

Medusae, siphonophores and ctenophores of the Alborán Sea, south western Mediterranean*

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SUMMARY: Fifty-eight species of planktonic Cnidaria and Ctenophora were observed and collected in the Alborán Sea (western Mediterranean) during a cruise in April 1991 on the *RV Seward Johnson*. Eleven stations were sampled 10 to 21 nautical miles off the north coast of Morocco between the Strait of Gibraltar and the Cap de Trois Fourches: 26 dives using the manned submersible *Johnson-Sea-Link I* were made to bottom depths of 370–850 m, and at 5 of the same stations 7 blue-water SCUBA dives were made from the surface to about 15 m. Twelve species of hydroidomedusae, 18 species of siphonophores, 6 species of scyphomedusae, and 22 species of ctenophores were collected. The most numerous species seen from the submersible in deep water included *Solmissus albescens*, *Halicsera conica*, *Forskalia* (?) *formosa*, *Lensia conoidea*, *Abylopsis tetragona*, *Paraphyllina ransonii*, *Periphylla periphylla*, *Euplokamis stationis*, *Bathocyroe fosteri*, *Bolinopsis infundibulum*, an undescribed cydippid ctenophore, and an undescribed lobate ctenophore. Species that were most numerous near the surface were *Pandea conica*, *Solmaris leucostyla*, *Nanomia bijuga*, *Haeckelia beehleri*, *Pleurobrachia rhodopsis*, *Bolinopsis vitrea*, *Ocyropsis maculata immaculata*, *Beroe ovata*, and an undescribed cydippid ctenophore. Advantages of using a submersible for this study included the ability to collect in perfect condition fragile forms like siphonophores and ctenophores that fall apart when collected in nets, the possibility of obtaining a realistic image of small-scale distribution throughout the water column, and to sample plankton close to the sea floor.

Key words: Hydromedusae, Hydroidomedusae, Scyphomedusae, Siphonophora, Ctenophora, gelatinous zooplankton, Mediterranean, community structure, distribution.

INTRODUCTION

This study is part of an ongoing program of manned submersible investigations of mesopelagic gelatinous zooplankton. Over the past decade we have been fortunate to have had the opportunity to dive in a number of locations, mostly in the North Atlantic. Gelatinous zooplankton is abundant at depths that can be searched using the *Johnson-Sea-Link* submersibles (to 915 m), and is usually of sufficient size

to be accessible to scientists observing the water column from inside a submersible. Planktonic Cnidaria and Ctenophora have been abundant and readily visible on all of our excursions. In this paper we report on the medusae, siphonophores, and ctenophores seen on a cruise in the Alborán Sea in the western Mediterranean. When time and weather allowed, the submersible observations were augmented by blue-water SCUBA dives to examine the near-surface fauna.

The principal purpose of this cruise was a study of bioluminescence in the water column during the spring bloom. The Alborán Sea was investigated

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because there are a number of reports of intense surface displays of bioluminescence from this region. Specialists familiar with gelatinous zooplankton were included in the scientific party in order to help identify organisms responsible for bioluminescence. The bioluminescence data will be reported elsewhere (Widder *et al.*, submitted).

The original cruise plan was to sample in a circular path in the western Alborán Sea. We should have been able to compare the fauna along the Moroccan coast with the fauna along the Spanish coast, but very windy weather kept us from sampling at any of the Spanish stations. Thus we present here only the fauna of the northwestern Morocco Mediterranean coast.

In addition to a species list, we have tried to leave the reader with an impression of the spatial distribution of gelatinous plankton throughout the water column. Previous studies in the western Mediterranean using nets have included a number of small species that we did not collect, because it is very difficult to see specimens less than about 1 cm, especially transparent ones, from the submersible. On the other hand, we offer information on the fragile siphonophores and ctenophores, and on small-scale distribution, not previously available. Spring bloom conditions presented us with an unusually diverse surface gelatinous fauna, exempli-

fied especially by a large number of rather young ctenophores.

We have separately authored the sections on our respective taxonomic specialities, so the summaries of the hydroidomedusae and scyphomedusae are by C. E. Mills, siphonophores by P. R. Pugh, and ctenophores by G. R. Harbison and S. H. D. Haddock.

MATERIALS AND METHODS

Macrozooplankton in the Alborán Sea (western Mediterranean) were observed and collected during a cruise April 5–24, 1991 on the *RV Seward Johnson*. The ship sailed from Cádiz, Spain, through the Strait of Gibraltar, and along the coast of Morocco 10 to 21 nautical miles offshore, as far as the Cap de Trois Fourches. It then crossed the Alborán Sea east of Isla de Alborán and returned west along the coast of Spain, but the weather was too rough to sample during the northern leg of the voyage. The cruise stations (numbered 1–12, although no plankton samples were taken at Station 11, so it is omitted) are shown in Figure 1.

Animals were collected by the following methods: (a) using the manned submersible *Johnson-Sea-Link I (JSLI)*, (b) by SCUBA (designated here as BWP, for blue-water plankton dives), and (c) in the

TABLE 1. – *Johnson-Sea-Link I (JSLI)* submersible dives, *RV Seward Johnson* Alborán Sea cruise, 5–24 April 1991.

Cruise Station#	JSLI Dive#	Latitude	Longitude	Sphere Observer	Bottom (m)	DayMoYr	DiveTime (GMT+1 hr)
3	2929	35 29 N	04 26 W	Widder	479	06 Apr 91	1120-1430
3	2930	35 29 N	04 28 W	Bernstein	~479	06 Apr 91	2030-2330
4	2931	35 28 N	04 13 W	Pugh	508	07 Apr 91	1235-1542
4	2932	35 27 N	04 13 W	Widder	409	07 Apr 91	2053-0000
5	2933	35 28 N	04 01 W	Harbison	370	08 Apr 91	1300-1610
5	2934	35 30 N	04 09 W	Herring	557	08 Apr 91	2202-0030
6	2935	35 35 N	03 40 W	Mills	641	09 Apr 91	1253-1545
6	2936	35 35 N	03 37 W	Bernstein	687	09 Apr 91	2110-0000
7	2937	35 53 N	03 22 W	Pugh	839	10 Apr 91	1231-1531
7	2938	35 52 N	03 23 W	Widder	>542	10 Apr 91	2031-2343
8	2939	35 32 N	03 16 W	Harbison	821	11 Apr 91	1238-1545
8	2940	35 30 N	03 18 W	Herring	~716	11 Apr 91	2113-0007
9	2941	35 44 N	02 49 W	Mills	587	12 Apr 91	1312-1622
9	2942	35 45 N	02 45 W	Bernstein	580	12 Apr 91	2050-0010
12	2943	35 45 N	03 15 W	Pugh	~823	13 Apr 91	1345-1625
12	2944	35 46 N	03 13 W	Harbison	~847	14 Apr 91	1100-1408
12	2945	35 45 N	03 18 W	Widder	~792	14 Apr 91	1910-2124
12	2946	35 45 N	03 12 W	Mills	837	15 Apr 91	1059-1415
12	2947	35 45 N	03 14 W	Widder	~914	15 Apr 91	1917-2119
12	2948	35 46 N	03 15 W	Haddock	841	16 Apr 91	1230-1545
12	2949	35 44 N	03 16 W	Bernstein	805	16 Apr 91	2221-0135
10	2950	36 04 N	02 48 W	Pugh	719	17 Apr 91	1234-1442
10	2952	36 03 N	02 48 W	Herring	729	17 Apr 91	2204-0020
2	2953	35 34 N	04 48 W	Harbison	465	23 Apr 91	1412-1730
2	2954	35 34 N	04 46 W	Widder	472	23 Apr 91	2132-0048
1	2955	35 49 N	05 04 W	Mills	411	24 Apr 91	0727-1022

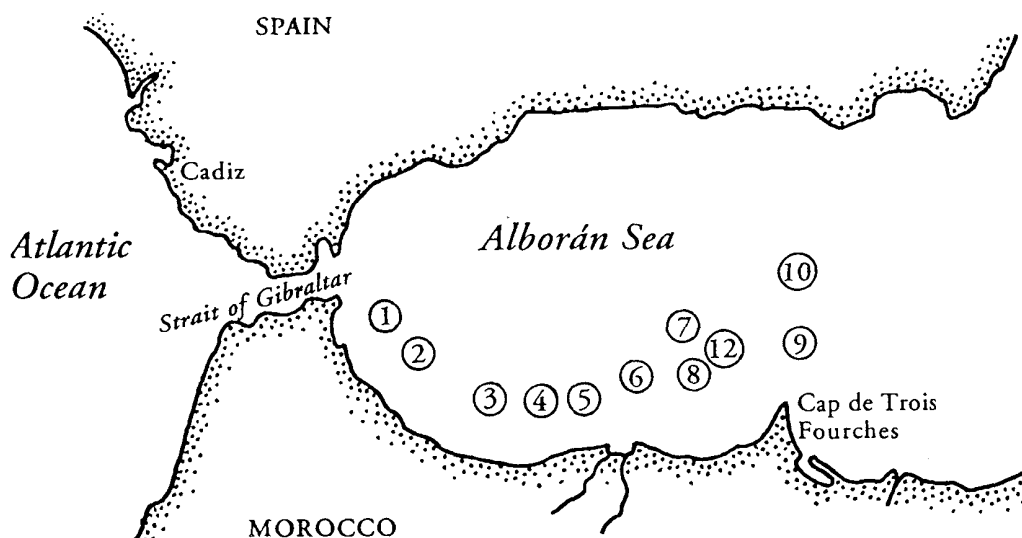


FIG. 1. – Map of the cruise stations for the RV Seward Johnson Alborán Sea cruise, 5-24 April 1991. Numbers 1-12 (there is no Station 11) correspond to the cruise station numbers of Tables 1 and 2.

case of one species of hydroidomedusa, using a plankton net. At a total of eleven stations, 26 submersible dives were made to bottom depths of 370–850 m (Table 1), and at five of the same stations a total of seven blue-water SCUBA dives from the surface to about 15 m (Table 2) accompanied the series of submersible dives.

