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ScienceDirect

Deep-Sea Research II 55 (2008) 119–125

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Vertical distribution and relative abundance of gelatinous zooplankton, *in situ* observations near the Mid-Atlantic Ridge

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Available online 26 December 2007

Abstract

Fourteen dives were conducted with the ROVs *Aglantha and Bathysaurus* to depths of 2335 m along the Mid-Atlantic Ridge (42°52′–53°17′N). The most frequently observed gelatinous fauna in order of overall abundance included medusae, ctenophores, siphonophores, appendicularians, and tunicates. All of these animals, except the tunicates, occurred throughout the water column. Their relative abundances differed with depth and location. Identification to species was limited to easily recognized fauna because relatively few gelatinous animals were collected.

Each group of gelatinous zooplankton tended to be most numerous in a region just south of the Charlie-Gibbs Fracture Zone. Medusae (mainly *Aeginura grimaldii*) were the most frequently encountered animals (up to 25 individuals per 100 m^3). On a vertical scale their abundance peaked from 550 to 800 m and these maxima were consistently within the SAIW and NACWe. In the NACW their densities were notably lower (up 2 individuals per 100 m^3) and the majority of the population was deeper, ranging from 800 to 1050 m. Ctenophores (mainly *Bathocyroe fosteri*) were most prominent (as many as 27 individuals per 100 m^3) in a zone from 300 to 600 m in the NACWe. Appendicularians (primarily oikopleurids) had a broader vertical distribution in all water masses, mainly from 450 to 1000 m. Up to 12 houses per 100 m^3 were noted in the NACWe, and these estimates are considered to be very conservative. Sorties near the sea floor (as deep as 2100 m) indicated these detritivores were a prominent component (up to 5 houses per 100 m^3) of the epibenthic macrozooplankton. Siphonophores (mostly calycophorans) reached densities of about 14 colonies per 100 m^3 in the NACWe and occurred mainly from 300 to 600 m, at most locations. Tunicates (salps and doliolids) were patchy in their distribution and infrequently observed. Salps were numerous (up to 3 solitary individuals per 100 m^3) at only one location (sta. 50) near the surface. Deep-living doliolids (up to 1 individual per 100 m^3) appeared from 400 to 500 m at this site and occasionally within the same depth range at most of the other stations.

Keywords: Gelatinous zooplankton; ROV; Distribution; Abundance; Mesopelagic

1. Introduction

Over the last two decades a relatively small number of research submersibles have provided unprecedented access to deep-water habitats. Most of the investigations with these undersea vehicles have focused on the benthos, surveying geological features, cataloging species diversity, and defining biogeochemical processes. A comparatively smaller number of observations in the pelagic realm have repeatedly encountered gelatinous fauna and gradually documented their diversity and abundance (Larson et al., 1992; Haddock et al., 2005; Raskoff et al., 2005). Although sporadic, except for the midwater program in Monterey Bay, and restricted mostly to coastal waters, these visual surveys have demonstrated that morphologically fragile animals are predictably more numerous in pelagic environments than have been revealed by collections in trawls and must be regarded as ecologically significant, especially in midwater regimes (Youngbluth et al., 1990; Robison, 2004).

The MAR-ECO project provided an unusual opportunity to visually quantify the vertical distribution of

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0967-0645/$ - see front matter
doi:10.1016/j.dsr2.2007.10.002

gelatinous zooplankton in the deep sea along the Mid-Atlantic Ridge in July 2004 (Bergstad and Godø, 2002). The discoveries presented in this paper are compared to direct observations previously conducted in this region and other oceans. Such information contributes to a quantitative phase in deep-sea biological exploration.

