Article

Bathykorus bouilloni: a new genus and species of deep-sea jellyfish from the Arctic Ocean (Hydrozoa, Narcomedusae, Aeginidae)

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Abstract

A new genus and species of a common deep-water narcomedusa is described from the Arctic Ocean. The species has four primary tentacles, four secondary tentacles, with three interradial manubrial pouches in each quadrant. A revision and taxonomic key of the family Aeginidae is presented to account for the new genus. Detailed information on its fine-scale vertical and horizontal distributions show that it occurs in a fairly narrow depth range between 1400–2000 meters. The species was observed 423 times at eleven stations, demonstrating that new species can be common in the under-explored regions of the ocean.

Key words: Jellyfish, ROV, biodiversity, vertical distribution, Cnidaria, medusae, Canada Basin, Northwind Ridge, Chukchi Plateau

Introduction

Narcomedusae Haeckel, 1879 is a group of diverse medusae that are primarily known from the deep sea. There are currently four families: Aeginidae, Cuninidae, Solmarisidae (Bouillon *et al.* 2006; Daly *et al.* 2007), and the recently added Tetraplatiidae (Collins *et al.* 2006a; Collins *et al.* 2008). Although there is great variation in body form, they are largely characterized by having few, non-contractile tentacles which root into the exumbrellar surface and that are often held aloft in front of the swimming medusae, and by their unusual axis of development from larvae to adult (Kramp 1961; Bouillon 1987; Bouillon *et al.* 2006; Daly *et al.* 2007). There have been few genetic studies of the group as a whole (Collins 2002; Collins *et al.* 2006a, b; Collins *et al.* 2008) and although the order Narcomedusae appears to be monophyletic, recent data point to several problematic issues at the family and generic level that still need attention (Collins *et al.* 2008; Haddock, Pers. Com.).

Narcomedusae has 13 commonly observed genera, with upwards of 45 species described, including several recently added genera and species (Xu & Zhang 1978; Arai *et al.* 2000; Bouillon *et al.* 2001; Bouillon *et al.* 2006; Collins *et al.* 2006a; Fuentes & Pagès 2006; Schuchert 2009). As was noted by Fuentes & Pagès (2006), virtually all new species to the family Aeginidae have required the creation of new genera, showing the description of diversity of the Aeginidae has been mainly at the generic level, not at the species level. This pattern of accumulating genera points to the absence of reliable species-level morphological characteristics and the need for detailed molecular data to elucidate the true relationships of these difficult to classify taxa.

The ecology of narcomedusae has been most studied in recent years with the advent and propagation of deep-diving submersible technologies. As the majority of these species are found in the deep sea and do not tend to survive the stress and abrasion in typical plankton nets, research on live specimens *in situ* is still an emerging field (Mills & Goy 1988; Raskoff 2002; Lindsay & Hunt 2005; Raskoff *et al.* 2005; Haddock 2007; Lindsay *et al.* 2008; Robison 2004; Raskoff *et al.* In press). These recent examinations of deep-sea environments around the globe have shown the narcomedusae to be abundant and important players in regional ecosystems.

The Arctic Ocean has been the subject of many gelatinous zooplankton surveys (Bigelow 1920; MacGinitie 1955; Grainger 1965; Uchida 1969; Shirley & Leung 1970; Stepanjants 1989; Kosobokova *et al.* 1998; Kosobokova & Hirche 2000; Søreide *et al.* 2003; and others). However in all of these studies, the new species described herein, *Bathykorus bouilloni*, was never reported. One likely explanation for this disparity is their extreme fragility. Collection with nets destroys most soft-bodied species or reduces them to unrecognizable fragments (Raskoff *et al.*, 2003). The other likely reason for their noted exclusion in previous studies is the fact that they superficially resemble another species, *Aeginopsis laurentii* Brandt, 1838 which also has four tentacles and could easily be confused for *Bathykorus bouilloni* if the specimen was sufficiently damaged.

Methods and materials

Specimens were collected on two cruises in the Arctic Ocean. A single specimen was collected at station AL10 at 2741m on August 22, 2002 at the Eastern edge of the Canada Basin/Beaufort Sea aboard the CCGS *Louis S. St-Laurent* (Table 1; see Raskoff *et al.* 2005 for additional information). All other specimens were observed and sampled during the summer of 2005, from June 29th through July 25th, aboard 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 (see Figure 1 in Raskoff *et al.* In Press for map and additional information). *In situ* observations and specimens were collected with the remotely operated vehicle (ROV) *Global Explorer* (Deep Sea Systems), a 2800m depth-rated vehicle equipped with a 720p High Definition (HDTV) video system. Live animals were captured with four, 6.5 liter "Detritus" samplers (Youngbluth, 1984a) and a carousel of twelve, 3.5-liter canisters that collect specimens using gentle suction (Youngbluth, 1984b).