The *Johnson-Sea-Link* submersibles have devices especially designed for the collection of gelatinous zooplankton. The submersible and its collection capabilities have been already been described by Pugh and Harbison (1986) and Youngbluth *et al.* (1988). The submersible carries one pilot and one observer in the front compartment, which is a transparent acrylic sphere about 2 m in diameter - this observer determines the program for each dive and is responsible for selection of specimens to be collected. Another observer and a technician are in an aft chamber with small observation ports. Both observers take notes (on paper, audiotape, or videotape) about animals seen through

the dive. Depth and temperature can be read off gauges in the sphere. Many of the specimens were videotaped *in situ* prior to being collected. Animals were individually collected, often without being touched, by either of two kinds of devices affixed to the front or top of the submersible. Dives lasted 2 to 3 1/2 hours. Animals were catalogued and processed within 30 minutes of the end of each dive at which time they were available for any scientist to study.

Animals collected on the blue-water SCUBA dives were individually collected in glass screw-top jars by divers attached to tethers from a central line. This technique is discussed at length by Hamner (1975). Specimens were brought to the ship, catalogued, and then made available for study, again within about 30 minutes of the end of each dive.

Figure 3 was compiled by computer from both film and videotape images that were scanned in and subsequently manipulated using Adobe Photoshop software.

TABLE 2. – Blue water plankton (BWP) SCUBA dive stations, RV Seward Johnson Alborán Sea cruise, 5-24 April 1991.

Cruise Station #	BWP Dive #	Latitude	Longitude	Depth (m)	DayMoYr	Dive Time (GMT+1 hr)
7	1894	35 53 N	03 22 W	0-15	10 Apr 91	1730-1814
9	1895	35 44 N	02 49 W	0-14	12 Apr 91	1715-1815
12	1896	35 46 N	03 13 W	0-14	14 Apr 91	1610-1705
12	1897	35 47 N	03 12 W	0-21	15 Apr 91	1630-1728
12	1898	35 46 N	03 15 W	0-20	16 Apr 91	1745-1830
10	1899	36 04 N	02 48 W	0-14	17 Apr 91	1530-1600
2	1900	35 34 N	04 48 W	0-17	23 Apr 91	1822-1912

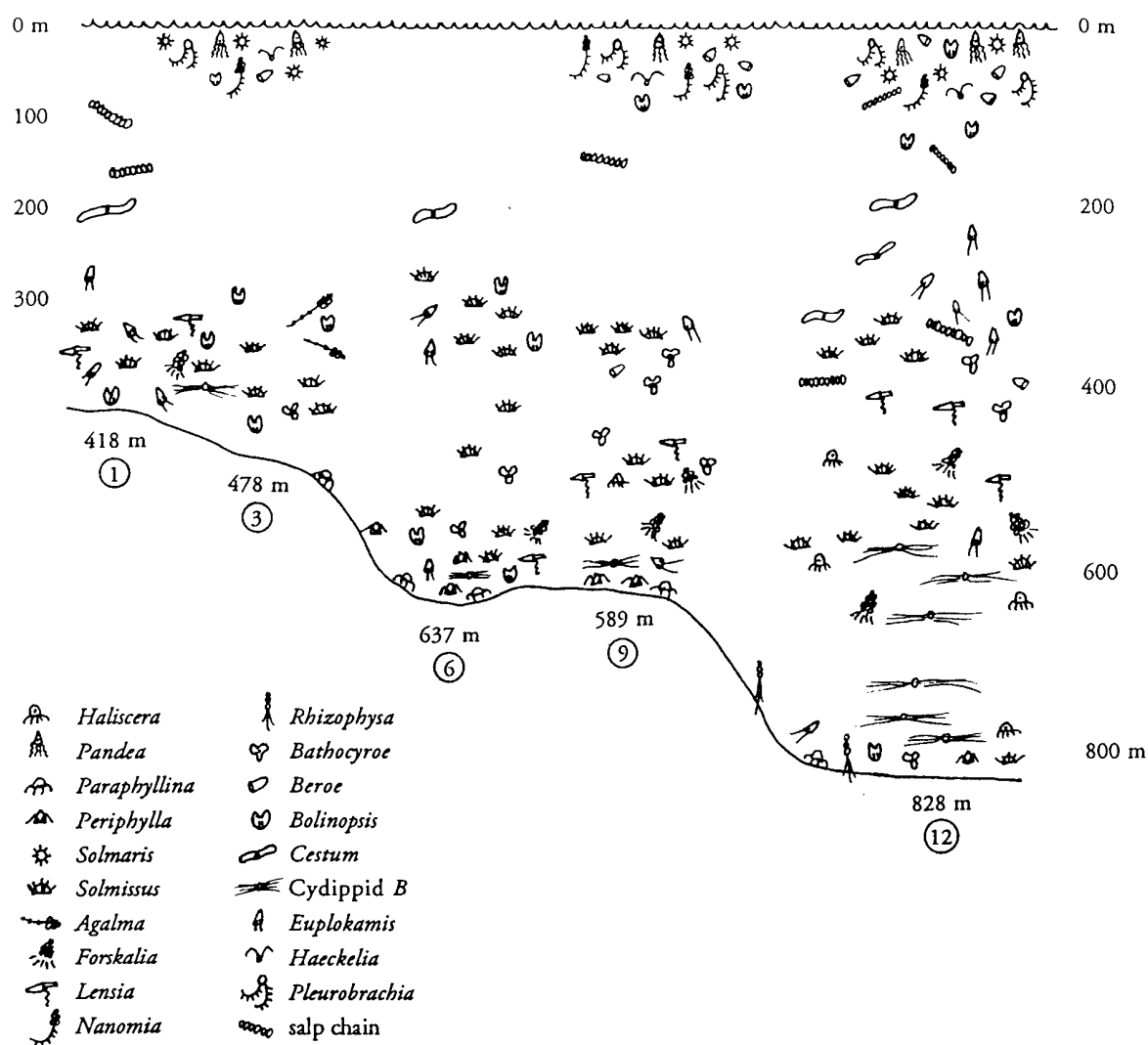


FIG. 2. – Cartoon depicting gelatinous zooplankton in a cross section of the Alborán Sea cruise track 5-24 April 1991. Animals in the water column and bottom profiles match observations moving from west to east (left to right in the cartoon) at Station 1 (JSLI dive 2955), Station 3 (JSLI dive 2929), Station 6 (JSLI dive 2935), Station 9 (JSLI dive 2941), Station 12 (JSLI dive 2946) (see Fig. 1, station map).

RESULTS AND DISCUSSION

We spent only about two weeks sampling in the Alborán Sea. Our studies allow us to provide a straightforward report of the species we observed. We are not able to further analyze our data to show either temporal or geographic variation, as has been done for planktonic Cnidaria further north along the Catalan coast (Gili *et al.*, 1987, 1988). We cannot even state for many of the species whether they are common inhabitants of this region or rare visitors.

Nevertheless, we can provide a detailed picture of the small-scale distribution of gelatinous zooplankton along the northwestern Moroccan coast for those two weeks in April 1991. Figure 2 is a cartoon image of the water column, moving from west to east, from

Station 1 to Station 12, simplified in order to be more generally readable. Diversity was quite high near the surface, as observed by SCUBA, then relatively few animals were seen in the remainder of the upper 300 m. Abundance increased below 300 m, with numbers continuing to increase in most locations towards the bottom. A few species, the coronates *Periphylla periphylla* and *Paraphyllina ransonii* and the siphonophore *Rhizophysa filiformis*, seemed to occur nearly exclusively very near the bottom.

The only species that could be described as dominating any part of the deepwater plankton landscape was the hydroidomedusa *Solmissus albescentis*. Other species provided an ever-present, but never abundant, part of the macroplankton community at all depths. On most submersible dives, 4-6

species each of medusae, siphonophores, and ctenophores were collected from the sub-surface water column. In one of the most jelly-rich bands, during *JSLI* dive 2950, at 1300 hrs GMT+1 and about 490 m, the proportions of predominant gelatinous macrozooplankton were observed to be: 20 *Solmissus albescens* to four *Abylopsis tetragona* to one *Haliscera conica* to one chaetognath, with occasional *Euplokamis stationis*. For scale, in this case, *S. albescens* were about one m apart, which converts to about $1.4 \times m^{-3}$ *S. albescens*, with the other species occurring at proportionately lower densities (formula in Mackie and Mills, 1983).

Gelatinous zooplankton is usually highly seasonal, and both species composition and abundance can be expected to change throughout the year. Many species of medusae are budded off benthic polyps at only certain times of the year. Even the holoplanktonic species of medusae, as well as the (holoplanktonic) siphonophores and ctenophores are seasonal, reproducing usually in the spring when their zooplankton prey are most abundant.