2. Materials and methods

The distribution and abundance of gelatinous zooplankton were assessed from vertical video profiles, using two remotely operated vehicles (ROV) *Aglantha* and *Bathysaurus* (2000 and 3000 m depth limit, respectively). The descent rate of these vehicles was $\leqslant 0.5\,\mathrm{m\,s^{-1}}$ for each vertical profile. On *Aglantha* a Sony EVI-401 color video camera [$\frac{1}{3}$-in CCD with Super HAD technology (440,000 pixels NTSC), 12× optical zoom and minimum object illumination of 1 lx] was available. On *Bathysaurus* a Sony FCB-471 video camera ($\frac{1}{4}$-in HAD CCD, 18× optical zoom, minimum sensitivity of 0.7 lx) was used. The field of view was illuminated by four 500-W halogen lights and two 150-W high intensity discharge (HID) gas-arc lights. The volume of water recorded by the video camera was calculated by multiplying a horizontal "surface area" with the distance moved vertically (Youngbluth and Båmstedt, 2001). Subsequent to a given dive, three observers simultaneously watched video records and confirmed the identity and depth of occurrence for each animal. Fauna were identified to the lowest possible taxonomic level. Abundances were integrated for vertical intervals of 50 m (volume = $115.50\,\mathrm{m^3}$) and standardized to individuals per $100\,\mathrm{m^3}$. The size of a given animal was determined with a dual beam laser or referenced to the size of a known part of the ROV in the field of view. Gelatinous fauna were captured with suction and static samplers (Tietze and Clark, 1986). Temperature, salinity, and dissolved oxygen in the water column were recorded with a CTD mounted on the ROV or from CTD casts at a given location. Søiland et al. (2008) describe the instrumentation and hydrographic data profiling with CTD casts.

3. Results

3.1. Hydrographic conditions

Several water masses occurred in the study area from 42°52′N to 53°17′N Latitude (Wenneck et al., 2008). Overviews of the hydrography from this cruise are provided elsewhere (Hosia et al., 2008; Søiland et al., 2008; Stemmann et al., 2008). Cooler, less saline Subarctic Intermediate Water (SAIW) characterized the upper water mass at the northernmost sampling sites (sta. 66–74) (Table 1). To the south of these stations the Subpolar Front (SPF) acted as a boundary separating the warmer, more saline surface waters that characterized the two, more southern clusters of stations (sta. 56–62 and sta. 44–50) where North Atlantic Central Water (NACW) occurred. The position of the SPF during the cruise was at about 52°N (Søiland et al., 2008). The Frontal Region south of this location (50–52°N) was characterized by a mixture of several water masses where SAIW dominated in the upper 1000 m. However, at Stations 56–62, just south of the Charlie–Gibbs Fracture Zone, a transitional, 60-km wide water mass called an NACW eddy (NACWe) was present (Stemmann et al., 2008). At mesopelagic depths the main pycnocline was prominent (Stemmann et al., 2008). In this regime cold and relatively fresh Labrador Sea Water (LSW) meandering from the north-west mixed with warm and salty Mediterranean water flowing from the southeast (Hosia et al., 2008; Vinogradov, 2005).

Table 1
The date, start time, station, location, and depth of ROV dives conducted near the Mid-Atlantic Ridge

Date	Start time	ROV dive	Station	Latitude–Longitude	Depth range (m)	Bottom depth (m)	Surface water mass
7/29/04	0429	17-A	74	53.17.13°N–36.47.06°W	0–1085	3051	SAIW
7/26/04	1128	15-B	68	53.07.62°N–34.47.33°W	0–2335	2335	SAIW
7/25/04	1422	14-A	66	53.01.69°N–33.36.63°W	0–655	3038	SAIW
7/27/04	0440	16-A	70	53.00.94°N–34.52.73°W	0–1517	1517	SAIW
7/17/04	1916	7-A	54	51.20.15°N–28.54.85°W	0–895	3506	SAIW
7/22/04	1638	11-A	62	51.53.56°N–30.24.09°W	0–1675	1685	NACWe
7/23/04	0714	12-B	56	51.45.17°N–29.35.01°W	0–1436	1436	NACWe
7/20/04	0026	10-A	60	51.30.78°N–30.20.13°W	0–975	975	NACWe
7/24/04	0717	13-B	58II	51.25.36°N–29.56.85°W	0–650	3242	NACWe
7/19/04	0455	9-A	58I	51.18.60°N–29.59.66°W	0–1000	3578	NACWe
7/13/04	2122	5-A	50	42.56.51°N–28.30.05°W	0–2092	2092	NACW
7/12/04	2239	4-B	44I	42.55.92°N–29.30.28°W	0–1228	1228	NACW
7/15/04	0219	6-A	44II	42.55.40°N–29.29.75°W	0–1045	1152	NACW
7/12/04	0138	3-B	48	42.52.35°N–29.06.17°W	0–1145	1145	NACW

Surface water masses are noted in the last column. A = ROV *Aglantha*; B = ROV *Bathysaurus*. SAIW = Subarctic Intermediate Water, NACWe = North Atlantic Central Water eddy, NACW = North Atlantic Central Water.