Live-collected animals were retrieved as soon as the ROV was recovered (i.e. within several hours of collection) and put into a dark, 1°C temperature-controlled environmental chamber equipped with special phototanks and planktonkreisels (see Fig 2 in Raskoff et al., 2003). The gentle collection procedures and tank designs made it possible to maintain live specimens for observations of more than a week.

Living specimens were observed under dissection (Leica MZ12) and compound (Leitz Laborlux) microscopes. Photographs were taken using a scope-mounted 2 MPx SPOT Insight Digital Camera and a 35mm macroscopic digital camera for whole animals. Nematocysts were imaged with a video camera on the compound microscope and MiniDV recorder, frame grabs were taken, and the resulting images analyzed on the computer for sizing.

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 *Bathykorus bouilloni* occurrences were collected and recorded in real-time, with augmentation using the recorded HDTV video tapes as needed. The species abundance was plotted by depth and station. The plot shows the number of individuals observed per hour of ROV observation, in 100m 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 individuals observed in the interval by the time spent searching 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 table 1 and in the text, but not included on the normalized contour figures. These data were contour plotted (SigmaPlot 11.0, Systat Software) along with the bottom depth of the stations when within the ROV's depth range (see Table 1). A few additional specimens were collected with a Hydro-bios Midi Multinet (mouth area 0.25 m^2) between 1000–2000m using 150μm mesh nets hauled vertically at ~0.5m/s (see Kosobokova & Hopcroft In press, for more net data).

Table 1. Observation, collection and location data for all known sightings of *Bathykorus bouilloni*. Maps and details on the stations can be found in Raskoff *et al.* 2005 and Raskoff *et al.* In press. "*" signifies a net trawl collection, "–" = no observations, nd = no data available.

Station	Date	Number Observed by ROV	Number Collected	Station Depth (m)	Max ROV Depth (m)	% water Column Surveyed	Dive Length (h)	Geographic Region	Latitude (N)	Longitude (W)
AL10	22 August 2002	1	1	2741	2741	nd	12	Canada Basin	73° 30'	136° 59'
3	30 June 2005	1	1	1530	1530	100	8.75	Chukchi Sea slope	72° 22'	155° 13'
5	04 July 2005	54	5	3853	2853	74	11.02	Canada Basin	73° 22'	153° 36'
6	07 July 2005	60	4	3854	1774	46	9.85	Canada Basin	74° 7'	153° 37'
7	09 July 2005	46	4	3800	2810	74	11.54	Canada Basin	74° 25'	151° 44'
8	11 July 2005	75	8	3840	2811	73	11.13	Canada Basin	74° 34'	151° 56'
9	14 July 2005	56	1*	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	5	–	1614	1614	100	9.22	Chukchi Basin	75° 59'	160° 39'
13	20 July 2005	14	–	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	111	1	2414	2414	100	10.62	Chukchi Sea slope	72° 51'	156° 58'

