



Jellies under ice: ROV observations from the Arctic 2005 hidden ocean expedition

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ABSTRACT

In order to provide a baseline understanding of gelatinous zooplankton biodiversity and distribution in the rapidly changing Arctic Ocean, 12 stations were sampled across the Canada Basin, Northwind Ridge, and Chukchi Plateau with detailed deep-water ROV observations and multinet tows down to 3000 m. The complex, multi-origin water layers of the Arctic Ocean provided the backdrop for examining the vertical and horizontal distributions of the poorly understood meso and bathypelagic gelatinous taxa. Over 50 different gelatinous taxa were observed across the stations, with cnidarians being the most common group. Medusae accounted for 60% of all observations, siphonophores for 24%, larvaceans for 10%, ctenophores for 5%, and numerous interesting and rarer taxa constituted the remaining 1% of observations. Several new species were found and many major range extensions were observed. Both the vertical and horizontal distribution of species appear to be linked to water mass characteristics, as well as bottom topography and geographic location within the study area. Shallow slope and ridge areas around the Canada Basin and Chukchi Plateau appear to harbor substantially lower gelatinous zooplankton biomass and diversity than the deeper locations. Shallow stations not only show reduced abundance, but also different relative abundance of the major taxa, where the shallow water stations are dominated by large numbers of siphonophores and ctenophores, the deep stations are dominated by medusae. Taxonomic issues and ecological observations of several important species are discussed, aided by the live collection of many undamaged and fragile species.

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1. Introduction

Among the major Oceans on Earth, the Arctic is the most inaccessible and the least studied. Within it, the Canada Basin is the least known and its hydrographic isolation is potentially predisposing it to the evolution of unique species. The exchange of deep-water biota between the world's deep oceans and the Arctic deep-sea is limited to the Fram Strait, but the Canada Basin remains even more isolated by the barriers imposed by the Lomonosov (e.g. Björk et al., 2007) and the Alpha-Mendeleev Ridges. This isolation has suggested that the Canada Basin may harbor a unique community of animals. Ninety percent of the world's ocean is deep-sea (Gage and Tyler, 1991) and more than half of the Arctic Ocean's surface lies beyond the shelf break. During winter months the Arctic Ocean is covered by sea ice that extends far into the Bering Sea. The ice typically reaches its minimum coverage and thickness in September but there is

considerable interannual variability in both parameters (e.g. Perovich et al., 2003). Record low ice coverage in recent years left the Beaufort and Chukchi Sea ice-free well above 75°N latitude (McPhee et al., 1998; Jeffers et al., 2001), and the most current estimates of sea ice extent and thickness paint an alarming picture of the region in the near future as global climate change enhances the sea ice melt (NSIDC, 2007).

The taxonomic composition and life history of the numerous crustaceans in the Arctic Ocean is relatively well known (Smith and Schnack-Schiel, 1990; Mumm et al., 1998; Deibel and Daly, 2007), because of their high abundance and ease of capture with traditional plankton nets. In contrast, relatively little is also known of the abundance, composition or ecology of the delicate gelatinous zooplankton such as ctenophores (Ospovat, 1985; Swanberg, 1974; Swanberg and Båmstedt, 1991), siphonophores, hydromedusae, scyphomedusae (e.g. Naumov, 1960, 1961; Stepanjants, 1989; Raskoff et al., 2005), and larvaceans (Pagès, 1997) in polar seas. The most obvious explanation for this disparity is their extreme fragility. Collection with nets destroys most soft-bodied species or reduces them to fragments (Raskoff et al., 2003). As a result the remaining parts are usually ignored,

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discarded, misidentified, or simply recorded as “jelly”. Not as apparent is the fact that nets commonly used to sample zooplankton are often too small in area (≤ 1 m diameter) to provide reliable estimates of dispersed taxa like the gelatinous zooplankton and greatly underestimate their diversity and abundance (e.g., Naumov, 1960, 1961; Ospovat, 1985; Stepanjants, 1989; Raskoff et al., 2005). Furthermore, conventional preservatives not only significantly distort many soft-bodied groups making identification difficult, but they often completely liquefy ctenophores. In addition, most of the previous scientific studies from various regions of the Arctic Ocean used vertically integrated net tows through the surface waters only, which provided no details of vertical distribution of taxa (i.e. Bigelow, 1920; MacGinitie, 1955; Johnson, 1956; Hand and Kan, 1961; Grainger, 1965, 1975; Uchida, 1969; Jinbiao and Mao, 2000; Søreide et al., 2003).

Larvaceans can be common in polar waters (Shiga et al., 1998; Hopcroft et al., 2005) and their grazing rates can be substantial. Similarly, the biomass of chaetognaths in the Arctic is generally large despite their low abundance (e.g. Kosobokova and Hirche, 2000; Hopcroft et al., 2005), and even in cold waters their grazing rates are substantial (Oresland, 1990). The ecological impact of larger gelatinous predators (i.e. medusae and jellyfish) can be considerable (Purcell, 2003; Purcell et al., 2000, 2010). There are indications that climate change has resulted in increased numbers of jellyfish in the Bering Sea in recent years (Brodeur et al., 1999). High abundances of predaceous jellyfish have the potential to profoundly shunt the availability of food away from sea-birds and marine mammals (Purcell et al., 2000; Purcell, 2003). Preliminary data collected in 2002 showed that large medusae (*Chrysaora melanaster* and *Cyanea capillata*) and ctenophores (*Mertensia ovum* and *Bolinopsis infundibulum*) were common in surface waters throughout the Canada Basin, physonect siphonophores were abundant in the intrusion of Atlantic water at 350–600 m depth, while several species of hydromedusae became most common at greater depth (Raskoff et al., 2005).

In this study we report on the fine-scale vertical and horizontal distributions of the major gelatinous taxa, with notes on the ecology of these groups collected during the 2005 Hidden Ocean cruise to the Canada Basin, Northwind Ridge, and Chukchi Plateau.

2. Methods and materials

Midwater fauna were sampled and assessed during the summer of 2005, from June 29th through July 25th, in 24 h daylight conditions. The platform for this research was the U.S. Coastguard Cutter *Healy*, which left from Point Barrow, headed North into the Canada Basin and then out onto the Northwind Ridge and into the Chukchi Plateau and back towards Point Barrow (Fig. 1). ROV data were collected at 12 stations across the cruise track, which sampled the coastal shelf north of Barrow, USA, several locations in the deep Canada Basin, and the shallow Northwind Ridge and deep portions of the Chukchi Plateau (Fig. 1 and Table 1; with two dives at station 15).

The results reported in this paper were collected with the Remotely Operated Vehicle (ROV) *Global Explorer* (Deep Sea Systems), an approximately 2800 m depth rated vehicle equipped with a 720p High Definition (HDTV) video system with a DVCPRO HD VCR. Live animals were obtained with four, 6.5 l “D” samplers (Youngbluth, 1984a) to collect intact individuals of gelatinous zooplankton and a carousel of 12, 3.5-l canisters that samples the smaller or less fragile specimens using gentle suction (Youngbluth, 1984b). A Seabird CTD was attached to the ROV to record

hydrographic data for all dives except for the first station (data storage failure).

Live collected animals were retrieved as soon as the ROV was recovered (i.e. within several hours of collection) and put into a dark, 0 °C temperature-controlled environmental chamber equipped with special phototanks and planktonkreisels (Raskoff et al., 2003). Specimens were identified to the lowest taxonomic level possible and extensively photographed and observed while living (Fig. 2). Many animals were preserved for morphological and genetic analysis. The gentle collection procedures and tank designs made it possible to maintain live specimens for observations of a week or more.

On each dive, the water column was traversed vertically to ascertain the distribution of gelatinous animals. Dives were conducted from the surface to the ocean floor, or to the depth limit of the ROV at the deepest stations (Table 1). Data on species occurrences were collected and recorded in real-time by the authors, with augmentation using the recorded HDTV video tapes as needed. Each individual organism observed, confirmed by 2–4 researchers observing simultaneously, was logged into a database with time, depth and annotation. *In situ* specimen identification was possible to the species level for many taxa due to the high quality of the HDTV video and relatively limited macroscopic diversity. For those species not known, or for those specimens that were not clearly viewable on the video, the lowest taxonomic category determined was recorded. In cases where live animals were collected, subsequent observation allowed for increased taxonomic resolution. Due to ROV technical problems at station 5, the observations were incomplete.

Taxa abundances were plotted by depth and station. The plots present the number of the specific taxa observed hour⁻¹ of ROV observation, in 100 m bin intervals from the surface to the maximum depth achieved for a particular station. This was accomplished by calculating the time the ROV spent in each depth interval (downcast and upcast integrated) and then dividing the number of a species observed in the interval by the time spent in that interval, yielding a normalized proxy of abundance, number hour⁻¹. This was done for every station except the first, station 3, as a CTD data storage failure prohibited the calculation of the time spent at depth for that station. Data for station 3 is discussed in the text, but not included on the normalized contour figures. These data were contour plotted (SigmaPlot 10.0, Systat Software) along with the bottom depth of the stations when within the ROVs depth range (see Table 1). Temperature and salinity data were obtained from the ROVs CTD, binned into 10 m depth intervals, and an average value was calculated for each interval. Video and CTD data streams were linked using a combination of time and depth. Graphs of temperature and salinity for each station were plotted on a log scale to highlight the complexities of the upper water masses (see McLaughlin et al., 2005).

Between ROV dives, traditional plankton nets were used to assess the “smaller” zooplankton. At these stations we employed a Hydro-bios Midi Multinet (mouth area 0.25 m²) to collect in strata of 0–25, 25–50, 50–100, 100–200, 200–300, 300–500, 500–1000, 1000–2000, and 2000–3000 m using 150 µm mesh nets hauled vertically at ~0.5 m/s. Formalin preserved samples were processed in their entirety for quantitative determination of species composition and abundance.

3. Results

3.1. Physical oceanography of the regions

The Arctic water column was characterized by a complex layering of water masses and transition zones at all stations

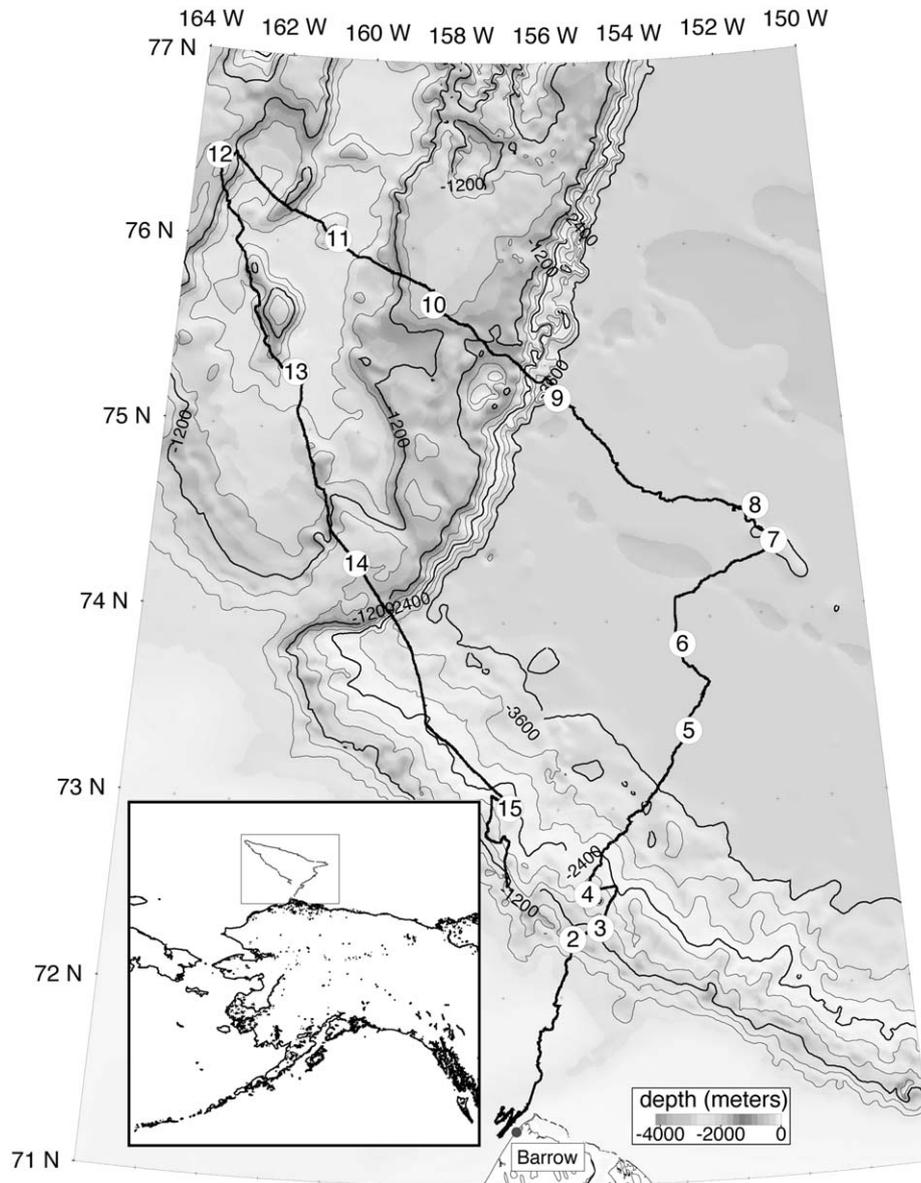


Fig. 1. Map of stations and cruise track on the USCGC *Healy* during the Hidden Ocean 2005 cruise. Not all stations were explored with the ROV. See Table 1 for list. Figure courtesy of Eric Mittelstaedt and Seung-Sep Kim, Hawaii Mapping Research Group.