3.2. Vertical distribution and abundance of gelatinous fauna

Investigations were conducted at pre-determined stations along the longitudinal axes of the Mid-Atlantic Ridge (Wenneck et al., 2008). The 14 ROV dives completed during this period occurred on an opportunistic basis in regard to time of day and geographic location (Table 1). Ten dives (sta. 54–74) were performed in the northern sector and four dives (sta. 44–50) occurred in the southern portion of the MAR-ECO Leg 2 cruise track (Table 1). In most cases, only one ROV dive was conducted at a given location. The depth of the water column, where vertical profiles were made, ranged from 975 to 3575 m. However, the extent of vertical excursions varied from 650 to 2335 m, and depended primarily on which ROV was deployed, its depth-time constraints, and the velocity of deep horizontal currents. Surface-to-bottom profiles were obtained on only seven dives, ranging from 975 to 2335 m.

Several gelatinous groups were commonly observed. Identification to species was restricted to easily recognized fauna because relatively few gelatinous animals were collected due to time constraints for a given ROV dive and control limitations of the vehicles. A total of 2042 animals were recorded. The most frequently observed animals in order of overall percent abundance included medusae (37%, $n = 748$), ctenophores (21%, $n = 432$), appendicularians (19%, $n = 397$), siphonophores (19%, $n = 394$), doliolids (3%, $n = 61$) and salps (1%, $n = 10$). All of these fauna, except salps, occurred throughout the water column and nearly all populations within each group were most abundant in the uppermost 1000 m. The percent of each gelatinous group (excluding data from sta. 54, 58II and 66 where ROV dive depths were less than 975 m) revealed that medusae composed of a somewhat larger (ca. 51 versus 37%) portion of the gelatinous fauna at the most northern sites (Fig. 1). Ctenophores showed the opposite trend (ca. 7% at the most northern station versus >18% at more southern stations). Appendicularians had a much smaller range (15–23 % from south to north). Siphonophores constituted a higher proportion (ca. 30%) of the gelatinous fauna at the southern stations in comparison to northern stations (ca. 17%) Doliolids formed only 5% of the gelatinous fauna at the more northern sites and were not observed at the southern stations. Salps were not seen at most stations. This group composed less than 1% at station 62 in the northern sector and 5% at station 50 in the southern sector.

Averaging enumeration data from stations where dives were 975 m or deeper (as noted above) indicated that gelatinous zooplankton (2–10 cm) tended to be most abundant from 350 to 750 m (Fig. 2). Vertical abundances of the major gelatinous groups observed at a single station in each water mass (Table 1) are compared in Fig. 3. Medusae were the most frequently encountered animals

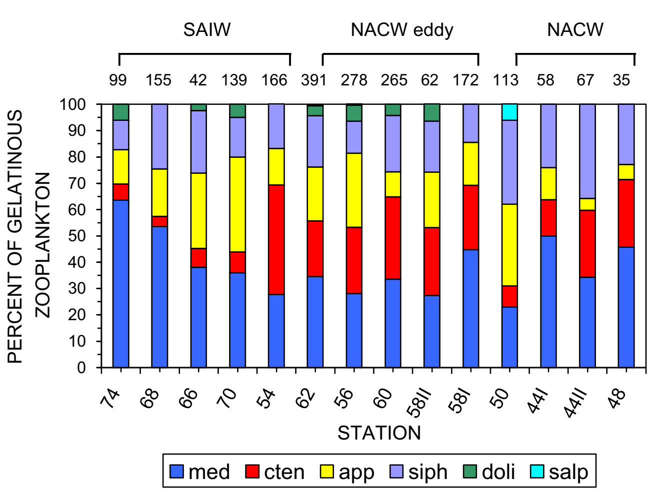

Fig. 1. The percent of gelatinous zooplankton observed during an ROV dive at each station is shown in a vertical bar. The legend at the bottom of the plot denotes the color used to distinguish each group: med = medusa, cten = ctenophore, app = appendicularian, siph = siphonophore, doli = doliolid, salp = salp. The total number of animals recorded for each dive is noted at the top of each bar. Abbreviations for water masses include: SAIW = Subarctic Intermediate Water, NACWe = North Atlantic Central Water eddy, NACW = North Atlantic Central Water.