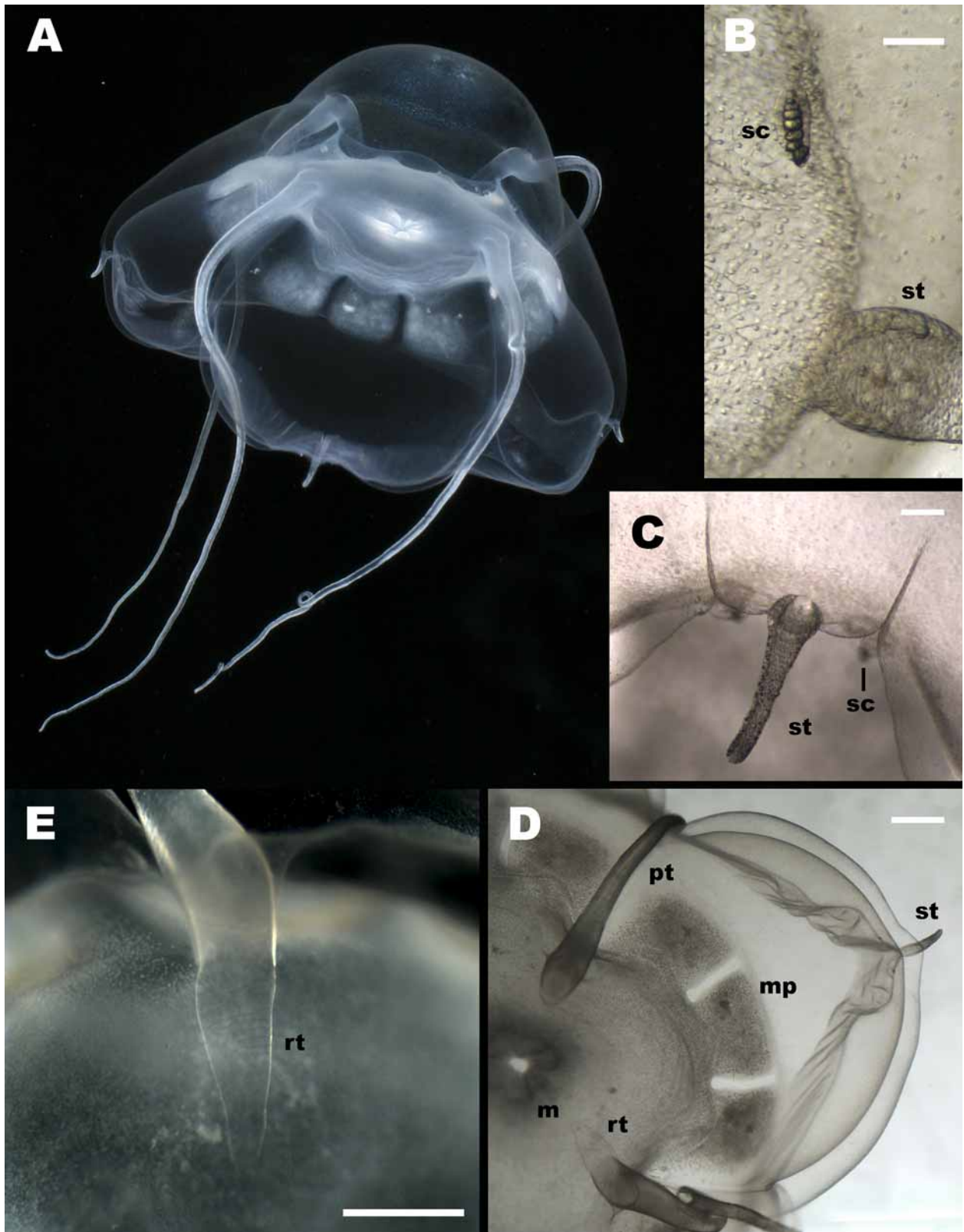*= net collection

nd= no data

FIGURE 1. *Bathykorus bouilloni*. All photographs obtained from a live specimen. A. Entire swimming medusa showing the positions of the primary and secondary tentacles, as well as the three interradial manubrial pouches per quadrant. B. Close up view of the base of the secondary tentacle and statocyst showing the 7 statoliths. sc, statocyst; st, secondary tentacle (scale bar = 200 µm). C. Close up view of the entire secondary tentacle (scale bar = 200 µm). D. Aboral view of one full quadrant of the medusa. m, mouth; mp, manubrial pouch; pt, primary tentacle; st, secondary tentacle; rt, tentacular root (scale bar = 1000 µm). E. Close up of the primary tentacular root (rt) (scale bar = 1000 µm).
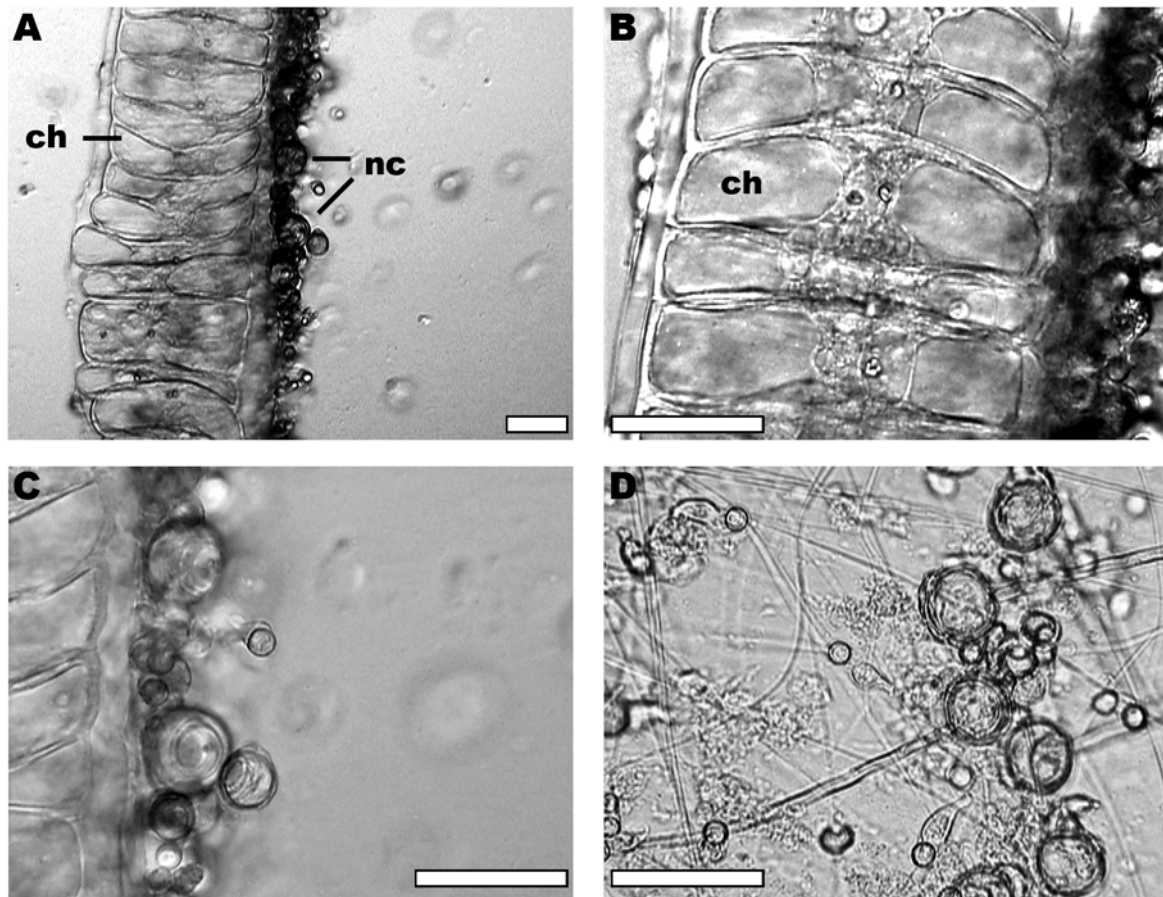
FIGURE 2. Cnidome of *Bathykorus bouilloni*. A. Primary tentacle showing the characteristic endodermal chordal cells (ch) inside the tentacle and the asymmetrical distribution of the nematocysts on the aboral (right) side of the tentacle (nc). B. Close up view of chordal cells and cellular matrix at the core of the tentacle. C. Undischarged nematocysts on tentacle showing the two main size classes. Coiled threads can be seen inside the capsules. D. Discharged large and small apotrichous isorhizae nematocysts. All scale bars = 50µm.

