

RESEARCH ARTICLE

# Trends in the Diversity, Distribution and Life History Strategy of Arctic Hydrozoa (Cnidaria)

Marta Ronowicz<sup>1\*</sup>, Piotr Kukliński<sup>1,2</sup>, Gillian M. Mapstone<sup>2</sup>

**1** Marine Ecology Department, Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland, **2** Life Science Department, Natural History Museum, London, United Kingdom

\* [martar@iopan.gda.pl](mailto:martar@iopan.gda.pl)



## OPEN ACCESS

**Citation:** Ronowicz M, Kukliński P, Mapstone GM (2015) Trends in the Diversity, Distribution and Life History Strategy of Arctic Hydrozoa (Cnidaria). PLoS ONE 10(3): e0120204. doi:10.1371/journal.pone.0120204

**Academic Editor:** Erik V. Thuesen, The Evergreen State College, UNITED STATES

**Received:** November 3, 2014

**Accepted:** January 20, 2015

**Published:** March 20, 2015

**Copyright:** © 2015 Ronowicz et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data Availability Statement:** All relevant data are within the paper and its Supporting Information files.

**Funding:** This work was supported by the Polish National Science Centre grant nrs 2012/04/M/NZ8/00670 to MR and 2011/03/B/NZ8/02872 to PK. The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

## Abstract

This is the first attempt to compile a comprehensive and updated species list for Hydrozoa in the Arctic, encompassing both hydroid and medusa stages and including Siphonophorae. We address the hypothesis that the presence of a pelagic stage (holo- or meroplanktonic) was not necessary to successfully recolonize the Arctic by Hydrozoa after the Last Glacial Maximum. Presence-absence data of Hydrozoa in the Arctic were prepared on the basis of historical and present-day literature. The Arctic was divided into ecoregions. Species were grouped into distributional categories according to their worldwide occurrences. Each species was classified according to life history strategy. The similarity of species composition among regions was calculated with the Bray-Curtis index. Average and variation in taxonomic distinctness were used to measure diversity at the taxonomic level. A total of 268 species were recorded. Arctic-boreal species were the most common and dominated each studied region. Nineteen percent of species were restricted to the Arctic. There was a predominance of benthic species over holo- and meroplanktonic species. Arctic, Arctic-Boreal and Boreal species were mostly benthic, while widely distributed species more frequently possessed a pelagic stage. Our results support hypothesis that the presence of a pelagic stage (holo- or meroplanktonic) was not necessary to successfully recolonize the Arctic. The predominance of benthic Hydrozoa suggests that the Arctic could have been colonised after the Last Glacial Maximum by hydroids rafting on floating substrata or recolonising from glacial refugia.

## Introduction

The class Hydrozoa is a monophyletic group in the phylum Cnidaria, consisting of approximately 3500 currently described species [1]. The basic life cycle of hydrozoans comprises a succession of developmental stages: planula larva, hydroid and dioecious hydromedusa [2]. Sessile polyps produce medusae through asexual budding. A medusa is a mobile reproductive stage. After fertilisation a planula larva develops. In about 70% of species a free swimming medusa is

suppressed [3,4]. In this case, the medusa does not leave the hydroid colony but gonophores are maintained on the polyp as sporosacs (fixed gonophores). The loss of the medusa is recognised as an evolutionary process [4,5]. The medusa stage can be reduced to medusoids, intermediary forms liberated from the polyp but short-lived, that disperse gametes over a short distance. There is also a group of species that completely lack a benthic stage (e.g. Trachymedusae, Narcomedusae, Siphonophorae). Planula larvae of benthic species live from hours to up to 20 days as given by Cornelius and Sommer and references cited therein [6,7]. They swim or crawl to a suitable substrate where they settle and metamorphose into a new polyp stage. Little is known about longevity and dispersal potential of planulae. We assume, after Jackson & Coates [8], Hughes [9] and Pagliara et al. [10], that lecithotrophic, non-feeding planula larvae are rather short-lived and possess restricted dispersal potential.

The Hydrozoa are a potentially good model for testing hypotheses about dispersal and the colonization of new regions because they have different dispersal strategies related to different life histories. Many Hydrozoa with circumglobal distributions are benthic [11] which may indicate that having medusa stage is not necessary for hydrozoan taxa to colonize distant places.

The Arctic region is a geologically young system and provides an opportunity for examination of dispersal. In recent geological history (back to Quaternary glaciations), the global sea level has fluctuated approximately 100 m between glacial lowstands and inter-glacial highstands [12,13]. The vast area of the Arctic continental shelf was frequently emergent and covered by glaciers, resulting in massive eradications of the shelf biota [12]. Only when deglaciation started approximately 14 ka (thousand years ago) could Arctic re-colonization begin. This was accomplished by survivors that had been able to retreat into the North Atlantic or North Pacific or take refuge either in the unglaciated shelf areas of the East Siberian and Beaufort Seas or in the deeper bathyal parts of the Arctic Ocean [14,15].

Despite extensive records of Hydrozoa in the Arctic from the end of XIX century [16,17] to recent descriptions of species new to science [18–21], there is a critical gap in the species inventory, distribution records and biodiversity comparisons amongst Arctic regions [22]. For instance, Hydrozoa were not included in the first pan-Arctic inventory of macrofauna species [23], although the benthic Hydrozoa number compiled in our study is higher than for Bryozoa in shelf regions of the Arctic [23]. Data on Arctic Hydrozoa are fragmentary (mostly local surveys) and scattered (dealing only with the benthic or pelagic domain). Basic knowledge on species distribution is fundamental to biodiversity research [24], and for future efforts to follow changes in marine ecosystems connected with global warming, especially in the Arctic region.

The main aims of this study are: (1) to compile an up-to-date list of Hydrozoa occurring in Arctic waters, with their zoogeographic affinities and life cycle strategies; (2) to explore patterns of Hydrozoa distribution and diversity within the Arctic region and (3) to analyse the effect of dispersal ability on distribution. This is the first attempt to create a comprehensive Arctic species register that covers the whole class Hydrozoa, encompassing both polypoid and medusa stages and including Siphonophorae.

We address the hypothesis that the presence of a pelagic stage (holo- and meroplanktonic) is not relevant to dispersal capabilities of Hydrozoa and colonization of the Arctic.

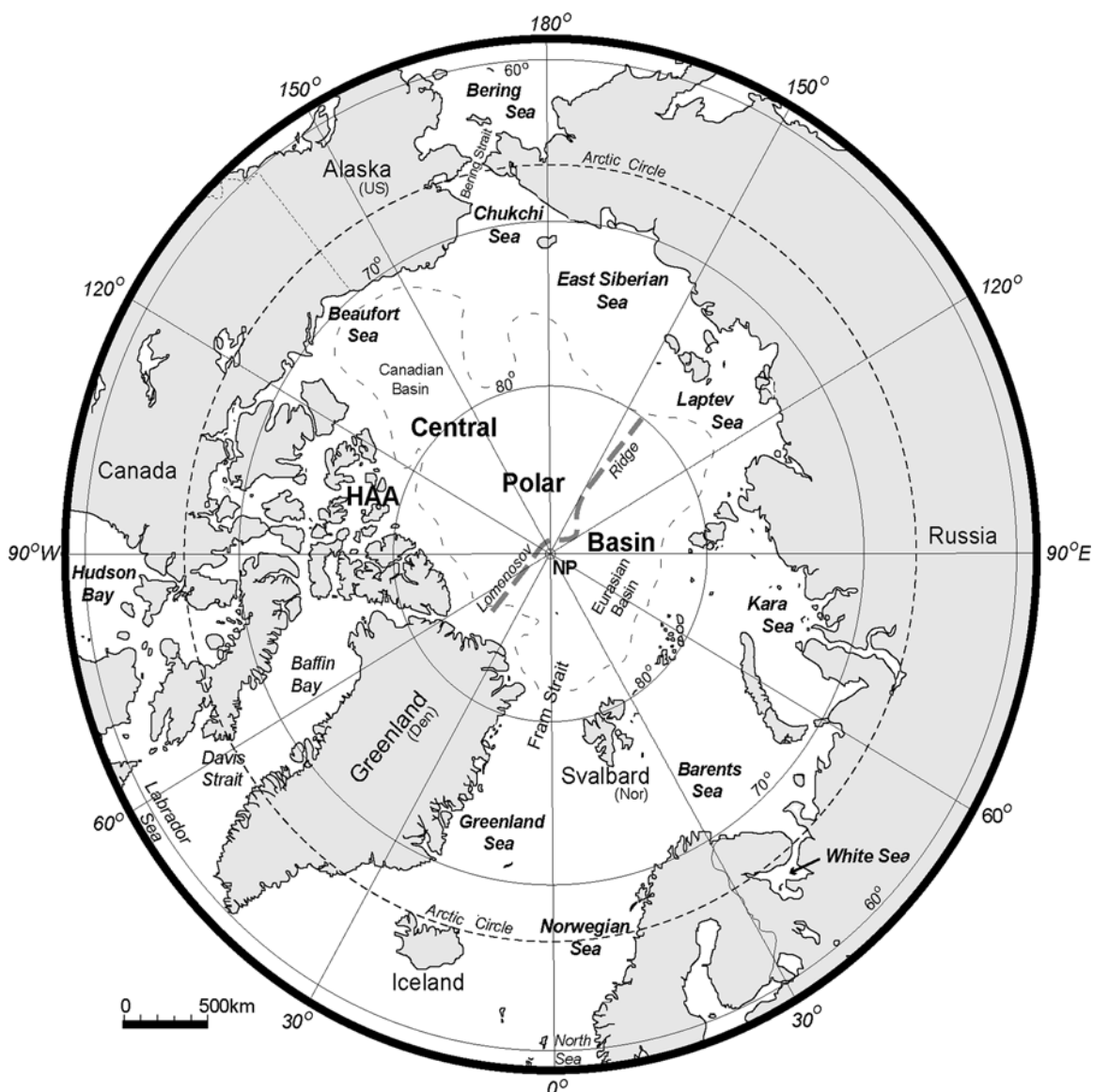
## Methods

### Study area

We use the Arctic Circle (66° 33.5' N) as the boundary of the Arctic, with some extensions. Thus, our area comprises the nearly landlocked Arctic Ocean, and adjacent shelf seas (Beaufort, Chukchi, East Siberian, Laptev, Kara, Barents Seas and the White Sea included), the Nordic Seas (Greenland and Norwegian seas with southern Greenland and Iceland included), the

Labrador Sea, Baffin Bay, Hudson Bay, the High Arctic Archipelago (HAA) (Fig. 1). The Bering Sea is also incorporated because of the climate conditions and the Arctic shelf which extends through it to the Aleutian Islands. In the centre of the Arctic Ocean there are two main deep basins—the Eurasian Basin and the Canadian Basin.

Warm waters of the Atlantic and Pacific Oceans flow northward to the Arctic. Atlantic waters flow into the Arctic Ocean over the 2500 m deep, 500 km wide Fram Strait and the Nordic seas. Pacific waters flow through the shallow and narrow Bering Strait [25]. The outflow of cold waters is through the Fram Strait via the East Greenland Current and the Canadian HAA. Surface currents move counter clockwise along the Arctic coast from Atlantic to Pacific on the Eurasian side and from Pacific to Atlantic on the North American side [26].



**Fig 1. The Arctic region.** An Azimuthal Equal-Area projection of the Arctic region, using the Arctic Circle (66° 33.5' N) as the boundary of the Arctic—approximately the limit of the midnight sun and polar night. All significant shelf seas are named, plus some seas that extend south of the Arctic Circle (eg. the Bering Sea). HAA identifies the Canadian High Arctic Archipelago. The Lomonosov Ridge crosses the Arctic Ocean near the North Pole (NP) and divides the Arctic's two main deep basins—the Canadian and Eurasian Basins. This aseismic ridge is 1 800km long, and rises 1 800–3 400m above the basin floor.

doi:10.1371/journal.pone.0120204.g001

## Data gathering and processing

An Arctic Hydrozoa list, including the zoogeographical affinity and reproductive strategy, is based on data extracted from the literature [16–21,27–87] (S1 Table). The species list was checked and rationalised for possible synonyms and the validity of each species verified with the World Register of Marine Species [88] (for list of synonyms see S2 Table). Species endemic to the Aleutian Islands and present only in Iceland were excluded from the analyses, as species occurring on the southernmost border of the study area were not good representatives of the Arctic region. The accuracy of the database extracted from historical sources may be limited by sampling biases (different sampling effort, types of gear), spatial resolution (area extension, lack of precise location information), taxonomic discrepancies (species misidentifications, mis-coding of medusa and hydroid stages) and also by uneven sampling of benthic and pelagic habitats (in favour of benthic forms).

The study area was divided into regions following Spalding's ecoregions [89] with some modifications resulting from, for example, poor representation of some regions, overlapping of bordering regions, lack of detailed coordinates of area sampled in some historical literature. We recognized the following regions: West Greenland, East Greenland, Iceland, Hudson Complex (including Hudson Bay and Strait, Foxe Basin and Ungava Bay), Beaufort Sea & High Arctic Archipelago, East Canada, Barents Sea (including Svalbard Archipelago), White Sea, Kara Sea, Laptev Sea, East Siberian Sea, Chukchi Sea, Alaska & Bering Sea, and the Central Polar Basin.

Species were classified into zoogeographical groups in relation to worldwide occurrence, as follows: 1) Arctic—noted only in high polar regions; 2) Arctic-boreal—occurring in both arctic and boreal waters; 3) boreal—found in temperate waters of the North Atlantic and North Pacific, in the present study found only in the sub-Arctic region, i.e. Iceland or/and the Bering Sea; 4) subtropical-Arctic—occurring from the Arctic to subtropical waters, with the Mediterranean region included; 5) cosmopolitan—distributed widely, and extending to tropical regions.

The species were categorised into three groups based on their life history strategy: 1) holoplanktonic species, spend their whole life as pelagic forms, 2) meroplanktonic species, have both a benthic and a pelagic stage, 3) benthic species, those that reproduce by means of fixed gonophores and those that produce short-lived, reduced medusae (eumedusoids and cryptomedusoids). For the purpose of the analyses, species that produce medusoids are grouped with benthic species because medusoids are short-lived and have limited dispersal ability (after Gibbons et al. [90]).

## Statistical analyses

Two diversity measures independent of sampling effort and sample size were employed to compare diversity at different taxonomic levels in different Arctic regions. Average taxonomic distinctness (AvTD) is the average taxonomic path length between all pairs of species [91]. Variation in taxonomic distinctness (VarTD) is the variance of the taxonomic distinctness between each pair of species about their mean value [91]. Five taxonomic levels were used in calculations: species, genus, family, order, subclass, and equal step levels between successive taxonomic levels were assumed. The master list was the species list of hydrozoan records in the Arctic (268 species). A sample data set was a species list from a particular region.

Multivariate analysis was used to identify patterns of hydroid species distribution. The similarity of species composition between Arctic regions was calculated with the Bray-Curtis index. These regions were then classified into groups by hierarchical agglomerative clustering using group-average linking, and the resulting classification presented as a dendrogram. Cluster and diversity analyses were performed with Primer package v. 6 [91].

Pearson's chi-square test was used to test for differences in the occurrence of hydrozoan species with medusa or polyp stage between the zoogeographical categories and to measure whether the proportions of the groups differed between polar regions.

## Results

### Diversity and composition

In the Arctic, the class Hydrozoa is represented by two subclasses, six orders, 54 families, 140 genera and 305 species (S1 Table, Table 1). In all, 37 species were excluded from further analyses due to uncertainty about their distribution or taxonomic status, or scarcity of worldwide records (see S1 Table, species marked with a star). Fifty two percent of the species belonged to 20 families of the order Leptothecata, and 32% to 18 families of Anthoathecata. The remaining species belonged to the orders Siphonophorae (7%), Trachymedusae (5%), Narcomedusae (3%) and Limnomedusae (1%).