Table 1

List of ROV stations.

Station	Date	Station depth (m)	Max ROV depth (m)	% water column surveyed	Dive length (h)	Geographic region	Latitude (N)	Longitude (W)
3	30 June 2005	1530	1530	100	8.75*	Chukchi Sea slope	72° 22'	155° 13'
5	04 July 2005	3853	2853	74	11.02	Canada Basin	73° 22'	153° 36'
6	07 July 2005	3854	1774	46	9.85	Canada Basin	74° 7'	153° 37'
7	09 July 2005	3800	2810	74	11.54	Canada Basin	74° 25'	151° 44'
8	11 July 2005	3840	2811	73	11.13	Canada Basin	74° 34'	151° 56'
9	14 July 2005	3859	2792	72	11.25	Canada Basin	75° 15'	155° 54'
10	15 July 2005	635	635	100	7.40	Northwind Ridge	75° 46'	158° 31'
11	16 July 2005	1614	1614	100	9.22	Chukchi Basin	75° 59'	160° 39'
13	20 July 2005	2110	2110	100	7.13	Chukchi Basin	75° 15'	161° 12'
14	22 July 2005	715	715	100	7.71	Northwind Ridge	74° 18'	159° 55'
15	23 July 2005	2414	2414	100	10.62	Chukchi Sea slope	72° 51'	156° 58'

Note that not all stations on the map (Fig. 1) were explored with the ROV.

Dive length (hours) of station 3 was determined from video recordings; all other dive lengths were calculated from CTD data files.

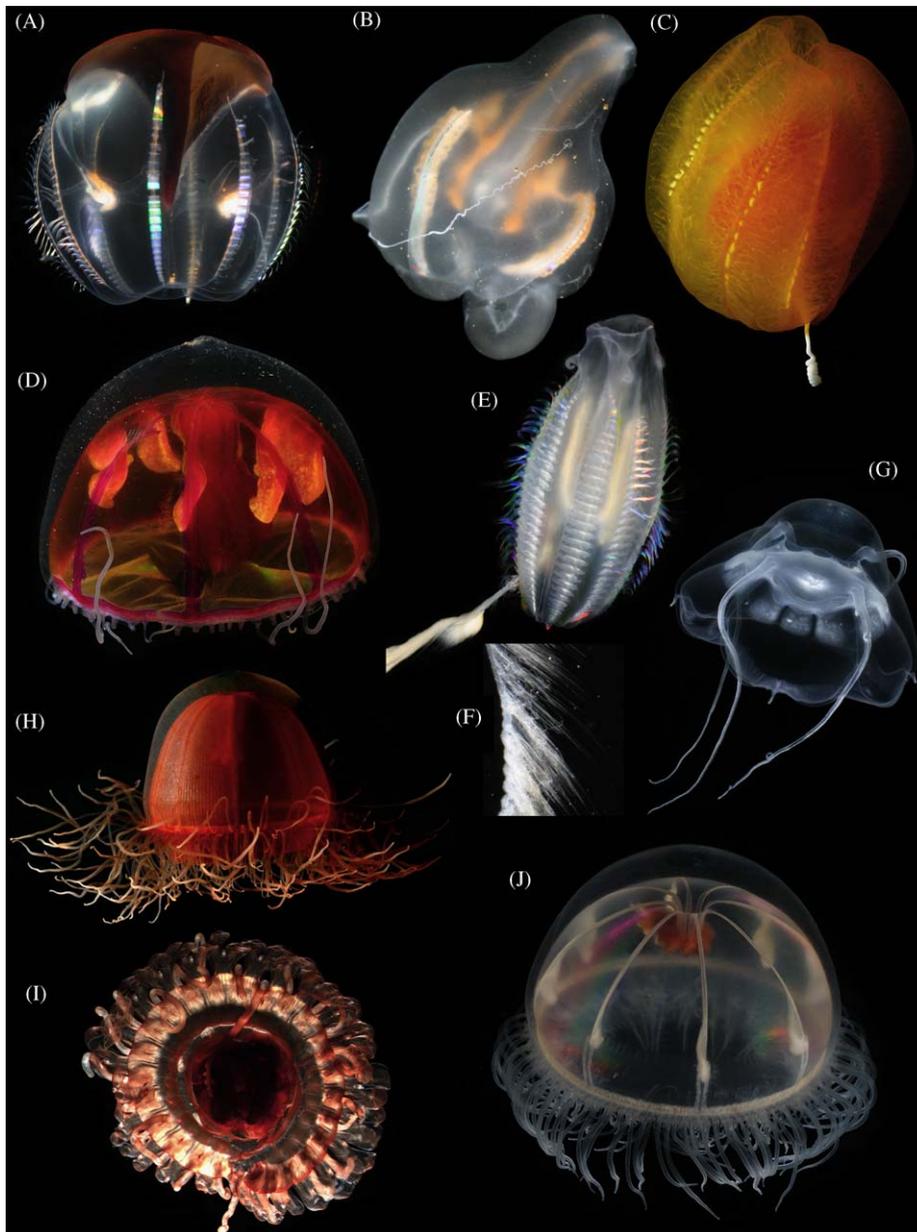


Fig. 2. Representative gelatinous zooplankton from the Arctic Ocean. (A) “Bathyctenid” cydippid ctenophore; (B) Epibenthic cydippid ctenophore; (C) cydippid ctenophore, *Aulacoctena* sp.; (D) trachymedusa, *C. millsae*; (E and F) “Horned” cydippid ctenophore; (F) Close-up view of tentacle and tentilla; (G) New Narcomedusae; (H) trachymedusa, *C. norvegica*; (I) scyphomedusa, *Atolla* sp. (*A. tenella*?); (J) trachymedusa, *Benthocodon hyalinus*. All photographed live. “I” taken on microscope by R. Hopcroft, all others with 35 mm camera system by K. Raskoff. Images are not to scale. See http://www.mpcf.aculty.net/kevin_raskoff/arctic05paper.htm for a color version of this figure and http://www.mpcf.aculty.net/kevin_raskoff/arctic.htm for additional species.

(Fig. 3). At an individual station, from the surface down to 20–40 m, the water was highly mixed with nearly constant temperature ($\sim -1.2^\circ\text{C}$) and slowly increasing salinity. Below this mixed zone were found the Pacific waters in which the temperature increased rapidly at a depth of 40–60 m by $\sim 1.0^\circ\text{C}$, depending on the station, and then decreased to a temperature minimum at 140–170 m. This temperature minimum marks the transition to the Atlantic water masses, which are characterized by a steady increase in both temperature and salinity to a depth of 400 m. The temperature maximum found at 400 m indicates the Fram Strait Branch waters (McLaughlin et al., 2005). Below this depth, the salinity stays high while the temperature decreases down to a depth of ~ 2000 m, at which point the waters transition for a final time to the Arctic deep basin bottom

waters, which have very long ventilation times and undergo little mixing with other water layers (McLaughlin et al., 2002; Timmermans et al., 2003).

3.2. Biological distributions

Over 50 unique gelatinous taxa were recorded during the 12 ROV dives with 7045 animal observations across all the stations (Table 1). Cnidarians accounted for the largest share of animals observed. Medusae were 60% of all observations. Siphonophores accounted for 24% of observations, with most of these animals being physonect colonies. Other non-cnidarian gelatinous plankton were also found in large numbers. Larvaceans accounted

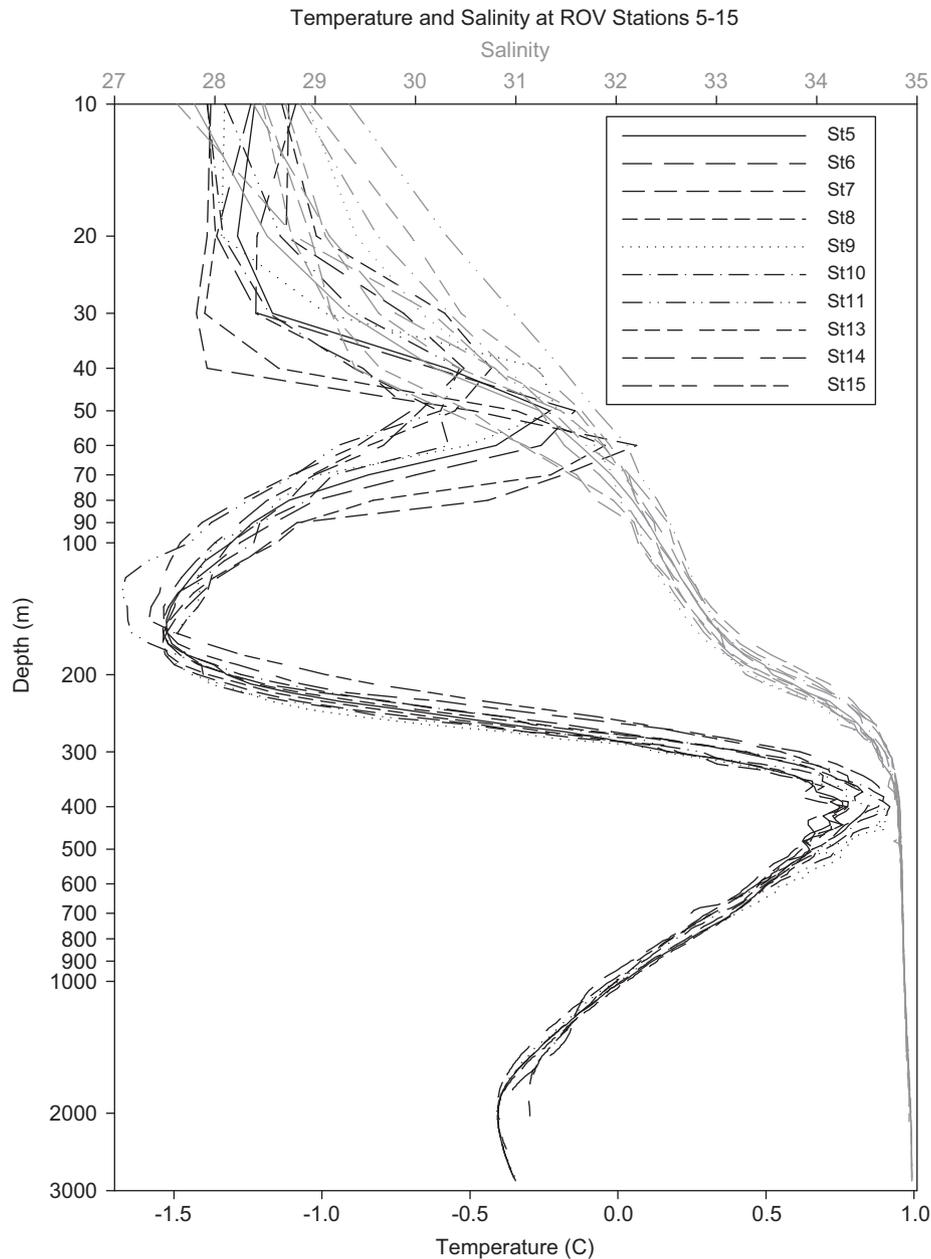


Fig. 3. Temperature and salinity plots of ROV stations 5–15 plotted on a log depth scale. Temperature in black, salinity in gray. Station information in Table 1. Station 3 data not was collected (see text).

for 10% of observations, ctenophores (mostly cydippids) for 5%, and numerous rarer taxa constituted the remaining 1% of observations. A total of 105 samples were collected by both the D samplers and the suction samplers comprising at least 31 different taxa. Laboratory-based macroscopic images of many of the gelatinous fauna discussed in this paper can be found at http://www.mpcfaculty.net/kevin_raskoff/arctic.htm.