Systematics

Phylum Cnidaria

Class Hydrozoa

Subclass Trachylina

Order Narcomedusae Haeckel, 1879

Family Aeginidae Gegenbaur, 1857

Genus *Bathykorus* gen. nov.

***Bathykorus bouilloni* gen. nov. sp. nov.**
(Figures 1–4)

Synonymy. "Unidentified narcomedusa" in Raskoff *et al.* 2005. "Narcomedusa" in Holland 2006. "New Narcomedusa" in Raskoff *et al.* In press. "Narcomedusae sp. nov." in Kosobokova & Hopcroft In press. "new narcomedusa" in Bluhm *et al.* In press.

Type material. The holotype and four paratype specimens have been deposited at the Smithsonian, National Museum of Natural History, Invertebrate Zoology Collection. USNM 1125360 Holotype, station 5, Canada Basin (73⁰ 22' N; 153⁰ 36' W), 4 July 2005 at 1607m depth. USNM 1125361, Paratypes, station 8, Canada Basin (74⁰ 34' N; 151⁰ 56' W), 11 July 2005 at 1514 m depth; four specimens.

Etymology. The generic name *Bathykorus* references the habitat and shape of the species. *Bathy* (Greek; from *bathus*, depth or deep) refers to the deep-sea habitat of the species, and *korus* (Greek; helmet) refers to the helmet-like shape of the bell. The specific epithet of *bouilloni* is named in honor of the late Dr. Jean Bouillon, (1926–2009). Dr. Bouillon's studies spanned over 60 years, and described 17 families, 34 genera, and 114 species. His work and his generous sprit continue to enlighten and inspire generations of biologists.
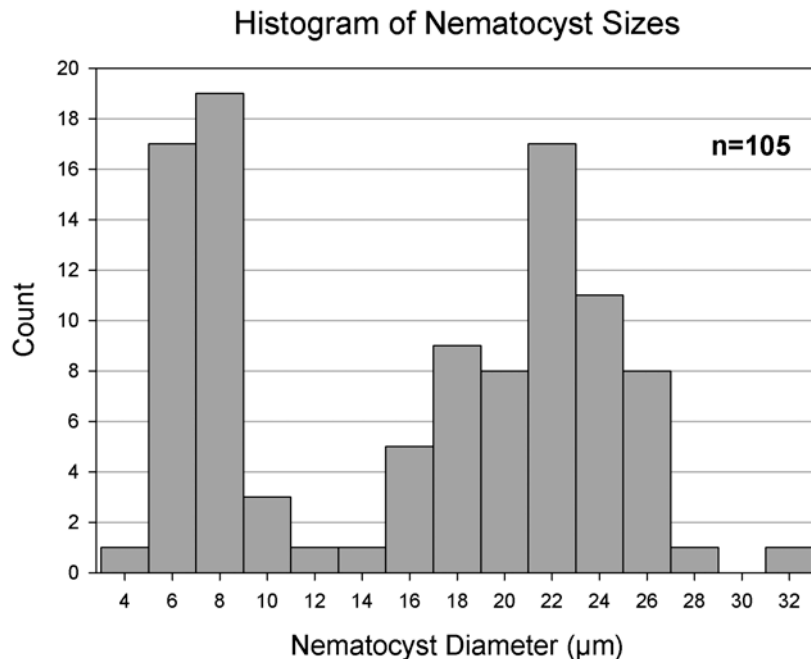

FIGURE 3. Histogram of nematocyst sizes in *Bathykorus bouilloni*. Nematocyst diameters (n=105) were measured from a random assortment of microscopic video stills taken of a live specimen. There are two statistically different size classes (Mann-Whitney rank sum, P = <0.001).

