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Western Atlantic midwater hydrozoan and scyphozoan medusae: *in situ* studies using manned submersibles

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Abstract

Little is known about the biology and ecology of mesopelagic medusae. In part, this is because midwater trawls are used to collect fragile medusae and other gelatinous macroplankton. Additionally, nets cannot provide data on behavior and on biotic associations. Herein, *in situ* observations on northwestern Atlantic midwater medusae made using the *Johnson-Sea-Link* submersibles are reported. Included are depth and temperature ranges; notes on pigments; locomotory behavior; and notes on prey and predators.

Introduction

Although there have been many studies on the midwater fauna of the North Atlantic, little is known about mesopelagic medusae. Recent studies using nets that sample at discrete depths have provided valuable data on vertical distributions (Thurston, 1977; Angel & Baker, 1982; Angel *et al.*, 1982; Mauchline & Harvey, 1983; Roe *et al.*, 1984; van der Spoel, 1987). Net studies have the disadvantage of biasing the data toward abundant and robust species. Less abundant taxa are not well sampled and delicate taxa are damaged beyond recognition or pass through the net. Furthermore, studies using nets provide little information on the biology of the animals collected. Consequently, oceanographers have failed to recognize the ecological importance of medusae in midwater.

Direct observation from submersibles is the best method for investigating the gelatinous midwater fauna (e.g., Pérès, 1958, 1959; Madin & Harbison, 1978; Smith, 1982; Vinogradov & Shushkina, 1982; Mackie & Mills, 1983; Youngbluth, 1984; Mackie, 1985; Harbison, 1986; Larson *et al.*, 1988b; Laval *et al.*, 1989). Not only can vertical distributions of even the most fragile species be studied, but behavioral observations can also be made. Here, we report the first detailed description of the midwater medusan fauna of the western North Atlantic from *in situ* observations.

Material and methods

Dives were made at 3 locations in the northwestern Atlantic to depths of 900 m using the

'Johnson-Sea-Link I & II' submersibles: 103 in the Bahama Islands (25–26° N 77–79° W) during October and November 1984, in October 1988 and in November 1989; 10 off the southern tip of Florida near the Dry Tortugas (24° N 82–83° W) in August and September 1987; and 23 in August and September 1986 and in August 1987 in 3 submarine canyons (Atlantis, Hydrographer and Veatch) off Georges Bank, New England (40° N 69–70° W).

Dives were of 3–4 h duration over a bottom depth of < 1000 m. Visual observations and color video recordings were made to record the species present and their behavior. Medusae were individually collected using a variety of samplers (Youngbluth, 1984). Specimens experienced only small temperature changes (< 5 °C) when brought to the surface because of the large volume of these samplers. Data reported herein are limited to medusae with bell diameters > 1 cm, because smaller specimens could not be seen.

Water temperatures in the upper 800 m ranged from < 5 °C to > 20 °C at the 3 sites (Table 1). Below 500 m, temperatures were uniformly low (4.8 to 7.2 °C) except in the Bahamas where they ranged from 7 to 16 °C.

Results

More than 300 specimens representing 55 species were collected and/or observed (Table 2). Three

orders (Trachymedusae, Narcomedusae and Coronatae) constituted 80–90% of the species and individuals. Most abundant were the hydromedusae *Aeginura grimaldii* Maas, *Colobonema sericeum* Vanhöffen, *Halicreas minimum* Fewkes, *Pantachogon haeckeli* Maas and *Solmissus incisa* (Fewkes); and the scyphomedusae *Pelagia noctiluca* Forskål, *Periphylla periphylla* (Péron & Lesueur) and *Poralia* sp. A. At least 15 of the taxa appear to be undescribed and many specimens represent new distribution records or have rarely been collected in the northwestern Atlantic.

Medusae were most diverse and numerous at mesopelagic depths (> 500–600 m) (Table 1). Only 9 species were seen above 500 m, and the intermediate zone (100–400 m) was nearly devoid of visible medusae: only one species was seen. There were no eurybathyal taxa, although *P. haeckeli* and *S. incisa* each occurred over about a 400 m depth range.