The fauna was dominated by the family Sertulariidae with 62 species (21% of the hydrozoan species known for the Arctic region). Sertulariidae was the most species-rich family in each studied Arctic region (from seven species in the Beaufort & High Arctic Archipelago (HAA) to 44 species in Alaska & Bering Sea). The next most species-rich families were Haleciidae (7%), and Campanulariidae (5%).

Highest species richness was noted in the Barents Sea, and lowest in the Hudson Complex, Beaufort Sea & HAA and Central Polar Basin (CPB) (Table 2).

The AvTD values for the studied regions generally fell within the 95% probability funnel. However, the value for most of the regions lay below the expected mean (Fig. 2a). Two regions had AvTD values below the expected average for the master list (White Sea and Iceland), and values for the next five regions were situated on the lower limit of the funnel (i.e., Hudson Complex, Kara, Norwegian and Barents Seas and Alaska & Bering Sea). The CPB and the Beaufort Sea & HAA, although having the lowest species richness had an AvTD significantly above expectation. In almost all regions (except Iceland) the VarTD fell within expected limits (Fig. 2b).

Cluster analysis was used to examine the similarity of species occurrence in different Arctic regions, and clustered regions into three groups. The first group comprised the CPB and the Beaufort Sea & HAA; the second group included Alaska & Bering Sea; the third group was split

**Table 1. Species richness (N) and percentage of Hydrozoa in the Arctic and globally.**

Orders	Arctic N	Arctic %	World N	World %
Leptothecata	148	53	1795	59
Anthoathecata	79	32	961	32
Siphonophorae	19	7	166	5
Limnomedusae	2	1	33	1
Narcomedusae	7	3	36	1
Trachymedusae	13	5	50	2
Actinulida	-	-	11	0.4
Total	268	100	3052	100

Global data after Gibbons et al., 2010a (extracted from Bouillon et al., 2006), excluding all doubtful or invalid species, or synonyms. N—number of species, %—percentage of species numbers of particular order in the total number of species.

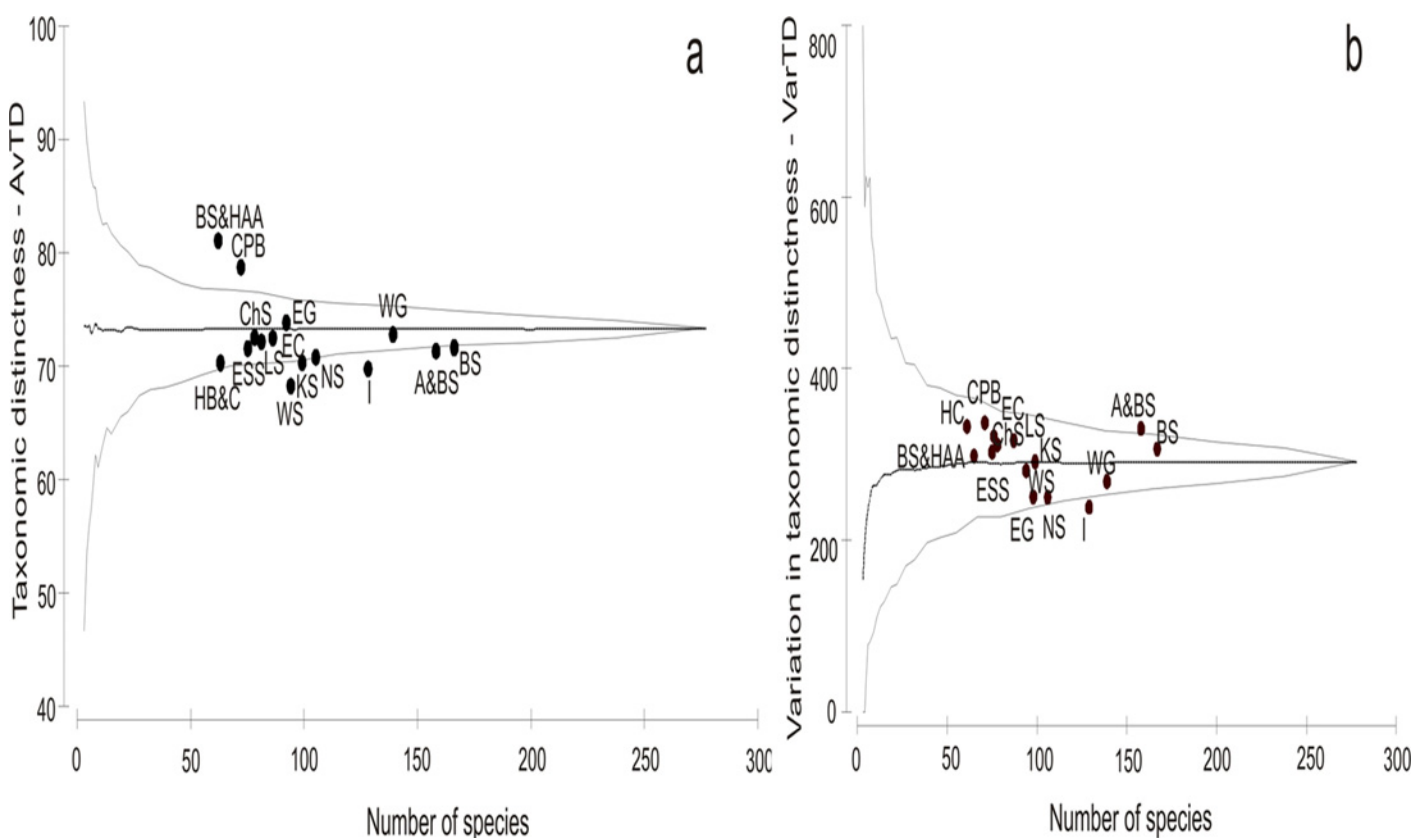
doi:10.1371/journal.pone.0120204.t001



**Table 2. Number of Hydrozoa taxa (N), average taxonomic distinctness (TD) and variation in taxonomic distinctness (VarTD) in the Arctic regions.**

Region	N of subclasses	N of orders	N of families	N of genera	N of species	TD	VarTD
Iceland—I	2	4	34	70	128	69.81	238.82
W Greenland—WG	2	6	35(36)	83	139	72.80	270.81
E Greenland—EG	2	6	33	63	92	73.86	245.86
Barents Sea—BS	2	6	38(39)	86	167	71.56	306.42
White Sea—WS	2	5	24(25)	49	94	68.25	281.23
Kara Sea—KS	2	6	29(30)	53	99	70.29	291.71
Laptev Sea—LS	2	6	26(27)	50	86	72.50	319.83
East Siberian Sea—ESS	2	6	25(26)	43	75	71.56	303.11
Chukchi Sea—ChS	2	6	23(24)	44	78	72.53	311.53
Alaska & Bering Sea—A&BS	2	6	39	73	149	71.33	330.37
Beaufort Sea & High Arctic Archipelago—BS&HAA	2	6	30(31)	56	57	80.98	304.81
East Canada—EC	2	5	28	53	82	72.92	321.98
Hudson Complex—HC	2	5	18	36	62	70.11	326.75
Central Polar Basin—CPB	2	6	40(41)	62	72	78.73	332.67

doi:10.1371/journal.pone.0120204.t002



**Fig 2. Funnel plot for simulated average taxonomic distinctness (AvTD) (a) and variation in taxonomic distinctness (VarTD) (b).** Funnel plot is based on presence/absence data of Hydrozoa against observed number of species, in each Arctic region (black points). Thick line denotes AvTD for the master list. Thin lines indicate 95% probability limits for simulated AvTD. Abbreviations of regions: I—Iceland, WG—West Greenland, EG—East Greenland, BS—Barents Sea, WS—White Sea, KS—Kara Sea, LS—Laptev Sea, ESS—East Siberian Sea, CHS—Chukchi Sea, A&BS—Alaska & Bering Sea, BS&HAA—Beaufort Sea & High Arctic Archipelago, EC—East Canada, HC—Hudson Complex, CPB—Central Polar Basin.

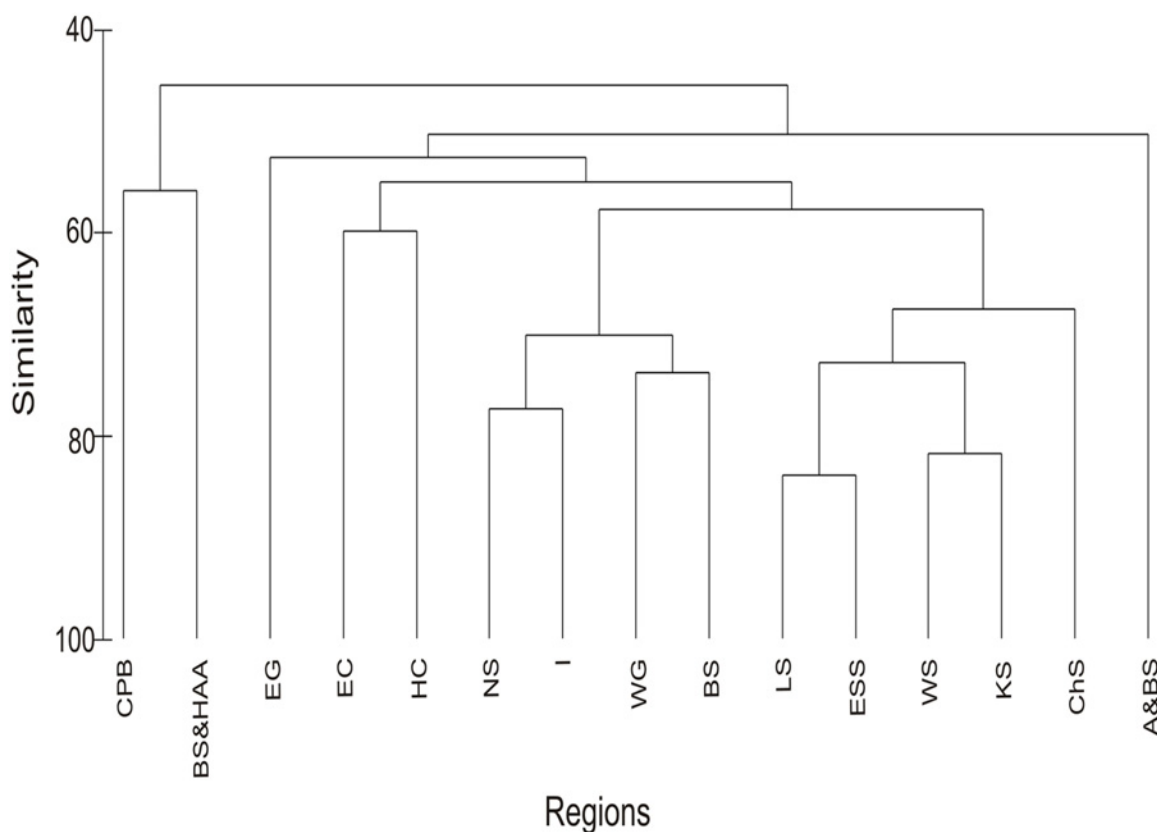
doi:10.1371/journal.pone.0120204.g002

into four subgroups: (a) East Canada and Hudson Complex, (b) Norwegian Sea, Iceland, the Barents Sea and Western Greenland, (c) White and Kara Seas, East Siberian and Laptev Seas and Chukchi Sea, and (d) Eastern Greenland (Fig. 3).

## Zoogeographical affinities

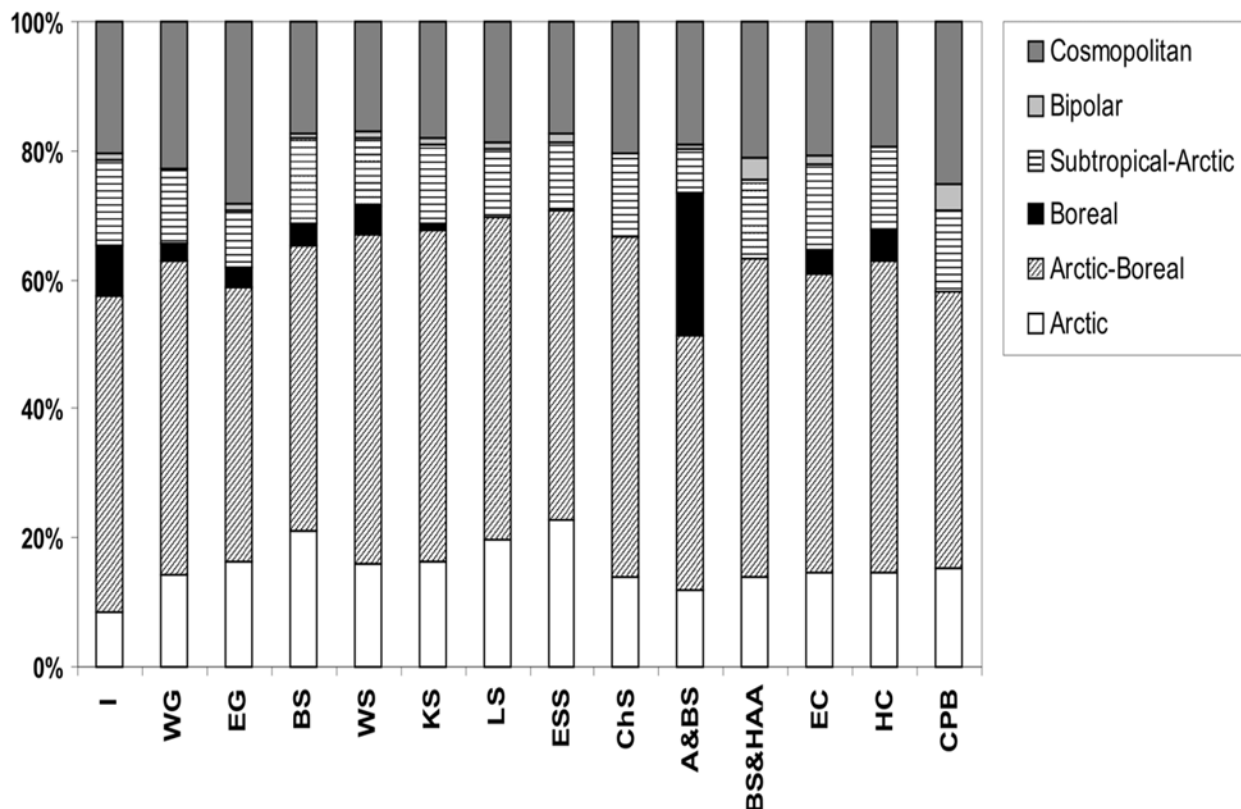
The zoogeographical affinity of each species is presented in the S1 Table. Most species (103 species, 38%) were classified as Arctic-boreal. Nineteen per cent of species (50 species) were endemic to the Arctic region. The proportions of widely distributed taxa such as those ranging from subtropical to Arctic and cosmopolitan were 10% and 19%, respectively. Boreal representatives (34 species) constituted 13% of the total number of species.

The proportions of zoogeographical groups were similar among the studied polar regions (Fig. 4). Each region was dominated by Arctic-Boreal species from 39% in Alaska & Bering Sea to 54% in the Chukchi Sea. The highest ratio of Arctic species (approximately 20%) was noted in the Barents and East Siberian Seas. Boreal species occurred in higher numbers only in Alaska & Bering Sea (22% of all species); in other regions this group reached from 0 to 8%.