Because of the special equipment for collection of planktonic animals on the *Johnson-Sea-Link* submersibles, this cruise yielded a much more elaborate species list than previous submersible cruises in the Mediterranean. Genovese *et al.* (1985) report their findings from 21 dives in May and June 1979 in the Strait of Messina using the mesoscaphe *Forel*. Laval *et al.* (1989) made eight dives in April 1986 in the Ligurian Sea using the French manned submersible *Cyana*. Both of the above papers report detailed small-scale distribution of six dominant species in the water column from the surface to 600-700 m, but neither present a full species list of the gelatinous zooplankton because of limited collecting ability of the submersibles. Trégouboff, Pérès, Picard, and Bernard used the French bathyscaphe *F.N.R.S. III* for many dives in the Ligurian Sea between 1954 and 1961 (Pérès, 1958; Trégouboff, 1958; and thirteen other papers cited by Mills and Goy, 1988). Based on many years of studying the regional plankton with other techniques, they made many detailed observations of fine-scale vertical stratification of plankton without the ability to collect samples from the bathyscaphe. Nonetheless, the plankton treatise by Trégouboff and Rose (1957) fails to recognize the presence of some species of gelatinous zooplankton (especially ctenophores) now known to be present in

TABLE 3. – Summary of numbers of species of medusae, siphonophores and ctenophores collected by submersible and by SCUBA divers, *RV Seward Johnson* Alborán Sea cruise, 5-24 April 1991.

	Total # Species	Species collected by submersible	Species collected by SCUBA
Hydroidomedusae	12	8	6
Siphonophores	18	13	5
Scyphomedusae	6	3	3
Ctenophores	22	11	13

the Ligurian Sea (C. E. Mills and C. Carré, personal observations).

Comparisons of the species that we found with planktonic Cnidaria and Ctenophora previously collected in the Alborán Sea are made under each major taxon. Our annotated species list for the April 1991 cruise is presented below. It can be assumed that with further study, the list of gelatinous zooplankton occurring in the Alborán Sea would be greatly expanded.

PHYLUM CNIDARIA

Class Hydrozoa

Sub-class Hydroidomedusae

Twelve species of hydroidomedusae [this term is being used instead of “hydromedusae”, as suggested by Bouillon *et al.* (1992)] were collected on the cruise. Sixty-three specimens comprising eight species were collected using the submersible; six species were collected by SCUBA, of which two were among those collected by submersible. One additional species was collected in a plankton net fished in the upper 5 m at Station 7 just prior to a SCUBA dive. Four of the six orders of Hydroidomedusae that produce medusae were represented in the collection.

Solmissus albescens was probably the single most numerous medusa, being seen at all stations on virtually all dives; this is a mesopelagic species that is capable of migrating to the surface at night.

From the sphere of the submersible many small clear trachymedusae were seen between about 300 and 700 m (*JSLI* dives 2929, 2935, 2941, 2946, 2950 and 2955 - Mills, personal observations). Nearly all of the specimens captured at these depths proved to be *Haliscera conica*, but it is possible that other species than those mentioned below were also present, but not collected.

All species collected were previously known from the Mediterranean Sea (Boero and Bouillon, 1993). Thirteen species of Hydroidomedusae have previously been reported from the Alborán Sea and Strait of Gibraltar (Goy, 1983; Rodríguez, 1983; Madin, 1991). Only four of the species that we found, *Lizzia blondina*, *Pandea conica*, *Solmissus albens*, and *Liriope tetraphylla*, were previously known there; the remaining eight species are new records for the Alborán Sea.

Order Anthomedusae

Lizzia blondina Forbes 1848. Several specimens were collected using a 153 µm mesh plankton net hauled from 5 m to the surface at Station 7, shortly before BWP dive 1894. None were seen by the SCUBA divers, but these 1 mm medusae were smaller than specimens normally collected using SCUBA. All *L. blondina* had medusa buds on the manubrium. This boreal, neritic species is well known from elsewhere in the western Mediterranean, NE Atlantic, and North Sea (Kramp, 1959).

Pandea conica (Quoy and Gaimard, 1827). Many specimens were collected by SCUBA divers: Station 2 (BWP dive 1900), Station 9 (BWP dive 1895), Station 10 (BWP dive 1899), and Station 12 (BWP dives 1896, 1897, 1898). This species was especially abundant at Station 12 where, in calm waters, hundreds could be seen at the surface even from the deck of the ship. All specimens were in the same size range, 8 to 15 mm in bell height, and appeared to be sexually mature. They had bright red gonads and red ocelli on the tentacles and intertentacular rudiments. In the laboratory, the medusae held their tentacles tightly coiled up and exhibited a strong crumple response when touched. Many of the medusae had one or more of an unidentified pink amphipod (sometimes with juveniles) clinging to the bell, usually on the subumbrellar surface. *P. conica* is known throughout the Mediterranean, as well as in boreal to tropical waters in the north and south Atlantic and in the Pacific (Kramp, 1959). This epipelagic species is frequently found offshore. It was also found in abundance by SCUBA divers in the Alborán Sea in spring, 1986 (Harbison, personal observations).

Order Leptomedusae

Laodicea undulata (Forbes and Goodsir, 1853). Two specimens were collected and more were seen

by SCUBA divers at Station 9 (BWP dive 1895). These immature medusae were about 7 mm in bell diameter. The hydroid of this species has been collected near the Strait of Gibraltar and off the coast of Morocco at 144 to 170 m (Ramil and Vervoort, 1992). This neritic species is widely distributed in the Atlantic and Mediterranean (Kramp, 1959, 1961).

Modeeria rotunda (= *Tiaranna*) (Quoy and Gaimard, 1827). A single specimen was collected by submersible at Station 1 (JSLI dive 2955) at 379 m. The medusa was 15 mm tall and wide, appeared to be sexually mature and, in spite of its very thick and stiff jelly, had a strong crumple response that brought the bell margin up inside the bell. This medusa was found at the station nearest to the Strait of Gibraltar; the hydroid of this species has also been reported from several locations along the coast of Spain in and around the Strait of Gibraltar at depths of 144 to 681 m (Ramil and Vervoort, 1992). This species is known mainly from deep water in the western Mediterranean, Atlantic, Pacific and Indian Oceans (Kramp, 1959; Ramil and Vervoort, 1992). The Family Tiarannidae, to which this species belongs, was recently moved from the Anthomedusae to the Leptomedusae (Bouillon, 1985).

Clytia hemisphaerica (Linné, 1767). Four specimens were collected by submersible: Station 1 (JSLI dive 2955) and Station 4 (JSLI dive 2934). Three specimens collected at Station 1, along with another two that were seen, but not collected, were all between 364 and 369 m, whereas the specimen at Station 4 was collected at 296 m. The four medusae collected were 7 to 10 mm in diameter, had mature gonads, and agreed with the description of *C. hemisphaerica* (= *Phialidium*) in Kramp (1961), except that the mouths were relatively large. This neritic species is found throughout the Atlantic and Mediterranean, also in the Indo-west-Pacific (Kramp, 1959). Garcíá-Carrascosa (1981) found the hydroid of *C. hemisphaerica* on the coast of Spain in the Alborán Sea east of Gibraltar.

Clytia sp. Two medusae were identified as "*Phialidium*" by SCUBA divers (Harbison and Haddock) at Station 12 (BWP dives 1897, 1898), but were not collected so could not be identified to species. *Phialidium* is a junior synonym of *Clytia*.

Octophialucium funerarium (Quoy and Gaimard, 1827). A single specimen was collected by submersible at Station 4 (JSLI dive 2931) at 393 m. This mature female, 23 mm in bell diameter, spawned in the ship's laboratory shortly after collection. The

species was originally described from the Strait of Gibraltar, is considered by Kramp (1959) to be a slope species, and is known from the Mediterranean and NE Atlantic.

Order Narcomedusae

Solmaris leucostyla (Will, 1844). This species was collected both by submersible and by SCUBA divers. Two specimens were collected by submersible at Station 4 (JSLI dive 2932) at 204 m; they were too small to be seen by observers in the submersible, but were found in a water sample taken at this depth. Large numbers of specimens were also seen on SCUBA dives at Station 2 (BWP dive 1900), Station 7 (BWP dive 1894), Station 9 (BWP dive 1895), Station 10 (BWP dive 1899), and Station 12 (BWP dives 1896, 1897, 1898). Two additional specimens were collected in a bucket of water dipped from the sea surface at Station 5. These medusae ranged from 1 to 5 mm in diameter - most were 3 to 5 mm. Specimens examined had 14 to 24 tentacles, the same number of lappets, and typically one statocyst per lappet. This species is an oceanic, epipelagic medusa that seems to be endemic to the Mediterranean (Kramp, 1959).

Solmissus albescens (Gegenbaur, 1856). Forty-one specimens were collected by submersible: Station 1 (JSLI dive 2955), Station 3 (JSLI dive 2929), Station 4 (JSLI dives 2931, 2932), Station 5 (JSLI dives 2933, 2934), Station 6 (JSLI dive 2935), Station 8 (JSLI dive 2939), Station 9 (JSLI dives 2941, 2942), and Station 12 (JSLI dives 2944, 2946, 2948). Many additional examples were seen from the windows of the sub, including at Station 2 (JSLI dive 2953), Station 7 (JSLI dive 2937), and Station 10 (JSLI dive 2950), so *S. albescens* was present at all stations. These medusae were collected from near the surface to 630 m depths, although during the day few were above 300 m (see below).