The net samples collected 26 taxa of cnidarians, ctenophores, larvaceans and pteropods (see Fig. 4 for a partial list). The most commonly collected taxa in the net were pteropods and larvaceans, accounting for 59% and 37% of all individuals sampled. Of the cnidarian and ctenophore taxa, trachymedusae accounted for 56.6%, siphonophores for 38.2%, ctenophores for 2.2%, anthomedusae for 1.5%, narcomedusae for 1.3%, and scyphomedusae for 0.1% of the total sampled.

3.2.1. Cnidarians

Hydromedusae, specifically both the trachymedusae and narcomedusae, were the most common group of gelatinous fauna at virtually every station according to the ROV data. Two species accounted for the majority of all medusae observations, *Sminthea arctica* and a new species of narcomedusae, herein termed the “new narcomedusa”. Other species of hydromedusae observed include: *Botrynema ellinorae*, *Botrynema brucei*, *S. bitentaculata*, *Crossota norvegica*, *Ptychogena hyperborea*, *Benthocodon hyalinus*, *Aglantha digitale*, *Aeginopsis laurentii*, and *Crossota millsae*.

The most common gelatinous zooplankton found in the midwater depths of the Arctic Ocean was the trachymedusan *S. arctica*. *S. arctica* occurred at all stations over a wide depth range (Fig. 5). It had the highest abundance of any group studied, with over 468 individuals seen at station 9 alone. *S. arctica*'s vertical distribution extended from ~100 m to over 2100 m, with the bulk

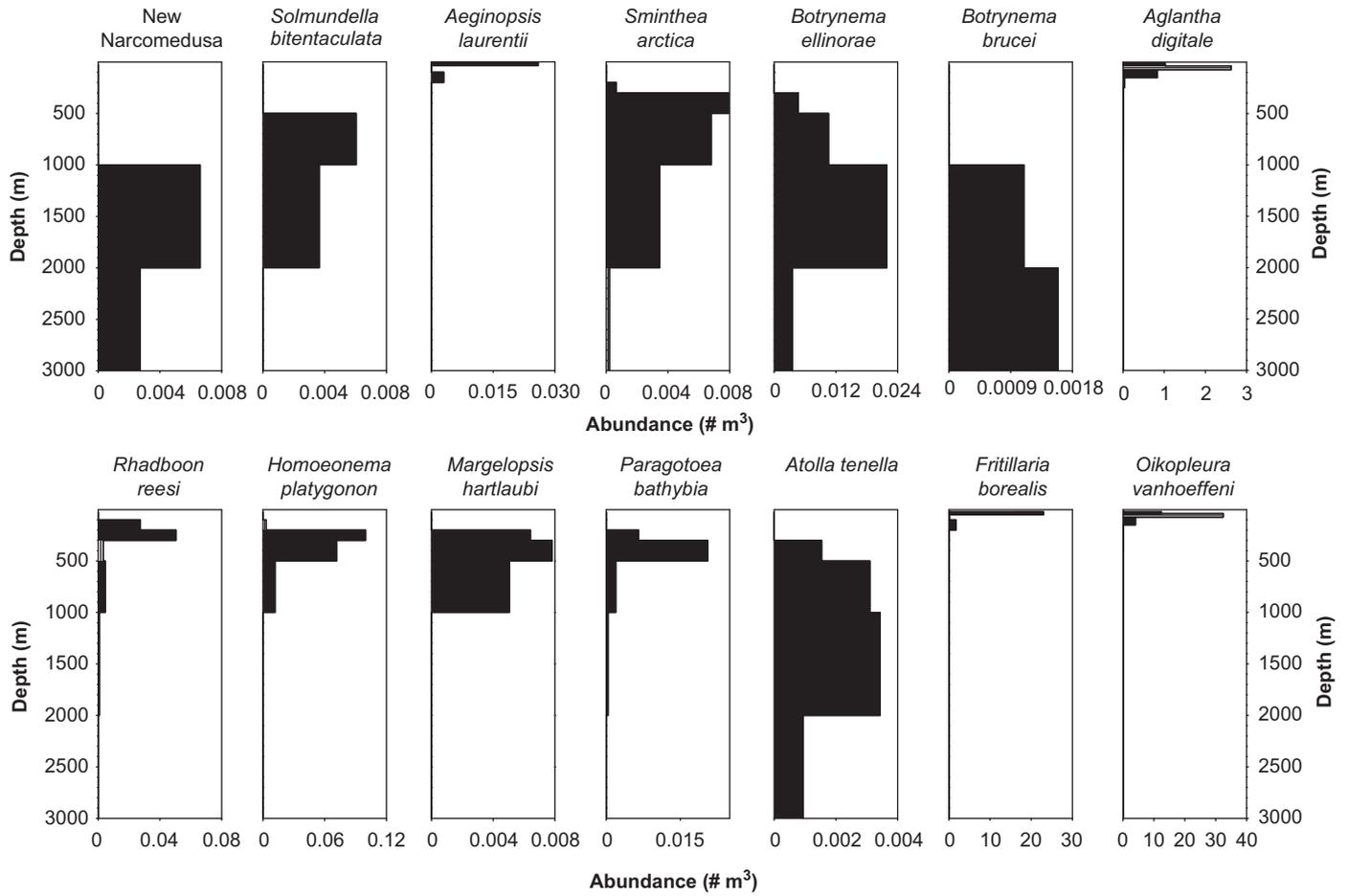


Fig. 4. Summary of abundance averages (ind/m³) of the multinet collections for 14 of the most important gelatinous taxa over the stations. Note the differing abundance axis scales in each plot. Depth strata are 0–25, 25–50, 50–100, 100–200, 200–300, 300–500, 500–1000, 1000–2000, and 2000–3000 m.

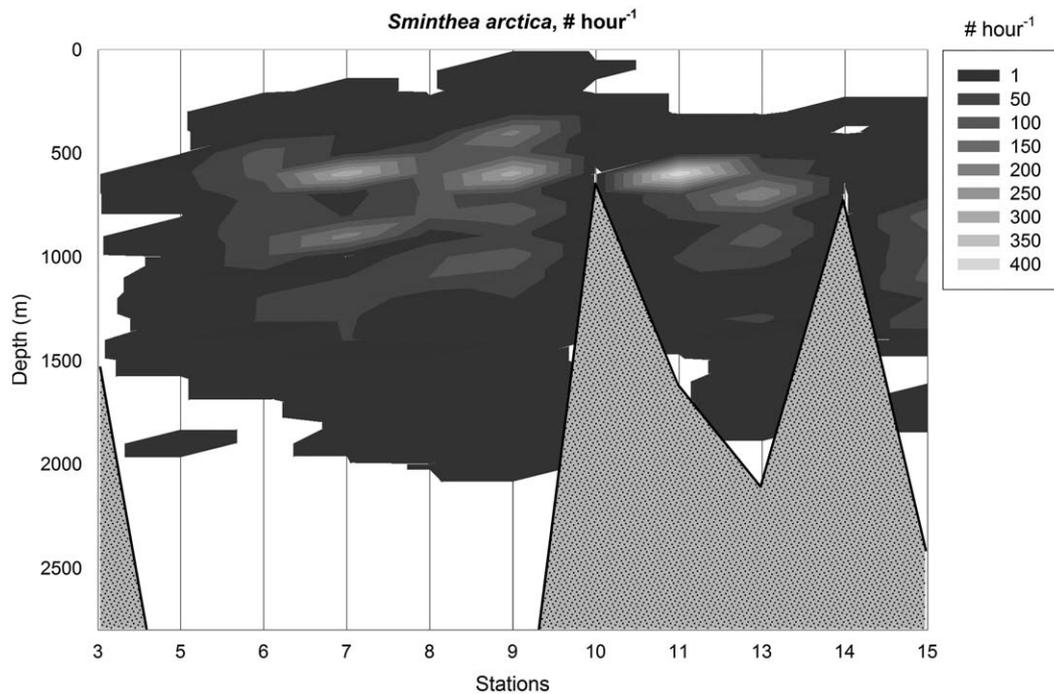


Fig. 5. Horizontal and vertical distribution of *Sminthea arctica* by depth and station. The plot shows the number of the individuals observed hour⁻¹ by ROV in 100 m depth bin intervals, from the surface to the maximum depth achieved for a particular station (see Table 1). The bottom depth, when within the ROV's depth range, is shown in gray. Note the differing abundance axis scales in Figs. 5–12.

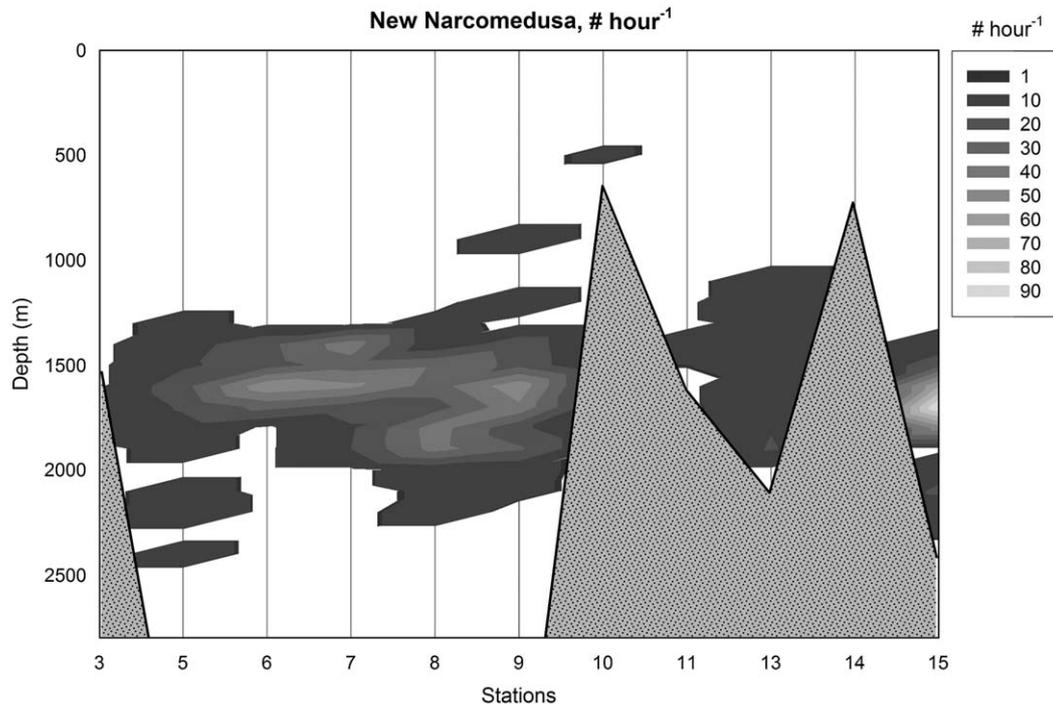


Fig. 6. Horizontal and vertical distribution of the New Narcomedusa by depth and station. Plot details as described in Fig. 5.

of the population found between 500 and 1000 m. *S. arctica* occurred infrequently at the three shallow stations (3, 10, and 14). The net data shows a similar vertical distribution of *S. arctica*, with the bulk of the population collected between 300 and ~2000 m (Fig. 4).

The second most common medusae was an undescribed species of narcomedusa (Fig. 2, G). This new species is superficially similar to *A. laurentii* because of the presence of four primary tentacles. *Aeginopsis laurentii* appears to be a shallower living species, inhabiting depths of less than 500 m in this study, determined from both ROV and net data. The distribution of the New Narcomedusa was generally restricted to waters deeper than 1300 m and it consistently occurred in a relatively narrow vertical range, from ~1400 to 2000 m (Fig. 6). The species was observed a single time at station 10 and not at all at station 14, which had bottom depths shallower than the species typical range. A single individual was found at station 3, where the bottom depth was 1530 m, and it was also present in low numbers at stations 11 and 13 over the Northwind basin, even though bottom depth was not as restrictive. The highest abundance was found at station 15, where 100 specimens were observed between 1500 and 1900 m. The superficially similar species *A. laurentii* was found at four stations from 172 to 464 m. It was only found over the Canada Basin [stn5: 195 m; stn 6: 339 m; stn 7: 464 m; stn 8: 172 m]. The net sampling of the New Narcomedusa was limited to 1000–3000 m while *A. laurentii* was sampled above 200 m (Fig. 4).