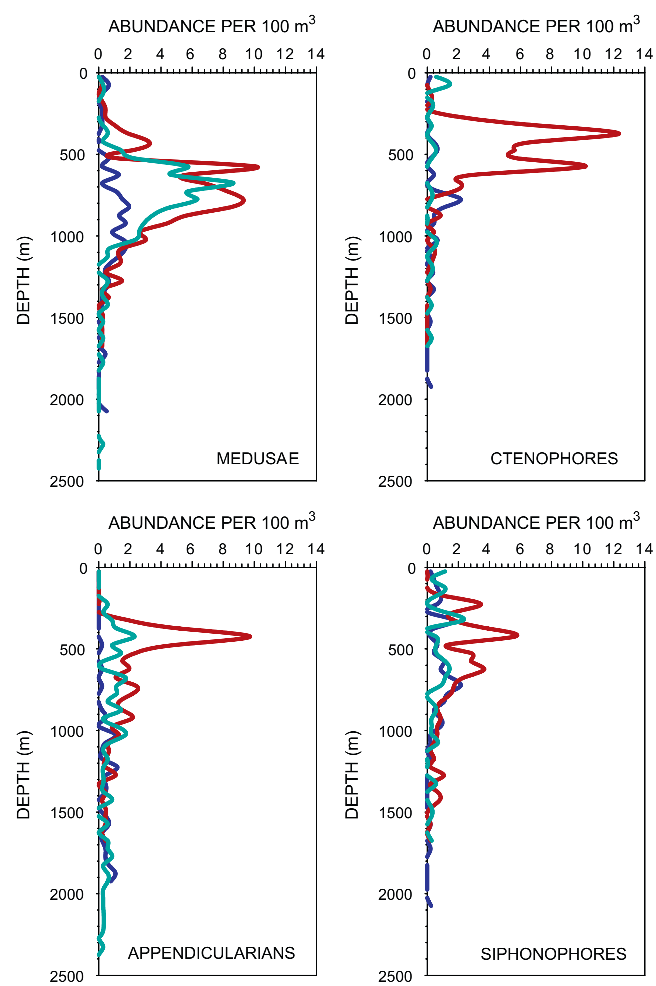

Fig. 2. The vertical distribution of gelatinous zooplankton averaged over all stations in each water mass. Only data from ROV dives that were greater than 975 m were plotted. Sta. 68–74 (green line, SAIW); sta. 581–62 (auburn line, NACWe); sta. 441–50 (blue line, NACW).