We had some difficulty in assigning a specific name to these narcomedusae (Fig. 3H). Mills originally called specimens caught early in the cruise (Stations 3, 4, 5, 6) *Solmissus marshalli* Agassiz and Mayer, 1902, based on comparisons with the summary descriptions of Kramp (1959, 1961) and her own collections at several locations in the western Atlantic. As the cruise progressed eastward, further into the Mediterranean, it was expected to find *S. albescens*, which is the only *Solmissus* thought to occur in Mediterranean waters, where it is considered endemic (Kramp, 1959). In fact, all

specimens looked the same, lacking the small, but distinct exumbrellar warts diagnostic of *S. albescens* (some had nematocyst patches extending above the lappets onto the bell). It was finally decided to use the name *S. albescens* for all *Solmissus* observed in the Alborán Sea, acknowledging that *S. marshalli* may turn out to be a junior synonym of *S. albescens*. It would be well worthwhile to make a careful comparison of all three *Solmissus* species to determine the validity of species names. (When examining the same submersible-collected specimens from the western Atlantic, C. E. Mills and R. J. Larson often independently assigned different species names, *S. marshalli* or *S. incisa*, to the same specimen, which exemplifies the difficulties even specialists have with the present species definitions.)

Solmissus albescens was the only really numerous medusa. By day, *S. albescens* typically occurred in a dense layer between about 300 and 500-600 m. On many dives, *S. albescens* medusae were as abundant as about 1 m apart within some of this layer, a numerical density equal to that observed by submersible for *S. albescens* in the Ligurian Sea in April 1986 (Mills and Goy, 1988). Small numbers of *S. albescens* occurred all the way to the bottom on most day dives. *S. albescens* is known to be a vertical migrator elsewhere in the Mediterranean (see Mills and Goy, 1988, for review), moving up into the upper 100 m during the night. Our night dives (used primarily for studies of bioluminescence) support that this migration also occurs in the Alborán Sea, although it appears that some animals remain at depth during the night in this location.

Several of the *Solmissus albescens* were feeding at the time of collection. We were able to recognize ctenophore comb plates in one specimen, another had eaten a small chain of *Salpa fusiformis*, another contained eight salps and a ctenophore *Euplokamis stationis* in its stomach, one had a single fish (?) egg in its gut, and several had featureless, unidentifiable, whitish food material in the stomach pouches. Two specimens had many small parasitic narcomedusae developing in the stomach pouches.

Order Trachymedusae

Liriope tetraphylla (Chamisso and Eysenhardt, 1821). A single medusa was collected using SCUBA at Station 12 (BWP dive 1897). This is a common cosmopolitan, oceanic epipelagic species, usually found in warm waters (Kramp, 1959).

Haliscera conica Vanhöffen, 1902. Eleven specimens were collected by submersible: Station 1 (JSLI dive 2955), Station 4 (JSLI dive 2931), Station 5 (JSLI dive 2933), Station 6 (JSLI dive 2935), Station 7 (JSLI dive 2938), Station 8 (JSLI dive 2939), Station 9 (JSLI dive 2941), and Station 12 (JSLI dives 2943, 2944). These medusae were collected between 334 and 591 m. Several more were seen (Mills observations) but not collected at Station 10 (JSLI dive 2950) and Station 12 (JSLI dive 2946) between 365 and 650 m. This species is colorless and very transparent. Medusae collected ranged between 9 and 17 mm in bell diameter - most seemed to have developing gonads that were also very transparent. The tentacles, all alike, are evenly distributed around the bell. Since the tentacles are rarely seen on net-collected animals, it should be mentioned that in life the tentacles are somewhat variable in length, but mostly extend down about the equivalent length of 3 bell diameters. The tentacles contract by coiling. These medusae (family Halicreatidae) are very strong swimmers, but do not have the fast escape swim typical of many trachymedusae in the family Rhopalonematidae (Mills *et al.*, 1985). *H. conica* is known worldwide from mesopelagic depths (Kramp, 1959; Mills, personal observations), where our submersible studies have shown that it is quite common.

Arctapodema sp. Two specimens were collected by submersible at Station 6 (JSLI dive 2935) and Station 7 (JSLI dive 2938) at 578 and 539 m, respectively. These medusae could not be clearly assigned to either *A. amplum* or *A. australe*, the species they most resembled. Both medusae were about 10 mm tall and 16 mm in bell diameter, with a small stomach that has orange-red pigment, and 4 simple lips. They had 8 rounded sac-like gonads immediately adjacent to the stomach on the 8 radial canals. One specimen had about 144 tentacles, the other had about 215 and both had 16 statocysts (2 per octant). On both specimens, a distinctive feature was that all 8 radial canals had several fine branches (or large neurons?) emerging from the lowest few mm and angling out towards the ring canal. We have collected specimens similar to these from around 800 m using the JSL submersibles in the Bahamas. *Arctapodema* is generally considered to be a deep water genus. A medusa identified as *A. amplum* was taken in an oblique plankton haul from deep water to the surface in the Alborán Sea (Ranson, 1936).

Ransonia krampi (Ranson, 1932). One specimen was collected by submersible at Station 12 (JSLI

dive 2943) at 499 m. The female medusa was 15 mm tall and was sexually mature. The muscle fields were remarkably refractile when illuminated and this medusa had a fast-escape swim strong enough to propel it out of its shallow container and onto the lab bench. This species is known from deep water in the western Alborán Sea and off the west coast of Africa. (Kramp, 1961).

Sub-class Siphonophorae

We collected 18 species of siphonophores [designated a sub-class by Bouillon *et al.* (1992)]. Sixty-six specimens, belonging to thirteen species, were collected during eighteen of the twenty-six submersible dives. Five additional species, represented by twenty-six specimens, were collected by SCUBA divers near the surface.

Siphonophores are classified according to whether there is present on the stem a float, or pneumatophore, and/or a series of swimming bells (nectosome) at the top of the stem. The calyccophoran species do not possess a float and, in general, they are small and fast-swimming. Such species were relatively abundant at depth, but were hard to see from the submersible and difficult to catch, such that only three species were collected with the submersible. Of these, *Lensia conoidea* and *Abylopsis tetragona* were predominant. Three more calyccophoran species were collected by SCUBA divers near the surface.

The larger physonect species, which possess both a float and a nectosome, proved to be uncommon in comparison with some other oceanic areas such as the Bahamas, and relatively low in species diversity. Submersible collection of these species is particularly useful as they are fragile organisms consisting of myriad parts and are easily destroyed during net collection. Nine species of physonects were collected with the submersible, of which three appear to belong to hitherto undescribed species. The most frequently seen and collected species belonged to the genus *Forskalia*, of which two species were collected, but neither could be identified with "recognized" Mediterranean species. Two species of physonects were collected by SCUBA divers, of which only *Nanomia bijuga* was common.

Cystonect species are relatively simple siphonophores that have a large float, with an apical pore, but no nectosome. Their long stems can reach considerable lengths when relaxed. Only a single species was collected.

Twenty species of siphonophores have previously been collected in the Alborán Sea [summarized by Madin (1991), which includes unpublished SCUBA observations of G. R. Harbison]. Of the 18 species that we collected, only six overlap with Madin's list, bringing the current known total to more than 30 species.

Order Cystonecta

Rhizophysa filiformis (Forsskål, 1775). Three specimens were collected by submersible: Station 6 (JSLI dive 2936), Station 10 (JSLI dive 2952), and Station 12 (JSLI dive 2946), at depths of 706, 729, and 833 m, respectively. The three large specimens were all green in colour. Although the stem can relax to a great length (tens of meters), all three specimens observed, of which we have excellent videos, were relatively contracted, and measured c. 2 m in stem length. However, their tentacles stretched down for tens of meters. All the specimens were collected in close proximity to the bottom, and it is quite possible that their tentacles were in contact with it. These animals, like their close relative *Physalia physalis*, the Portuguese Man O'War, have the ability to inflict a powerful and painful sting (Haddock, personal observation). They feed mainly on fish, and possibly derive their green pigmentation from their prey's bile pigments. There is not a great deal of information on the geographical and depth distribution of cystonect siphonophores as they are difficult to collect in nets. However, SCUBA divers have collected many young specimens in the warm-er waters of the Atlantic and Pacific Oceans, and these are known to have a considerable predation impact on fish larvae stocks in certain areas (c.f. Purcell, 1981, 1985).

In addition to collection of the three *R. filiformis* specimens, a large, free-floating egg mass that, because of its greenish coloration, almost certainly was derived from *R. filiformis*, was collected at Station 8 (JSLI dive 2940) at 595 m. Such an egg mass, actually a detached, highly proliferated gonodendron from the parent colony, looks like numerous asexual swimming bells superimposing an agglomeration of eggs. This, we believe, is the first time that the free-floating egg mass of a cystonect siphonophore, with the possible exception of *Physalia physalis*, has ever been seen. Since the animals are single sexed, this method of dispersion of the gametes is of great interest as it certainly is putting your many millions of eggs (see Totton, 1960) into one basket! It has yet to be established that the

male gametes are released in a similar manner, but it is interesting to note that all three of the *R. filiformis* specimens collected were male; and one had a gonodendron with nectophores almost as well developed as those found with the free-floating egg mass.