B. ellinorae and *B. brucei* were also common species. *B. ellinorae* was found from 400 to 1400 m (Fig. 7). *B. brucei* was found from 900 to 2600 m (Fig. 8). Although the two species have some vertical overlap, the bulk of the populations remain well segregated. The highest abundance for both species occurred at station 9, with 21 *B. ellinorae* and 46 *B. brucei* observed. Neither *B. ellinorae* nor *B. brucei* were found at station 3, the shallowest site, and they appeared in very low numbers over the shallow Northwind Ridge, at stations 10 and 14. Many *B. brucei* occurred on and just off of the bottom at stations 13 and 15. Only those individuals which could be positively identified to the species

level are included in the figures. The net sampling of both *B. ellinorae* and *B. brucei* agreed well with the ROV observations (Fig. 4). *B. ellinorae* was found below 300 m and largely above 2000 m. *B. brucei* was sampled exclusively below 1000 m, with the highest abundance between 2000 and ~3000 m.

S. bitentaculata was observed 28 times in total and at all stations except 6, 10, and 14. Several individuals were found at almost every station in the Canada Basin and over the Barrow Slope, with only a few seen in the shallower Chukchi Plateau. This species was noticeably absent over the Northwind Ridge. Depths of occurrence ranged from 519 to 2846 m. It was collected in the nets between 500 and ~2000 m, also in low numbers (Fig. 4). The deep red colored *C. norvegica* was observed at station 9 at 2605 m and collected at 1595 m at station 11 (Fig. 2, H). The collected specimen had 10 radial canals, as opposed to eight radial canals common to other species of *Crossota* (see http://www.mpcfaculty.net/kevin_raskoff/arctic05paper.htm for additional photos of this specimen). It was collected in the nets only between 1000 and ~2000 m. *C. millsae* was collected from station 11 on the bottom at 1614 m, and two were observed on-bottom at station 13 at 2093 m (Fig. 2, D). *P. hyperborea* was observed and collected once at station 6 at 980 m. A milky-white, translucent *B. hyalinus* was found ten times at station 10, on the bottom or within a few meters of bottom, at 620 and 630 m and once on bottom at station 13 at 2093 m (Fig. 2, J). These observations are the first records of this species from the Arctic. Mesoplanktonic sized gelatinous zooplankton (0.2–20 mm) were frequently observed, but were unable to be classified to absolute taxonomic groupings. An example of these are the so called “mystery balls”, which were among the top 25 taxa observed (Table 2). From several particularly good sections of video it is thought these were very small hydromedusae, with deployed, very fine tentacles, which gave the species a “fuzzy” appearance which would collapse to a small, unresolved mass when the tentacles were contracted towards the bell. Analysis of the net data point to several candidate species which co-occur in these same depth ranges, such as: *Rhabdoon reesi*, *Paragotoea bathybia*, *Margelopsis hartlaubi*,

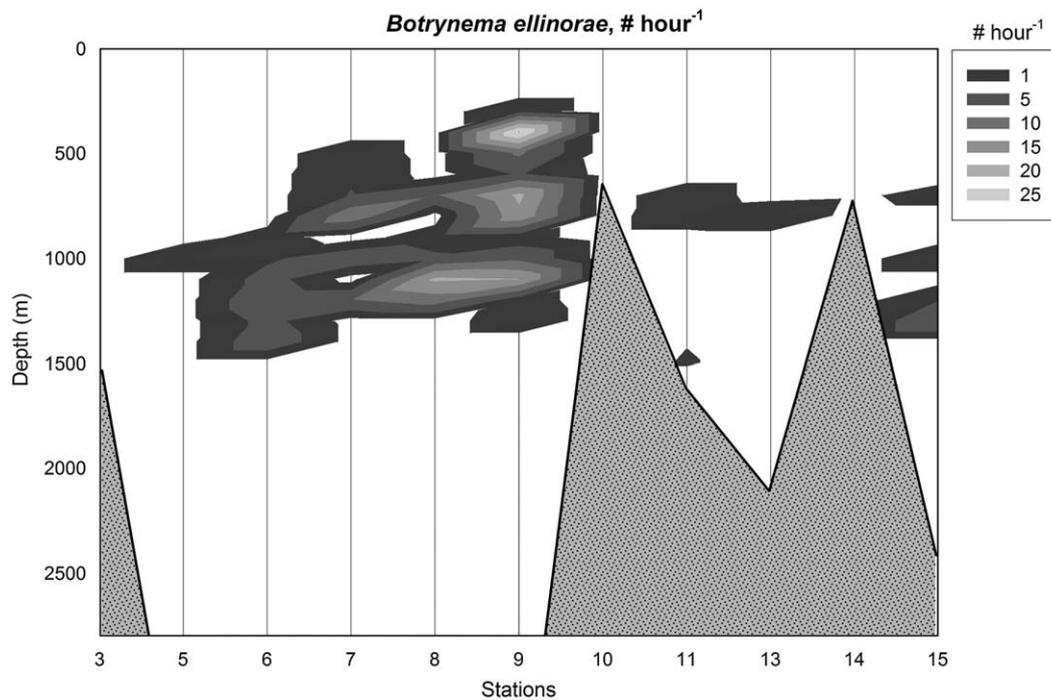


Fig. 7. Horizontal and vertical distribution of *Botrynema ellinorae* by depth and station. Only those individuals which could be positively identified as *B. ellinorae* are included. Many other generic observations of *Botrynema* were made but are not shown. Plot details as described in Fig. 5.

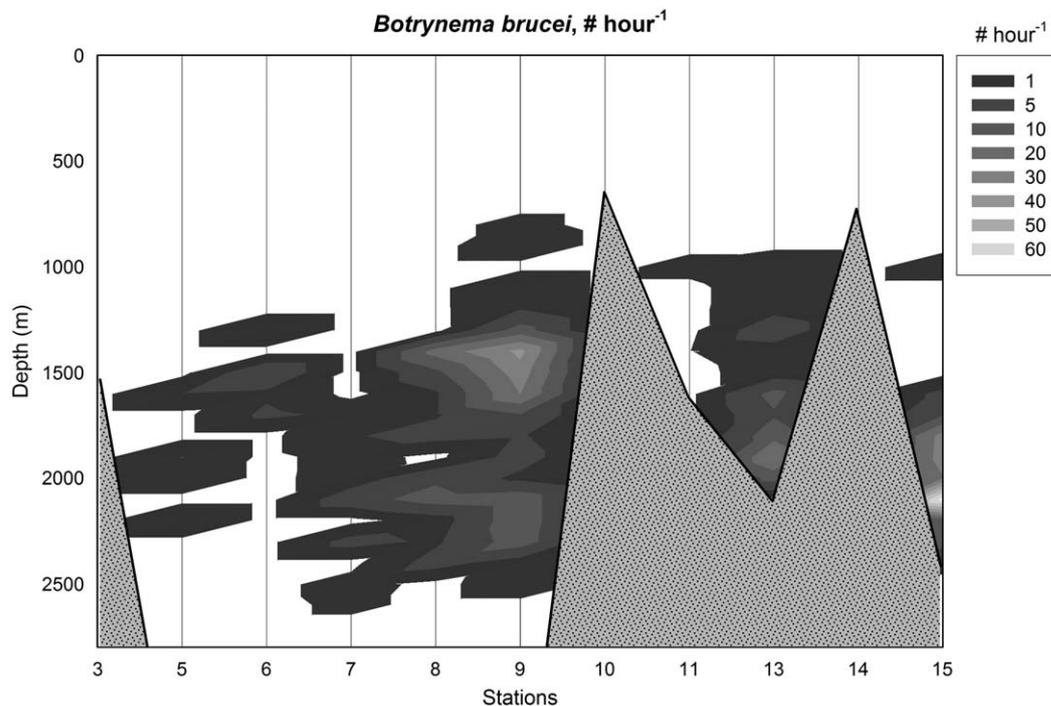


Fig. 8. Horizontal and vertical distribution of *Botrynema brucei* by depth and station. Only those individuals which could be positively identified as *B. brucei* are included. Many other generic observations of *Botrynema* were made but are not shown. Plot details as described in Fig. 5.

Homoeonema platygonon, and *A. digitale*, which were all quite small (Fig. 4). However, due to tentacle number, *H. platygonon* and very small *A. digitale* remain the most likely candidates.

Scyphozoan medusae commonly seen were *C. melanaster* and *Atolla* sp., with single sightings of *Nausithoe limpida* and *Cyanea* sp. *C. melanaster* was exclusively found in the surface waters between 10 and 80 m. Fifty one medusae were observed, with the highest abundance at stations 8, 9 and 13. Further analysis of *C. melanaster*

populations is reported elsewhere (Purcell et al., 2010). An *Atolla* sp. (presumed to be *A. tenella* based on available literature), a large coronate scyphomedusae, occurred in relatively high numbers at every station except at our shallowest stations 10 and 14 (Figs. 21 and 9). The vertical distribution of *Atolla* sp. was between 650 and 2200 m, with the majority of the population found in a relatively narrow band between 900 and 1200 m. The highest abundance appeared over the Canada Basin, at stations 6, 7, 8, and 9. In the

Table 2

Abundance of the 25 most common gelatinous taxa observed with ROV by station, with taxa composition of each station in percentage.

Taxa	Station												Total
	3	5	6	7	8	9	10	11	13	14	15	15b	
<i>Sminthea arctica</i>	38	32	386	258	239	468	19	313	245	17	213	132	2360
%	26.4	15.0	48.4	43.7	34.4	43.8	4.3	47.4	34.3	5.4	23.8	36.5	
Physonect siphonophores	47	57	116	75	84	136	241	157	94	171	112	41	1331
%	32.6	26.8	14.5	12.7	12.1	12.7	55.1	23.8	13.1	54.6	12.5	11.3	
Larvaceans	6	13	15	24	15	47	26	55	168	44	175	53	641
%	4.2	6.1	1.9	4.1	2.2	4.4	5.9	8.3	23.5	14.1	19.6	14.6	
Shrimps		2	70	56	110	64	59	42	74	5	82	37	601
%		0.9	8.8	9.5	15.8	6.0	13.5	6.4	10.3	1.6	9.2	10.2	
<i>Botrynema</i> spp.		11	27	38	60	157	1	16	33	3	76	10	432
%		5.2	3.4	6.4	8.6	14.7	0.2	2.4	4.6	1.0	8.5	2.8	
New narcomedusa	1	54	60	46	75	56	1	5	14		107	4	423
%	0.7	25.4	7.5	7.8	10.8	5.2	0.2	0.8	2.0		12.0	1.1	
<i>Atolla</i> sp.	2	18	33	25	31	42		19	20		22	29	241
%	1.4	8.5	4.1	4.2	4.5	3.9		2.9	2.8		2.5	8.0	
<i>Cydidippid</i> ctenophores	19	4	35	7	11	10	35	16	14	26	35	14	226
%	13.2	1.9	4.4	1.2	1.6	0.9	8.0	2.4	2.0	8.3	3.9	3.9	
Calycophoran siphonophore(s)	8	2	8	1	1		1	2	5	33	32	8	101
%	5.6	0.9	1.0	0.2	0.1		0.2	0.3	0.7	10.5	3.6	2.2	
Hydromedusae		9	14	12	15	17	11	1	6	1	6	1	93
%		4.2	1.8	2.0	2.2	1.6	2.5	0.2	0.8	0.3	0.7	0.3	
Mystery Balls			19	21	14	30	1	1	2			1	89
%			2.4	3.6	2.0	2.8	0.2	0.2	0.3			0.3	
Siphonophore eudoxids			5	3	10	9	24	19	13		5		88
%			0.6	0.5	1.4	0.8	5.5	2.9	1.8		0.6		
<i>Chrysaora melanaster</i>	4	3	1	7	10	10	2	2	10	1	1	12	63
%	2.8	1.4	0.1	1.2	1.4	0.9	0.5	0.3	1.4	0.3	0.1	3.3	
<i>Bolinopsis infundibulum</i>	10	1		4	1	5	9	1	4	8	6	10	59
%	6.9	0.5		0.7	0.1	0.5	2.1	0.2	0.6	2.6	0.7	2.8	
<i>Dinemertes</i> sp.		2	1	6	8	11			1		2		31
%		0.9	0.1	1.0	1.2	1.0			0.1		0.2		
<i>Mertensia ovum</i>	5				3			2	4	2	6	6	28
%	3.5				0.4			0.3	0.6	0.6	0.7	1.7	
<i>Solmundella bitentaculata</i>		3		1	5	2		2	1		11	2	27
%		1.4		0.2	0.7	0.2		0.3	0.1		1.2	0.6	
<i>Gonatus fabricii</i>	2			1	1	1	2	1		1			9
%	1.4			0.2	0.1	0.1	0.5	0.2		0.3			
<i>Beroe</i> sp.	2						4					2	8
%	1.4						0.9					0.6	
<i>Aeginopsis laurentii</i>		2	1	3	1								7
%		0.9	0.1	0.5	0.1								
Lobate ctenophores			2					2	3				7
%			0.3					0.3	0.4				
<i>Aulacoctena</i> sp.			3	1	1			1					6
%			0.4	0.2	0.1			0.2					
<i>Crossota millsae</i>						1	1	1	3				6
%						0.1	0.2	0.2	0.4				
<i>Nectopyramis</i> sp.			1	1		3		1					6
%			0.1	0.2		0.3		0.2					
<i>Cirroteuthis muelleri</i>			1					1	1		3		6
%			0.1					0.2	0.1		0.3		
Total	144	213	798	590	695	1069	437	660	715	312	894	362	6889

net collections, *Atolla* sp. were found over a wide depth range, between 300 and 3000 m, with the bulk of the population between 500 and 2000 m (Fig. 4). A single *Cyanea* sp. was noted at 49 m at station 14. A single *N. limpida* was collected at station 12 at 980 m.