Many mesopelagic medusae have a dark red, brown or purple-black pigment over the gut and umbrella. About 35% of the taxa collected below 500 m were darkly pigmented, but the majority at all depths were transparent. Most pigmented species were scyphomedusae, although some hydromedusae, including *A. grimaldii*, *Chromatone-ma rubrum* Fewkes, *Crossota pedunculata* H.B. Bigelow, *Crossota rufrobrunnea* (Kramp), and *Pandea rubra* H.B. Bigelow were also dark.

Table 1. Vertical distribution of numbers of medusan species and temperatures at three submersible dive sites in the northwestern Atlantic.

Depth (m)	Bahamas		Dry Tortugas		New England	
	T(°C)	No. species	T(°C)	No. species	T(°C)	No. species
0–100	> 25	5	> 28	1	12–17	1
101–200	25–20	0	28–21	0	12–9	1
201–300	20–19	0	21–16	0	9–7.4	0
301–400	19–17	0	16–8.8	0	7.4–6	0
401–500	17–16	3	8.8–7.2	1	6–5.3	2
501–600	16–13	9	7.2–6.4	1	5.3–5	3
601–700	13–11	16	6.4–5.7	2	5–4.9	4
701–800	11–10	19	5.7–5.4	12	4.9–4.8	15
801–900	10–7	26	5.4–5.0	17	ND*	ND*

* ND = No dives at this depth.

Table 2. Medusae seen and/or collected using the *Johnson-Sea-Link* submersibles (+ denotes medusa but depth was undetermined.)

TAXA	Depth of Collection		
	Bahama Islands	New England	Dry Tortugas
HYDROMEDUSAE			
<i>Aegina citrea</i> Eschscholtz	680–740	705	
Aeginidae n.g., n.sp.	+		890
<i>Aeginura grimaldii</i> Maas	700–880	670–780	845
<i>Amphogona apicata</i> Kramp	630–660		
<i>Amphogona</i> n.sp.			825–885
<i>Arctapodema ?australis</i> (Vanhöffen)	840		
<i>Arctapodema</i> n.sp. A	890		+
<i>Arctapodema</i> n.sp. B	830		
<i>Arctapodema</i> n.sp. C	860		
<i>Arctapodema</i> n.sp. D			820
<i>Botrynema brucei</i> Browne	810		865
<i>Bythotiara murrayi</i> Günther	431		
Calycopsidae n.g. A, n.sp.	900		
Calycopsidae n.g. B, n.sp.	765		
Calycopsidae n.g. C, n.sp.	520		
<i>Chromatonema rubrum</i> Fewkes		745–780	
<i>Colobonema sericeum</i> Vanhöffen	520–875	760–770	775
Corymorphidae n.g., n.sp.	900		
<i>Crossota pedunculata</i> H. B. Bigelow	830–910		
<i>Crossota rufobrunnea</i> (Kramp)			765
<i>Eutiara mayeri</i> H. B. Bigelow	60		
<i>Halicreas minimum</i> Fewkes	605–900	700–790	765
<i>Haliscera bigelowi</i> Kramp	720–880		790–885
<i>Haliscera conica</i> Vanhöffen	540–855		
<i>Halitrephes maasi</i> H. B. Bigelow	590–885	760	610–855
<i>Halitrephes valdiviae</i> Vanhöffen	605–785		710–745
Mitrocomidae n.g., n.sp.	735		860
<i>Orchistoma pileus</i> (Lesson)	25		
<i>Pandea rubra</i> H.B. Bigelow		745	
<i>Pantachogon haeckeli</i> Maas		425–790	785–835
<i>Pegantha clara</i> R.P. Bigelow	640		
Ptychogastridae n.g., n.sp.	700		
<i>Solmaris corona</i> (Keferstein & Ehlers)	675–695		
<i>Solmaris flavescens</i> (Kölliker)	865–900		
<i>Solmissus incisa</i> (Fewkes)	470–894	762	475–760
<i>Solmissus marshalli</i> Agassiz & Mayer	610–810		
<i>Solmundella bitentaculata</i> (Quoy & Gaimard)	760–900	700–740	720
<i>Tiaropsis</i> n.sp.	610		
CUBOMEDUSAE			
<i>Carybdea alata</i> Reynaud	505–580		
<i>Carybdea marsupialis</i> (Linnaeus)	80		
SCYPHOMEDUSAE			
<i>Atolla parva</i> Russell	910		760–855
<i>Atolla vanhoeffeni</i> Russell	655–850	715–755	810–820