Diagnosis. Generic Diagnosis

Genus *Bathykorus* gen. nov.

Four (rarely 5) primary tentacles and peronia, manubrial pouches 3x tentacle number (rarely more); peripheral canal system absent or reduced; with secondary marginal tentacles in equal number to primary tentacles; no otoporpae.

Species description

***Bathykorus bouilloni* sp. nov.**

Bell. The medusae shows primarily tetramerous symmetry with the umbrella being dome-shaped and the apex having a pronounced thickening of the mesoglea; with a maximum observed diameter of 1.5cm and height of 1.1cm (Figure 1). The mesoglea becomes thinner at the margins and has a uniform light blue coloration in life which turns milky-white when preserved. The bell is incised or lobed below the origin of the

primary tentacles forming the peronia (Figure 1D). There is a thin velum on the inside edge of the umbrellar margin.

Tentacles. There are four primary, solid, noncontractile tentacles which originate above the umbrellar margin and peronia (one specimen of 25 collected was found with five tentacles) that are two to three times as long as the medusa is wide. These primary tentacles have deep endodermal tentacular roots that anchor into the mesoglea through the exumbrellar surface (Figure 1E). On the margin of the bell there is one secondary tentacle per quadrant hanging free from the edge of the lappet (one specimen was found with two secondary tentacles in a single quadrant) (Figure 1C&D). The core of the tentacles is made of very large vacuolated endodermal chordal cells (Figure 2 A&B).

Subumbrella. The mouth is simple and circular, but can fold into irregular patterns with muscular movement. The mouth extends into a wide and flat gastric cavity that leads into the interradial manubrial pouches, a feature characteristic of the Aeginidae. There are typically three manubrial pouches per primary tentacle (Figure 1D), although one specimen was observed with four pouches in one of its quadrants. There are an equal number of simple canals to the tentacles (usually four) which quickly bifurcate into the peripheral and peronial canals which follow along the margin of each interradial lappet. It was not determined if the canals are hollow, or solid as is common for some narcomedusae.

Statocysts. There are typically two free hanging, ecto-endodermic statocysts found in each quadrant, one on each side of the secondary tentacle. In one specimen there were two secondary tentacles in a quadrant and there were three statocysts, alternating with the tentacles. The statocysts have 5–7 statoliths in each cluster (Figure 1B). They appear to be similar to the "closed" marginal sensory clubs found in *Sigiweddellia benthopelagica* (Cuninidae; Bouillon *et al.* 2001), but it is unclear based on their drawings and description. In *Bathykorus bouilloni* the hanging statocysts are not found within distinct pockets in the ectoderm, as is seen in *S. benthopelagica*.

Cnidome. Cnidocysts are found in an asymmetrical pattern on the main tentacles such that the dense collection of cnidocysts are on the aboral (exumbrellar) side of the tentacles (Figure 2 A&B). This is the side that would contact prey when the tentacles are held aloft in their typical foraging position. There were very few cnidocysts found on the oral side of the tentacles. The cnidome mainly consists of two different sizes of cnidocysts, with two major size fractions of nematocysts found, as is typically described for other narcomedusae (Carré et al. 1989; Purcell & Mills 1988) (Figure 2 C&D). Both of these nematocyst types appear to be apotrichous isorhizas. The large macroisorhizas had a diameter of 22.6 µm ± 0.44 (Mean ± SE; N=65), while the smaller sized microisorhizas had a diameter of 8.3 µm ± 0.19 (Mean ± SE; N=40), with these differences (Figure 3) statistically significant (P = <0.001) using a Mann-Whitney rank sum test.

Gonads. Although 25 specimens were examined, no obvious mature gonads were observed under a dissection microscope at up to 100x magnification. Although some thickened, dense tissue was found in the distal area of the interradial manubrial pouches, no definitive determination was made of its type. Either the population was immature at this time of the year, or the gonads are not obvious and a careful compound microscopic exploration is needed.

Discussion. Modification to Aeginidae

The family Aeginidae is now modified to include species that have between one and four interradial manubrial pouches between each primary tentacle. A new diagnosis and key to genera, based on Bouillon *et al.* 2006, is provided.

Family Aeginidae Gegenbaur, 1857

Manubrial pouches interradial, undivided or divided into two to four parts, bearing the ''gonads''; with or without peripheral canal system; exumbrellar, perradial, primary tentacles between marginal lobes; with or without secondary tentacles on umbrellar margin. Primary tentacles originating above manubrial pouches. With or without otoporpae.