Order Physonecta

Agalma clausi Bedot, 1888. Six specimens were collected by submersible: Station 3 (JSLI dive 2929), Station 4 (JSLI dive 2931), and Station 7 (JSLI dive 2938). All were collected between 260 and 369 m. The present data indicate that this species occurs over a relatively narrow depth range, but has a relatively widespread distribution throughout the study area, although the majority were found toward the west and inshore. This species (Fig. 3D) was described by Bedot (1888) from three specimens collected at Villefranche-sur-Mer, but it has not been recorded in the Mediterranean since. Indeed, Totton (1965) had some reservations regarding the distinctiveness of this species. However, there are other records for this species from SCUBA diving collections in the tropical Atlantic; and the amphipods that occur on them have been recorded by Harbison *et al.* (1977).

Because of the dearth of information on this species, it is worth reporting that it is a rigid stemmed form, that is the siphosomal stem apparently cannot be relaxed, as is also the case for its close relative *Agalma okeni*, and unlike *A. elegans*, which is able to relax its stem. Like these two species, *A. clausi* has tricornuate tentilla, but the structure of the involucre, which usually encloses the central ampulla, distinguishes *A. clausi* from the other species. One of the chief characteristics is the presence of deep red pigment spots on the bracts, particularly the younger ones. In the collection jar these spots were seen to rupture and the specimen "inked" itself, rather like the release of pigment from the palpons of *Forskalia* spp. Dr. Peter Herring (personal communication) observed during the Alborán Sea cruise that the bracts emitted a diffuse luminescence, rather like the nectophores of *Hippopodius hippopus*, but the red pigment itself did not bioluminesce. Our video sequences show that this species is a powerful swimmer, with a large number of biserially arranged nectophores present on the nectosome.

Totton (1965) included another *Agalma* species, *A. haeckeli* Bigelow, 1911, which was originally described, inadequately, by Haeckel (1888) under the improper name *A. eschscholtzii*. The only

worthwhile character recorded was that its bracts had a patchwork of reddish pigment spots borne on ribs. As this is also a characteristic of *A. clausi*, we consider that *A. haeckeli* is a junior synonym of this species.

Agalma elegans (Sars, 1846). One specimen was collected by submersible at Station 10 (JSLI dive 2950) at 387 m. This is a relatively well known species with a world-wide distribution, mainly in warmer waters, and is well known from the Mediterranean. Whether some previous records, particularly from the Mediterranean, may actually refer to *A. clausi* is not known, but the latter species was certainly more abundant in the present study. Little is known about the depth distribution of *A. elegans*, but specimens have been collected near the surface by SCUBA divers, and at epi- and mesopelagic depths.

Cordagalma cordiforme Totton, 1932. One specimen was collected by submersible at Station 10 (JSLI dive 2952) at 726 m. This species was originally described from the Great Barrier Reef, but is fairly well known from the Mediterranean and other warmer waters. Most of the records come from shallow depths, and several specimens have been caught by SCUBA divers, but not during this particular cruise. However, Mackie (1985) reports it to be fairly common at depths between 200 and 500 m (temperature around 9° C, Mills personal records), based on submersible observations and collections near the Strait of Georgia, British Columbia.

Totton (1932) originally ascribed the specific name *cordiformis* to this species; but recently it has been pointed out that this does not conform with the generic name, which is neuter. In consequence the specific name *cordiforme* has been suggested as an alternative. There are close similarities between the bracts and tentilla of this species and those of *Anthemodes ordinata* Haeckel, 1888, although the nectophores differ markedly. None the less, we are inclined to adopt the name *Cordagalma ordinata* (Haeckel, 1888) for this species. The generic name *Anthemodes* cannot be used, as it was originally established for *A. canariensis* Haeckel, 1869, which is a junior synonym of *Nanomia bijuga* (Chiaje, 1841). Thus *Anthemodes* is a junior synonym of *Nanomia*.

Nanomia bijuga (Chiaje, 1841). Nineteen specimens were caught only by SCUBA divers: Stations 2 (BWP dive 1900), Station 7 (BWP dive 1894), Station 9 (BWP dive 1895), and Station 12 (BWP dives 1896, 1897, 1898). Although present at four of the five stations sampled by SCUBA, it was most

abundant at Station 12, where three dives were made. One of the specimens was seen to have the parasitic pelagic nudibranch, *Cephalopyge*, on its stem. This small physonect species is well known from the warmer waters of the world's oceans, and usually has been collected from close to the surface, although occasionally at deeper depths.

Lychnagalma utricularia (Claus, 1879). Five specimens were collected by submersible: Station 6 (JSLI dive 2935), Station 7 (JSLI dive 2938), Station 9 (JSLI dive 2941), and Station 12 (JSLI dive 2943). In order of stations, specimens were collected at 628 (2 spec.), 308, 558, and 608 m. As with *Agalma clausi*, this species was first described from the Mediterranean (Strait of Messina), but has never been recognised since from that sea. This is probably due to a certain resemblance of the nectophores (which may be found individually in plankton samples) to other physonects, for instance *Agalma* and *Halistemma* spp. Once again, with the use of submersibles, this species has been found to be abundant around the Bahamas, and other regions of the western Atlantic (Pugh and Harbison, 1986). These authors also suggest that the species *Lychnagalma vesicularia* Haeckel, 1888 should be regarded as a junior synonym of this species. Altogether, we have now collected 41 other specimens of this species. It is interesting to note that Pugh and Harbison (1986) mainly found the species in the 500-700 m range, averaging 620 m. The present records are in general accord with this, although one specimen was found at 308 m. This species is of interest because of the shape of its tentilla, that have a terminal ampulla surrounded, at the base, by 8 filaments. It has been suggested (Pugh, 1989) that this might be an example of aggressive mimicry, as Purcell (1980) has suggested for other siphonophore species. However, we know nothing about the preferred diet of this species. *L. utricularia* was the only non-bioluminescent physonect that we collected in the Alborán Sea.

Physophora hydrostatica Forskål, 1775. One specimen was caught by SCUBA divers at Station 9 (BWP dive 1895). This is an almost cosmopolitan species, and has frequently been collected in the Mediterranean. In most cases it has been taken close to the surface, or at epipelagic depths, but occasionally it can occur deeper (Pugh, unpublished data).

Forskalia (?) *formosa* Keferstein and Ehlers, 1860. Twenty specimens were collected by submersible: Station 1 (JSLI dive 2955), Station 2 (JSLI dive 2953), Station 6 (JSLI dive 2935),

Station 7 (*JSLI* dives 2937, 2938), Station 8 (*JSLI* dive 2939), Station 9 (*JSLI* dive 2941), and Station 12 (*JSLI* dives 2943, 2944). This species occurred between 355 and 600 m, with most specimens captured below 450 m, and was widely distributed throughout the Alborán Sea, except at the stations closest to the Moroccan coast. It was the most frequently collected siphonophore, and many other specimens were observed, but not collected, during the dives. The video sequences show that the animals were powerful swimmers, and that they rotated, usually in an anti-clockwise direction, as they swam. The nectosome had a relatively narrow and consistent diameter. The siphosome is broader than the nectosome and, in some specimens, was about three times the length of the latter. The siphosomal stem clearly was spiralled, but in such a way that the gastrozooids appeared to be arranged in rows.

It has become apparent, through SCUBA and submersible collections over the past decade or so, that the taxonomy of the genus *Forskalia* is not fully understood. Totton (1965) listed five species, plus one species inquirenda. Moreover, he considered that three of the five species were of dubious authenticity. It is now well established, from SCUBA collections, that one of these dubious species, *Forskalia tholoides* Haeckel, 1888, is completely valid. The identity of another of these, *Forskalia cuneata* Chun, 1888, remains uncertain should be, although we now know that the bracts that Totton (1965) suggested might belong to that species in fact belong to *Frillagalma vitiazi* Daniel, 1966 (see Mackie *et al.*, 1987, p. 117).

The third dubious species included by Totton (1965) is *Forskalia formosa* Keferstein and Ehlers, 1860. The description of this species given by Keferstein and Ehlers (1861) is brief and perhaps the only important character given is that the nectophores are deeply incised, on the stem side, to produce two unequal lobes. Such an asymmetry in the lobes of the nectophores of the present specimens is very apparent and so we tentatively ascribe the specimens to this species. The species appears to have been collected regularly by Moser (1917) in the Villefranche-sur-Mer region (Ligurian Sea), but no useful descriptive details are given. There are no other reports of this species in the Mediterranean, but Daniel (1985) and Stepanjants (1977) have found it in the Indian and Pacific Oceans, respectively.

Forskalia sp. 1. Three specimens were collected

by submersible, one each at Station 3 (*JSLI* dive 2929), Station 8 (*JSLI* dive 2939), and Station 9 (*JSLI* dive 2942) at depths of 432, 476, and 384 m, respectively. This species (Fig. 3C) does not conform to the description of any of the currently recognised species; it most closely resembled *Forskalia leuckarti* Bedot, 1893, but never had a disc-shaped, pigmented rete in the pedicular canal of the nectophore. There has been much confusion in the past with regard to descriptions of this latter species, but the pigmented rete appears to be a consistent part of these descriptions. The two, somewhat truncated, lobes on the nectophores are of almost equal size. There is a video sequence of the former of the two specimens that shows that the nectosome and siphosome are of almost equal length. The nectosome has a greater diameter than the siphosome and is dome-shaped. There is still a lot to learn about *Forskalia* spp. and at least one other type has been collected by submersible.

Altogether four specimens of three physonect species that appear to be new to science were collected. All have nectophores that are virtually ridgeless, and have straight lateral radial canals on the nectosac. The cnidoband of the tentillum is straight and unspiralled in all three species.