**Fig 3. Dendrogram resulting from cluster analysis of the Bray—Curtis similarities in Arctic and subarctic water basins.** Analysis based on presence/absence data of hydrozoan species list. Abbreviations of regions: I—Iceland, WG—West Greenland, EG—East Greenland, BS—Barents Sea, WS—White Sea, KS—Kara Sea, LS—Laptev Sea, ESS—East Siberian Sea, CHS—Chukchi Sea, A&BS—Alaska & Bering Sea, BS&HAA—Beaufort Sea & High Arctic Archipelago, EC—East Canada, HC—Hudson Complex, CPB—Central Polar Basin.

doi:10.1371/journal.pone.0120204.g003



**Fig 4. Proportion of different zoogeographical groups of Hydrozoa in the Arctic regions.** Abbreviations of regions: I—Iceland, WG—West Greenland, EG—East Greenland, BS—Barents Sea, WS—White Sea, KS—Kara Sea, LS—Laptev Sea, ESS—East Siberian Sea, ChS—Chukchi Sea, A&BS—Alaska & Bering Sea, BS&HAA—Beaufort Sea & High Arctic Archipelago, EC—East Canada, HC—Hudson Complex, CPB—Central Polar Basin.

doi:10.1371/journal.pone.0120204.g004

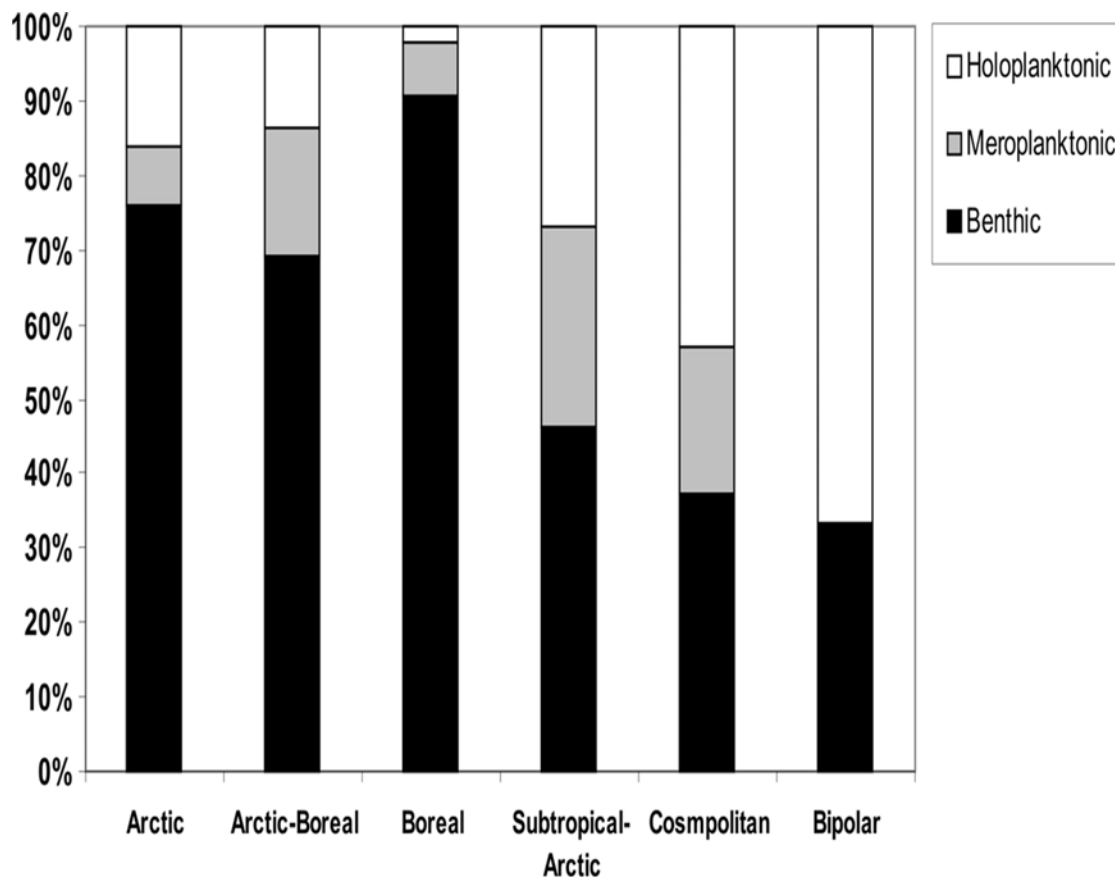
## Life history strategy

Most of the species in the studied region was benthic (64%, 171 species). Twenty percent of species (54 species) displayed a holoplanktonic life history, while 16% (43 species) possessed both benthic and planktonic stages. The number of species with various life cycle strategies differed between the Arctic species pool and the global species pool (data extracted from Bouillon et al. [2] after Gibbons et al. [90]) (Pearson Chi-square goodness of fit test:  $\chi^2 = 10.5$ ,  $df = 2$ ,  $p = 0.005$ ). While benthic species represented a similar ratio in both pools, the number of holoplanktonic species was proportionally greater in the Arctic and the number of meroplanktonic species lower.

Frequency distribution of species with different life history strategies varied among zoogeographical groups (Pearson Chi-square test of independence:  $\chi^2 = 44.48$ ,  $df = 8$ ,  $p < 0.001$ ) (Fig. 5). Benthic species dominated in the Arctic, Arctic-Boreal and Boreal groups (70–90%), while species having a pelagic life stage (meroplanktonic and holoplanktonic) were more frequent in the subtropical-Arctic, cosmopolitan and bipolar groups (they comprised from 54 to 67%).

The CPB and Beaufort Sea & HAA had a higher proportion of species with a pelagic stage (mostly holoplanktonic taxa) during their life history (i.e. more than 50%), compared to the other regions where, in contrary, benthic species constituted more than 60% (Fig. 6).





**Fig 5. Proportion of Hydrozoa life history strategy by zoogeographical groups.**

doi:10.1371/journal.pone.0120204.g005

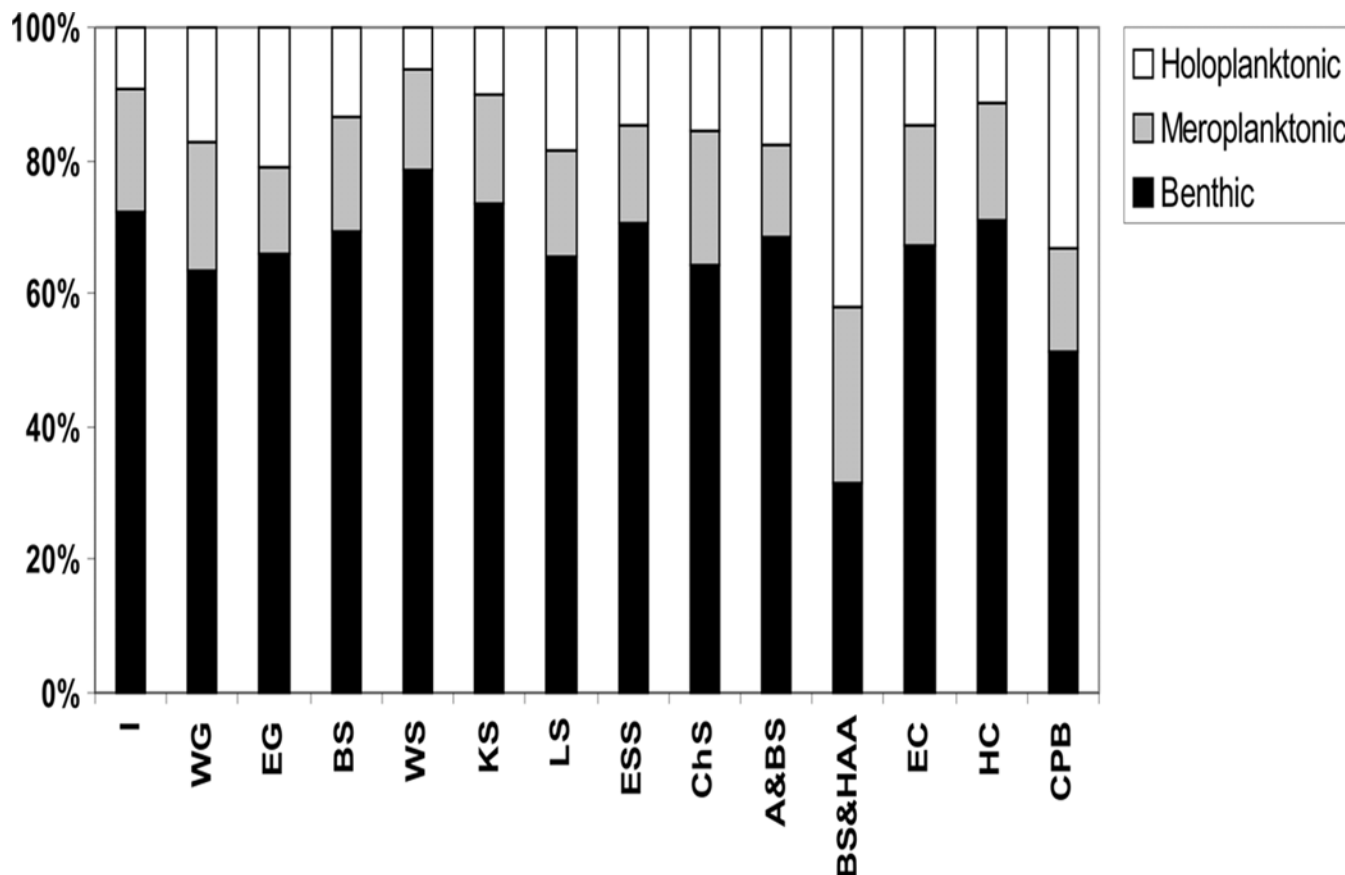
## Discussion

### Species richness and composition

The species list compiled from the literature revealed an overall hydrozoan species richness for the Arctic of 268. Species in the order Leptothecata dominate (55%), with Anthoathecata forming the second largest group (29%). Such proportion almost mirrors that of the global species pool, where the global ratio between these two orders is 59% to 32% [90]. Slightly higher numbers of species of Siphonophorae, Narcomedusae and Trachymedusae are observed in the Arctic region compared to the global data set, while Limnomedusae constitute 1% of hydroid species in both the Arctic and globally.

The most species rich families in the Arctic are Sertulariidae (21%) which dominated in each studied region, Haleciidae (7%) and Campanulariidae (5%). These families are the most speciose in many areas in the world, including, for example, the Indian Ocean [92], Bay of Fundy [93], west coast of Australia [94], Kurile Islands [95] and Antarctica [96]. Globally, Sertulariidae is also the most speciose family in the Hydrozoa (17%) [2].

Species richness (S) and other diversity indices (e.g., Shannon index) are heavily dependent on sampling effort [91]. When sampling effort is unknown or unequal (especially when it relates to historic data sets as in our case) any comparison of diversity using standard measures is problematic [91]. In addition to species richness, we used other tools (taxonomic distinctness indices) that measure biodiversity at the taxonomic level and allow comparison of species-related diversity between unbalanced samples.



**Fig 6. Proportion of Hydrozoa life history strategies in different Arctic regions.** Abbreviations of regions: I—Iceland, WG—West Greenland, EG—East Greenland, BS—Barents Sea, WS—White Sea, KS—Kara Sea, LS—Laptev Sea, ESS—East Siberian Sea, ChS—Chukchi Sea, A&BS—Alaska & Bering Sea, BS&HAA—Beaufort Sea & High Arctic Archipelago, EC—East Canada, HC—Hudson Complex, CPB—Central Polar Basin.

doi:10.1371/journal.pone.0120204.g006

Most of the Arctic regions (except the White Sea and Iceland) fall into the probability funnel for simulated average taxonomic distinctness (AvTD) and variation in taxonomic distinctness (VarTD), revealing that they involve good representatives of Arctic taxonomic diversity. The Iceland species list is not complete because boreal species that were only present in Iceland were not included in the Arctic master list (S1 Table). The species composition in Iceland can only be treated as an approximation. The White Sea sublist includes species that are most closely related, i.e. AvTD is the lowest. Ninety four of these species belong to five orders and 24 families, which means that almost every four species belong to the same family.

Some regions share patterns of taxonomic relatedness of species. For instance, Alaska & Bering Sea and the Barents Sea are characterized by high species richness and a VarTD value also above the expected level, while AvTD is at the lower limit of the funnel. Low AvTD and high VarTD values can be attributed to the relatively lower number of higher taxonomic ranks (compared to the number of species) and uneven species distribution across the hierarchical taxonomic tree.

In the Beaufort Sea & High Arctic Archipelago (HAA) and the Central Polar Basin (CPB) both AvTD and VarTD reached their highest values, even though species richness was low in these regions. This indicates that these groups of species were taxonomically very distinct (about every second species in a different family). These results confirm the independence of both taxonomic distinctness indices from the sampling effort and species richness. Increased

taxonomic distinctness of assemblages has been attributed to greater stability of environmental conditions both in an evolutionary and an ecological context [97]. The Beaufort Sea & HAA and the CPB are characterized by greater overall depth compared to other shelf regions in the Arctic and successful faunistic exchange across the underwater ridges [50].

Cluster analysis was used to analyze the similarity of species occurrence in different Arctic regions. Regions separated into two main clusters: firstly, the CPB and Beaufort Sea & HAA, at 55% similarity. As mentioned above, both regions shared similar trends in diversity indices: low species richness but taxonomically very distinct (high AvTD and VarTD) and in species composition: lack of boreal species, lower percentage of benthic taxa and higher percentage of taxa having a pelagic phase (mostly holoplanktonic).

Secondly, a more diverse assemblage, consisting of three groups and two regions split off from the rest. The distinction of Alaska & Bering Sea is clearly noticeable. This region is geographically the most isolated from the Arctic Ocean. The Bering Strait is a shallow (50 m deep) and narrow (82 km wide at its narrowest point) connection between the Bering Sea and the Chukchi Sea. Thirty six species were found exclusively in Alaska & Bering Sea and did not enter the Bering Strait and Arctic Ocean. Of them, 21 species are boreal and the Bering Sea is the northernmost limit of their distribution. Fourteen species of the family Sertulariidae are absent from other Arctic regions.

E Greenland is another region separated from the remaining groups. This is due to the single occurrence of six rare species that were exclusively noted in this region. Cosmopolitan siphonophores (*Heteropyramis crystallina*, *H. maculata* and *Muggiaea kochi*) and the hydromedusa (*Hebella scandens*) were most likely occasional visitors. Single records of *Lafoea symmetrica* and *Hydractinia arctica* are known only from deep waters. When these species are excluded from the analysis the grouping is totally different, with E Greenland combining with W Greenland, E Canada, Iceland, the Barents and Norwegian Seas. Analyses with a presence/absence database introduce bias resulting from giving equal weight to all species, regardless of whether they are rare or common [91].

Surprisingly, the Chukchi Sea hydroid fauna is more similar to the Arctic Russian seas fauna (i.e., Laptev, East Siberian, White, Kara) than to the Alaska & Bering Sea fauna. The majority of species in the Chukchi Sea have a circumpolar distribution. Only 4 species were restricted to Pacific Arctic waters: *Earleria cellularia* and *Thuiaria cylindrica* occur only in Pacific waters, while two others *Aegina citrea* and *Nectadamas diomedae* have a cosmopolitan distribution. The affinity of the Chukchi Sea hydroid fauna to Pacific waters is not noticeable in the species composition. This result is not in accordance with earlier studies by Dunton [14] who observed that the benthic assemblages of the Chukchi and East Siberian seas are dominated by Pacific fauna, nor those by Stepanjants [76], who noted the separation of hydroid fauna into western and eastern regions delimited by the Kara and Laptev seas.

The next group, in which the Norwegian and Barents seas, W Greenland and Iceland are clustered together, is under the direct influence of Atlantic waters, which may explain the similarity in species composition in these regions. Relatively warm and saline Atlantic water flows northward with the main inflow along the Norwegian and Barents seas and west Svalbard continental margins [98]. Another branch, a continuation of the North Atlantic Drift, flows parallel to the western coast of Greenland as the West Greenland Current [99]. Thus it is not unexpected that the fauna of W Greenland is more similar to that of the Barents Sea than, for example, the fauna of E Canada and Hudson Complex, which is under the influence of Arctic water flowing from the north. Fresh and cold Arctic water, mostly of Pacific origin, enters Baffin Bay through the HAA on the north and runs south along the shelf edge of western Baffin Bay and throughout the Hudson Complex to the Labrador Sea [99]. The majority of species found in this region have a circumpolar distribution with records noted from the Alaska &

Bering Sea (85% of species in Hudson Complex and 70% in E Canada) which indicates that they are of Pacific origin colonizing these regions from the North.

