles (Madin and Harbison, 1978; Child and Harbison, 1986; Widder et al., 1989). For example, Mills and Goy (1988) observed the narcomedusa *Solmissus* feeding on *Cavolinia* pteropods at night, whereas all simultaneously net-collected *Solmissus* had empty stomachs, night and day. Similarly, we have been able to observe active feeding by midwater squids (Fig. 3).

The abundance and exact position in the water column of deep megaplanktonic and micronektonic organisms can be determined precisely from submersibles, whereas nets homogenize the microdistributions of these organisms in a single sample. Studies from the submersible PISCES revealed that species of plankton were distributed in unexpectedly very narrow and sharply defined layers (Mackie and Mills, 1983). Laval et al. (1989) observed for the first time in the western Mediterranean Sea populations of fragile ctenophores and appendicularians that had never been captured during a 25-year period of regular sampling with plankton nets. Comparisons between counts from the submersible CYANA and catches with simultaneously-towed Isaacs-Kidd midwater trawls indicate a 2:1 underestimation of abundance of some species by these nets. The ratio in favor of the submersible is even higher for species that actively avoid the net (Laval and Carré, 1988). Our observation of *Lolliguncula brevis* at a depth of 507 m near a vertical wall that could not have been sampled by trawling, extends the known depth range of this supposedly inshore species by over 475 m. We also have documentation of *L. brevis* actively swimming in hypoxic (0.7 mg/liter) bottom waters on the Louisiana continental shelf, indicating that this species is even more eurytopic than previously believed.

Ornithoteuthis antillarum has been considered to be rare based on net sampling (Roper and Young, 1975), but our observations from submersibles indicate that this species is very common. Clearly, this rapid swimmer avoids nets but is not threatened enough by submersibles to escape before being observed. Species thought to be exclusively pelagic, e.g., species of *Mastigoteuthis* and *Histioteuthis*, now are known from in situ observations to descend, at least on occasion, to very near the bottom. While this refutes traditional inferences based on indirect evidence from trawls, it explains the previously puzzling occurrence of these "mesopelagic" squids in the stomachs of exclusively benthic deep-sea fishes (C. F. E. Roper, unpubl.). Furthermore, we now know that *Illex illecebrosus* commonly rests on the sediment surface on the continental slope.

None of these results suggest that we should abandon traditional sampling methods, but they do confirm that observations from submersibles provide data and information applicable to problems that are intractable by traditional techniques. We certainly concur with Laval et al. (1989) who recommend that major oceanographic studies of pelagic ecosystems should be supplemented by use of submersibles.

Janssen et al. (1986) and Alldredge et al. (1984) made discoveries from submersibles about hatchetfish swimming behavior and copepod diapause state, respectively, that could not have been realized by traditional methods. Miller and Pawson (1990) precisely documented swimming behavior in bathyal and abyssal holothurians based on in situ observations and videotapes, a study that would have been impossible without submersibles. Carrying this to the extreme, Pawson and Foell (1986) described a new species of benthopelagic holothurian based solely on collected photographs and videotapes, not specimens. Our work has already yielded fortuitous information on fragile taxonomic and morphological characters that are not visible on trawl-caught and preserved specimens, e.g., the rows of pigment-free spots on *Opisthoteuthis*. Especially enlightening are observations on

functional morphology; examples include the relationship of tentacles and tentacular sheaths in *Chiroteuthis* and *Mastigoteuthis*, the autotomizing tail of "Doraptosis" paralarvae, medusoid swimming by several deep-sea octopod species, and a probable locomotory function in the mantle opening of *Alloposis*. Behavioral observations are numerous and unexpected, e.g., the "J" posture of several species, the cockatoo posture of cranchiids, and the ability of *Ornithoteuthis* to bend its mantle double to use the ventral arms for removal of irritants from the fins and tail.

Critics of submersibles as tools for observing deep-sea animals, including cephalopods, argue that observed behaviors are biased by the presence of the submersible and therefore are unnatural and invalid. While it is true that some postures and behaviors observed are a result of stimuli from the submersible, it is unlikely that all observations are thus influenced. Furthermore, the stresses on animals observed in situ are less than those of capturing the animal, transporting it to the surface, and then observing it in the confinement of an aquarium. If what we are seeing are defensive postures, then at least we now know what defensive postures look like. The important point is that these observations, recorded on videotape, represent some of the first data available on living deep-sea cephalopods in their natural environments. They allow us a glimpse, however incomplete, into the lives and habits of these important members of marine ecosystems.

For us, the use of submersibles represent an effective and invaluable tool that enables us to investigate numerous aspects of the behavior, morphology, systematics, and ecology of deep-sea cephalopods.

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ADDRESSES: (M.V.) National Marine Fisheries Service, Systematics Laboratory, National Museum of Natural History, Washington, DC 20560; (C.F.E.R.) Department of Invertebrate Zoology (Mollusks), National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.