Key to Family Aeginidae

1. 2 tentacles .... *Solmundella*
- 4 or more tentacles..2
2. with secondary tentacles 3
- without secondary tentacles 4
3. 4 (or 5) primary tentacles, manubrial pouches 3x tentacle number... *Bathykorus*
- 8 (or more) primary tentacles, manubrial pouches 2x tentacle number... *Aeginura*
4. 4–6 tentacles 5
- 8 or more tentacles 6
5. 4 tentacles, 8 peronia and manubrial pouches 4x tentacle number.. *Aeginopsis*
- 4 to 6 tentacles, 4–6 peronia and manubrial pouches 2x tentacle number..*Aegina*
6. 8 tentacles, 8 manubrial pouches (7–9), with peripheral canal; with otoporpae .... *Otoporpa*
- 30+ tentacles, equal number undivided manubrial pouches, without otoporpae....................... *Jubanyella*

Habitat and distribution. Over the course of the two cruises, 423 individuals of this species were observed. The single observation in 2002 is in stark contrast to the 422 observations made during the 2005 cruise. In 2005, *Bathykorus bouilloni* ranked as one of the most common mesopelagic species observed in the Arctic Ocean. It is not known if this disparity in abundance between cruises was the result of a true change in abundance, or the result of the significant improvements in the ROV video system from NTSC to HDTV, which allowed for visual identifications of specimens in 2005 that were not possible in 2002. The distribution of *Bathykorus bouilloni* was generally restricted to waters deeper than 1300m and it occurred in a narrow vertical range, from ~1400–2000m (Figure 4). The species was not observed at stations that had bottom depths shallower than the species' typical range (Figure 4; Table 1). A single individual was found at station 3, where the bottom depth was 1530m, 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 1900m. The superficially similar species *Aeginopsis laurentii,* which is often found in Arctic waters (Bigelow 1920; Uchida 1969; Shirley & Leung 1970; Kosobokova & Hirche 2000) was found at 4 different stations, from 172–464m over the Canada Basin. Sampling of *B. bouilloni* by more traditional plankton nets was limited to 1000–3000m while *Aeginopsis laurentii* was only sampled above 200m. It is likely that some of the deepwater medusae identified as *A. laurentii* in previously collected net-tows in the Arctic Ocean basins may have been misidentified *Bathykorus bouilloni* (Kosobokova, Personal Communication). A reexamination of old samples, where the specimens are in sufficiently good condition is advised. A superficially similar species has been reported from Japanese waters (Kitamura et al., 2008; Lindsay & Miyake, 2009) but awaits description.

Tentacles and Cnidae. The core of the tentacles, like those of most narcomedusans, are made of very large vacuolated endodermal chordal cells, which provide the stiff reinforcement needed to raise the tentacles up in front of the swimming medusa (Figure 2 A&B). An analysis of the nematocysts of *Bathykorus bouilloni* shows two clearly identifiable types (Figure 2C&D; Figure 3) of differing size. While difficult to see with the compound microscope, both types appeared to have small spines along their length, making them apotrichous isorhizas, as have been observed in many other species of Narcomedusae (Purcell & Mills 1988; Carré *et al.* 1989; Arai *et al.* 2000). No staining was done on the cnidocysts, so additional sub-categories of nematocyst type, observable only with staining, as was found in Arai *et al.* 2000, should be considered in future studies.

Behaviors. In life, medusae typically swim with the noncontractile tentacles angled up over the top of their umbrellar surface, leading forward of the medusae in the direction of travel. This foraging behavior is typical for many species of Narcomedusae (Mills 1981; Mills & Goy 1988; Raskoff 2002) and has been hypothesized to aid in the capture of prey that might otherwise sense the bow wave of the swimming medusa (Raskoff 2002). The bulk of prey items captured by this so-called "stealth predation" in past studies have been other gelatinous zooplankton, primarily ctenophores, siphonophores, and medusae. Although hundreds of *Bathykorus bouilloni* were observed and dozens collected, no prey items were found in their gastric cavities, so their diet remains unknown. There are many other gelatinous species that co-occur with *B. bouilloni* at their habitat depth between 1400–2000m and several of these could be either prey or predators