## Zoogeographical affinity, life history and dispersal strategy

The hydrozoan fauna in the Arctic is dominated by Arctic-boreal species and includes a small fraction of exclusively Arctic species (19%). The dominance by Arctic-boreal forms, the lack of endemism of higher taxa and the very low level of species endemism is typical of Arctic fauna and flora [76,100,101]. The key explanation for this phenomenon might be the very short evolutionary history of the Arctic ecosystem and the fact that the Arctic is not geographically isolated [13,14,100]. The Arctic Ocean acquired its cold-water attribute (e.g., temperature drop, perennial ice cover) in the Pliocene, approximately 4 million years ago [13]. At that time, there were cycles of glacial and inter-glacial conditions with resultant ice sheet changes and global sea level variation. These events caused destruction of marine life in vast areas of the Arctic shelf biota [14]. Recolonization began relatively recently on the geological time scale. The last glaciation ended approximately 13–12 ka, enabling the present-day Arctic community to start developing. Therefore, the Arctic region is considered to be a young biota that is not yet completely established, but is still in a phase of colonization [13,14]. The species that are endemic to the Arctic and some boreal-Arctic species, most likely survived glaciations in refugia (i.e. isolated ice-free areas that retained the environmental conditions previously more widespread) [102]. Geological evidence indicates that extensive southern glacial refugia existed during the Last Glacial Maximum, 25–18 ka [15]. Lately, results of molecular studies suggest the existence of small, periglacial isolated northern ice-free areas [15], but no fossil evidence has so far been found to confirm continuous *in situ* survival of macrofauna in these areas [103]. The Chukchi, Beaufort, Laptev and East Siberian seas were unglaciated during this period but largely emergent [104,105]. Some shelf fauna may have moved southwards into the Atlantic and Pacific, retreated into unglaciated areas, or found refuge in the deeper Arctic basin [106], the latter theory being supported by the relatively large numbers of species found today within the Arctic Ocean which inhabit both shelves and continental slopes [107].

The Arctic is influenced by both Pacific and Atlantic waters, but more so by the Atlantic [26]. The connection with the Atlantic and Pacific suggests that colonization from the boreal seas could take place relatively easily unless physiological barriers (e.g., caused by differences in water temperature) are also important. These influences are reflected in the predominance of the Arctic-boreal component of the Arctic fauna which dominates each region studied. The proportion of different zoogeographical groups is similar across all regions in the Arctic, with the exception of Alaska & Bering Sea where boreal forms contributed a higher share.

Predominance of benthic species over holo- and meroplanktonic species is a common attribute of Hydrozoa worldwide. In the Arctic, 64% of species are benthic and have only a planula larva for their dispersal stage. Even in the CPB and Beaufort & HAA, benthic species constitute a high proportion of the community. The largest number of more widespread species in the Arctic (present in most ecoregions) belong to families that completely lack the medusa stage, including Sertulariidae and Haleciidae. Moreover, many cosmopolitan hydrozoans both in the Arctic (present study) and globally lack a pelagic stage [11]. Therefore, the presence of a pelagic stage (holo- or meroplanktonic) was not necessary for successful recolonization of the Arctic. However, recent molecular analyses suggest that some benthic cosmopolitan species (e.g., *Obelia geniculata*, *Lafoea dumosa*, *Nemertesia antennina*, *Plumularia setacea*) could in fact be cryptic species complexes [11,108,109]. Unfortunately, Arctic specimens have not been incorporated in such analyses as yet.

The traditional view of Hydrozoa is that holo- and meroplanktonic species will have a better dispersal potential and a more extensive distribution than benthic species, whose only means of dispersal is a rather short-lived, lecithotrophic planula larva [110,111]. This idea has been derived from the general concept of a positive relationship between the length of the planktonic larval stage and geographic distribution in marine benthic invertebrates [112,113]. However, this idea has been demonstrated to be false in, for example, some gastropods [114], ascidians, scleractinian corals, most bryozoans and hydroids [115]. The successful colonization of remote habitats like Rockall island by benthic species with no planktonic larva [114] or the Azores predominantly by hydrozoans lacking a medusa phase [6], are good examples of far away colonization without a long-lived mobile stage. In most cases, it is a benthic stage that is responsible for long distance dispersal via rafting on floating objects [115]. Hydrozoans are reported to be very common rafters [6,116], with a great ability to disperse (from <100 km up to > 5000 km) on other organisms, pieces of wood, ships, and plastic items [110,116–118]. Dispersal during the benthic stage may be advantageous over long-lived larval or medusae dispersal. To establish a population in a distant area, two medusae (male and female) have to arrive at that place at the same time to mate. The probability that this may happened decreases with distance, due to the medusae's life span and diffusion in the open ocean. Similarly, once larvae reach a distant place it must be a suitable one for settlement and metamorphosis into a hydroid colony. This colony can asexually grow and expand but in order to complete the life cycle, another colony must be present in the vicinity to provide gametes of another sex. In contrast, rafting may supply a group of individuals, probably sometimes of both sexes, which can reproduce amongst themselves. If a fertilized female colony rafts, it will brood planulae, which after settlement may establish a new population. Other means of dispersal are also known in Hydrozoa. The free hydranths may detach from a colony, travel for up to 30 days and resettle or release larvae [119,120]. Frustules or larva-like propagules produced by budding may cover some distance and themselves become reproductive [121]. If hydrozoans survived the last glaciations in northern glacial refuges (no evidence is available so far), this would also have allowed them to expand their distribution from these refuges into the nearby shelf areas with gradually retreating ice. However, this probably applies only to the most adaptable species or to species that are able to survive critical environmental stress by the formation of tolerant resting stages. Extreme physical stress causes many hydroids to transform into dormant phases, and colony regeneration follows the return of favourable conditions [122]. Different kinds of species quiescence, including dormant cysts and resting eggs, or dormant tissues in stems and stolons occur in many Arctic species (e.g. *Eudendrium album* and *Sertularia argentea* [122], *Clava multicornis* [123], *Gonothyraea loveni* [124]).

A totally different strategy is employed by holoplanktonic siphonophores, most of which are hermaphrodite, or monoecious (both sexes present on the same colony) [53] to reduce the risk of not finding a mate in a vast ocean. This may be the reason why most Siphonophora are successful cosmopolitans [125]. The majority of widely distributed hydrozoan species are mero- or holoplanktonic. Although Kramp [48] has remarked that both the medusae stage and the planula are too short lived to cross oceanic distances, pelagic stage may play a role in dispersal. Wide distribution of holopelagic hydrozoans worldwide and in the waters off South Africa has been demonstrated by Gibbons et al. [90,126].

## Limitations of the data collected

Data collected and analysed in the present study are subject to bias resulting from variation in the sampling effort undertaken through historical time in particular regions, extension of ecoregions and their accessibility. There is also a strong imbalance in the literature which

underestimates the pelagic community of Hydrozoa in favour of higher sampling effort of benthic habitats; this imbalance is further exacerbated by the destructive nature of net sampling which destroys delicate jellyfish zooplankton into unrecognizable blobs. Another potential limitation of the present study (and any meta-analysis) results from integration of data through time and space when and where different people identified species in different time and regional scales. We tried to eliminate this issue by checking all possible synonyms ([S2 Table](#)).

## Conclusions

The total species richness of Hydrozoa in the Arctic was 268 with Sertulariidae being the most speciose family. The hypothesis that the presence of a pelagic stage (holo- or meroplanktonic) was not necessary for successful recolonization of the Arctic is supported by our analyses. The predominance of benthic Hydrozoa suggests that the Arctic could have been colonised after the Last Glacial Maximum by hydroids rafting on floating substrata, or recolonizing from glacial refuges. Nevertheless, as holoplanktonic or meroplanktonic species outweigh the benthic species in widely distributed categories such as cosmopolitan, subtropical-Arctic and bipolar, we cannot deny that having the medusa or pelagic stage (e.g. as in the case for Siphonophora) is also an important mean of dispersal. Most Arctic hydrozoan species have Arctic-boreal distributions. The hydrozoan fauna shows a very low level of endemism, a common phenomenon in other Arctic macrofaunal groups.

We acknowledge the severe problem of imbalance in knowledge of particular regions in the Arctic as well as in sampling effort between pelagic versus benthic domains. The results of our comparative analyses may therefore change with time, when more data are available.

## Supporting Information

**S1 Table. List of Arctic species with their life history strategies and zoogeographical affinities.**

(DOC)

**S2 Table. Arctic species with their synonyms used in particular reference item.**

(DOC)

## Acknowledgments

Special thanks to Brian Rosen who kindly offered constructive criticism at the very early draft of manuscript. We are indebted to Peter Schuchert for discussions on various aspects of presented ideas and help in collecting literature and to Kevin Raskoff and anonymous reviewers for valuable comments on this paper. We thank Barry Mapstone for preparing a map of the Arctic.

## Author Contributions

Conceived and designed the experiments: MR PK. Performed the experiments: MR PK. Analyzed the data: MR PK. Contributed reagents/materials/analysis tools: MR GM. Wrote the paper: MR PK GM.

## References

1. Daly M, Brugler MR, Cartwright P, Collins AG, Dawson MN, Fautin DG, et al. The phylum Cnidaria: A review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa*. 2007; 182: 127–182.
2. Bouillon J, Gravili C, Pagès F, Gili J-M, Boero F. An introduction to Hydrozoa. Muséum national d'Histoire naturelle: Paris, France; 2006.



3. Cornelius PFS. Evolution in leptolid life-cycles (Cnidaria: Hydrozoa). *J Nat Hist*. 1990; 24: 579–594.
4. Leclère L, Schuchert P, Cruaud C, Couloux A, Manuel M. Molecular phylogenetics of Thecata (Hydrozoa, Cnidaria) reveals long-term maintenance of life history traits despite high frequency of recent character changes. *Syst Biol*. 2009; 58(5): 509–526. doi: [10.1093/sysbio/syp044](https://doi.org/10.1093/sysbio/syp044) PMID: [20525605](https://pubmed.ncbi.nlm.nih.gov/20525605/)
5. Cartwright P, Nawrocki A. Character evolution in Hydrozoa (phylum Cnidaria). *Integr Comp Biol*. 2010; 50(3): 456–472. doi: [10.1093/icb/icq089](https://doi.org/10.1093/icb/icq089) PMID: [21558215](https://pubmed.ncbi.nlm.nih.gov/21558215/)
6. Cornelius PFS. The Azores hydroid fauna and its origin, with discussion of rafting and medusa suppression. *Arquipélago*. 1992a; 10: 75–99. PMID: [25606133](https://pubmed.ncbi.nlm.nih.gov/25606133/)
7. Sommer C. Larval biology and dispersal in *Eudendrium racemosum* (Hydrozoa, Eudendriidae). *Sci Mar*. 1992; 56: 205–211.
8. Jackson JBC, Coates AG. Life-cycles and evolution of clonal (modular) animals. *Philos Trans R Soc Lond B Biol Sci*. 1986; 313: 7–22.
9. Hughes RN. A functional biology of clonal animals. London: Chapman and Hall; 1989.
10. Pagliara P, Bouillon J, Boero F. Photosynthetic planulae and planktonic hydroids: contrasting strategies of propagule survival. *Sci Mar*. 2000; 64(Suppl.1): 173–178.
11. Schuchert P. High genetic diversity in the hydroid *Plumularia setacea*: A multitude of cryptic species or extensive population subdivision? *Mol Phylogenet Evol*. 2014; 76: 1–9. doi: [10.1016/j.ympev.2014.02.020](https://doi.org/10.1016/j.ympev.2014.02.020) PMID: [24602986](https://pubmed.ncbi.nlm.nih.gov/24602986/)
12. Golikov AN, Scarlato OA. (1989) Evolution of Arctic ecosystems during the Neogene period. In: Herman Y, editor. *The Arctic Seas Climatology, Oceanography, and Biology*. New York: Van Nostrand Reinhold; 1989. pp. 257–279.
13. Piepenburg D. Recent research on Arctic benthos: common notions need to be revised. *Polar Biol*. 2005; 28: 733–755.
14. Dunton K. Arctic biogeography: the paradox of the marine benthic fauna and flora. *Trends Ecol Evol*. 1992; 7(6): 183–189. doi: [10.1016/0169-5347\(92\)90070-R](https://doi.org/10.1016/0169-5347(92)90070-R) PMID: [21236004](https://pubmed.ncbi.nlm.nih.gov/21236004/)
15. Maggs CA, Castilho R, Foltz D, Henzler C, Jolly MT, Kelly J, et al. Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology*. 2008; 89(11): 108–122. PMID: [19097488](https://pubmed.ncbi.nlm.nih.gov/19097488/)
16. Clark SF. Report on the hydroids collected on the coast of Alaska and the Aleutian Islands, by W. H. Dall, U.S. coast survey, and party, from 1871 to 1874 inclusive. *Proc Acad Nat Sci Philadelphia*. 1877; 28: 209–238.
17. Marktanner-Turneretscher G. Hydroiden von Ostspitsbergen. *Zool Jahrb, Abt Syst Geogr Tiere*. 1895; 8: 391–438.
18. Miglietta MP. *Hydractinia antonii* sp. nov.: a new, partially calcified hydractiniid (Cnidaria: Hydrozoa: Hydractiniidae) from Alaska. *J Mar Biol Assoc U.K.* 2006; 86: 993–996.
19. Raskoff KA. *Bathylorus bouillonii*: a new genus and species of deep-sea jellyfish from the Arctic Ocean (Hydrozoa, Narcomedusae, Aeginidae). *Zootaxa*. 2010; 2361: 57–67.
20. Ronowicz M, Schuchert P. *Halecium arcticum*, a new hydroid from Spitsbergen (Cnidaria: Hydrozoa). *Zootaxa*. 2007; 1549: 55–62.
21. Piraino S, Bluhm BA, Gradinger R, Boero F. *Sympagohydra tuuli* gen. nov. and sp. nov. (Cnidaria: Hydrozoa) a cool hydroid from the Arctic sea ice. *J Mar Biol Assoc U.K.* 2008; 88: 1637–1641.
22. Cusson M, Archambault P, Aitken A. Biodiversity of benthic assemblages on the Arctic continental shelf: historical data from Canada. *Mar Ecol Prog Ser*. 2007; 331: 291–304.
23. Piepenburg D, Archambault P, Ambrose WG Jr, Blanchard AL, Bluhm BA, Carroll ML, et al. Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. *Mar Biodivers*. 2011; 41: 51–70.
24. Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B. How many species are there on Earth and in the ocean? *PLoS Biol*. 2011; 9: e10001127.
25. Tomczak M, Godfrey JS. *Regional oceanography: an introduction*, 2nd edn. Pergamon, Tarrytown, New York; 1994.
26. Jones EP. Circulation in the Arctic Ocean. *Polar Res*. 2001; 20: 139–146.
27. Arai MN, Brinkmann-Voss A. Hydromedusae of British Columbia and Puget Sound. *Can Bull Fish Aquat Sci*. 1980; 204: 1–192.
28. Bonnevie K. Hydrozoa. The Norwegian North-Atlantic Expedition 1876–1878. 1899; 7: 1–103.
29. Broch H. Die Hydroiden der arktischen Meere. *Fauna Arctica*. 1909; 5: 127–248.
30. Broch H. Stylasteridae. The Danish Ingolf-Expedition. 1914; 5(5): 1–26.