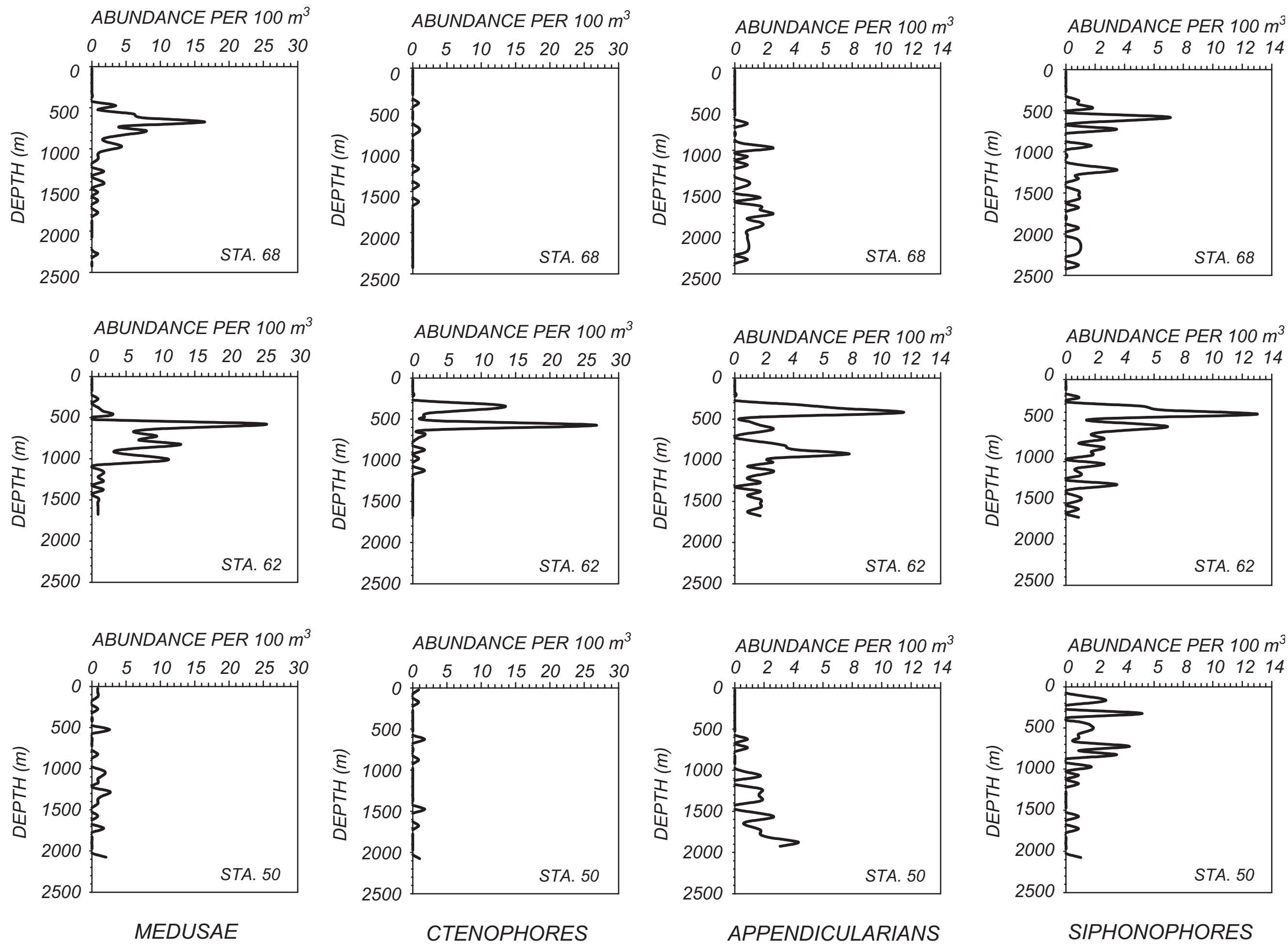

Fig. 3. The vertical distribution of gelatinous zooplankton is profiled at a single (sta. 68, 62, and 50) station in each water mass. Only data from the deepest (1675–2335 m) ROV dives that profiled the entire water column are presented.

(up to 25 individuals per 100 m^3). *Aeginura grimaldii*, the most common species in this group, was observed from 519 to 1572 m. Approximately 70% ($n = 236$ total individuals) of this species was seen between 600 and 900 m with peak abundances near 750 m. *Aeginura grimaldii* was consistently numerous in the northern and middle sectors (sta. 54–74). In both of these regions the vertical distribution coincided with the base of the permanent pycnocline (Stemmann et al., 2008). In the southern sector (sta. 44–50) the bulk of medusae was deeper (ranging from 800 to 1050 m) and less numerous, most frequently about 2 individuals per 100 m^3. Other species of medusae observed included *Solmissus* sp., *Aglantha digitale*, *Atolla* sp., *Periphylla periphylla*. *Solmissus* sp. was observed during every dive and ranged from 279 to 1333 m; 51% ($n = 50$ total individuals) occurred from 500 to 700 m and most sightings occurred in the northern middle set. *Atolla* sp. occurred at eight stations, ranging from 440 to 1450 m with 63% ($n = 32$ total individuals) between 500 and 700 m. This species was common at the more northern stations and rare in the southernmost cluster of stations (sta. 44–52). *Aglantha digitale* appeared at five stations (all within the NACW eddy) and was most numerous at stations 58I, 60, and 62, ranging from 291 to 1288 m; 73% ($n = 33$ total individuals) occurred from 700 to 1000 m. *Periphylla periphylla* was observed at four stations (sta. 58I, 60, 62, 74) and ranged from 99 to 693 m, 40% ($n = 10$ total individuals) occurred from 500 to 700 m. Unidentified medusae averaged 48% ($n = 746$ total individuals) of all medusae observed at a given location.