(Raskoff *et al.* In press). That a new genus and species can be found by the hundreds in a single expedition demonstrates how much is left to be discovered about the inhabitants of the deep sea, especially in the polar regions.
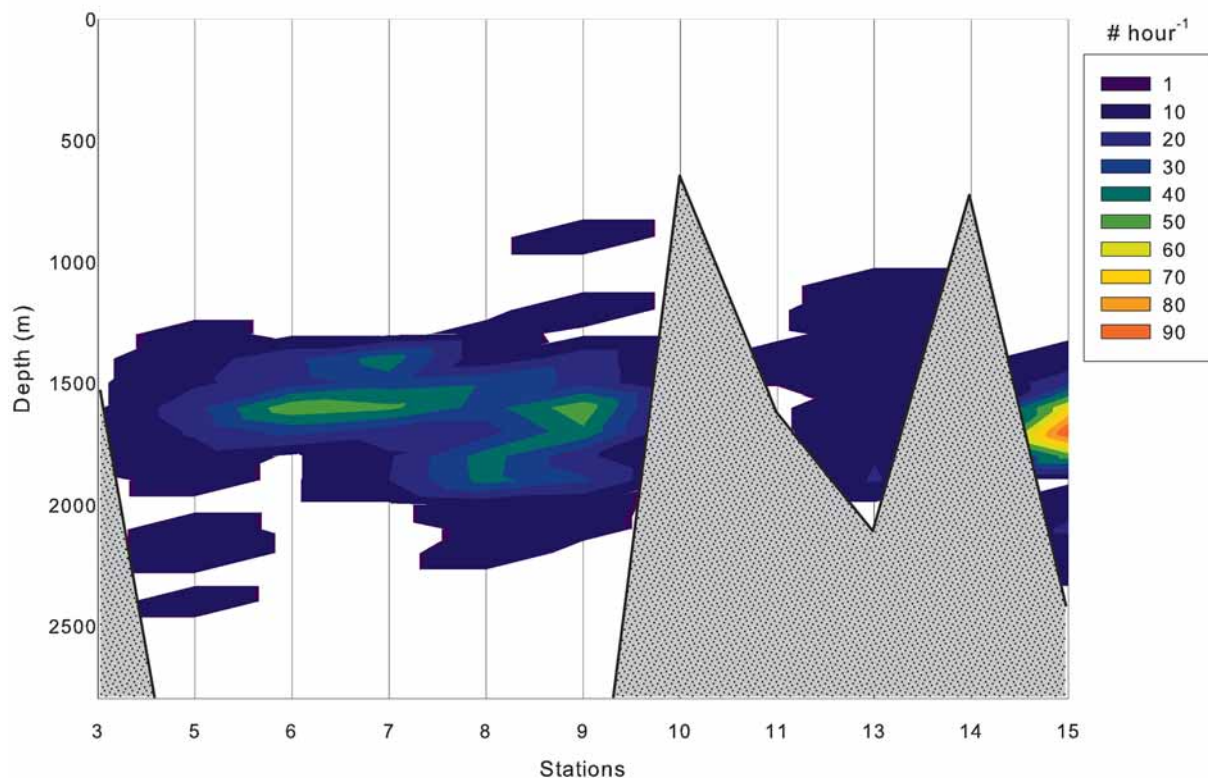

FIGURE 4. Horizontal and vertical distribution of *Bathykorus bouilloni* in the Canada Basin, Northwind Ridge and Chukchi Plateau Region, summer 2005. The number of individuals observed per hour by the ROV is presented in 100m depth bin intervals, from the surface to the maximum depth achieved for a particular station (see Table 1). The bottom depth, when within the ROV's depth range, is shown in gray.

Acknowledgments

References

Arai, M.N., Cavey, M.J. & Moore, B.A. (2000) Morphology and distribution of a deep-water Narcomedusa (Solmarisidae) from the northeast Pacific. *Scientia Marina*, 64, 55–62.

Bigelow, H.B. (1920) Medusae and Ctenophores from the Canadian Arctic Expedition, 1913-1918. Part H. Medusae and Ctenophora. *In: Report of the Canadian Arctic Expedition VIII: Mollusks, Echinoderms, Coelenterates, etc.* Kings Printer, Ottawa, pp. 3–19.

Bluhm, B.A., Iken, K. & Hopcroft, R.R. (In press) Observations and exploration of the Arctic's Canada Basin and the

Chukchi Sea: the Hidden Ocean and RUSALCA expeditions. *Deep-sea research II*.

Bouillon, J. (1987) Considérations sur le développement des Narcoméduses et sur leur position phylogénétique. *Indo-Malayan Zoology*, 4, 189–278.

Bouillon, J., Pagès, F. & Gili, J.M. (2001) New species of benthopelagic hydromedusae from the Weddell Sea. *Polar Biology*, 24, 839–845.

Bouillon, J., Gravili, C., Pagès, F., Gili, J.M. & Boero, F. (2006) An introduction to Hydrozoa. *Mémoires du Muséum national d'Histoire naturelle*, 194, 1–591.

Carré, D., Carré, C. & Mills, C.E. (1989) Novel cnidocysts of narcomedusae and a medusivorous ctenophore, and confirmation of kleptocnidism. *Tissue and Cell*, 21, 723–734.

Collins, A.G. (2002) Phylogeny of Medusozoa and the evolution of cnidarian life cycles. *Journal of Evolutionary Biology*, 15, 418–432.

Collins, A.G., Bentlage, B., Matsumoto, G.I., Haddock, S.H.D., Osborn, K. & Schierwater, B. (2006a) Solution to the phylogenetic enigma of *Tetraplatia*, a worm-shaped cnidarian. *Biology Letters*, 2, 120–124.

Collins, A.G., Schuchert, P., Marques, A.C., Jankowski, T., Medina, M. & Schierwater, B. (2006b) Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Systematic Biology*, 55, 97–115.