31. Cairns SD, Lindner A. A revision of Stylasteriidae (Cnidaria, Hydrozoa, Filifera) from Alaska and adjacent waters. *ZooKeys*. 2011; 158: 1–88. doi: [10.3897/zookeys.158.1910](https://doi.org/10.3897/zookeys.158.1910) PMID: [22303109](https://pubmed.ncbi.nlm.nih.gov/22303109/)
32. Calder DR. Thecate hydroids from the shelf waters of Northern Canada. *J Fish Res Board Can*. 1970; 27(9): 1501–1547.
33. Calder DR. Some athecate hydroids from the shelf waters of Northern Canada. *J Fish Res Board Can*. 1972; 29(3): 217–228.
34. Cooney RT. Bering Sea zooplankton and micronekton communities with emphasis on annual production. In: Hood DW, Calder JA, editors. *The eastern Bering Sea shelf: Oceanography and Resources*. Vol. 2. Seattle: University of Washington Press; 1981. pp. 947–974.
35. Cornelius PFS. North-west European thecate hydroids and their medusae. Part 1. Synopses of the British Fauna (New Series). 1995a; 50.
36. Cornelius PFS. North-west European thecate hydroids and their medusae. Part 2. Synopses of the British Fauna (New Series). 1995b; 50.
37. Dunbar MJ. Marine macroplankton from the Canadian Eastern Arctic. II. Medusae, Siphonophora, Ctenophora, Pteropoda and Chaetognatha. *Can J Res*. 1942; 20(D): 71–77.
38. Fisher WK. Hydrocorals of the North Pacific Ocean. In: *Proceedings of the United States National Museum*, Tom 84. U.S. Government Printing Office; 1938. pp. 493–554.
39. Fraser CM. Hydroids of the Atlantic coast of North America. The University of Toronto Press, Toronto; 1944.
40. Grainger EH. Zooplankton from the Arctic Ocean and adjacent Canadian waters. *J Fish Res Board Can*. 1965; 22(2): 543–564.
41. Grainger EH, Grohe K. Zooplankton data from the Beaufort Sea, 1951 to 1975. *Fish Mar Serv Res Dev Tech Rep*. 1975; 591.
42. Hand C, Kan LB. The medusae of Chukchi and Beaufort seas of the arctic ocean including the description of a new species of *Eucodonium* (Hydrozoa: Anthomedusae). *Arctic Institute of North America; technical papers*. 1961; 6: 1–23.
43. Jäderholm E. Die Hydroiden des Eisfjords. Bihang till Kungliga Svenska Vetenskapsakademiens Hand-lingar. 1916; 54(4): 1–14.
44. Kramp P. Hydroids collected in West-Greenland Fjords in 1911 and 1912. *Meddelelser om Grønland*. 1932; 91: 1–35.
45. Kramp P. Siphonophora. The Godthaab Expedition 1928. *Meddelelser om Grønland*. 1942; 80(8): 3–24.
46. Kramp P. The zoology of East Greenland. Hydroida. *Meddelelser om Grønland*. 1943; 121: 1–52.
47. Kramp P. Medusae. Part III. Trachylina and Scyphozoa, with zoogeographical remarks on all the medusae of the northern Atlantic. *Danish Ingolf Expedition*. 1947; 5: 1–66.
48. Kramp P. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana-Report*. 1959; 46: 1–283.
49. Kramp P. Synopsis of the medusae of the world. *J Mar Biol Assoc U.K*. 1961; 40: 1–469.
50. Kosobokova K, Hirche H-J. Zooplankton distribution cross the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. *Deep Sea Res Part 1 Oceanogr Res Pap*. 2000; 47: 2029–2060.
51. Kosobokova K, Hanssen H, Hirche H-J, Knickmeier K. Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993. *Polar Biol*. 1998; 19: 63–76.
52. Kosobokova K, Hopcroft RR, Hirche H-J. Patterns of zooplankton diversity through the depths of the Arctic's central basin. *Mar Biodivers*. 2011; 41: 29–50.
53. Mapstone GM. Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters. NRC Research Press, Ottawa, Ontario, Canada; 2009.
54. Margulis RYa. The distribution of siphonophores in the western North Atlantic in summer of 1974. *Vestnik Moskovskogo Universiteta, Ser. XVI Biologiya*. 1978; 3: 1–11.
55. Margulis RYa. A new siphonophore *Rudjakovia plicata* gen. n., sp. n., (Coelenterate, Hydrozoa) from the Polar Basin and some notes on other siphonophores. *Zoological Journal*. 1982; 61: 440–444.
56. Motoda S, Minoda T. Plankton of the Bering Sea. In: Hood DW, Kelly J, editors. *Oceanography of the Bering Sea; Proceedings of the International Symposium for Bering Sea Studies*, Hakodate, Japan, 21 January to 4 February, 1972. University of Alaska, Fairbanks; 1974. pp. 207–241.
57. Naumov DV. Hydroids and Hydromedusae of the USSR. Jerusalem: Israel Program for scientific translation; 1969.

58. Nutting CC. Papers from the Harriman Alaska Expedition. XXI. The hydroids. Proceedings of the Washington Academy of Science. 1901; 3: 157–216.
59. Palerud R, Gulliksen B, Brattegard T, Snell J-A, Vader W. The marine macro-organisms in Svalbard waters. In: Prestrud P, Strøm H, Goldman HV, editors. A catalogue of the terrestrial and marine animals of Svalbard. Tromsø: Norwegian Polar Institute; 2004. pp. 5–56.
60. Petersen KW. Evolution and taxonomy in capitate hydroids and medusae (Cnidaria: Hydrozoa). Zool J Linn Soc. 1990; 100: 101–231.
61. Pugh PR, Pagès F. Is *Lensia reticulata* a diphyine species (Siphonophorae, Calycophora, Diphyidae)? A re-description. Sci Mar. 1995; 59(2): 181–192.
62. Raskoff KA, Purcell JE, Hopcroft RR. Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. Polar Biol. 2005; 28: 207–217.
63. Raskoff KA, Hopcroft RR, Kosobokova KN, Purcell JE, Youngbluth M. Jellies under ice: ROV observations from the 2005 Hidden Ocean Expedition. Deep Sea Res 2 Top Stud Oceanogr. 2010; 57: 111–126.
64. Ronowicz M. Benthic hydroids (Cnidaria: Hydrozoa) from Svalbard waters—biodiversity and distribution. J Mar Biol Assoc U.K. 2007; 87: 1089–1094.
65. Ronowicz M, Włodarska-Kowalczyk M, Kukliński P. Hydroid epifaunal communities in Arctic coastal waters (Svalbard): effects of substrate characteristics. Polar Biol. 2013a; 36: 705–718.
66. Ronowicz M, Włodarska-Kowalczyk M, Kukliński P. Depth- and substrate-related patterns of species richness and distribution of hydroids (Cnidaria, Hydrozoa) in Arctic coastal waters (Svalbard). Mar Ecol. 2013b; 34: 165–176.
67. Schuchert P. Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). Meddelelser om Grønland, Bioscience. 2001; 53: 1–184.
68. Schuchert P. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1. Rev Suisse Zool. 2006; 113: 325–410.
69. Schuchert P. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 3. Rev Suisse Zool. 2008a; 115: 221–302.
70. Schuchert P. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 4. Rev Suisse Zool. 2008b; 115: 677–757.
71. Schuchert P. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 2. Rev Suisse Zool. 2010; 117: 337–555.
72. Schuchert P (2012) North-West European Athecate Hydroids and their Medusae. Synopses of the British Fauna (New Series). 2012; 59.
73. Shirley WD, Leung Y-M (1970) Medusae of the Central Arctic. In: Kobayashi HE, editor. Taxonomic Guides to Arctic Zooplankton II [Technical report no 3, 1960–1970]. University of Southern California Los Angeles, Department of Biological Sciences, Los Angeles; 1970.
74. Shih CT, Figueira AJG, Grainger EH. A synopsis of Canadian marine zooplankton. Bull Fish Res Board Can. 1971; 176: 1–264.
75. Stepanjants SD. Siphonophores of the seas of the USSR and the northern part of the Pacific Ocean. Opredeleteli po Faune SSSR; 1967.
76. Stepanjants SD. Hydrozoa of the Eurasian Arctic Seas. In: Herman Y, editor. The Arctic Seas Climatology, Oceanography, and Biology. New York: Van Nostrand Reinhold; 1989. pp. 397–430.
77. Stepanjants SD. Hydrozoa of the East Siberian Sea. Issledovaniya Fauny Morei. 1994; 48: 116–142.
78. Stepanjants SD. Subphylum Medusozoa. Classes Hydrozoa, Siphonophora, Scyphozoa. In: Sirenko BI, editor. List of species of free-living Invertebrates of Eurasian Arctic Seas and Adjacent deep waters. Issledovaniya Fauny Morei. 2001; 51(59): 31–36.
79. Stepanjants SD, Kosobokova KN. Medusae of the genus *Rhabdoon* Hydrozoa: Anthomedusae: Tubularioidea in the Arctic Ocean. Mar Biol Res. 2006; 2(6): 388–397.
80. Stepanjants SD, Svoboda A. The genus *Gymnogonos* (Anthoathecata: Capitata: Corymorphidae)—redescription of known species and description of a new species from the North Pacific. J Mar Biol Assoc U.K. 2008; 88: 1619–1629.
81. Thiel ME. Übersicht über die Hydromedusen der Arktis. Fauna Arctica. 1932; 6: 119–158.
82. Uchida T. Medusae from the Arctic Ocean. Publications of the Seto Marine Biological Laboratory. 1969; 17(4): 285–287.
83. van Soest RWM. Planktonic coelenterates collected in the North Atlantic Ocean. Bijdragen tot de Dierkunde. 1973; 43(1): 119–125.

84. Voronkov A, Stepanjants SD, Hop H. Hydrozoan diversity on hard bottom in Kongsfjorden, Svalbard. *J Mar Biol Assoc U.K.* 2010; 90: 1337–1352.
85. Węśławski JM, Kwaśniewski S, Wiktor J. Winter in a Svalbard fiord ecosystem. *Arctic.* 1991; 44(2): 115–123.
86. Yashnov VA. Hydromedusae. In: Gaevskoy NL, editor. Check List Fauna Flora northern seas U.S.S.R., Moscow; 1948. pp. 65–74.
87. Zelickman EA. Distribution and ecology of the pelagic hydromedusae, siphonophores and ctenophores of the Barents Sea, based on perennial plankton collections. *Mar Biol.* 1972; 17: 256–264.
88. World Register of Marine Species website. Available: <http://www.marinespecies.org>. Accessed 2014 Jul 2.
89. Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, et al. Marine Ecoregions of the World: a bioregionalization of coast and shelf areas. *BioScience.* 2007; 57: 573–583.
90. Gibbons MJ, Janson LA, Ismail A, Samaai T. Life cycle strategy, species richness and distribution in marine Hydrozoa (Cnidaria: Medusozoa). *J Biogeo.* 2010a; 37: 441–448.
91. Clarke KR, Warwick RM. Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth; 2001.
92. Gravier-Bonnet N, Bourmaud C. Hydroids (Cnidaria, Hydrozoa) of coral reefs: preliminary results on community structure, species distribution and reproductive biology in the Îles Glorieuses (Southwest Indian Ocean). In: Proceedings of the 10th International Coral Reef Symposium, Okinawa, Japan; 2006. pp. 188–196.
93. Henry L-A, Kenchington E. Differences between epilithic and epizoic hydroid assemblages from commercial scallop grounds in the Bay of Fundy, northwest Atlantic. *Mar Ecol Prog Ser.* 2004; 266: 123–134.
94. Watson JE. Distribution and biogeographic relationships of the hydroid fauna of the Australian West coast: a preliminary account. *Sci Mar.* 1996; 60(1): 75–83.
95. Antsulevich AE. Observations on the hydroid fauna of the Kurile Islands. *Sci Mar.* 1992; 56(2–3): 213–216.
96. Peña Cantero AL. How rich is the deep-sea Antarctic benthic hydroid fauna? *Polar Biol.* 2004; 27: 767–774.
97. Warwick RM, Clarke KR. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar Ecol Progr Ser.* 1995; 129: 301–305.
98. Rudels B, Friedrich HJ, Quadfasel D. The Arctic Circumpolar Boundary Current. *Deep Sea Res 2 Top Stud Oceanogr.* 1999; 46: 1023–1062.
99. Jones EP, Swift JH, Anderson LG, Lipizer M, Civitarese G, Falkner KK, et al. Tracing Pacific water in the North Atlantic Ocean. *J Geophys Res.* 2003; 108: C4, 3116.
100. Curtis MA. The marine benthos of arctic and sub-arctic continental shelves. *Polar Records.* 1975; 17 (111): 595–626.
101. Schmid MK, Piepenburg D. The benthos zonation of the Disko Fjord, West Greenland. *Meddelelser om Grønland, Bioscience.* 1993; 37: 1–21.
102. Provan J, Bennett KD. Phylogeographic insights into cryptic glacial refugia. *Trends Ecol Evol.* 2008; 23(10): 564–571. doi: [10.1016/j.tree.2008.06.010](https://doi.org/10.1016/j.tree.2008.06.010) PMID: [18722689](https://pubmed.ncbi.nlm.nih.gov/18722689/)
103. Brochmann C, Gabrielsen TM, Nordal I, Landvik JY, Elven R. Glacial survival or tabula rasa? The history of North Atlantic biota revisited. *Taxon.* 2003; 52: 417–450.
104. Nürnberg D, Fütterer DK, Niessen F, Nørgaard-Pedersen N, Schubert CJ, Spielhagen RF, et al. The depositional environment of the Laptev Sea continental margin: Preliminary results from the R/V POLARSTERN ARK IX-4 cruise. *Polar Res.* 1995; 14(1): 43–53.
105. Darby DA, Polyak L, Bauch HA. Past glacial and interglacial conditions in the Arctic Ocean and marginal seas—a review. *Prog Oceanogr.* 2006; 71: 129–144.
106. Nesis KN. A hypothesis of the origin of western and eastern ranges of marine bottom animals. *Biologiya Morya.* 1983; 5: 3–13.
107. Bluhm BA, Ambrose AG Jr, Bergmann M, Clough LM, Gebruk AV, Hasemann C, et al. Diversity of the Arctic deep-sea benthos. *Mar Biodivers.* 2011; 41: 87–107.
108. Govindarajan AF, Halanych KM, Cunningham CW. Mitochondrial evolution and phylogeography in the hydrozoan *Obelia geniculata* (Cnidaria). *Mar Biol.* 2005; 146: 213–222.
109. Moura CJ, Harris DJ, Cunha MR, Rogers AD. DNA barcoding reveals cryptic diversity in marine hydroids (Cnidaria, Hydrozoa) from coastal and deep-sea environments. *Zool Scr.* 2008; 37: 93–108.