The most conspicuous siphonophores were the physonect *Marrus orthocanna*, the calycophorans *Nectopyramis* and *Crystallophyes*, and several routinely unidentifiable smaller physonects, diphyid calycophorans and eudoxid stages, including primarily *Dimophyes arctica* and *Muggiaea bargmannae*. *M. orthocanna* and the other, smaller, physonects were common on all dives, second to only the trachymedusa *S. arctica* in numbers (Fig. 10). The bulk of the populations were found between 200 and 800 m in depth, with infrequent observations down to 2100 m at station 9. The

upper limit of these depth distributions marks the beginning of the Atlantic water mass and the populations spanned the Fram Strait Branch waters. The highest abundances were found over the shallow Northwind Ridge, at stations 10 and 14 from 300 to 500 m. Numerous siphonophores were collected at virtually all depths in the net tows. They were found from 25 to ~3000 m, and included several different species that have yet to be worked up by a specialist. The depth ranges with the highest values were between 100 and 500 m, which agrees closely with the ROV data.

3.2.2. Ctenophores

The cydidippid *M. ovum* and the lobate *B. infundibulum* were both very common in the surface mixed layer (surface to ~50 m).

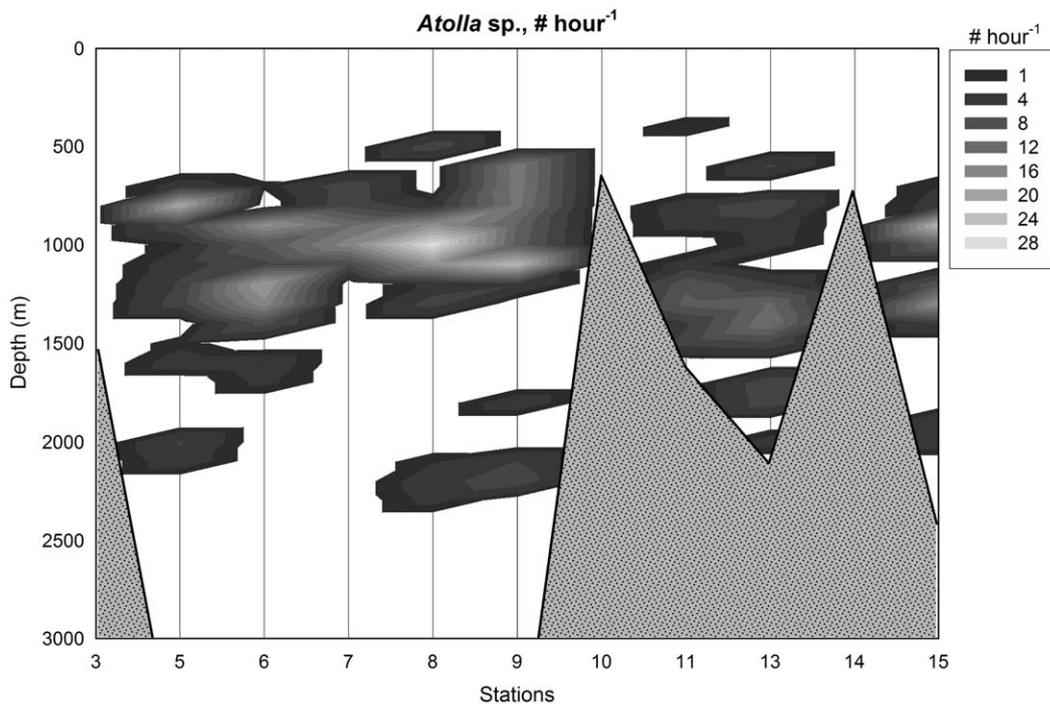


Fig. 9. Horizontal and vertical distribution of *Atolla* sp. by depth and station. Plot details as described in Fig. 5.

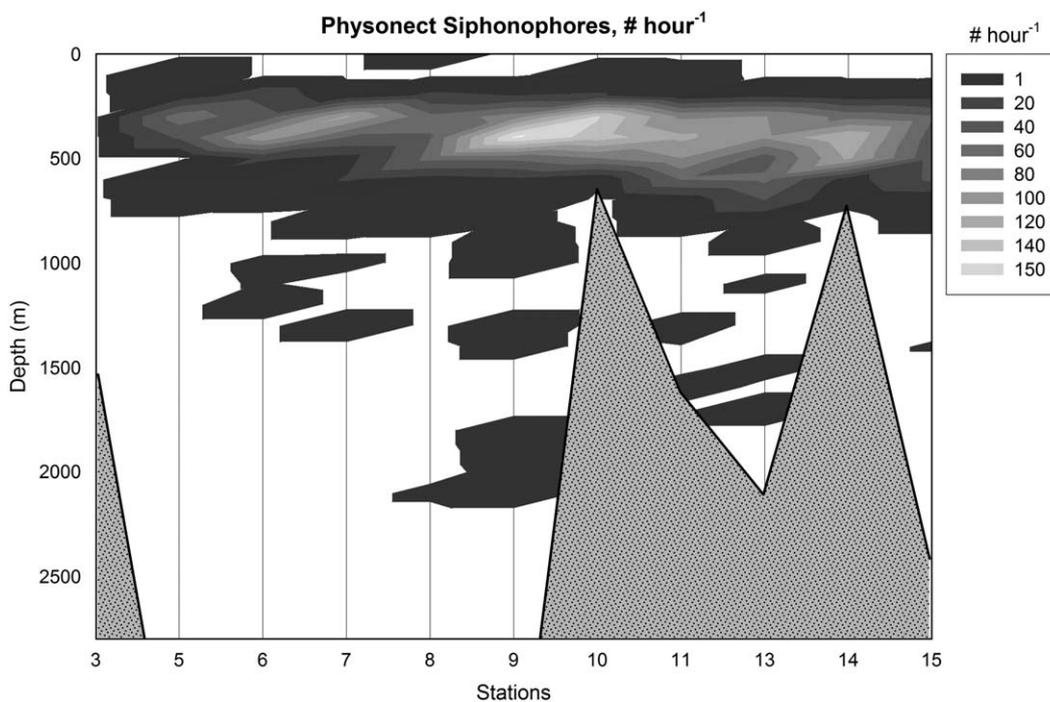


Fig. 10. Horizontal and vertical distribution of the physonect siphonophores by depth and station. Plot details as described in Fig. 5.

A *Beroe* sp. (presumed to be *B. cucumis* from previous Arctic literature) and the cydippid *Dryodora glandiformis* were observed several times by the ROV and were also collected by divers in the surface waters. *Beroe* sp. and *M. ovum* were collected in the net tows only in the surface water strata, between 0 and 25 m. The surface water ctenophores are addressed in more detail in other reports (Purcell et al., 2010). Deep-water lobate and cydippid ctenophores were numerous (Fig. 11). An unidentified cydippid was the most frequently observed ctenophore between 240 and

420 m, with the highest abundance found at stations 6, 10, 14, and 15. Additional unidentified cydippid ctenophores were also collected in the net tows at a variety of depths between 0 and 1000 m. An undescribed red-lipped cydippid, likely a Bathyctenid (see Bathyctenid sp. A in Lindsay and Hunt, 2005) was a common deep-water species between 1300 and 2400 m (Fig. 2, A). Lobate taxa resembling *Bolinopsis* were observed several times, but their transparency made identification difficult and none were able to be collected. A large (15 cm+ long), bright orange *Aulacoctena* sp.

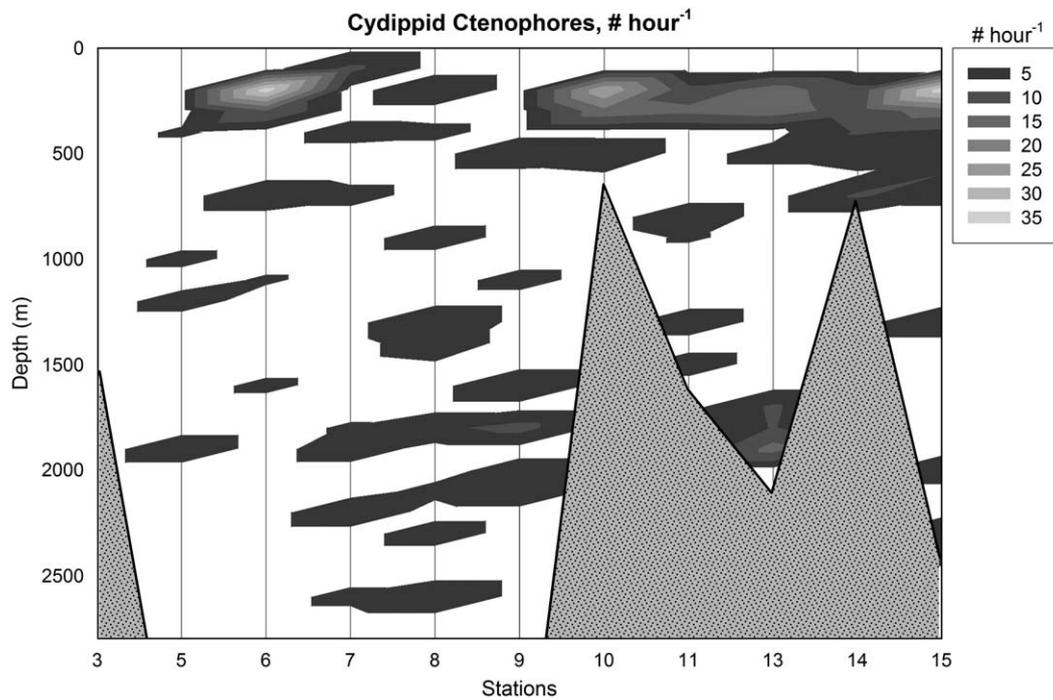


Fig. 11. Horizontal and vertical distribution of the cydippid ctenophores by depth and station. Plot details as described in Fig. 5.