Physonect sp. 1. Two specimens were collected by submersible, one each at Station 7 (*JSLI* dive 2938) and Station 2 (*JSLI* dive 2953) at 360 and 372 m, respectively. The siphosomal stem is pale orange, as are the cnidobands of the tentilla. The gastrozooids are light reddish brown, with dark brown hepatic spots. The otherwise colourless palpons had terminal ampullae that could be filled with reddish pigment. The latter could be discharged ("inked") in a similar way to *Forskalia* species.

Physonect sp. 2. One specimen was collected by submersible at Station 8 (*JSLI* dive 2940) at 549 m. This was a large physonect with a total length of c. 5 m, whose nectosome was c. 40 cm long and bore a large number (>70) of biserially arranged nectophores (Fig. 3A).

Physonect sp. 3. One specimen was collected by submersible at Station 8 (*JSLI* dive 2940) at 492 m. This magnificent animal, which measured c. 3+ m in length, was observed *in situ* to be coiled into a helix of expanding diameter from top to bottom (Fig. 3B). From the direction of approach of the submersible, this coiling gave to the animal the appearance of an inner space galaxy. The vast majority of the length of the animal was made up by the siphosome, and the nectosome was relatively small.

Order Calycophora

Hippopodius hippopus (Forsskål, 1776). A single detached nectophore of this species was collected by SCUBA divers at Station 12 (BWP dive 1898). The remainder of this common, warm water, epipelagic species was not found.

Sulculeolaria quadrivalvis Blainville, 1834. Two specimens were collected by SCUBA divers, one each at Station 7 (BWP dive 1894) and Station 12 (BWP dive 1897). Again, this is a well known, warm water, epipelagic species.

Lensia conoidea (Keferstein and Ehlers, 1860). Ten specimens were collected by submersible: Station 1 (JSLI dive 2955), Station 2 (JSLI dive 2953), Station 4 (JSLI dive 2932), Station 6 (JSLI dive 2935), Station 9 (JSLI dive 2941), and Station 12 (JSLI dives 2943, 2944). This species was located between 390 and 560 m. The collections of this common calycophoran are somewhat erratic, probably as a result of its small size. It is an abundant species, particularly in the colder waters of the North Atlantic Ocean. Siphonophores of this size, c. 3-4 cm, are difficult to observe from a submersible, but the striking fishing posture of this species, with the nectophores horizontal and the siphosome hanging vertically down between them, helped to identify them. However, we know little about the fishing postures of other *Lensia* species.

Muggiaea atlantica Cunningham, 1892. Three specimens were collected by SCUBA divers at Station 12 (BWP dives 1897, 1898) and more specimens were seen, but not collected. *M. atlantica* is an abundant neritic siphonophore, and probably would have been found at other inshore stations if SCUBA dives had been made.

Clausophyes ovata (Keferstein and Ehlers, 1860). Three specimens were collected by submersible at Station 7 (JSLI dive 2937) and Station 12 (JSLI dives 2943, 2948) at 483, 556, and 753 m, respectively. The classification of the genus *Clausophyes* has become extremely confused (see Pugh and Pagès, 1993) and the species referred to here is that well described by Keferstein and Ehlers (1861), as *Diphyes ovata*, and not the species that Moser (1925) and subsequent authors associated with this name. The latter species must now be called *Clausophyes moserae* Margulis, 1988. Because of the confusion in taxonomy it is difficult to know which of the past records refer to which species. In the North Atlantic *C. moserae* certainly is much more abundant than *C. ovata*, but it is not certain if this is the case in the Mediterranean, where *C. ovata*

has been recorded under its junior synonym *C. mas-siliana* Patrìti, 1969.

Abylopsis tetragona (Otto, 1823). Ten specimens were collected by submersible: Station 1 (JSLI dive 2955), Station 2 (JSLI dive 2953), Station 10 (JSLI dive 2950). This species was found between 294 and 488 m. Although it was collected at the most easterly station could be, the majority of collections and sightings occurred at Stations 1 and 2, close to the Strait of Gibraltar could be, and of the small number of siphonophores collected at these stations, this species predominated. This is of interest as previous net collections, for instance Furnestin (1958), have found abyloid species, of which *A. tetragona* is one, to be the predominant species in this area. Despite the small size of the specimens, the characteristic shape of this species made it very easy to recognise from the submersible. It was found to have a very interesting bimodal bioluminescence spectrum (Haddock, personal observations).

Class Scyphozoa

Forty-seven scyphomedusae were collected on the cruise, representing six species. Most numerous were the two species of coronate scyphomedusae, *Paraphyllina ransonii* and *Periphylla periphylla*, collected by submersible. Both were quite abundant below about 500 m and were found primarily near the bottom; differences in depths collected reflect mostly different bottom depths between dives (see Fig. 1). These coronates were seen at most of the Moroccan stations except those nearest the Strait of Gibraltar, which were the shallowest. Four species of sennaeos-tome medusae were also collected, but each was represented by only one or two specimens. Of these, one species was collected only by submersible in the upper mid-water and the other three species occurred near the surface. All of these scyphomedusae have previously been collected in the Mediterranean Sea (Kramp, 1961; Russell, 1970), although no scyphomedusae have specifically been reported in the Alborán Sea prior to this study (Madin, 1991).

Order Coronatae

Paraphyllina ransonii Russell, 1956. Eighteen specimens were collected by submersible: Station 4 (JSLI dive 2931), Station 6 (JSLI dives 2935, 2936), Station 7 (JSLI dives 2937, 2938), Station 8 (JSLI dive 2939), and Station 12 (JSLI dives 2946, 2948). This species was collected at depths ranging

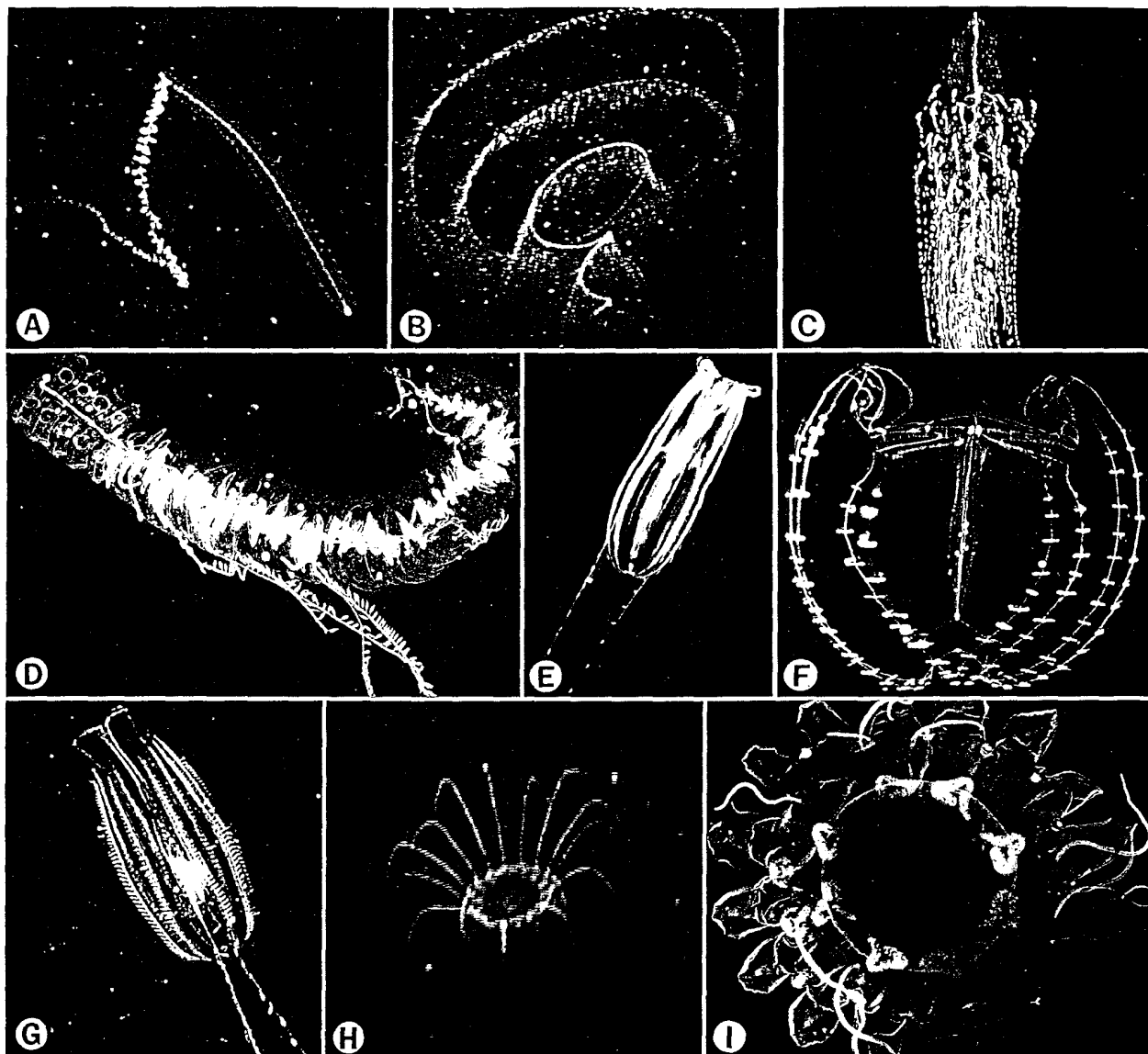


FIG. 3. — Some species of gelatinous zooplankton from the Alborán Sea. (A) *Physonect* sp. 2 from *in situ* video, nectosome about 40 cm long, total length about 5 m; (B) *Physonect* sp. 3 from *in situ* video, total length 3–4 m; (C) *Forskalia* sp. 1 photographed live in the ship's laboratory, total length about 30 cm; (D) *Agalma clausi* photographed live in the ship's laboratory, total length about 8 cm; (E) *Lampea paucispina* photographed live in the ship's laboratory, body height 30 mm; (F) *Detiopea kaloktenota* photographed live in the ship's laboratory, body height 44 mm; (G) *Euplokamis stationis* photographed live in the ship's laboratory, body height about 30 mm; (H) *Solmissus albescens* from *in situ* video, bell diameter about 28 mm; (I) *Paraphyllina ransoni*, preserved specimen, coronal diameter 12 mm.