110. Cornelius PFS. Life cycle, dispersal and distribution among the Hydroida. Porcupine Newsletter. 1981; 2(3): 47–50.
111. Boero F. The ecology of marine hydroids and effects of environmental factors: a review. Mar Ecol. 1984; 5: 93–118.
112. Mileikovsky SA. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a reevaluation. Mar Biol. 1971; 19: 193–213.
113. Scheltema RS, Williams IP. Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and Western Pacific mollusks. Bull Mar Sci. 1983; 33: 545–565.
114. Johannesson K. The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? Mar Biol. 1988; 99: 507–513.
115. Jackson JBC. Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. Bull Mar Sci. 1986; 39(2): 88–606.
116. Thiel M, Gutow L. The ecology of rafting in the marine environment. II. The rafting organisms and community. Oceanogr Mar Biol. 2005; 43: 279–418.
117. Thiel M, Haye PA. The ecology of rafting in the marine environment. III. Biogeographical and evolutionary consequences. Oceanogr Mar Biol. 2006; 44: 323–429.
118. Cornelius PFS. Medusa loss in leptolid Hydrozoa (Cnidaria), hydroid rafting, and abbreviated life-cycles among their remote-island faunae: an interim review. Sci Mar. 1992b; 56(2–3): 245–261.
119. Rungger D. Autotomy in *Tubularia crocea* and its ecological and physiological significance. Pubbl Stn Zool Napoli. 1969; 37: 95–139.
120. Gravier-Bonnet N. Cloning and dispersal by buoyant autotomised hydranths of a Thecate hydroid (Cnidaria; Hydrozoa). Sci Mar. 1992; 56: 229–236.
121. Berrill NJ. Growth, development and pattern. San Francisco: W.H. Freeman; 1961.
122. Calder DR. Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina, U.S.A. Can J Zool. 1990; 68: 442–450.
123. Broch H. Biographie vom Tier aus. Naturwissenschaften. 1925; 13: 447–452.
124. Kinne O. Zur Ökologie der Hydroidpolypen des Nordostsee-kanals (*Laomedea loveni* Allman, *Cordylophora caspia* Pallas, *Perigonimus megas* Kinne). Zeitschrift für Morphologie und Ökologie der Tiere. 1956; 45: 217–249. doi: [10.1107/S0108767309007235](https://doi.org/10.1107/S0108767309007235) PMID: [19349661](https://pubmed.ncbi.nlm.nih.gov/19349661/)
125. Mapstone GM. Global Diversity and Review of Siphonophorae (Cnidaria: Hydrozoa). PloS One. 2014; 9(2): e87737. doi: [10.1371/journal.pone.0087737](https://doi.org/10.1371/journal.pone.0087737) PMID: [24516560](https://pubmed.ncbi.nlm.nih.gov/24516560/)
126. Gibbons MJ, Buecher E, Thibault-Botha D, Helm RR. Patterns in marine hydrozoan richness and biogeography around southern Africa: implications of life cycle strategy. J Biogeo. 2010b; 37: 606–616.

**Appendix 1.** List of Arctic species with their synonyms used in particular reference item (number of item after dash). For list of references see below.

Species	Synonyms	References
<b>Aequoreidae</b>		
<i>Aequorea forskalea</i> Péron & Lesueur, 1810		9,32
<b>Aglaopheniidae</b>		
<i>Aglaophenopsis bonnevieae</i> (Jäderholm, 1909)	<i>Aglaophenia compressa</i> -2; <i>Aglaophenopsis compressa</i> -32	2,32,44
<i>Aglaophenopsis cornuta</i> (Fewkes, 1881)	<i>Aglaophenopsis cornuta</i> -3	3,44
<i>Cladocarpus campanulatus</i> Ritchie, 1912		44
<i>Cladocarpus formosus</i> Allman, 1877	<i>Aglaophenia formosa</i> -2	2,3,20,44,53
<i>Cladocarpus integer</i> (Sars, 1873)		44,53
<i>Cladocarpus pourtalesii</i> Verrill, 1879		53,55
<i>Lytocarpia myriophyllum</i> (Linnaeus, 1758)	<i>Thecocarpus myriophyllum</i> -22	22,44
<b>Bonneviellidae</b>		
<i>Bonneviella grandis</i> (Allman, 1876)		3,32,44,53
<i>Bonneviella laevigata</i> Naumov, 1960		32
<i>Bonneviella regia</i> (Nutting, 1901)		32
<i>Bonneviella superba</i> Nutting, 1915		32
<b>Campanulariidae</b>		
<i>Campanularia crenata</i> Allman, 1876	<i>Campanularia bigena</i> -32; <i>C. speciosa</i> -7,12,32; <i>Tulpa speciosa</i> -53; <i>T. crenata</i> -55	6,12,32,44,53,55
<i>Campanularia groenlandica</i> Levinsen, 1893		3,6,12,22,32,44,53
<i>Campanularia hincksii</i> Alder, 1856		3,44,53
<i>Campanularia volubilis</i> (Linnaeus, 1758)		2,3,6,12,20,22,29,32,40,44,53,61,
<i>Clytia gracilis</i> (Sars, 1850)		43,52,60
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	<i>Campanularia johnstoni</i> -3,64	3,5,11,43,52,63
<i>Clytia languida</i> (A. Agassiz, 1862)		
<i>Gonothyraea loveni</i> (Allman, 1859)	<i>Obelia loveni</i> -32,53; <i>Laomedea hyalina</i> -3,20	3,5,15,19,31,39,43,52
<i>Hartlaubella gelatinosa</i> (Pallas, 1766)	<i>Obelia plicata</i> -6; <i>Laomedea dichotoma</i> -3	
<i>Laomedea flexuosa</i> Alder, 1857	<i>Obelia flexuosa</i> -32,53	3,32,53,61
<i>Obelia dichotoma</i> (Linnaeus, 1758)	<i>Obelia plicata</i> -6; <i>Laomedea dichotoma</i> -3	3,6,44
<i>Obelia geniculata</i> (Linnaeus, 1758)		3,6,32,44,53,58,64
<i>Obelia longissima</i> (Pallas, 1766)	<i>Laomedea longissima</i> -20,22	3,6,9,20,32,40,44,53,61,64,22
<i>Orthopyxis integra</i> (MacGillivray, 1842)	<i>Campanularia integra</i> -3,6,12,20,22,29,32,40,53	3,6,12,20,22,29,32,40,44,53,61,
<i>Rhizocaulus chinensis</i> (Marktanner-Turneretscher, 1890)	<i>Verticillina chinensis</i> -32	32
<i>Rhizocaulus verticillatus</i> (Linnaeus, 1758)	<i>Verticillina verticillata</i> -32; <i>Campanularia verticillata</i> -6,12,20,22,29,32	3,6,12,20,22,29,32,40,44,53
<b>Campanulinidae</b>		
<i>Calycella syringa</i> (Linnaeus, 1767)		3,6,20,22,29,32,40,42,44,53,61
<i>Campanulina pumila</i> (Clark, 1875)	<i>Opercularella nana</i> -3,32,55	3,32,40,44,55
<i>Cuspidella humilis</i> (Alder, 1863)		
<i>Cuspidella procumbens</i> Kramp, 1911		
<i>Cuspidella quadridentatum</i> Hincks, 1874		
<i>Lafoeina maxima</i> Levinsen, 1893		3,6,20,22,32,40,43,44,53
<i>Lafoeina tenuis</i> Sars, 1874		3,29,32,44
<i>Opercularella lacerata</i> (Johnson, 1847)	<i>Campanulina lacerata</i> -3,20,32,53	3,6,20,32,40,43,44,53
<b>Eirenidae</b>		
<i>Eutonina indicans</i> (Romanes, 1876)	<i>Eirine indicans</i> -9,32	1,9,32,24,44
<b>Haleciidae</b>		
<i>Halecium arcticum</i> Ronowicz & Schuchert, 2007	<i>H. undulatum</i> -6	6,41
<i>Halecium beanii</i> (Johnston, 1838)		3,29,32,43,44,53
<i>Halecium birulai</i> Spassky, 1929		32,44,53
<i>Halecium corrugatum</i> Nutting, 1899		3,32,53,55
<i>Halecium curvicaule</i> Lorenz, 1886	<i>H. kukenthali</i> -29	3,6,20,22,29,32,40,43,44,53,55
<i>Halecium groenladicum</i> Kramp, 1911		6,20,22,32,44,53
<i>Halecium halecinum</i> (Linnaeus, 1758)		3,22,29,32,53,61
<i>Halecium harrimani</i> Nutting, 1901		33
<i>Halecium irregulare</i> Bonnevie, 1899		
<i>Halecium laeve</i> Kramp, 1932		20,44



<i>Halecium labrosum</i> Alder, 1859		3,6,20,22,29,32,44,53,61
<i>Halecium marsupiale</i> Bergh, 1887		32,53
<i>Halecium minutum</i> Broch, 1903		3,6,20,22,40,43,44
<i>Halecium mirabile</i> Schydlowsky, 1902		3,32,40,43
<i>Halecium muricatum</i> (Ellis & Solander, 1786)		2,3,6,16,20,22,32,33,40,43,44,53
<i>Halecium ornatum</i> Nutting, 1901		3,33
<i>Halecium reversum</i> Nutting, 1901		32,33,53
<i>Halecium scutum</i> Clark, 1877	<i>H. beringi</i> -32	3,6,32,33,55
<i>Halecium speciosum</i> Nutting, 1901		6,32,33,40,43,53
<i>Halecium tenellum</i> Hincks, 1861		3,20,22,32,44,53,61
<i>Halecium textum</i> Kramp, 1911		40,43,44
<i>Halecium undulatum</i> Billard, 1921		
<b>Halopterididae</b>		
<i>Nuditheca dalli</i> (Clark, 1876)	<i>Macrorhynchia dalii</i> -8	8,32
<i>Nuditheca tetrandra</i> Naumov, 1960		32
<i>Schizotricha polaris</i> Naumov, 1960		32,53
<i>Schizotricha variabilis</i> Bonnevie, 1899	<i>Plumularia variabilis</i> -2	2,32,44,53
<b>Hebellidae</b>		
<i>Hebella scandens</i> (Bale, 1888)	<i>H. calcarata</i> -22	22
<b>Kirchenpaueriidae</b>		
<i>Kirchenpaueria fragilis</i> (Hamann, 1882)	<i>Plumularia fragilis</i> -2,32,53	2,32,53,55
<i>Kirchenpaueria plumularioides</i> (Clark, 1877)	<i>Halecium plumularioides</i> -8	8
<b>Lafoeidae</b>		
<i>Acryptolaria conferta</i> (Allman, 1877)	<i>Cryptolaria profunda</i> -32	32,44
<i>Acryptolaria flabellum</i> (Allman, 1888)	<i>Cryptolaria flabellum</i> -32	32
<i>Filellum serpens</i> (Hassall, 1848)		3,6,20,22,32,40,44,53,61
<i>Grammaria abietina</i> (M. Sars, 1850)	<i>Lafoea abietina</i> -2	2,3,6,20,22,44,53,61
<i>Grammaria borealis</i> (Levinson, 1893)	<i>Cryptolaria borealis</i> -6,32; <i>Acryptolaria borealis</i> -53	3,6,20,32,44,53
<i>Grammaria immersa</i> Nutting, 1901		3,6,22,32,44,53
<i>Halisiphonia arctica</i> Kramp, 1932		44
<i>Lafoea dumosa</i> (Fleming, 1820)	<i>L. gracillima</i> -6,20,29; <i>L. pocillum</i> -8,32,53; <i>L. fruticosa</i> -2,3,6,32	2,3,6,8,20,29,32,43,44,53,61
<i>Lafoea grandis</i> Hincks, 1874		32,53
<i>Lafoea symmetrica</i> Bonnevie, 1899		2
<i>Zygophylax pinnata</i> (Sars, 1873)		53,55
<b>Laodiceidae</b>		
<i>Ptychogena hyperborea</i> Kramp, 1942		19,25,39
<i>Ptychogena lactea</i> Agassiz, 1865		6,9,13,24,32,50,53,54,55,58,63,64
<i>Staurostoma mertensii</i> (Brandt, 1834)	<i>Staurophora mertensi</i> -50,58,59,63; <i>Cuspidella mertensii</i> -32	32,50,53,55,58,59,63,64
<b>Lovenellidae</b>		
<i>Eucheilota ventricularis</i> McCrady, 1859		25
<i>Lovenella producta</i> (G.O. Sars, 1874)	<i>Campanulina producta</i> -3	3,44
<b>Melicertidae</b>		
<i>Melicertum octocostatum</i> M.Sars, 1835	<i>Melicertum campanula</i> -9,32,64	9,14,24,25,32,50,53,54,58,63,64
<b>Mitrocomidae</b>		
<i>Cosmetira pilosella</i> Forbes, 1848		
<i>Earleria cellularia</i> (A.Agassiz, 1862)	<i>Halistaura cellularia</i> -24,50	24,25,50
<i>Halopsis ocellata</i> Agassiz, 1863		21,25,32,53,63,64
<i>Mitrocomella polydiademata</i> (Romanes, 1876)	<i>Cuspidella grandis</i> -32; <i>C. polydiademata</i> -32,64	25,32,53,54,55,62,63,64
<b>Phialellidae</b>		
<i>Phialella quadrata</i> (Forbes, 1848)		61
<b>Plumulariidae</b>		
<i>Nemertesia antennina</i> (Linnaeus, 1758)	<i>Antennularia antennina</i> -3	3,6,20,32,44,53
<i>Polypiumaria gracillima</i> (Sars, 1873)	<i>Polynemertesia gracillima</i> -32,53	22,32,44,53
<b>Sertulariidae</b>		
<i>Abietinaria abietina</i> (Linnaeus, 1758)	<i>Diphasia abietina</i> -3,20	3,6,20,22,32,44,53,55
<i>Abietinaria compressa</i> (Merezhkovskii, 1878)		32
<i>Abietinaria filicula</i> (Ellis & Solander, 1786)	<i>Diphasia abietina</i> var. <i>filicula</i> -3; <i>Sertularia filicula</i> -8	3,6,8,32,44,53
<i>Abietinaria fusca</i> (Johnston, 1847)		32,44,53
<i>Abietinaria gigantea</i> (Clark, 1877)	<i>Thuiaria gigantea</i> -8	8,32
<i>Abietinaria gracilis</i> Nutting, 1904		31
<i>Abietinaria inconstans</i> (Clark, 1877)	<i>Thuiaria costata</i> -33	32,33