Ctenophores (mainly *Bathocyroe fosteri*) appeared at all stations, ranging from 28 to 1616 m. This group was numerous only in the cluster of stations just south of the Charlie–Gibbs Fracture Zone. The two peaks in abundance at 350 and 550 m were *B. fosteri*, up to 27 individuals per 100 m^3 (Figs. 2 and 3). The second most common (appearing at 12 of the 14 stations) species *Bolinopsis infundibulum* was less numerous (0.4–3 individuals per 100 m^3) and occurred from 42 to 659 m. The bulk of this species often overlapped with the shallower portion of the *B. fosteri* distribution. Although it was not always possible to distinguish between these two species because of their transparency, their position in the light field, and the descent rate of the ROV, these two lobates composed of 75–95% of all ctenophores observed. Two, small (ca. 1–2 cm body length with tentacles that extended as much as 30 cm) unidentified cydippids were common at the NACW eddy stations, appearing most often between 500 and 600 m and ranged from 333 to 1013 m. One and two *Beroe* spp. occurred at two sites (646 m at sta. 50; 511 and 1126 m at sta. 62, respectively).

Appendicularian houses (primarily oikopleurids and some fritillarids) were conspicuous and consistently present at all stations, ranging from 233 to 2212 m overall. It was not always possible to confirm that every house was occupied. Unoccupied houses are usually deflated or laden with particulate matter and difficult to distinguish from large aggregates of marine snow and such particles were not recorded as houses. Most houses were about 2–4 cm in diameter; a few larger houses, up to 10 cm in diameter were seen. Peaks in abundance (up to 12 houses per 100 m^3) were noted at about 400 m in the two northern sites (Figs. 2 and 3). All estimates of abundance are considered very conservative because houses were easily disrupted and cryptic, especially when large amorphous aggregates co-occurred in the water column. Appendicularian houses were a prominent and obvious component of the epibenthic macrozooplankton communities but quantitative estimates of appendicularians were not conducted during ROV surveys in the benthic boundary zone. At sta. 50 (Fig. 3) appendicularian houses were more (2–4 times) abundant below 1000 m and most numerous (up to at least 5 houses per 100 m^3) near the sea floor.

Siphonophores (mostly small, 2–3 cm long calycophorans and a few physonects ranging from 10–30 cm) occurred mainly from 300 to 600 m. Densities were highest (nearly 14 calycophoran colonies per 100 m^3 around 425 m, (sta. 62 in the NACW eddy cluster), averaging up to 6 colonies per 100 m^3. At the most northern and southern sites, the highest abundances averaged about 2 calycophoran colonies per 100 m^3 at 325 m (Fig. 2) but ranged up to ca. 6 colonies per 100 m^3 at 570 and 325 m (sta. 68 and 50, respectively).

Tunicates were infrequently observed. Up to 3 solitary salps per 100 m^3 occurred near the surface (0–50 m) at one location (sta. 50) in the southern zone. Deep-living doliolids (up to 1 individual per 100 m^3) appeared from 400 to 500 m at station 62 and occasionally within the same depth range at most of the other stations. These estimates of doliolid abundance could be low because some doliolids may have been identified as physonect siphonophores.

4. Discussion

The dynamics of deep-water zooplankton communities and the roles of deep-living gelatinous predators are inevitably linked to shifts in advective processes and surface productivity (Vinogradov et al., 2002; Piontkovski et al., 2003; Raskoff, 2004). The interplay of these conditions is complex (e.g., Canziani, 1999) and requires more rigorous spatial and temporal investigations of community structure and behavior (e.g., Parsons, 2002) than were conducted in this study. A general impression of zoogeographic affinities among pelagic cnidarians and water masses that transect the MAR-ECO cruise track are discussed elsewhere (Hosia et al., 2008; Stemmann et al., 2008). Furthermore, although this study focused on quantifying vertical patterns of distribution and abundance of these fragile zooplankton, our glimpses of what appeared to be undescribed medusae, ctenophores, doliolids and appendicularians suggest that the diversity of gelatinous species in deep oceanic regimes remains understudied (e.g., Godeaux and Harbison, 2003; Hopcroft, 2004; Lindsay et al., 2004; Raskoff and Matsumoto, 2004; Hosia et al., 2008).