Collins, A.G., Bentlage, B., Lindner, A., Lindsay, D.J., Haddock, S.H.D., Jarms, G., Norenburg, J.L., Jankowski, T. & Cartwright, P. (2008) Phylogenetics of Trachylina (Cnidaria: Hydrozoa) with new insights on the evolution of some problematical taxa. *Journal of the Marine Biological Association of the United Kingdom*, 88, 1673–1685.

Daly, M., Brugler, M.R., Cartwright, P., Collins, A.G., Dawson, M.N., Fautin, D.G., France, S.C., McFadden, C.S., Opresko, D.M., Rodrigues, E., Romano, S.L. & Stake, J.L. (2007) The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa*, 1668, 127–182.

Fuentes, V. & Pagès, F. (2006) Description of *Jubanyella plemmyris* gen. nov. et sp. nov. (Cnidaria: Hydrozoa: Narcomedusae) from a specimen stranded off Jubany Antarctic station, with a new diagnosis for the family Aeginidae. *Journal of Plankton Research*, 28, 959–963.

Grainger, E.H. (1965) Zooplankton from the Arctic Ocean and adjacent Canadian waters. *Journal of Fisheries Resources of Canada*, 22, 543–564.

Haddock, S.H.D. (2007) Comparative feeding behavior of planktonic ctenophores. *Integr. Comp. Biol.*, 47, 847–853.

Holland, J.S. (2006) Ice-Water Aliens. *National Geographic Magazine*, December, 210, p.26.

Kitamura, M., Miyake, H., and Lindsay, D.J. (2008) Cnidaria in: Deep-sea life -Biological observations using research submersibles. (eds Fujikura K, Okutani T, Maruyama T). Tokai University Press, Kanagawa, p. 295–320.

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 Biol.*, 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-Oceanographic Research Papers*, 47, 2029–2060.

Kosobokova, K.N. & Hopcroft, R.R. (In press) Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. *Deep-sea research II*.

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 United Kingdom*, 85, 503–517.

Lindsay, D.J. & Miyake, H. (2009) A checklist of midwater cnidarians and ctenophores from Japanese waters -species sampled during submersible surveys from 1993–2008 with notes on their taxonomy. Kaiyo Monthly 41(8): 417–438.

Lindsay, D.J., Pagès, F., Corbera, J., Miyake, H., Hunt, J.C., Ichikawa, T., Segawa, K. & Yoshida, H. (2008) The anthomedusan fauna of the Japan Trench: preliminary results from *in situ* surveys with manned and unmanned vehicles. *Journal of the Marine Biological Association of the United Kingdom*, 88, 1519–1539

MacGinitie, G.E. (1955) Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. *Smithsonian Miscellaneous Collections*, 128, 1–201.

Mills, C.E. (1981) Diversity of swimming behaviors in hydromedusae as related to feeding and utilization of space. *Marine Biology*, 64, 185–189.

Mills, C.E. & Goy, J. (1988) *In situ* observations of the behavior of mesopelagic *Solmissus* narcomedusae (Cnidaria, Hydrozoa). *Bulletin of Marine Science*, 43, 739–751.

Purcell, J.E. & Mills, C.E. (1988) The correlation between nematocyst types and diets in pelagic hydrozoa. *In:* Hessinger, D.A. & Lenhoff, H.M. (Eds.) *The biology of nematocysts*. Academic Press, New York, pp. 463–485.

Raskoff, K.A. (2002) Foraging, prey capture, and gut contents of the mesopelagic narcomedusa, *Solmissus* spp. (Cnidaria: Hydrozoa). *Marine Biology*, 141, 1088–1107.

Raskoff, K.A., Hopcroft, R.R., Kosobokova, K.N., Purcell, J.E. & Youngbluth, M. (In press) Jellies under ice: ROV observations from the Arctic 2005 Hidden Ocean Expedition. *Deep-sea research II*, doi:10.1016/j.dsr2.2009.08.010.

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.

Raskoff, K.A., Sommer, F.A., Hamner, W.M. & Cross, K. (2003) Collection and culture techniques for gelatinous zooplankton. *Biological Bulletin*, 204, 68–80.

Robison, B.H. (2004) Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology*, 300, 253–272.

Schuchert, P. (2009) The Hydrozoa Directory, Version 18. Available from: http://www.ville-ge.ch/mhng/hydrozoa/hydrozoa-directory.htm (accessed June 24, 2009)

Shirley, W.D. & Leung, Y.-M. (1970) Medusae of the Central Arctic. *In:* H.A., K. (Ed.) *Taxonomic Guides to Arctic Zooplankton. II.* Technical Report University of Southern California, Department of Biological Sciences, 51.

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, 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.

Uchida, T. (1969) Medusae from the Arctic Ocean. *Publications of the Seto Marine Biological Laboratory*, 17, 285–287.

Xu, Z. & Zhang, J. (1978) On the hydromedusae, siphonophores and scyphomedusae from the coast of the east Guangdong province and South Fujian province, China. *Acta scientiarum naturalium, Universitatis Amoiensis*, 17, 19–64.