<i>Abietinaria kincaidi</i> (Nutting, 1901)		32
<i>Abietinaria pulchra</i> (Nutting, 1904)	<i>Diphasia pulchra</i> -6,20	6,20,32,40,43,44,53
<i>Abietinaria thuiarioides</i> (Clark, 1877)	<i>Sertularia thuiarioides</i> -8	8,32,44
<i>Abietinaria turgida</i> (Clark, 1877)	<i>Thuiaria turgida</i> -8	6,8,32,53,55
<i>Abietinaria variabilis</i> (Clark, 1877)	<i>Diphasia variabilis</i> -3; <i>Sertularia variabilis</i> -8	3,8,32
<i>Diphasia attenuata</i> (Hincks, 1866)		44
<i>Diphasia fallax</i> (Johnston, 1847)	<i>Dynamena fala</i> -2	2,3,22,32,44,53
<i>Diphasia rosacea</i> (Linnaeus, 1758)		3,6,32,44,53
<i>Dynamena pumila</i> (Linnaeus, 1758)	<i>Sertularia pumila</i> -3	3,6,32,44,53
<i>Hydrallmania falcata</i> (Linnaeus, 1758)		2,3,22,32,44,53
<i>Sertularella albida</i> Kirchenpauer, 1884		32
<i>Sertularella complexa</i> Nutting, 1904		32
<i>Sertularella erratum</i> Vervoort & Watson, 2003	<i>Sertularella reticulata</i> -32	32
<i>Sertularella fusiformis</i> (Hincks, 1861)	<i>Sertularella pellucida</i> -32,53	6,22,32,53
<i>Sertularella gayi</i> (Lamouroux, 1821)		3,44
<i>Sertularella gigantea</i> Mereschowsky, 1878		3,20,22,32,53,55
<i>Sertularella pinnata</i> Clark, 1876 (?)		3,6,32
<i>Sertularella polyzonias</i> (Linnaeus, 1758)	<i>S. polyzonias</i> var. <i>gigantea</i> -3,20,22	2,3,6,8,20,22,32,33,43,44
<i>Sertularella rugosa</i> (Linnaeus, 1758)		3,8,32,40,43,44,53
<i>Sertularella tenella</i> (Alder, 1856)		3,6,22,32,40,43,44,53
<i>Sertularia albimaris</i> Mereschowsky, 1878		3,32,40,43,53,55
<i>Sertularia argentea</i> Linnaeus, 1758	<i>S. cupressina</i> -6,32,53	6,32,40,43,44,53
<i>Sertularia converrucosa</i> Naumov, 1960		32
<i>Sertularia cupressoides</i> Clark, 1876		8,32,33,40,43,53,55
<i>Sertularia fabricii</i> Levinsen, 1893		3,6,20,43,44
<i>Sertularia mirabilis</i> (Verrill, 1873)	<i>Diphasia mirabilis</i> -8	3,6,8,20,32,40,43,44,53
<i>Sertularia plumosa</i> (Clark, 1876)	<i>Thuiaria plumosa</i> -8	3,6,8,32,53,55
<i>Sertularia robusta</i> (Clark, 1876)	<i>Thuiaria robusta</i> -8	3,6,8,32
<i>Sertularia schmidtii</i> Kudelin, 1914		6,32,40,43,44
<i>Sertularia similis</i> Clark, 1877		6,8,32,40,43,44,53
<i>Sertularia tenera</i> Sars, 1874		3,6,20,22,29,32,44,53
<i>Sertularia tolli</i> (Jäderholm, 1908)		32,53
<i>Symplectoscyphus pinnatus</i> (Clark, 1876)		32,55
<i>Symplectoscyphus tricuspidatus</i> (Alder, 1856)	<i>Sertularella tricuspidata</i> -2,6,20,22,32,53	2,6,20,22,29,32,40,43,44,53,61
<i>Tamarisca tamarisca</i> (Linnaeus, 1758)	<i>Sertularella tamarisca</i> -3; <i>Sertomma tamarisca</i> -20	3,32,43,44,53,55
<i>Thuiaria alternitheca</i> Levinsen, 1893		3,6,20,44,53
<i>Thuiaria arctica</i> (Bonnevie, 1899)	<i>Saleginopsis arctica</i> -2	2,3,32,44,53
<i>Thuiaria articulata</i> (Pallas, 1766)	<i>T. barentsi</i> -32; <i>T. lonchitis</i> -6,53	2,6,32,40,43,44,53
<i>Thuiaria breiifussi</i> (Kudelin, 1914)		32,53,55
<i>Thuiaria carica</i> Levinsen, 1893	<i>T. kirchenpaueri</i> -29	3,6,29,32,44,53
<i>Thuiaria cedrina</i> (Linnaeus, 1758)		32
<i>Thuiaria cornigera</i> Kudelin, 1914		32
<i>Thuiaria cupressoides</i> (Lepechin, 1783)		32,53
<i>Thuiaria cylindrica</i> Clark, 1876		3,8,32,53,55
<i>Thuiaria decemserialis</i> (Merezhkovskii, 1878)		3,32,53
<i>Thuiaria hartlaubi</i> (Nutting, 1904)		32,44
<i>Thuiaria hippuris</i> Allman, 1874		22
<i>Thuiaria kudelini</i> Naumov, 1960		32
<i>Thuiaria laxa</i> Allman, 1874		3,6,22,32,40,43,44,53
<i>Thuiaria mereschkovskii</i> Kudelin, 1914		32
<i>Thuiaria obsoleta</i> (Lepechin, 1781)	<i>Saleginopsis obsoleta</i> -2	2,3,32,53
<i>Thuiaria pinaster</i> (Lepechin, 1783)		3
<i>Thuiaria sachalini</i> Kudelin, 1914		44
<i>Thuiaria uschakovii</i> Naumov, 1960		32,54
<i>Thuiaria thuja</i> (Linnaeus, 1758)		3,6,20,22,32,44,53
<b>Tiarannidae</b>		
<i>Chromatonema rubrum</i> Fewkes, 1882		58
<i>Modeeria rotunda</i> (Quoy & Gaimard, 1827)	<i>Stegopoma fastigiatum</i> -3,20,32	3,20,32,53
<i>Stegopoma plicatile</i> (M. Sars, 1863)	<i>Modeeria plicatile</i> -53	3,6,22,32,40,44,53,55
<b>Tiaropsidae</b>		
<i>Tiaropsis multicirrata</i> (Sars, 1835)		10,13,14,24,25,32,50,53,54,55,58,63

**Order: Anthoathecata****Suborder: Capitata****Acaulidae**

*Acaulis primarius* Stimpson, 1854

22,32,44,55

**Boreohydridae**

*Boreohydra simplex* Westblad, 1937

44,45

**Candelabridae**

*Candelabrum phrygium* (Fabricius, 1780)

*Myriothela phrygia*-2,3,7,32

2,3,7,20,32,44,45,53,61

*Candelabrum verrucosum* (Bonnievie, 1989)

2,45

*Monocoryne gigantea* (Bonnievie, 1898)

7,45,53,55

**Corymorphidae**

*Branchiocerianthus reniformis* Broch, 1918

44

*Corymorpha carnea* (Clark, 1876)

*Rhizonema carnea*-8

8

*Corymorpha glacialis* Sars, 1859

*Monocaulus glacialis*-55

3,32,44,53,55

*Corymorpha groenlandica* (Allman, 1876)

*Monocaulus groenlandica*-55; *Lampra purpurea*-2

2,3,7,32,44,48,53,55

*Corymorpha nana* Alder, 1857

2,48,49

*Corymorpha nutans* M. Sars, 1835

3,16,44,48,49

*Corymorpha typica* (Uchida, 1927)

*Gotoea typica*-51

51

*Euphysa aurata* Forbes, 1848

*Corymorpha aurata*-32,64

25,32,44,48,53,55,58,64

*Euphysa flammea* (Linko, 1905)

*Corymorpha flammea*-9,32,64

9,10,13,14,24,32,50,53,55,58,59,62,63,64

*Euphysa tentaculata* Linko, 1905

*Corymorpha tentaculata*-32,64

1,21,32,48,53,58,64

*Gymnogonos crassicornis* Bonnievie, 1898

42,43,44,48,53,57

*Gymnogonos obvolutus* Kramp, 1933

*Corymorpha obvoluta*-22

22,48,53,57

*Paragotoea bathybia* Kramp, 1942

*Paragotoea elegans*-18

18,19,39,48,53,57

**Corynidae**

*Coryne hincksi* Bonnievie, 1898

7,44

*Coryne pusilla* (Gaertner, 1774)

*Sarsia brachygaster* Grönberg, 1898 sp. inq.

*Sarsia lovenii* (M. Sars, 1846)

*Coryne lovenii*-32,53

22,32,40,43,44,53

*Sarsia princeps* (Haeckel, 1879)

*Coryne princeps*-32; *Coryne principes*-9

9,10,13,14,18,24,32,50,53,55,58,63,64

*Sarsia tubulosa* (M. Sars, 1835)

*Coryne tubulosa*-9,32,64; *C. sarsi*-20; *S. barentsi*-58

1,7,9,10,20,24,25,32,44,53,58,61,63,64

*Stauridiosarsia gemmifera* (Forbes, 1848)

*Sarsia gemmifera*-64

64

*Stauridiosarsia producta* (Wright, 1858)

32,44,55

**Tubulariidae**

*Bouillonina cornucopia* (Bonnievie, 1898)

*Tubularia cornucopia*-2

2,44,48,53

*Ectopleura larynx* (Ellis & Solander, 1786)

*Tubularia larynx*-2,4,32,55

2,3,32,44,53,55

*Hybocodon prolifer* Agassiz, 1860

*Tubularia prolifer*-2,9,32,53,64; *H. christinae*-63

1,2,9,10,24,32,44,48,50,53,54,55,58,63,64

*Tubularia indivisa* Linnaeus, 1758

*Tubularia simplex*-32,55

3,8,32,44,53,55

*Tubularia regalis* Boeck, 1860

*T. variabilis*-2

2,3,7,8,20,34,44,53,54

*Zyzyzus robustus* Petersen, 1990

34

**Protohydridae**

*Protohydra leuckarti* Greeff, 1870

53,55

*Sympagohydra tuuli* Piraino et al. 2008

35

**Capitata incertae sedis**

*Plotocnide borealis* Wagner, 1885

*Eucodonium arctica*-15,50

15,18,19,48,50,51,53,54,55,58,59,63,64

*Rhabdoon reesi* (Shirley & Leung, 1970)

*Yakovia polinae*-17,18,56; *Pararhysomedusa reesi*-51

17,18,19,39,48,51,53,56

**Suborder: Filifera****Bougainvilliidae**

*Bougainvillia principis* (Steenstrup, 1850)

24,32,53,54,58,63,64

*Bougainvillia superciliaris* (L. Agassiz, 1849)

9,10,15,24,42,43,50,53,54,55,58,62,63,64

*Chiarella centripetalis* Maas, 1897

*Rathkea jaschnowi*-9,32; *Ch. jaschnowi*-24

9,24,32

*Dicoryne conferta* (Alder, 1856)

3,44,53

*Garveia polarsterni* Stepanjants, 2001

53,55

*Rhizorhagium roseum* Sars, 1874

*Perigonimus roseus*-32

3,7,32,40,42,43,44,53

**Bythotiaridae**

*Bythotia depressa* Naumov, 1960

32

*Calycopsis birulai* (Linko, 1913)

*Eumedusa birulai*-13,18,50

13,14,18,32,50,53,54,55,63,64

*Calycopsis nematomorpha* Bigelow, 1913

*C. nematophora*-9,32

1,9,24,32,58

*Meator rubatra* Bigelow, 1913

24

**Eudendriidae**

*Eudendrium album* Nutting, 1898

*E. islandicum*-40

40,42,43,44,47

<i>Eudendrium annulatum</i> Norman, 1864		3,20,32,40,42,43,44,47,53
<i>Eudendrium arbuscula</i> Wright, 1859		42,43
<i>Eudendrium capillare</i> Alder, 1856		3,7,20,29,32,42,43,44,47,53
<i>Eudendrium rameum</i> (Pallas, 1766)		2,3,7,22,29,32,40,42,43,44,47,53
<i>Eudendrium ramosum</i> (Linnaeus, 1758)		3,22,32,40,43,44,47,53,55
<i>Eudendrium tenellum</i> Allman, 1877 sp.inq.		
<i>Eudendrium unispirum</i> Schuchert, 2008		42,43,47,49
<i>Eudendrium vaginatum</i> Allman, 1863		12,42,43,47,49,61
<b>Hydractiniidae</b>		
<i>Clava multicornis</i> (Forsskål, 1775)	<i>C. squamata</i> -3,22	3,22,32,42,43,44,53
<i>Clavactinia serrata</i> (Kramp, 1943)	<i>Hydractinia serrata</i> -22,32,42,43,46,53,54	22,32,42,43,44,46,53,54
<i>Hydractinia arctica</i> (Jäderholm, 1902)		44,46
<i>Hydractinia carica</i> Bergh, 1887	<i>H. minuta</i> -2	2,7,12,32,43,44,46,53,55,61
<i>Hydractinia echinata</i> (Fleming, 1828)		3,12,32,44,46,53,55
<i>Hydractinia ingolfi</i> Kramp, 1932		20,44,46
<i>Hydractinia monocarpa</i> Allman, 1876		3,7,29,32,44,46,53
<i>Hydractinia</i> cf. <i>monoon</i> (Hirohito, 1988)		42
<i>Hydractinia sarsii</i> Steenstrup, 1850		2,44,46
<i>Podocoryna borealis</i> (Mayer, 1900)		3,44
<i>Podocoryna carnea</i> (M. Sars, 1846)		3,44,53,58
<i>Schuchertinia allmani</i> (Bonnevie, 1898)	<i>Hydractinia allmani</i> -2,20,32,44,46,53	2,3,22,32,44,46,53,55
<i>Schuchertinia antonii</i> (Miglietta, 2006)		30
<b>Margelopsidae</b>		
<i>Margelopsis hartlaubi</i> Browne, 1903		19
<b>Oceaniidae</b>		
<i>Rhizogeton nudus</i> Broch, 1910	<i>R. nudum</i> -3,53	3,7,20,22,42,43,44,53,61
<i>Similomerona nematophora</i> (Antsulevich, 1986)	<i>Rhizogeton nematophorum</i> -53	42,43,53,55
<b>Pandeiidae</b>		
<i>Catablema multicirratum</i> Kishinouye, 1910	<i>C. multicirrata</i> -59	24,25,58,59
<i>Catablema vesicarium</i> (A. Agassiz, 1862)	<i>C. vesicaria</i> -53	10,18,24,25,49,50,53,54,55,58,62,63
<i>Halitholus cirratus</i> Hartlaub, 1913		10,13,14,25,49,50,54,58,61,63
<i>Halitholus pauper</i> Hartlaub, 1913		10,25,50,58
<i>Halitholus yoldiaarcticae</i> (Birula, 1897) sp. inq.	<i>Perigonimus yoldia-arcticae</i> -3,9,32,64	3,9,18,22,32,43,44,53,55,64
<i>Leuckartiara nobilis</i> Hartlaub, 1914		15,24,25,50
<i>Neoturris abyssi</i> (G.O. Sars 1874)	<i>Perigonimus abyssi</i> -3,32,64,2,22	2,3,22,32,64
<i>Neoturris brevicornis</i> (Murbach & Shearer, 1902)	<i>Perigonimus brevicornis</i> -9,32; <i>Leuckartiara brevicornis</i> -15,24,50,58	9,10,15,24,25,32,50,58
<b>Protiariidae</b>		
<i>Paratiara digitalis</i> Kramp & Damus, 1925		54
<b>Rathkeidae</b>		
<i>Rathkea octopunctata</i> (M. Sars, 1835)		1,10,15,24,25,50,53,54,58,62,63,64
<b>Stylasteridae</b>		
<i>Crypthelia trophostega</i> Fisher, 1938		5,11,32
<i>Cyclohelix lamellata</i> Cairns, 1991		5
<i>Distichopora borealis</i> Fisher, 1938		5
<i>Errinopora dichotoma</i> Cairns & Lindner, 2011		5
<i>Errinopora disticha</i> Cairns & Lindner, 2011		5
<i>Errinopora fisheri</i> Cairns & Lindner, 2011		5
<i>Errinopora nanneca</i> Fisher, 1938		3,11
<i>Errinopora undulata</i> Cairns & Lindner, 2011		5
<i>Errinopora zarhyncha</i> Fisher, 1938		3,11
<i>Stylaster alaskanus</i> Fisher, 1938		11
<i>Stylaster brochi</i> (Fisher, 1938)	<i>Allopora brochi</i> -11,32	3,5,11,32
<i>Stylaster campylecus</i> (Fisher, 1938)	<i>Allopora polyorchis</i> -11,32	3,11,32
<i>Stylaster elassotomus</i> (Fisher, 1938)		11
<i>Stylaster erubescens groenlandicus</i> Zibrowius & Cairns, 1992		46
<i>Stylaster gemmascens</i> (Esper, 1794)		4,32,46
<i>Stylaster leptostylus</i> (Fisher, 1938)		
<i>Stylaster parageus parageus</i> (Fisher, 1938)		3
<i>Stylaster repandus</i> Cairns & Lindner, 2011		5
<i>Stylaster roseus</i> (Pallas, 1766)		5