Vertical distribution profiles from ROV (this study) and UVP (Stemmann et al., 2008) dives were remarkably consistent in regard to the estimates of location and abundance of gelatinous fauna in each water mass where sampling was conducted concurrently. A minor exception was that more (ca. 2x, mostly small forms) siphonophores were recorded with the UVP in the upper 400 m in the NACW eddy. Previous visual surveys of gelatinous fauna near the Charlie–Gibbs Fracture Zone in the same season have shown that gelatinous fauna, principally medusae and mainly *Aeginura grimaldii*, are most numerous from 600 to 1000 m (Vinogradov, 2005). Similarly, during that study small siphonophores were observed to peak from 300 to 600 m. Ctenophores appeared in low densities throughout the water column. As in this study, appendicularians were abundant near the seafloor. It is worth noting that the abundances of gelatinous fauna recorded in the present investigation were 2–10 times higher than reported previously (Vinogradov et al., 2002; Vinogradov, 2005). This discrepancy may represent temporal variation or methodological bias.

The reasons underlying the pronounced association of gelatinous zooplankton for the depth zone 350 to 750 m in the NACW eddy remain unknown. Abundances of the four major groups (medusae, ctenophores, appendicularians, and siphonophores) were clearly largest in this midwater region, although medusae were also relatively numerous within this midwater region at the SAIW stations. Small mesopelagic crustaceans, probably copepods, which are potential prey for medusae, ctenophores, and siphonophores, were not notably numerous in this deep-water sector (L. Stemmann, per. comm.). Layers of particles in the size range that would be suitable as food for appendicularians were also not obvious from UVP profiles (L. Stemmann, per. comm.).

By way of conclusion, the current trend to instrument the oceans for monitoring purposes is crucial for documenting, quantifying, and modeling long-term and large-scale events. However, reliance on that approach and integrated sampling with net tows will overlook the coupling of small-scale environmental phenomena and short-term animal behavior (Graham et al., 2001; Pagès et al., 2001; Robison et al., 2005). Recognizing that the water column is layered in time and space and that gelatinous pelagic fauna respond to vertical boundaries, especially in the deep sea, is generally not appreciated. For example, gelatinous marine organisms often concentrate, segregate and feed at water column boundaries such as isolumes, pycnoelines, and fronts on diel and seasonal scales (Angel, 1989; Swanberg et al., 1990; Youngbluth et al., 1990; Youngbluth and Båmstedt, 2001; Toyokawa et al., 2003; Frank and Widder, 2004). This study confirms and contributes to previous studies that have shown several kinds of gelatinous zooplankton persist in specific deep-water zones (e.g., Mills, 1995; Vinogradov and Shushkina, 2002; Lindsay and Hunt, 2005). The stability of biodiversity in such trophic guilds and the predictability of their impact on ecosystem function in the deep sea require a continuation of *in situ* investigations.

5. Conclusions

The most frequently observed gelatinous fauna in order of overall abundance included medusae, ctenophores, appendicularians, siphonophores, and tunicates. The majority of these animals were relatively small (1–10 cm). The highest abundance of gelatinous fauna consistently occurred from 350 to 750 m in the region just south of the Charlie–Gibbs Fracture Zone.

Acknowledgments

This study was supported in part by the MAR-ECO project, a field study of the Census of Marine Life programme, the Whiteley Center, and the Harbor Branch Oceanographic Institution. The camaraderie of fellow scientists, ROV technicians from Argus Remote Systems, Laksevåg, and the Institute of Marine Research, Bergen, and crew of the Norwegian research vessel G.O. Sars made this cruise productive. Special thanks to Toktleder Odd Aksel Bergstad and nature photographer par excellence David Shale. HBOI Contribution No. 1692.

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