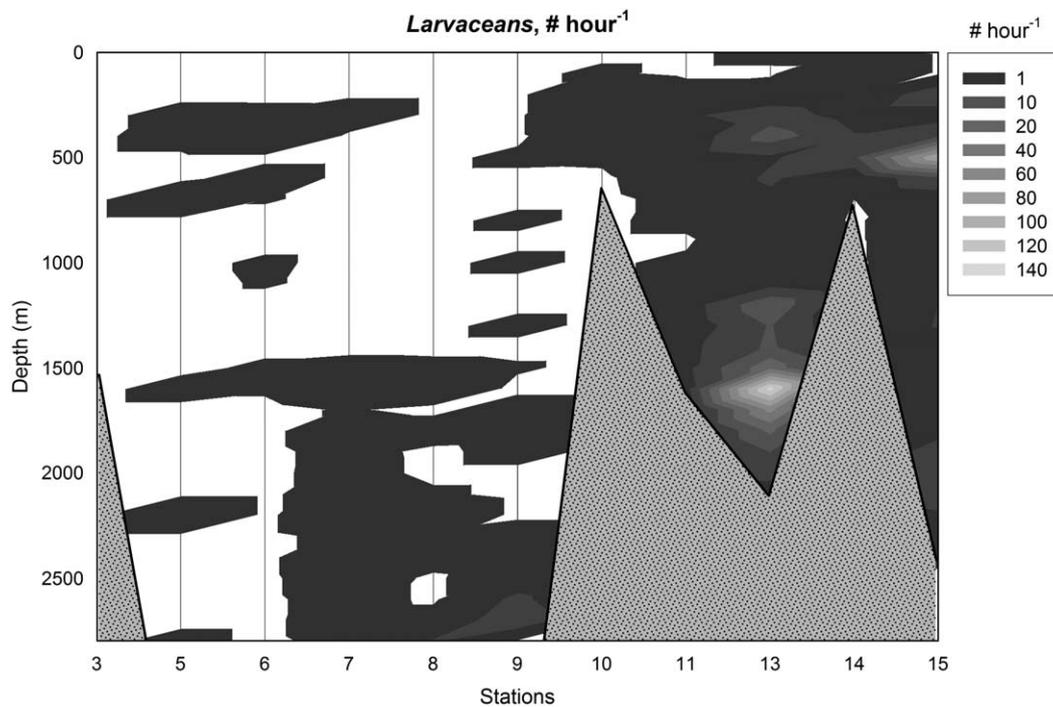


Fig. 12. Horizontal and vertical distribution of the larvaceans by depth and station. Plot details as described in Fig. 5.

was observed on six occasions, at stations 6, 7, 8, and 11 (Fig. 2, C). Several other undescribed species of cydippid ctenophores were observed: a small, white species with oral “horns” or keeled species with long comb plates and remarkably fine and dense secondary tentilla, which gave the tentacles a “furry” appearance (Fig. 2, E and F); a very small (<1 cm) cydippid which had tiny, ball-like coiled secondary tentilla on the tentacles; an undescribed epibenthic species was observed 13 times on or

attached to the bottom at stations 10 and 14 on the Northwind Ridge (630 m; 707 m) (Fig. 2, B).

3.2.3. Larvaceans

The pelagic tunicates were represented by several species of larvaceans (Fig. 12). The surface waters, above 50 m, were populated by *Oikopleura vanhoffeni* especially at station 15 where

a bloom occurred near the ice-edge with numbers too large to count with the ROV (not shown in Fig. 12; estimates of density $\sim 20/\text{m}^3$). Large numbers of this species were also sampled by the net system (Fig. 4). The highest abundance was found in the top 100 m (up to $32 \text{ ind}/\text{m}^3$), with substantially fewer found persistently down to the deepest strata at 2000–3000 m. Other species of larvaceans were common in the deeper waters, with an undescribed species of *Oikopleura* most common below 1000 m, as well as a lesser abundant undescribed large species of *Fritillaria*. The net collections also sampled *Fritillaria borealis* in large numbers (up to $23 \text{ ind}/\text{m}^3$) from 0 to 50 m, with lower numbers found deeper to 2000–3000 m (Fig. 4). Larvaceans were consistently numerous in benthic boundary regimes as well, especially at station 13, which had over 140 h^{-1} observed.

3.2.4. Other taxa

The nemertean *Dinonemertes* sp. was common at seven stations from 835 to 2777 m. Six of the naked gymnosome pteropods *Clione limacina* were noted at four stations from 69 to 348 m. *C. limacina* were collected in large numbers in the net tows from 0 to 50 m and infrequently down to 200–300 m. The thecosome *Limacina helicina* was found from the surface—2000 m, with the bulk of the abundance from the surface—500 m. Nine of the Armhook Squid, *Gonatus fabricii*, were found at seven stations from 303 to 1792 m. Six of the finned octopod, *Cirroteuthis muelleri*, were found at four stations, from 969 to 2404 m. Chaetognaths, shrimp, polychaetes, and amphipods were often very common and too abundant to count *in situ* and are not reported herein (see Kosobokova and Hopcroft, 2010 for additional net data).

4. Discussion

4.1. Water mass and vertical distributions

As was found in our previous pelagic ROV dives in the region, there was a complex layering of water masses and transition zones at all stations (Fig. 3) (Raskoff et al., 2005). The mixed layer was found from the surface down to 20–40 m and is characterized by nearly constant temperature and slowly increasing salinity. The largest species of gelatinous zooplankton, such as the medusae *C. melanaster* and *C. capillata*, and the ctenophores *M. ovum*, *B. infundibulum*, *Beroe* sp., and *D. glandiformis* occurred in this mixed layer, as did several species that were sampled with the net system, such as *A. digitale*, *A. laurentii*, *L. helicina*, *C. limacina*, *F. borealis*, and *O. vanhoeffeni* (Fig. 4). Kosobokova and Hirche (2000) found similar depth distributions for *C. limacina*, *F. borealis*, and *O. vanhoeffeni* in the mixed layer and *C. melanaster*, *C. capillata*, *A. digitale*, *M. ovum*, *B. infundibulum*, and *B. sp.* were observed in the Canada Basin in the mixed layer by Raskoff et al. (2005). Shirley and Leung (1970) used opening-closing nets to study the vertical distribution of the gelatinous fauna of the Central Arctic and collected several species in the mixed layer, including: *A. laurentii*, *M. ovum*, *Beroe* sp., *A. digitale*, and *H. platygonon*. Many other studies have examined the surface waters of various regions of the Arctic Ocean and collected a fair number of these same gelatinous taxa (Bigelow, 1920; MacGinitie, 1955; Johnson, 1956; Hand and Kan, 1961; Grainger, 1965, 1975; Uchida, 1969; Kosobokova et al., 1998; Jinbiao and Mao, 2000; Søreide et al., 2003), however, most of these studies were limited to integrated vertical tows through the top several 100 m, so there is very low resolution concerning the vertical distributions of any of these taxa. This mixed-layer depth zone is difficult to sample in the daylight with the ROV due to the bright down-welling light and bright background. In order to be observed, the shallow water

species had to be either large and opaque (such as *C. melanaster* and *C. capillata*), or caught illuminated in Snell's window against a slightly darker background. In any case, the examination of zooplankton in the mixed layer is difficult and any observations must be viewed in very rough terms and will necessarily represent a significant undercount of the true values. The major objective of the dives was to determine patterns of vertical distribution and to collect unknown species in the deep waters. For finer-scale examination of distribution and abundance in the mixed layer, the use of divers and specially designed nets will be of great importance in assessing accurate numbers and community composition of the shallow water plankton.

Below the surface mixed zone the Pacific waters show a rise and then drop in temperature to a minimum at 140–170 m (from ~ 0.0 to -1.5 °C). Few animals were observed in these Pacific waters, with the exceptions of *C. melanaster* and a few *C. limacina*, however the lighting is still not optimal in this region due to down-welling light. The net data show a similar pattern, with few species found in the Pacific water layer, with the exception of *A. digitale*, *F. borealis*, and *O. vanhoeffeni* (Fig. 4). The transition between the populated mixed layer (surface to ~ 40 m) and the Pacific water layer corresponded with an abrupt, pronounced decrease in gelatinous zooplankton of all types. Across all stations, only 3.4% of all observations occurred above 170 m and most of these were from the mixed layer.

Below the Pacific water, at ~ 140 –170 m is the beginning of the Atlantic water, which is characterized by slowly rising temperature and salinity to a depth of 400 m (from -1.5 to ~ 0.75 °C and ~ 32.75 to 34.75). Atlantic waters were teeming with gelatinous zooplankton compared to the depauperate Pacific waters. Transition to the Atlantic water mass showed a rapid increase in zooplankton, especially cydippid ctenophores, physonect and calycophoran siphonophores, and larvaceans. These species tended to be small, highly transparent, and difficult to observe and collect. The net data show a marked increase in the abundance of several groups, including the small medusae *H. platygonon*, *M. hartlaubi*, *P. bathybia*, *R. reesi*, and *S. arctica*, the pteropod *L. helicina*, and the larvacean *F. borealis* (Fig. 4). Shirley and Leung (1970) found many of the same depth patterns in the Central Arctic, with *A. digitale*, *H. platygonon*, *S. bitentaculata*, several siphonophores, *B. ellinorae*, and *S. arctica* prominent in the Atlantic Waters. Kosobokova and Hirche (2000) found a similar pattern over the Lomonosov Ridge with some of the small medusae, such as *H. platygonon*, *S. arctica*, and *A. laurentii*, and the larvaceans *F. borealis*, and *O. vanhoeffeni*. *S. arctica*, siphonophores, and other gelatinous groups were reported in the Atlantic Waters of the Canada Basin by Raskoff et al. (2005), and *A. laurentii* and *H. platygonon* were recorded at these depths from the Laptev Sea (Sirenko et al., 1996).

The temperature maximum found at 400 m indicates the Fram Straight Branch waters. Below this depth the salinity remains high and stable while the temperature decreases (to ~ -0.5) to a depth of 2000 m. It is in this water layer that the bulk of the gelatinous zooplankton occurred. 86.7% of all observations in this study were made in the Atlantic and Fram Straight Branch waters. Interestingly, the net data show the opposite pattern of abundance at these depths. With $\sim 750 \text{ m}^3$ of water sampled from the surface down to 3000 m using the listed methods, the nets recorded only $\sim 0.2\%$ of all gelatinous plankton abundance at these depths. Even if only the non-pteropod and larvacean groups are considered, only $\sim 6\%$ of the overall abundance occurred in these layers. Shirley and Leung (1970) recorded *A. digitale*, *S. bitentaculata*, *B. brucei*, *B. ellinorae*, *S. arctica*, and *Atolla tenella* between 400 and 1500 m. These previous species, as well as *H. platygonon* and a narcomedusa (recorded as *A. laurentii* but which may have been the New Narcomedusa), were previously known from these

depths (Kosobokova and Hirche, 2000). Raskoff et al. (2005) also recorded *S. arctica*, *A. tenella*, various siphonophores, and ctenophores from these depths. At a depth of ~2000 m, the Fram Straight Branch waters transition to the slightly warmer Arctic deep basin bottom waters, which have very long ventilation times and little mixing with other water layers (McLaughlin et al., 2005). Although this water mass contained rare and undescribed deep-water species, only 9.9% of observations were made below 2000 m. The nets recorded only ~1% of abundance from these deepest of waters. The rarely documented groups of animals found in deep basin waters include: larvaceans, the finned pelagic octopod, *C. muelleri*, nemertean worms, cydippid and lobate ctenophores, the hydromedusae *B. brucei*, *S. bitentaculata*, and *C. norvegica*, and the scyphomedusa *Atolla tenella*. *B. brucei* and *B. ellinorae* were previously reported from the Laptev Sea at these extreme depths (Sirenko et al., 1996).

The complex and layered water masses of the Arctic Ocean are possible boundaries for biodiversity and development. Hydrographic structure may restrict the vertical distributions of various species to particular depth intervals and water masses. A species' tolerance to the physical and biological environment (temperature, salinity, dissolved oxygen, pressure, food, competition, predation), which continually changes with depth from the surface to the bottom, could be of importance to the success of that species in the various water masses and depths of the Arctic Ocean, however further factor analysis would be needed to definitively address this. Søreide et al. (2003) found that the water mass was the most important predictor for macrozooplankton variability in the Barents Sea, followed by the geographic position, season, and bottom depth. Individual species tolerances and responses to these and many other important physical and biological factors need to be investigated to provide a more complete view of the factors which lead to the strong vertical zonation observed throughout the water column.

4.2. Bottom topography

Relationships between the bottom topography and taxa found at each station need further study. Some species, such as *S. arctica*, were found in approximately the same numbers in the Canada Basin and in the Chukchi Plateau (Fig. 5). Other species, such as the "New Narcomedusa" (Fig. 6) and *B. ellinorae* and *B. brucei* (Figs. 7 and 8) appeared in much reduced numbers in the Chukchi Plateau compared with the Canada Basin, even though the water depth and other measured physical factors were quite similar. Still other species (several physonect siphonophores and cydippid ctenophores) appeared to occur in high numbers in the shallower waters over the Northwind Ridge (Figs. 8 and 9). In the case of the siphonophores, even though the species were found at virtually all stations, abundance over the ridge was an order of magnitude higher than over the basins. The factors underlying these relationships are unclear, but previous studies have found high nitrates in this general area (McLaughlin et al., 2005) and future investigations into the current regimes of the area, rates of primary production, and transport of production down into the mesopelagic depths are needed.