<i>Stylaster stejnegeri</i> (Fisher, 1938)	<i>Allopora stejnegeri</i> -11	11
<i>Stylaster trachystomus</i> (Fisher, 1938)		11
<i>Stylaster verrilli</i> (Dall, 1884)	<i>Allopora verrilli</i> -32	3,32
<b>Zancleidae</b>		
<i>Zanclea</i> sp.		
<b>Order: Siphonophorae</b>		
<b>Clausophyidae</b>		
<i>Chuniphyes moserae</i> Totton, 1954		31,52
<i>Chuniphyes multidentata</i> Lens & van Riemsdijk, 1908		21,60
<i>Crystallophyes amygdalina</i> (Moser, 1925)		27,59,60
<i>Heteropyramis crystallina</i> (Moser, 1925)	<i>Thalassophyes crystallina</i> -60	60
<i>Heteropyramis maculata</i> Moser, 1925		27
<b>Diphyidae</b>		
<i>Dimophyes arctica</i> (Chun, 1897)		9,10,13,17,21,26,27,28,31,37,50,51,52,53,60,64
<i>Gilia reticulata</i> (Totton, 1954)	<i>Lensia reticulata</i> -27,31	27,31,36,52
<i>Lensia achilles</i> Totton, 1941		27,31,52
<i>Lensia conoidea</i> (Keferstein & Ehlers, 1860)		21,27,60
<i>Muggiaea bargmannae</i> Totton, 1954		14,17,27,28,31,39,53,59
<i>Muggiaea kochi</i> (Will, 1844)		60
<b>Hippopodiidae</b>		
<i>Vogtia serrata</i>		9,21,31,52
<b>Pyrostephidae</b>		
<i>Bargmannia</i> sp.		
<b>Prayidae</b>		
<i>Nectadamas diomedea</i> (Bigelow, 1911)	<i>Nectopyramis diomedea</i> -51,53	51,52,53
<i>Rosacea plicata</i> Bigelow, 1911		
<b>Agalmatidae</b>		
<i>Agalma okeni</i> Eschscholtz, 1825		51
<i>Nanomia cara</i> Agassiz, 1865	<i>Stephanomia cara</i> -21	21,27,60
<i>Marrus orthocanna</i> (Kramp, 1942)	<i>Stephanomia orthocanna</i> -21; <i>M. antarcticus pacifica</i> -52	21,26,27,28,39,52,53,64
<i>Rudjakovia plicata</i> Margulis, 1982		28,53,54
<b>Apolemiidae</b>		
<i>Apolemia vitiazi</i> (Stepanjants, 1967)	<i>Ramosia vitiazi</i> -31,52; <i>Ramosa vitiazi</i> -9	9,31,52
<b>Physophoridae</b>		
<i>Physophora hydrostatica</i> Forskål, 1775		21,53,60,64
<b>Order: Trachymedusae</b>		
<b>Ptychogastridae</b>		
<i>Ptychogastria polaris</i> Allman, 1878		17,19,25,32,39,50,53,54,55,58,64
<b>Halicreatidae</b>		
<i>Botrynema brucei</i> Browne, 1908		9,17,19,25,39,51,55
<i>Botrynema ellinorae</i> (Hartlaub, 1909)		17,18,19,25,37,39,51,55,58
<i>Halicreas minimum</i> Fewkes, 1882	<i>H. papilio</i> -58	9,25,32,58,64
<i>Halicera bigelowi</i> Kramp, 1947		32,53
<i>Homoeonema platygonon</i> Browne, 1903		17,18,19,25,32,37,51,53,54,55,58,63,64
<b>Rhopalonematidae</b>		
<i>Aglantha digitale</i> (O.F. Müller, 1776)		9,10,13,14,17,18,23,25,37,39,50,51,53,54,55,58,59,63,64
<i>Benthocodon hyalinus</i> Larson & Harbison, 1990		19
<i>Crossota brunnea</i> Vanhöffen, 1902		9
<i>Crossota millsae</i> Thuesen, 2003		19,39
<i>Crossota norvegica</i> Vanhöffen, 1902		19,39
<i>Crossota rufobrunnea</i> (Kramp, 1913)		1,17,23,39,55,58
<i>Pantachogon haeckeli</i> Maas, 1893		1,9,23,24,25,32,50,54,58,63,64
<i>Sminthea arctica</i> (Hartlaub, 1909)		17,19,25,37,39,51,58,59
<b>Order: Limnomedusae</b>		
<b>Monobrachiidae</b>		
<i>Monobrachium parasitum</i> Mereschkowsky, 1877		2,3,32,44,53
<b>Olindiidae</b>		
<i>Eperetmus typus</i> Bigelow, 1915		25,58
<i>Gonionemus vertens</i> A. Agassiz, 1862		25
<b>Order: Narcomedusae</b>		

**Aeginidae**

<i>Aegina citrea</i> Eschscholtz, 1829	<i>Aegina rosea</i> -9,32,50,58	9,32,50,58
<i>Aeginopsis laurentii</i> Brandt, 1835		10,13,14,15,17,18,25,50,51,53,54,55,58,59,64
<i>Aeginura grimaldii</i> Maas, 1904		24,25,32,58
<i>Bathykorus bouilloni</i> Rascoff, 2010		19,38
<i>Solmundella bitentaculata</i> (Quoy & Gaimard, 1833)		19,32,39,51

**Cuninidae**

<i>Solmissus incisa</i> (Fewkes, 1886)		24,25,58
--	--	----------

**Solmarisidae**

<i>Solmaris corona</i> (Keferstein & Ehlers, 1861)		24,64
--	--	-------

**References**

1. Arai MN, Brinkmann-Voss A (1980) Hydromedusae of British Columbia and Puget Sound. Canadian Bulletin of Fisheries and Aquatic Sciences 204: 1-192.
2. Bonnevie K (1899) Hydroida. The Norwegian North-Atlantic Expedition 1876-1878 7: 1-103.
3. Broch H (1909) Die Hydroiden der arktischen Meere. Fauna Arctica 5: 127-248.
4. Broch H (1914) Stylasteridae. The Danish Ingolf-Expedition 5(5): 1-26.
5. Cairns SD, Lindner A (2011) A revision of Stylasteriidae (Cnidaria, Hydrozoa, Filifera) from Alaska and adjacent waters. ZooKeys 158: 1-88.
6. Calder DR (1970) Thecate hydroids from the shelf waters of Northern Canada. Journal of the Fisheries Research Board of Canada 27(9): 1501-1547.
7. Calder DR (1972) Some athecate hydroids from the shelf waters of Northern Canada. Journal of the Fisheries Research Board of Canada 29(3): 217-228.
8. Clark SF (1877) Report on the hydroids collected on the coast of Alaska and the Aleutian Islands, by W. H. Dall, U.S. coast survey, and party, from 1871 to 1874 inclusive. Proceedings of the Academy of Natural Sciences of Philadelphia 28: 209-238.
9. Cooney RT (1981) Bering Sea zooplankton and micronekton communities with emphasis on annual production. In: Hood DW, Calder JA, eds. The eastern Bering Sea shelf: Oceanography and Resources. Vol. 2. Seattle: University of Washington Press. pp. 947-974.
10. Dunbar MJ (1942) Marine macroplankton from the Canadian Eastern Arctic. II. Medusae, Siphonophora, Ctenophora, Pteropoda and Chaetognatha. Can J Res 20(D): 71-77.
11. Fisher WK (1938) Hydrocorals of the North Pacific Ocean. In: Proceedings of the United States National Museum, Tom 84. U.S. Government Printing Office. pp. 493-554.
12. Fraser CM (1944) Hydroids of the Atlantic coast of North America. The University of Toronto Press, Toronto. 451 p.
13. Grainger EH (1965) Zooplankton from the Arctic Ocean and adjacent Canadian waters. Journal of the Fisheries Research Board of Canada 22(2): 543-564.
14. Grainger EH, Grohe K (1975) Zooplankton data from the Beaufort Sea, 1951 to 1975. Fish Mar Serv Res Dev Tech Rep 591. 54 pp.
15. Hand C, Kan LB (1961) The medusae of Chukchi and Beaufort seas of the arctic ocean including the description of a new species of *Eucodonium* (Hydrozoa: Anthomedusae). Arctic Institute of North America; technical papers 6: 1-23.
16. Jäderholm E (1916) Die Hydroiden des Eisfjords. Bihang till Kungliga Svenska Vetenskapsakademiens Hand-lingar 54(4): 1-14.



17. Kosobokova K, Hirche H-J (2000) Zooplankton distribution cross the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. Deep Sea Res Part 1 Oceanogr Res Pap 47: 2029-2060.
18. Kosobokova K, 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: 63-76.
19. Kosobokova K, Hopcroft RR, Hirche H-J (2011) Patterns of zooplankton diversity through the depths of the Arctic's central basin. Mar Biodivers 41: 29-50.
20. Kramp P (1932) Hydroids collected in West-Greenland Fjords in 1911 and 1912. Meddelelser om Grønland 91: 1-35.
21. Kramp P (1942) Siphonophora. The Godthaab Expedition 1928. Meddelelser om Grønland 80(8): 3-24.
22. Kramp P (1943) The zoology of East Greenland. Hydroida. Meddelelser om Grønland 121: 1-52.
23. Kramp P (1947) Medusae. Part III. Trachylina and Scyphozoa, with zoogeographical remarks on all the medusae of the northern Atlantic. Danish Ingolf Expedition 5: 1-66.
24. Kramp P (1959) The Hydromedusae of the Atlantic Ocean and adjacent waters. Dana-Report 46: 1-283.
25. Kramp P (1961) Synopsis of the medusae of the world. J Mar Biol Assoc U.K. 40: 1-469.
26. Mapstone GM (2009) Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters. NRC Research Press, Ottawa, Ontario, Canada. 302 p.
27. Margulis RYa (1978) The distribution of siphonophores in the western North Atlantic in summer of 1974. Vestnik Moskovskogo Universiteta, Ser. XVI Biologiya 3: 1-11.
28. Margulis RYa (1982) A new *siphonophore* *Rudjakovia plicata* gen. n., sp. n., (Coelenterate, Hydrozoa) from the Polar Basin and some notes on other siphonophores. Zoological Journal 61: 440-444.
29. Marktanner-Turneretscher G (1895) Hydroiden von Ostspitsbergen. Zoologische Jahrbücher, Abteilung Systematik und Geographie der Tiere 8: 391-438.
30. Miglietta MP (2006) *Hydractinia antonii* sp. nov.: a new, partially calcified hydractiniid (Cnidaria: Hydrozoa: Hydractiniidae) from Alaska. J Mar Biol Assoc U.K. 86: 993-996.
31. Motoda S, Minoda T (1974) Plankton of the Bering Sea. In: Hood DW, Kelly J, eds. Oceanography of the Bering Sea; Proceedings of the International Symposium for Bering Sea Studies, Hakodate, Japan, 21 January to 4 February, 1972. University of Alaska, Fairbanks. pp. 207-241.
32. Naumov DV (1969) Hydroids and Hydromedusae of the USSR. Jerusalem: Israel Program for scientific translation. 660 p.
33. Nutting CC (1901) Papers from the Harriman Alaska Expedition. XXI. The hydroids. Proceedings of the Washington Academy of Science 3: 157-216.
34. Petersen KW (1990) Evolution and taxonomy in capitate hydroids and medusae (Cnidaria: Hydrozoa). Zool J Linn Soc 100: 101-231.
35. Piraino S, Bluhn BA, Gradinger R & Boero F (2008) Sympagohydra tuuli gen. nov. and sp. nov. (Cnidaria: Hydrozoa) a cool hydroid from the Arctic sea ice. J Mar Biol Assoc U.K. 88: 1637-1641.
36. Pugh PR, Pagès F (1995) Is *Lensia reticulata* a diphyine species (Siphonophorae, Calycophora, Diphyidae)? A re-description. Scientia Marina 59(2): 181-192.
37. Raskoff KA, Purcell JE, Hopcroft RR (2005) Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. Polar Biol 28: 207-217.

38. Raskoff KA (2010) *Bathycorus bouilloni*: a new genus and species of deep-sea jellyfish from the Arctic Ocean (Hydrozoa, Narcomedusae, Aeginidae). Zootaxa 2361: 57-67.
39. Raskoff KA, Hopcroft RR, Kosobokova KN, Purcell JE, Youngbluth M (2010) Jellies under ice: ROV observations from the 2005 Hidden Ocean Expedition. Deep Sea Res 2 Top Stud Oceanogr 57: 111-126 .
40. Ronowicz M (2007) Benthic hydroids (Cnidaria: Hydrozoa) from Svalbard waters - biodiversity and distribution. J Mar Biol Assoc U.K. 87: 1089-1094.
41. Ronowicz M, Schuchert P (2007) *Halecium arcticum*, a new hydroid from Spitsbergen (Cnidaria: Hydrozoa). Zootaxa 1549: 55-62.
42. Ronowicz M, Włodarska-Kowalczyk M, Kukliński P (2013a) Hydroid epifaunal communities in Arctic coastal waters (Svalbard): effects of substrate characteristics. Polar Biol 36: 705-718.
43. Ronowicz M, Włodarska-Kowalczyk M, Kukliński P (2013b) Depth- and substrate-related patterns of species richness and distribution of hydroids (Cnidaria, Hydrozoa) in Arctic coastal waters ( Svalbard ). Mar Ecol 34: 165-176.
44. Schuchert P (2001) Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). Meddelelser om Grønland, Bioscience 53: 1-184.
45. Schuchert P (2006) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1. Rev Suisse Zool 113: 325-410.
46. Schuchert P (2008a) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 3. Rev Suisse Zool 115: 221-302.
47. Schuchert P (2008b) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 4. Rev Suisse Zool 115: 677-757.
48. Schuchert P (2010) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 2. Rev Suisse Zool 117: 337-555.
49. Schuchert P (2012) North-West European Athecate Hydroids and their Medusae. Synopses of the British Fauna (New Series) 59. 164 p.
50. Shih CT, Figueira AJG, Grainger EH (1971) A synopsis of Canadian marine zooplankton. Bulletin of the Fisheries Research Board of Canada 176: 1-264.
51. Shirley WD, Leung Y-M (1970) Medusae of the Central Arctic. In: Kobayashi HE, ed. Taxonomic Guides to Arctic Zooplankton II [Technical report no 3, 1960-1970]. University of Southern California Los Angeles, Department of Biological Sciences, Los Angeles.
52. Stepanjants SD (1967) Siphonophores of the seas of the USSR and the northern part of the Pacific Ocean. Opredeliteli po Faune SSSR 96. 216 p.
53. Stepanjants SD (1989) Hydrozoa of the Eurasian Arctic Seas. In: Herman Y, ed. The Arctic Seas Climatology, Oceanography, and Biology. New York: Van Nostrand Reinhold. pp. 397-430.
54. Stepanjants SD (1994) Hydrozoa of the East Siberian Sea. Issledovaniya Fauny Morei 48: 116-142.
55. Stepanjants SD (2001) Subphylum Medusozoa. Classes Hydrozoa, Siphonophora, Scyphozoa. In: Sirenko BI, ed. List of species of free-living Invertebrates of Eurasian Arctic Seas and Adjacent deep waters. Issledovaniya Fauny Morei 51(59): 31- 36.
56. Stepanjants SD, Kosobokova KN (2006) Medusae of the genus *Rhabdoon* Hydrozoa: Anthomedusae: Tubularioidea in the Arctic Ocean. Mar Biol Res 2(6): 388-397.
57. Stepanjants SD, Svoboda A (2008). The genus *Gymnogonos* (Anthoathecata: Capitata: Corymorphidae) - redescription of known species and description of a new species from the North Pacific. J Mar Biol Assoc U.K. 88: 1619-1629.

58. Thiel ME (1932) Übersicht über die Hydromedusen der Arktis. *Fauna Arctica* 6: 119-158.
59. Uchida T (1969) Medusae from the Arctic Ocean. *Publications of the Seto Marine Biological Laboratory* 17(4): 285-287.
60. van Soest RWM (1973) Planktonic coelenterates collected in the North Atlantic Ocean. *Bijdragen tot de Dierkunde* 43(1): 119–125.
61. Voronkov A, Stepanjants SD, Hop H (2010) Hydrozoan diversity on hard bottom in Kongsfjorden, Svalbard. *J Mar Biol Assoc U.K.* 90: 1337-1352.
62. Węśławski JM, Kwaśniewski S, Wiktor J (1991) Winter in a Svalbard fiord ecosystem. *Arctic* 44(2): 115-123.
63. Yashnov VA (1948) Hydromedusae. In: Gaevskoy NL, ed. *Check List Fauna Flora northern seas U.S.S.R., Moscow*. pp. 65-74.
64. Zelickman EA (1972) Distribution and ecology of the pelagic hydromedusae, siphonophores and ctenophores of the Barents Sea, based on perennial plankton collections. *Mar Biol* 17: 256–264.