Table 2. (Continued)

TAXA	Depth of Collection		
	Bahama Islands	New England	Dry Tortugas
<i>Atolla wyvillei</i> Haeckel	700–910	685–790	
<i>Atorella octogonos</i> Mills, Larson & Youngbluth	480–885		855
<i>Aurelia aurita</i> (Linnaeus)	0		
<i>Nausithoe atlantica</i> Broch	895–900	760	750
<i>Paraphyllina intermedia</i> Maas	585–685		
<i>Paraphyllina ransoni</i> Russell	900–915		
<i>Palephyra</i> n.sp.	695		
<i>Pelagia noctiluca</i> (Forskål)	+	0–185	0–90
<i>Periphylla periphylla</i> (Péron & Lesueur)	560–910	490–760	710–855
<i>Periphyllopsis ?galatheae</i> Kramp			870
<i>Periphyllopsis braueri</i> Vanhöffen	890		
<i>Poralia</i> sp. A	775–910	700–790	880
<i>Poralia</i> sp. B			870–880
Totals: 55 taxa	46	16	25

Midwater medusae were observed to be mostly inactive foragers that either drifted or slowly swam with relatively short stiff tentacles extended out to the side and/or below the bell. The only medusae that had filiform contractile tentacles were the anthomedusae *C. rubrum* and *P. rubra*; the leptomedusa *Tiaropsis* sp., and an undescribed mitrocomid; and the sennaeostomes *Poralia* spp. Some species had well developed escape responses. *Atolla* spp. and *P. periphylla* were mostly seen swimming rapidly with tentacles held either compressed downward against the umbrella (*Atolla* spp.) or up over the umbrella (*P. periphylla*), in apparent response to the submersible's lights. Quiescent *Atolla* spp. and *P. periphylla* held their tentacles respectively below or straight out from the bell margin. *Halitrephes maasi* H.B. Bigelow was often seen drifting passively when first detected, but as the submersible approached individuals would then rapidly swim upward for many meters with their tentacles trailing. Other trachymedusae showed a brief but rapid escape response of a few pulsations (as described by Mills *et al.*, 1985), but normally were inactive with rigid, outstretched tentacles. Narcomedusae slowly pulsed with their tentacles held outwards

or upwards (as described by Mills & Goy, 1988, and Larson *et al.*, 1989).

We rarely saw prey in the guts of the meso-pelagic medusae. One *S. incisa* was collected with an ingested ctenophore; two others were seen with veliger shells in their guts. However, prey-derived oil droplets were seen in many medusae, indicating that they had recently fed. We saw more evidence of predation on medusae. Many narcomedusae and coronate scyphomedusae had shortened or missing tentacles, possibly eaten by predators. We saw several crustaceans feeding on medusae at depth. Off New England, we observed a large red caridean shrimp *Notostomus robustus* Smith feeding on a specimen of *Atolla wyvillei* Haeckel. When first observed at 790 m, the medusa was vigorously swimming, apparently attempting to escape. Even after bringing them to the surface the shrimp continued to feed on the medusa, and consequently all but one of the tentacles were missing and some pedalia were damaged. The hyperiid amphipod *Parathemisto gaudichaudi* (Guerin-Meneville) was often seen feeding on medusae and siphonophores. These amphipods were attracted in vast numbers by the lights of the submersible. Several times when we

collected medusae some *P. gaudichaudi* entered the collection chambers and ate most of them. One *P. periphylla* was collected in the Bahamas with 3 pycnogonids *Pallenopsis* (*Bathypallenopsis*) *scoparia* Fage attached to it that had eaten most of its tentacles (Child & Harbison, 1986). Additional pycnogonids were found on *C. pedunculata* and on *A. grimaldii*. Also, we saw and collected a large apolemid siphonophore feeding on 2 *P. periphylla*.