from 503 to 837 m, but was always within 100 m of the bottom; over the shallower bottoms in its range, it was on or within a few m of the bottom. Many of the specimens (Fig. 3I) had gonads shaped more like a "V" than the "W" described by Russell (1956, 1970), but they otherwise agreed with the species description. Although the stomach was always deeply pigmented, the subumbrella and lappets ranged in coloration from clear and unpigmented to a dark brick red. Specimens identified as *P. intermedia* have been collected NE of the

Alborán Sea off the Spanish Catalan coast (Gili, 1986; Gili *et al.*, 1987). Both species are mesopelagic, and have been found in limited, but widely separated geographical locations worldwide (Kramp, 1961; Van Der Spoel, 1987; Mills, personal observations).

Periphylla periphylla (Péron and Lesueur, 1809). Twenty-four specimens were collected by submersible: Station 5 (*ISLI* dive 2934), Station 6 (*ISLI* dives 2935, 2936), Station 7 (*ISLI* dives 2937, 2938), Station 8 (*ISLI* dives 2939, 2940), and

Station 12 (*JSLI* dives 2946, 2948). It was collected at depths ranging from 496 to 823 m. Like *Paraphyllina ransonii*, most *P. periphylla* were found within 100 m of the bottom, although a few young specimens (coronal diameters 6-10 mm) were collected as much as 300 m above the bottom (at a depth of about 500 m). *P. periphylla* is a common, cosmopolitan, mesopelagic medusa (Kramp, 1959, 1961; Russell, 1970).

Order Semaestomeae

Phacellophora camtschatica Brandt, 1838. A single specimen was collected by submersible at Station 1 (*JSLI* dive 2955) at 216 m. This animal was about 40 cm in diameter, with 16 sets of tentacles that extended 10-15 m. The stomach was brilliant orange and the rest of the bell was colorless and transparent except for yellow warts on the lappets and just above this area on the exumbrella. *P. camtschatica* is a cosmopolitan species, often found in cold waters, and infrequently reported from the Mediterranean (Kramp, 1961).

Chrysaora hysoscella (Linnaeus, 1766). A single specimen was collected with SCUBA at Station 12 (BWP dive 1897) near the surface. This species is well known in the Mediterranean and North Atlantic (Kramp, 1961; Gili, 1986).

Pelagia noctiluca (Forskål, 1775). One specimen was seen from the submersible at Station 1 (*JSLI* dive 2955) at 9 m, and a second specimen was collected using SCUBA at Station 12 (BWP dive 1897). *P. noctiluca* is a common epipelagic oceanic species in most of the world oceans (Kramp, 1961), as well as in the Mediterranean, where it sometimes reaches bloom proportions (summarized by Goy *et al.*, 1989).

Order Rhizostomeae

Rhizostoma pulmo (Macri, 1778). A single specimen was collected using SCUBA at Station 12 (BWP dive 1896). This species is found throughout the Mediterranean and North Atlantic; it was collected near Mallorca by Gili (1986).

PHYLUM CTENOPHORA

The Alborán Sea has a diverse ctenophore fauna. Half of the 22 species we collected were epipelagic, in marked contrast with other regions where we have

compared submersible and SCUBA collections; usually the mesopelagic fauna is much more diverse. Nine species were collected only by the submersible, although two of these, *Bolinopsis infundibulum* and *Lampea pancerina*, frequently occur in surface waters. There was little overlap between our SCUBA and submersible collections, with only two species (*Beroë* "ovata" and *Cestum veneris*) collected with both methods. The diversity of the epipelagic ctenophore fauna in comparison with the mesopelagic fauna is made even more dramatic when one considers that our SCUBA diving effort was much less intense than the submersible effort. We made only seven SCUBA dives, averaging about 45 minutes each, while 26 submersible dives were made, each lasting several hours (Tables 1 and 2).

The ctenophores collected included nine species of cydippid ctenophores. Four of these species were collected with the submersible, of which two have been described and two have not. Five additional species of cydippids were collected only by SCUBA diving; four of these have been described, and one has not. Three species of lobates were collected with the submersible and four more species were collected with SCUBA diving. Also we collected two thalassocalycids by submersible (one undescribed), two cestids, and two beroids.

Madin (1991) reports five species of ctenophores for the Alborán Sea (all taken by blue water diving with SCUBA by G. R. Harbison in spring, 1986). We have now expanded that list to 23 species (only *Pleurobrachia pileus* was collected in 1986 and not in 1991). Of the 22 species we collected on the present cruise, eight represent new records for the Mediterranean: cydippid sp. A, cydippid sp. B, cydippid sp. C, *Haeckelia beehleri*, *Ocyropsis maculata immaculata*, *Bathocyroe fosteri*, *Thalassocalyce inconstans* and *Thalassocalycid* sp. A. Several of the epipelagic species are widely distributed in the North Atlantic, and may not penetrate much farther than the Alborán Sea into the Mediterranean. It is probable, however, that the mesopelagic species are more widespread in the Mediterranean, since three of them (*Euplokamis stationis*, *Deiopea kaloktenota* and *T. inconstans*) were collected by Chun (1880) in the Gulf of Naples.

Order Cydippida

Euplokamis stationis Chun, 1879. Thirty-one specimens were collected by submersible: Station 1 (*JSLI* dive 2955), Station 2 (*JSLI* dives 2953, 2954),

Station 4 (*JSLI* dive 2931), Station 5 (*JSLI* dive 2933), Station 6 (*JSLI* dive 2935), Station 7 (*JSLI* dives 2937, 2938), Station 10 (*JSLI* dives 2950, 2952), and Station 12 (*JSLI* dives 2943, 2944, 2946, 2948). It was collected at depths ranging between 183 and 729 m. Only eight specimens were collected above 200 m and only two were collected below 600 m. *Euplokamis stationis* appears to be a true deep-sea species that can be brought to the surface by upwelling. This species (Fig. 3G) may be quite common, although it has only rarely been reported (Chun, 1879, 1880).

Haeckelia beehleri (Mayer, 1912). Twenty-four specimens were collected by SCUBA divers: Station 2 (BWP dive 1900), Station 7 (BWP dive 1894), Station 10 (BWP dive 1899), and Station 12 (BWP dives 1896, 1897, 1898). This is the first record of this species in the Mediterranean, although it is common in tropical and subtropical waters of the North Atlantic and North and South Pacific (Harbison *et al.*, 1978; Harbison, 1985; Haddock, personal observations). Although it has been reported that this ctenophore feeds on siphonophores (Harbison, 1985), it also fed on *Solmaris leucostyla* in the ship's laboratory.

Haeckelia bimaculata Carré and Carré, 1989. Three specimens were collected by SCUBA divers at Station 12 (BWP dives 1897, 1898). In addition to its original collection location in the Ligurian Sea in the Mediterranean (Carré and Carré, 1989), this species has also been found off California (Haddock, personal observations). It too preyed upon *Solmaris leucostyla* in the ship's laboratory.

Haeckelia rubra (Kölliker, 1853). Six specimens were collected by SCUBA divers: Station 7 (BWP dive 1894), Station 9 (BWP dive 1895), Station 10 (BWP dive 1899), and Station 12 (BWP dives 1897, 1898). This species, which is reported to feed on medusae (Mills and Miller, 1984), is widely distributed, and has been collected in the North Atlantic and North Pacific. We regard it noteworthy that all three species of *Haeckelia* that we collected fed on *Solmaris leucostyla* in the laboratory, since this medusa was extremely abundant on all of our SCUBA dives. Since *H. beehleri* is also known to eat siphonophores (Harbison, 1985), we consider it likely that the other species of *Haeckelia* will do so as well. Harbison (1985) suggested that cydippid ctenophores with simple tentacles (lacking tentilla) specialize on tentaculate prey (such as medusae, siphonophores, and ctenophores), while those cydippids that have tentacles with tentilla feed on prey that lack tentacles. Our

observations support this speculation.

Lampea pancerina (Chun, 1879). Five specimens were collected by submersible: Station 1 (*JSLI* dive 2955), Station 2 (*JSLI* dive 2953), Station 7 (*JSLI* dive 2937), and Station 12 (*JSLI* dives 2943, 2946). This species (Fig. 3E) was collected at depths ranging between 280 and 837 m. It feeds primarily on salps, occurs world-wide (Harbison *et al.*, 1978), and is frequently found in surface waters in the Mediterranean and eastern Atlantic, although we did not collect it with SCUBA diving on this cruise. Because of its typically broad depth distribution, *L. pancerina* cannot be regarded as a truly mesopelagic species.