4.3. ROV/net comparison

Several groups that were very common from the ROV observations were not well represented in the net collections, and the converse was true that some of the most numerous species collected in the nets were rarely observed with the ROV. This is only to be expected as the multinet sampled the more common species, including, importantly, many of the smaller

jellies generally invisible to the ROV, such as *A. digitale*, *H. platygonon*, *M. hartlaubi*, *P. bathybia*, *R. reesi*, the smaller pteropods, such as *L. helicina*, and the larvaceans, *F. borealis* and *O. vanhoffeni*, which are all often only a few mm in size. However, the net system under sampled many of the rarer, and/or larger species, such as the very common New Narcomedusa, *S. arctica*, *Botrynuma* spp., *Atolla* sp., *C. melanaster*, and the larger lobate ctenophores and siphonophores. The difference in the sampling volume between the two methods is pronounced. The net system has an opening of 0.25 m², whereas the video field of view is based on the combination of the angle of view of the camera, the lighting, and the distance away from the camera at which the organism can be observed and identified. Even for small, difficult to observe taxa, it is estimated that this field of view is 10 times to 100 times larger than the net mouth area. Therefore it appears the two survey methods are a good compliment to each other as they each have their own bias. When used together they paint a more complete picture of the community as a whole.

4.4. Biological patterns across stations

There was great variation in the numbers of total animals and within groups between all the stations (Fig. 13). The lowest total abundance of gelatinous zooplankton was found at stations 3, 5, 10, and 14. Station 3 on the Barrow Slope was relatively shallow (1530 m) and also our first station, so real-time *in situ* annotation was likely less proficient. Stations 10 and 14 over the Northwind Ridge were the two shallowest stations (635 and 715 m). Because much less water was surveyed (due to the shallow depths) than at the other stations, the total dive and annotation time was reduced (Table 1). However, with all of this factored out (Fig. 13 data normalized for dive duration), it does appear that the shallow slope and ridge areas around the Canada Basin and Chukchi Plateau harbor lower gelatinous zooplankton biomass and numbers than at the deeper stations. An apparent anomaly in this pattern is station 5, which although quite deep (3853 m) and well removed from the slope or ridge, shows low total counts of organisms, however, due to ROV and camera malfunction on this dive, there were significantly fewer observations, and video

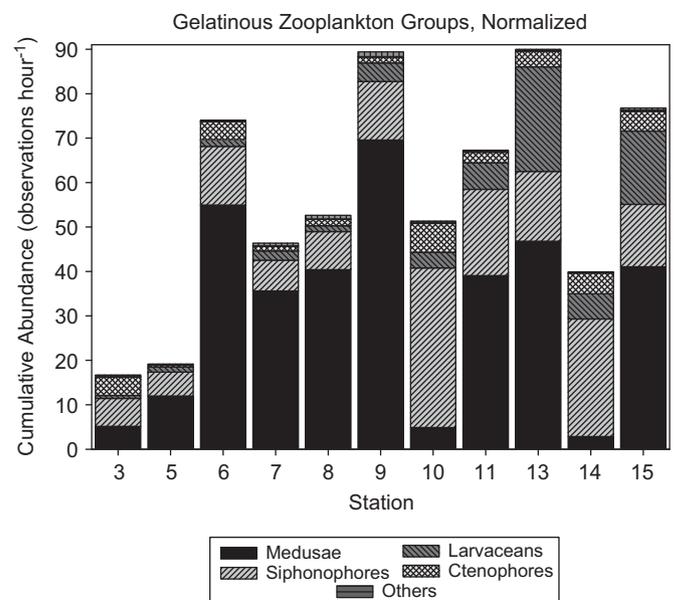


Fig. 13. Cumulative abundance of the five major gelatinous zooplankton groups by station. Each group calculated as the number of observations hour⁻¹ at each station.

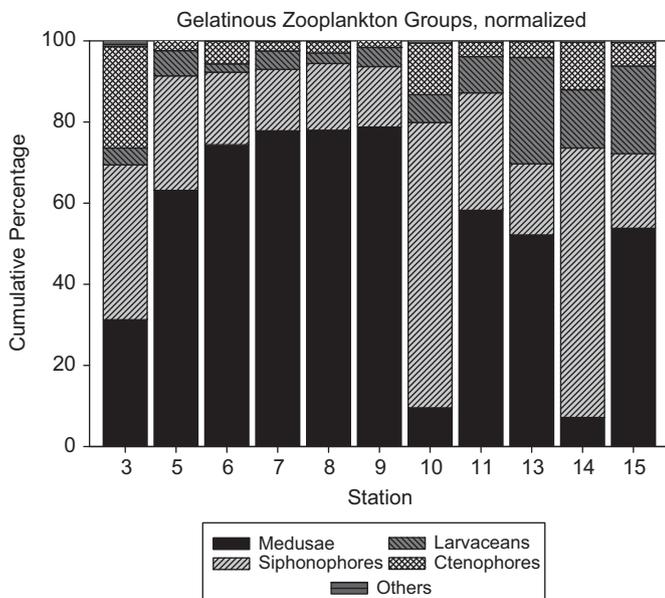


Fig. 14. Cumulative percentage of the five major gelatinous groups by station.

quality was reduced. These problems made the data from station 5 incomplete.

An examination of the cumulative percentage of all taxa at each station (Fig. 14) revealed that the relative importance or representation of the major taxa shows many interesting patterns across the stations. The highest abundance of total organisms was found at station 9, at the edge of the Canada Basin and Northwind Ridge. Shallow stations 3, 10, and 14 show not only a lower number of individuals, but also a different relative abundance of the major taxa (Figs. 13 and 14). The shallow water stations were dominated by large numbers of siphonophores and ctenophores. The deep stations were dominated by medusae. This contrast is most evident between Station 9 and 10, where there is a transition from the Canada Basin onto the Northwind Ridge. Fewer medusae were observed over the shallow ridge and the numbers of siphonophores and ctenophores were much higher.

The somewhat surprising variation observed between similar stations (with regard to physical properties, location, and bottom depth) raises many questions regarding the spatial and/or temporal variation of species distributions. Many species and higher taxa showed large variations in abundance and vertical distributions from one station to another, a result which has been noted by other researchers (Lindsey and Hunt, 2005; Raskoff et al., 2005). Are these differences due to inherent (and unmeasured) differences in stations, or do they point to the stochastic and variable nature of these poorly studied systems? Single sampling events at each station do not allow us to do more than speculate on the longevity or reproducibility of the observed distributions of taxa at a particular station.

4.5. Biological notes

Our observation with the ROV endeavored to be quantitative and focused on the large-scale vertical and horizontal patterns of the regions of study. However, over the course of the cruise several noteworthy taxonomic and qualitative biological observations were recorded. In our investigations, some previous taxonomic uncertainties were identified. The trachymedusae *B. hyalinus* is here reported for the first time from the Arctic Ocean (Fig. 2, J). In the past, *B. hyalinus* may have been confused

with *Ptychogastris polaris*, which has been widely reported from the Arctic, or with other trachymedusae, such as *Crossota* (see Raskoff et al., 2005). When viewed from the water column by ROV, camera sled, etc., *P. polaris* and *B. hyalinus* can look almost identical, but are quite distinct when viewed closely due to several important characteristics found in *B. hyalinus*, including the lack of any centripetal canals, quite different gonad shape and placement (partially pendant at the distal end), a pronounced gastric peduncle between the manubrium and the stomach, and tentacles lacking adhesive disks (Larson and Harbison, 1990). All of these characters require careful and close examination that is usually not possible from the ROV, even with HDTV quality, and requires careful collection and subsequent examination in the laboratory. *B. hyalinus* was described from Antarctica waters in McMurdo sound in shallow waters at -1.5°C , and was hypothesized to also occur in deeper waters, as many other normally deep-water medusae are found in the shallow Antarctic waters due to the lack of a significant thermocline (Larson and Harbison, 1990), which is in sharp contrast to the physical clines observed in the Arctic ocean. The only other records of *B. hyalinus* are from deep waters in Monterey Bay and a possible sighting in St. Croix, U.S. Virgin Islands (Larson et al., 1992; Raskoff, unpublished data). Since almost all previous records of benthic trachymedusae in the Arctic are reported to be *P. polaris* (i.e. Stübing and Piepenburg 1998; Panteleeva et al., 1999; Sirenko, 2001), extreme care should be taken by researchers to not assume the taxonomy of benthic medusae without adequate specimen sampling and examination of appropriate characters. During our cruise, further time on the bottom examining station 10 by the benthic research group recorded an additional 20 medusae, which we believe were likely *B. hyalinus* based on our previous specimen and video observations.

Another surprising finding was the large number of the mesopelagic, coronate scyphomedusa *Atolla* sp. (presumed to be *A. tenella*; Fig. 2, I), which was found in high numbers at all stations, except for the two shallow stations over the Northwind Ridge (Fig. 9). The numbers observed of *Atolla* in the Arctic were very high compared to the number of *Atolla* spp. in other mesopelagic regions world-wide, such as Japan (Hunt and Lindsay, 1999; Lindsey et al., 2004), Monterey, CA (Widder et al., 1989; Raskoff unpublished data), and Antarctic regions (Pagès et al., 1996). Shirley and Leung (1970) observed *A. tenella* at similar depths as in this current study.

The cydippid ctenophore, *Aulacoctena* sp., is one of the most spectacular species of this phylum (Fig. 2, C). It is quite large (15 cm+ in length) and its thick unbranched tentacles show amazing adhesion underwater to all manner of materials, both human-made and biological. Much about their ecology remains unknown, including details on their diet, or the source of their conspicuous orange coloration. Several researchers have observed this genus, at many locations, and the number species world-wide still seems up for some debate (Lindsey, 2005; Haddock, 2007; Lindsey and Miyake, 2007; see http://www.mpcfaculty.net/kevin_raskoff/arctic.htm for photos). One of the specimens collected of *Aulacoctena* sp. in this study ejected its gastric contents in the sampling container. Microscopic analysis of this material showed the presence of a nemertean stylet, along with copious orange digested tissue. The orange nemertean worm *Dinonemertes* sp. (Jon Norenburg, personal communication) was a frequent member of the mesopelagic and was found to co-occur with *Aulacoctena*. The conspicuously similar orange coloration of both *Aulacoctena* and *Dinonemertes* are striking and, combined with the gut content data, strongly suggest that *Aulacoctena* preys on nemerteans, at least in the Arctic. The strong swimming ability of *Dinonemertes* may also help explain the adaptation of the incredibly strong and sticky tentacles of *Aulacoctena*.

Another interesting ctenophore observed was *D. glandiformis*. This species has a well described and specialized diet of larvaceans, which the ctenophore captures in a specialized “vestibule” outside its mouth (Haddock, 2007). *Dryodora* was found at 30–50 m depth, co-occurring with the larvacean *O. vanhoeffeni* at several stations, most notably station 15, which had a very dense bloom of larvaceans.

An undescribed species of epibenthic ctenophore was observed 13 times on or attached to the bottom at stations 10 and 14, along the Northwind Ridge (Fig. 2, B). This epibenthic species was attached with one or both tentacles (filaments?) to the bottom substrate with its mouth facing into the current. The species has many unusual characteristics, including the eight ctenes rows which are fused into four pairs of two rows which run down the length of the body. This species reportedly resembles a species found on seamounts in the deep-water off California (Haddock, personal communication), and it also resembles a species found in Japan (Lindsey and Miyake, 2007), however separate filaments were never detected in any of the *in situ* observations, only the two primary tentacles, nor were filaments seen when observing the many collected specimens. The opacity of the tissue could have precluded detection of secondary filaments, but with lengthy video observation *in situ*, and close-up observation of the many collected specimens, it seems unlikely they would have been missed.

The gelatinous zooplankton community of the Arctic Ocean is quite diverse and represented by a number of new and poorly studied species. The data collected in this study, although much more detailed than anything previously done, are still very coarse, with large geographic distances between neighboring stations. Consequently, large scale, or overly generalized patterns of taxonomic distribution are also necessarily rough. However, many patterns emerge that show the region to have great heterogeneity in the distribution of species with respect to water depth, geographic area, and physicochemical properties of the water. Much is yet to be understood about the natural history and ecology of the gelatinous species reported herein. Piecing together the ecological interactions of these deep-sea species will require a concerted effort towards the study of the reproductive, trophic, and behavioral biology of these fragile, and difficult to study taxa. Their large numbers, diversity, and biomass show them to be a critical link in the Arctic ecosystem, yet their responses to a changing climate and changing ocean conditions are mostly unknown. As increased attention is turned towards the poles in our study of climate change and its direct and indirect effects on sea ice, the ecological fate of the pelagic deep ocean may largely rest on these gelatinous organisms.