Discussion

Although we tried to document the entire pelagic coelenterate fauna we were unable to see and collect very small specimens. This bias was mostly limited to near the surface where small medusae predominate. Most midwater medusae are large enough to be visible.

In the deep sea, medusae are probably better known than any other group of gelatinous macroplankton. Nevertheless, undescribed species are still being collected using submersibles (Mills *et al.*, 1987; Larson *et al.*, 1988a). We found at least 15 new species of medusae as well as collected a number of rarely reported species. For example, the large but very fragile semaestome medusa *Poralia* sp. was previously known from the western Atlantic from only a few specimens reported by Bigelow (1938) off Bermuda. However, we found that this medusa was fairly common below 700 m at all 3 sites. Twelve *Poralia* sp. A were seen on one dive in the Bahamas, where it was most numerous within 100 m of the bottom. (There are two *Poralia* spp. in the western Atlantic and it is uncertain which is *P. rufescens*.) Smith (1982), using the submersible *Alvin*, reported that *P. rufescens* was rather numerous near the bottom off southern California. Another unusual occurrence was the sighting and collection of numerous *Crossota pedunculata* H.B. Bigelow in the Bahamas at 800–900 m. This benthopelagic species has not been reported since it was originally described from off Oregon by Bigelow (1913).

The vertical distributions reported here can be

compared with those reported by Thurston (1977) and Roe *et al.* (1984) from the eastern North Atlantic at 53–60° N 20° W and 44° N 13° W, respectively. Both employed discrete-depth sampling, open-closing midwater trawls. All 3 studies revealed the greatest species diversity and highest number of individuals at greater depths, but some differences were evident between the vertical distributions of the various species (Larson *et al.*, 1988b).

Physical factors have been thought to regulate midwater vertical distributions. Although temperature may determine the overall distribution of a species, other factors regulate the range within these broad limits. For example, *P. periphylla* occurs at temperatures as high as 20 °C; yet even where water column temperatures are uniform or are much lower, such as at high latitudes, *P. periphylla* is always most numerous at mesopelagic depths (Larson, 1986). We found that highest diversity in the Bahamas occurred at temperatures of 7–13 °C, whereas in the Dry Tortugas and off New England highest diversity was at <5 °C. Thus temperature was probably not the primary factor controlling the observed vertical distribution patterns.

Light may be an important factor in medusa distribution since in the upper layers they might be seen and avoided by prey or be seen and eaten by predators such as decapod crustaceans and fishes. However, light does not seem to determine the overall depth limits. This is indicated by the shallower depth distributions of medusae in the clear waters in the Bahamas in comparison with New England where the water is more turbid. Yet light undoubtedly does affect some medusae, as is evidenced by its control of vertical migrations (Mills, 1983; Mackie, 1985).

Within broad limits set by temperature and light, if there are limits, biological factors may be even more important in controlling vertical distributions. Prey availability is often a limiting factor for neritic gelatinous predators (Reeve & Walter, 1978; Purcell, 1981; Larson, 1987), so it might be expected that the vertical distributions of midwater taxa throughout the oceans would be correlated with those of their prey. However, lack

of information on the prey of midwater medusae precludes drawing conclusions.

Bioluminescence of ingested prey may have been a selection factor, through predation, causing the evolution of dark pigmentation in midwater medusae (Herring, 1972; Bonnett *et al.*, 1979). It should be noted, however, that the majority of deep water medusae are transparent. Possibly the presence or absence of pigment over the gut is a function of diet since bioluminescent prey in the stomach of a transparent medusa could make the medusa visible to predators.

We know more about mesopelagic cnidarians as prey than as predators. Mesopelagic medusae are important in the diets of amphipods, mysids, decapod shrimps, fish and leatherback turtles (Tchindonova, 1959; Thurston, 1977; Roe *et al.*, 1984; Hopkins, 1985, 1987; Mrosovsky, 1987; Moore & Rainbow, 1989). Our report of the decapod *Notostomus* feeding on the medusa *A. wyvillei* is the first direct observation of midwater carideans feeding on cnidarians. These studies emphasize that gelatinous zooplankton may be important midwater prey, but further work is needed to clarify the role of medusae as predators in midwater food webs.

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