Pleurobrachia rhodopsis Chun, 1880. Twenty-two specimens were collected by SCUBA divers: Station 2 (BWP dive 1900), Station 9 (BWP dive 1895), and Station 12 (BWP dives 1896, 1897, 1898). This species may be identical with *Pleurobrachia pileus* (Müller, 1776), which is widely distributed across the temperate North Atlantic.

Cydippid sp. A. A single specimen was collected by submersible at Station 12 (*JSLI* dive 2948) at 815 m. We have commonly collected this distinctive species in the western North Atlantic. It has a heavily pigmented, purple-red colored stomodaeum. It seldom occurs above 600 m, and is presently being described (Harbison, unpublished data).

Cydippid sp. B. Twenty-three specimens were collected by submersible: Station 2 (*JSLI* dive 2954), Station 8 (*JSLI* dives 2939, 2940), and Station 12 (*JSLI* dives 2943, 2944, 2946, 2948). It was collected at depths ranging between 363 and 827 m, with only two specimens collected above 500 m. This species, which is being described elsewhere (Harbison, unpublished data), is transparent and very easily damaged, so that many of the specimens were in fragmentary condition.

Cydippid sp. C. Thirteen specimens of this undescribed species were collected by SCUBA divers: Station 7 (BWP dive 1894), Station 9 (BWP dive 1895), Station 10 (BWP DIVE 1899), and Station 12 (BWP dives 1897, 1898). Because of its red tentacles and small size, this animal has perhaps been assumed to be a juvenile of *Pleurobrachia rhodopsis*. It and two other species belonging to the same genus are presently being described (Harbison and Mills, unpublished data). This species is known from the North Atlantic (Harbison, personal observations) and North Pacific (Mills and Haddock, personal observations).

Order Lobata

Bathocyroe fosteri Madin and Harbison, 1978. Thirteen specimens were collected by submersible: Station 1 (*JSLI* dive 2955), Station 2 (*JSLI* dive 2954), Station 4 (*JSLI* dives 2931, 2932), Station 6 (*JSLI* dive 2935), Station 8 (*JSLI* dive 2939), Station 9 (*JSLI* dives 2941, 2942), and Station 12 (*JSLI* dives 2944, 2946). It was found at depths ranging between 352 and 827 m. This mesopelagic species is widely distributed, and sightings of it probably constitute the majority of observations made from submersibles of red-gutted lobate ctenophores that swim slowly by flapping their oral lobes. However, it should be noted that there are several other less common species with which it can be confused (Harbison, personal observations).

Bolinopsis infundibulum (Müller, 1776). Sixteen specimens were collected by submersible: Station 2 (*JSLI* dive 2953), Station 3 (*JSLI* dive 2929), Station 4 (*JSLI* dive 2931), Station 5 (*JSLI* dive 2933), Station 7 (*JSLI* dive 2937), and Station 12 (*JSLI* dives 2947, 2948). This species was collected at depths ranging between 274 and 831 m. It is widely distributed in temperate and boreal waters, where it is common in surface waters (Vanhöffen, 1903; Harbison *et al.*, 1978).

Bolinopsis vitrea (Milne Edwards, 1841). Thirty-six specimens were collected by SCUBA divers: Station 7 (BWP dive 1894), Station 9 (BWP dive 1895), Station 10 (BWP dive 1899), and Station 12 (BWP dives 1896, 1897, 1898). This species is widely distributed in tropical and subtropical waters (Harbison *et al.*, 1978).

Deiopea kaloktenota Chun, 1879. Three specimens were collected by submersible: Station 5 (*JSLI* dive 2933) and Station 12 (*JSLI* dives 2944, 2948). It was collected at depths ranging between 245 and 302 m. This transparent ctenophore (Fig. 3F) can become quite large, and has been found in widely separated mesopelagic regions of the North Atlantic. Although it is probably a mesopelagic species, it has been collected infrequently in surface waters of the Mediterranean, North Atlantic (Chun, 1880; Harbison, personal observations), and North Pacific (Haddock, personal observations). It should also be noted that on BWP SCUBA dive 1899, a larval lobate was collected that most probably belongs to this species.

Eurhamphaea vexilligera Gegenbaur, 1856. A single specimen was collected with SCUBA at Station 9 (BWP dive 1895). It is widely distributed in tropical and subtropical regions of the Atlantic and

Pacific (Harbison *et al.*, 1978; Harbison, personal observations).

Leucothea multicornis (Quoy and Gaimard, 1825). Five specimens were collected by SCUBA divers: Station 2 (BWP dive 1900), Station 7 (BWP dive 1894), Station 9 (BWP dive 1895), and Station 12 (BWP dive 1896). This species is also widely distributed in subtropical and temperate waters (Harbison *et al.*, 1978).

Ocyropsis maculata immaculata Harbison and Miller, 1986. Eleven specimens were collected by SCUBA divers: Station 2 (BWP dive 1900), Station 7 (BWP dive 1894), Station 9 (BWP dive 1895), Station 10 (BWP dive 1899), and Station 12 (BWP dives 1897, 1898). This is the first record of this widely distributed tropical and subtropical species (Harbison *et al.*, 1978) for the Mediterranean.

Order Thalassocalycida

Thalassocalyce inconstans Madin and Harbison, 1978b. Two specimens were collected with the submersible at Station 6 (*JSLI* dive 2935) and Station 12 (*JSLI* dive 2946), from 632 and 828 m depths, respectively. Although this species is mesopelagic, it is sometimes found in great numbers by SCUBA divers. This is the first record of its occurrence in the Mediterranean, although small *Thalassocalyce* sp. have also been collected in the Ligurian Sea (Mediterranean) (C. Carré, personal communication). These observations support the suggestion of Madin and Harbison (1978) that a small specimen figured by Chun (1880), and called by him a larval stage of *Leucothea multicornis*, was in reality a *Thalassocalyce*.

Thalassocalycid sp. A. Eleven specimens were collected by submersible: Station 1 (*JSLI* dive 2955), Station 2 (*JSLI* dive 2953), Station 4 (*JSLI* dive 2932), Station 9 (*JSLI* dive 2942), Station 10 (*JSLI* dive 2950), and Station 12 (*JSLI* dives 2943, 2944). It was found at depths ranging between 255 and 493 m. This distinctive ctenophore, which is large, transparent and extremely delicate, occurs widely in the North Atlantic, and is presently being described (Harbison, unpublished data).

Order Cestida

Cestum veneris Lesueur, 1813. Four specimens were collected by submersible, at Station 8 (*JSLI* dive 2940) and Station 12 (*JSLI* dives 2946, 2949). It was found at depths ranging between 192 and 333 m. One specimen was also collected with SCUBA at

Station 2 (BWP dive 1900). This is a well-known epipelagic species, which occurs world-wide in tropical and subtropical waters (Harbison *et al.*, 1978).

Velamen parallelum (Fol, 1869). One specimen was collected with SCUBA at Station 7 (BWP dive 1894). This species is more common than *Cestum veneris* in epipelagic temperate waters of the Atlantic, and never attains the great size of the latter (Harbison *et al.*, 1978).

Order Beroida

Beroe forskalii Milne Edwards, 1841. Seven specimens were collected by SCUBA divers: Station 2 (BWP dive 1900), Station 7 (BWP dive 1894), Station 10 (BWP dive 1899), and Station 12 (BWP dive 1898).

Beroe "ovata" Eschscholtz, 1829. Forty-one specimens were collected by SCUBA divers at Stations 2, 7, 9, 10, and 12 (BWP dives 1894-1900), and five additional specimens were collected by submersible at depths ranging between 271 and 485 m: Station 2 (*JSLI* dive 2953), Station 4 (*JSLI* dive 2931), Station 9 (*JSLI* dive 2941), and Station 12 (*JSLI* dive 2944). This species, which was illustrated and called *Beroe ovata* Eschscholtz, 1829 by Chun (1880), was also illustrated and called *Beroe cucumis* Fabricius, 1780 by Mayer (1912). European zoologists have used the nomenclature of Chun (1880), while American zoologists have used the nomenclature of Mayer (1912), creating considerable confusion. It appears that both names are incorrect, since although Chun (1880) credits Eschscholtz (1829) with the original description, Bruguère (1789) had previously described an animal he called *Beroe ovatus*, which is cited in Eschscholtz (1829). Bruguère's description is, unfortunately, based on several different species, including a species of *Beroe* described and figured by Browne (1756) from Jamaica, the description and illustration by Baster (1761) from Holland of what appears to be *Pleurobrachia pileus* (Müller), and the description and drawing by Martens (1675) of *Bolinopsis infundibulum* collected near Spitzbergen. To add to the confusion, the species that Mayer (1912) illustrates and calls *Beroe ovata* Chamisso and Eysenhardt, 1821 is distinct from the European *Beroe ovata*. Although Mayer (1912) credits Chamisso and Eysenhardt (1821) with the original description of *B. ovata*, the latter authors credit Bosc (they give no date - perhaps it is Bosc, 1802). On the other hand, the ctenophore that Mayer illustrates and

calls *Beroe cucumis* is not the same species as that first described from Greenland by Fabricius (1780), which appears to be restricted to polar regions and mesopelagic depths.

Given the confusion that exists within the genus, and the necessity for its complete revision, we simply note that the species we call *Beroe "ovata"* follows the nomenclature of Chun (1880). This species is distributed world-wide in tropical and subtropical waters.

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