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References

- Bigelow, H.B., 1920. In: Medusae and Ctenophores from the Canadian Arctic Expedition, 1913–1918. Part H. Medusae and Ctenophora. Report of the Canadian Arctic Expedition VIII: Mollusks, Echinoderms, Coelenterates, etc. Kings Printer, Ottawa, pp. 3–19.
- Björk, G., Jakobsson, M., Rudels, B., Swift, J.H., Anderson, L., Darby, D.A., Backman, J., Coakley, B., Winsor, P., Polyak, L., Edwards, M., 2007. Bathymetry and deep-water exchange across the central Lomonosov Ridge at 88°–89°N. *Deep-Sea Research Part I* 54, 1197–1208.
- Brodeur, R.D., Mills, C.E., Overland, J.E., Walters, G.E., Schumacher, J.D., 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fisheries Oceanography* 8, 296–306.
- Deibel, D., Daly, K.L., 2007. Zooplankton processes in Arctic and Antarctic polynyas. In: Smith, W.O., Barber, D.G. (Eds.), *Arctic and Antarctic Polynyas*. Elsevier, Amsterdam, pp. 44.
- Gage, J.D., Tyler, P.A., 1991. In: *Deep-sea Biology: a Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, Cambridge.
- Grainger, E.H., 1965. Zooplankton from the Arctic Ocean and adjacent Canadian waters. *Journal of Fisheries Resources of Canada* 22, 543–564.
- Grainger, E.H., 1975. Biological productivity of the southern Beaufort Sea: the physical-chemical environment and the plankton. *Beaufort Sea Technical Report*, Victoria, p. 82.
- Haddock, S.H.D., 2007. Comparative feeding behavior of planktonic ctenophores. *Integrative and Comparative Biology* 47, 847–853.
- Hand, C., Kan, L.B., 1961. The medusae of the Chukchi and Beaufort Seas of the Arctic Ocean including the description of a new species of *Eucodinium* (hydrozoa: anthomedusae). *Arctic Institute of North America*.
- Hopcroft, R.R., Clarke, C., Nelson, R.J., Raskoff, K.A., 2005. Zooplankton Communities of the Arctic's Canada Basin: the contribution by smaller taxa. *Polar Biology* 28, 197–206.
- Hunt, J.C., Lindsay, D.J., 1999. Methodology for creating an observational database of midwater fauna using submersibles: results from Sagami Bay, Japan. *Plankton Biology and Ecology* 46 (1), 75–87.
- Jeffers, S., Agnew, T.A., Alt, B.T., Abreu, R.D., McCourt, S., 2001. Investigating the anomalous sea-ice conditions in the Canadian High Arctic (Queen Elizabeth Islands) during summer 1998. *Annals of Glaciology* 33, 507–512.
- Jinbiao, Z., Mao, L., 2000. The hydromedusae from Chukchi Sea and its distribution. *Chinese Journal of Polar Research* 12 (3), 169–182.
- Johnson, M.W., 1956. In: *The plankton of the Beaufort and Chukchi Sea Areas of the Arctic and its Relation to Hydrography*. Arctic Institute of North America, Montreal.
- Kosobokova, K.N., Hanssen, H., Hirche, H.-J., Knickmeier, K., 1998. Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993. *Polar Biology* 19, 63–73.
- Kosobokova, K., Hirche, H.J., 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. *Deep-Sea Research Part I* 47 (11), 2029–2060.
- Kosobokova, K.N., Hopcroft, R.R., 2010. Diversity and distribution of mesozooplankton in the Arctic's Canada Basin. *Deep-Sea Research Part II* 57, 96–110.
- Larson, R.J., Harbison, G.R., 1990. Medusae from McMurdo Sound, Ross Sea [Antarctica] including the descriptions of two new species, *Leukartiara brownei*, new species and *Benthocodon hyalinus*, new genus new species. *Polar Biology* 11, 19–26.
- Larson, R.J., Matsumoto, G.I., Madin, L.P., Lewis, L.M., 1992. Deep-sea benthic and benthopelagic medusae: recent observations from submersibles and a remotely operated vehicle. *Bulletin of Marine Science* 51 (3), 277–286.
- Lindsay, D.J., 2005. Planktonic communities below 2000 m depth. *Bulletin of the Plankton Society of Japan* 52 (2), 113–118.
- Lindsay, D.J., Furushima, Y., Miyake, H., Kitamura, M., Hunt, J.C., 2004. The scyphomedusan fauna of the Japan Trench: preliminary results from a remotely-operated vehicle. *Hydrobiologia* 530/531, 537–547.
- Lindsay, D.J., Hunt, J.C., 2005. Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and north-western Pacific. *Journal of the Marine Biological Association of the U.K.* 85, 503–517.
- Lindsay, D.J., Miyake, H., 2007. A novel benthopelagic ctenophore from 7,217 m depth in the Ryukyu Trench, Japan, with notes on the taxonomy of deepsea cydippids. *Plankton and Benthos Research* 2 (2), 98–102.
- MacGinitie, G.E., 1955. Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. *Smithsonian Miscellaneous Collections* 128 (9), 1–201.
- McLaughlin, F., Carmack, E., Macdonald, R., Weaver, A.J., Smith, J., 2002. The Canada Basin, 1989–1995: upstream events and far-field effects of the Barents Sea. *Journal of Geophysical Research* 107 (C7), 1–20.
- McLaughlin, F., Shimada, K., Carmack, E., Itoh, M., Nishino, S., 2005. The hydrography of the southern Canada Basin, 2002. *Polar Biology* 28, 182–189.
- McPhee, M.G., Stanton, T.P., Morison, J.H., Martinson, D.G., 1998. Freshening of the upper ocean in the central Arctic: is perennial sea ice disappearing?. *Geophysical Research Letters* 25, 1729–1732.
- Mumm, N., Auel, H., Hanssen, H., Hagen, W., Richter, C., Hirche, H.-J., 1998. Breaking the ice: large-scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises. *Polar Biology* 20, 189–197.
- Naumov, D.V., 1960. Hydroids and hydromedusae of the USSR. Pavlovskii, E.N. (Ed.), *Keys to the Fauna of the USSR, Vol. 70*. Zoological Institute of the Academy of Sciences of the USSR, Moscow-Leningrad, pp. 660.

- Naumov, D.V., 1961. In: Scyphozoan medusae of the seas of the USSR. Nauka Press, Moscow-Leningrad.
- National Snow and Ice Data Center (NSIDC), 2007. Arctic Sea Ice Shatters All Previous Record Lows. <http://nsidc.org/news/press/2007_seaiceminimum/20071001_pressrelease.html>, 1 October, 2007.
- Oresland, V., 1990. Feeding and predation impact of the chaetognath *Eukrohnia hamata* in Gerlache Strait, Antarctic Peninsula. *Marine Ecology Progress Series* 63, 201–209.
- Ospovat, M.F., 1985. On phylogeny and classification of the type Ctenophora. *Zoologicheskii Zhurnal* 64, 965–974.
- Pagès, F., White, M.G., Rodhouse, P.G., 1996. Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in summer 1994. *Marine Ecology Progress Series* 141 (1–3), 139–147.
- Pagès, F., 1997. The gelatinous zooplankton in the pelagic system of the Southern Ocean: a review. *Annales de l'Institut Océanographique* 73 (2), 139–158.
- Panteleeva, N.N., Frolova, E.A., Sheiko, O.V., 1999. New records of the benthic medusa *Ptychogasteria polaris* Allman, 1878 (Trachylida, Hydrozoa) in the Barents Sea and off the Kurile Islands (Pacific Ocean). *Polar Biology* 22 (6), 372–378.
- Perovich, D.K., Grenfell, T.C., Richter-Menge, J.A., Light III, B., Eicken, W.B.T., 2003. Thin and thinner: sea ice mass balance measurements during SHEBA. *Journal of Geophysical Research (C Oceans)* 108.
- Purcell, J.E., Brown, E.D., Stokesbury, K.D.E., Haldorson, L.H., Shirley, T.C., 2000. Aggregations of the jellyfish *Aurelia labiata*: abundance, distribution, association with age-0 walleye pollock, and behaviors promoting aggregation in Prince William Sound, Alaska, USA. *Marine Ecology Progress Series* 195, 145–158.
- Purcell, J.E., 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Marine Ecology Progress Series* 246, 137–152.
- Purcell, J.E., Whittledge, T.E., Kosobokova, K.N., Hopcroft, R.R., 2010. Distribution, abundance, and predation effects of epipelagic ctenophores and jellyfish in the western Arctic Ocean. *Deep-Sea Research II* 57, 127–135.
- Raskoff, K.A., Sommer, F.A., Hamner, W.M., Cross, K.M., 2003. Collection and culture techniques for gelatinous zooplankton. *Biological Bulletin* 204, 68–80.
- Raskoff, K.A., Purcell, J.E., Hopcroft, R.R., 2005. Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. *Polar Biology* 28, 207–217.
- Shiga, N., Takagi, S., Nishiuchi, K., 1998. Interannual variation and vertical distribution of appendicularians in the south of St. Lawrence Island, northern Bering Sea shelf, in summer. *Memoirs of the Faculty of Fisheries, Hokkaido University* 45, 48–51.
- Shirley, W.D., Leung, Y.-M., 1970. Medusae of the Central Arctic. In: Kobayashi, H.A. (Ed.), *Taxonomic Guides to Arctic Zooplankton*. II. Technical Report of the University of Southern California, Dept. Biol. Sci., pp. 51.
- Sirenko, B.I., Markhaseva, E.L., Buzhinskaya, G.N., Golikov, A.A., Menshutkina, T.V., Petryashov, V.V., Semenova, T.N., Stepanjants, S.D., Vassilenko, S.V., 1996. Preliminary data on suprabenthic invertebrates collected during the RV *Polarstern* cruise in the Laptev Sea. *Polar Biology* 16, 345–352.
- Sirenko, B.I., 2001. List of species of free-living invertebrates of Eurasian Arctic Seas and adjacent deep waters. *Explorations of the Fauna of the Seas Russian Academy of Sciences*. St. Petersburg, vol. 51, pp. 1–129.
- Smith, S.L., Schnack-Schiel, S.B., 1990. Polar Zooplankton. In: Smith Jr., W.O. (Ed.), *Polar Oceanography, Part B: Chemistry, Biology, and Geology*. Academic Press, San Diego, pp. 527–598.
- Søreide, J., Hop, H., Falk-Petersen, S., Gulliksen, B., Hansen, E., 2003. Macrozooplankton communities and environmental variables in the Barents Sea marginal ice zone in late winter and spring. *Marine Ecology Progress Series* 263 (28), 43–64.
- Stepanjants, S.D., 1989. Hydrozoa of the Eurasian Arctic Seas. In: Herman, Y. (Ed.), *The Arctic Seas: Climatology, Oceanography, Geology, and Biology*. Van Nostrand Reinhold, New York, pp. 397–430.
- Stübing, D., Piepenburg, D., 1998. Occurrence of the benthic trachymedusa *Ptychogasteria polaris* Allman, 1878 (Cnidaria: Hydrozoa) off Northeast Greenland and in the northern Barents Sea. *Polar Biology* 19 (3), 193–197.
- Swanberg, N.R., Båmstedt, U., 1991. Ctenophora in the Arctic: the abundance, distribution, and predatory impact of the cydippid ctenophore *Mertensia ovum* (Fabricius) in the Barents Sea. *Proceedings of the Pro Mare Symposium on Polar Marine Ecology*. *Polar Research* 10, 507–524.
- Swanberg, N., 1974. The feeding behaviour of *Beroe ovata*. *Marine Biology* 24, 69–76.
- Timmermans, M.-L., Garrett, C., Carmack, E., 2003. The thermohaline structure and evolution of the deep waters in the Canada Basin, Arctic Ocean. *Deep-Sea Research I* 50, 1305–1321.
- Uchida, T., 1969. Medusae from the Arctic Ocean. *Publications of the Seto Marine Biological Laboratory* 17 (4), 285–287.
- Widder, E.A., Bernstein, S.A., Bracher, D.F., Case, J.F., Reisenbichler, K.R., Torres, J.J., Robison, B.H., 1989. Bioluminescence in the Monterey Submarine canyon: image analysis of video recordings from a mid-water submersible. *Marine Biology* 100, 541–551.
- Youngbluth, M.J., 1984a. In: *Manned submersibles and sophisticated instrumentation: tools for oceanographic research*. Proceedings of SUBTECH 1983. Society of Underwater Technology, London, pp. 335–344.
- Youngbluth, M.J., 1984b. Water column ecology: *in situ* observations of marine zooplankton from a manned submersible. Fleming, N.C. (Ed.), *Divers, submersibles and marine science*. Memorial University of Newfoundland, *Occasional Papers in Biology*, vol. 9; 1984, pp. 45–57.