

Ctenophore diversity of Atlantic Canada: a synthesis

Florian Lüsrow ^{a,b} and Hunter Stevens ^c

^aDepartment of Earth, Ocean and Atmospheric Sciences, The University of British Columbia, Vancouver, BC, Canada; ^bInstitute for the Oceans and Fisheries, The University of British Columbia, Vancouver, BC, Canada; ^cCanadian Parks and Wilderness Society – Nova Scotia Chapter, Halifax, NS, Canada

Corresponding author: Florian Lüsrow (email: flueskow@eoas.ubc.ca)

Abstract

Ctenophores (comb jellies) are part of the diverse gelatinous zooplankton that have received growing research interest in recent decades. However, scientific dedication varies vastly across regions. Ctenophores have historically attracted limited attention in Atlantic Canada (four easternmost provinces and Quebec) despite their documented (seasonal) considerable food web impacts. In this part of the Northwest Atlantic known for bio-invasions and climate change-facilitated northward distribution shifts, we reviewed literature and open-access biodiversity repositories to improve our understanding of ctenophore seasonal population dynamics, spatial distributions, and trophic interactions. From the peer-reviewed literature, we listed four extant species (*Beroe cucumis* Fabricius, 1780; *Bolinopsis infundibulum* (O.F. Müller, 1776); *Mertensia ovum* (Fabricius, 1780); and *Pleurobrachia pileus* (O.F. Müller, 1776)), which are common cold-water species found across the boreal/sub-arctic North Atlantic, one species recorded more than a century ago (*Dryodora glandiformis* (Mertens, 1833)), and one extinct species (*Daihuoides jakobvintheri*[†] Klug, Kerr, Lee & Cloutier, 2021). In addition, online platforms (Ocean Biodiversity Information System, Global Biodiversity Information Facility, and iNaturalist[®]) revealed up to seven additional species. Some of them are doubtful. We discussed the complementary species lists and caveats of the (community) scientific approaches. We formulated research priorities to overcome historically rooted knowledge gaps on gelatinous zooplankton, and ctenophores in particular, in Atlantic Canadian territorial shelf waters.

Key words: biodiversity, comb jellies, gelatinous zooplankton, monitoring, Northwest Atlantic

Introduction

The phylum Ctenophora contains more than 200 recognized marine gelatinous species globally (Mills 2001; Giribet and Edgecombe 2020). They are characterized by the presence of ctenes, comb-like structures composed of cilia that they use as a method of locomotion (Tamm 2014; Dunn et al. 2015). The two main classes of ctenophores (or comb jellies) are Tentaculata, which have retractile tentacles, and Nuda, lacking tentacles (Gibbons et al. 2021).

Within marine ecosystems, ctenophores play important ecological roles as consumers of fish eggs, larvae, and various zooplankton species, including other ctenophores (e.g., Purcell 1997; Purcell et al. 2001; Sullivan and Gifford 2004). They are also prey for various marine predators, such as fish, turtles, and pelagic cnidarians (Arai 2005; Purcell et al. 2007; Dischereit et al. 2024). Besides these trophic interactions (see jelly web; Chi et al. 2021), ctenophores are important hosts for symbionts (Selander et al. 2009), host distinct microbial communities (Hao et al. 2015), and contribute to the global carbon cycle (Luo et al. 2020). Ctenophores, among other gelatinous zooplankton species, are known to be indicators of water masses of different properties and origins (Colebrook 1977; Raymont 1983; Mańko et al. 2020).

Some ctenophores exhibit population explosions under certain oceanographic conditions, reaching extremely high densities (e.g., Oguz et al. 2008). This can cause strong top-down and bottom-up impacts on pelagic communities (McNamara et al. 2010; Schroeder et al. 2023). Furthermore, several ctenophore species have proven to be successful as invaders by establishing populations and expanding into regions outside their native range, as is the case of *Mnemiopsis leidyi* A. Agassiz, 1865 and *Beroe ovata* Bruguière, 1789 in the Black Sea (Shiganova et al. 2024).

In the waters of Atlantic Canada (AC) (provinces of New Brunswick, Newfoundland and Labrador, Nova Scotia, and Prince Edward Island), marine research has a centuries-old history and focused primarily on commercially important fauna such as finfish and shellfish (reviewed by Arai 1992; Myers et al. 1997; Lander et al. 2012; Greenan et al. 2019), invasive species (e.g., *Ciona intestinalis* (Linnaeus, 1767); Ramsay et al. 2009), and marine mammals (Whitehead et al. 1997). While lower trophic organisms like phyto-, meso-, and macrozooplankton were mostly investigated as indicators of water masses and food resources for predators (Simard and Harvey 2010; Debertain et al. 2017), ctenophores and other gelatinous zooplankton taxa received only limited attention.

Elaborate studies such as the one by Fraser (1970) on the ecology of *Pleurobrachia pileus* (O.F. Müller, 1776) in Scottish waters do not exist in Canadian waters. Stimpson (1854), Bigelow (1909), and Mayer (1912) were probably the first to describe the diversity and distribution of ctenophores along the Atlantic coast of North America. They stated in their works that only 21 ctenophore species occur from the Arctic in the north to Florida and the Greater and Lesser Antilles in the south. Within the sub-region of AC, they mentioned *Beroe cucumis* Fabricius, 1780, *Bolinopsis infundibulum* (O.F. Müller, 1776), *Mertensia ovum* (Fabricius, 1780), and *P. pileus*. The latter three were described to occur seasonally in high abundance. Since these dedicated works, very little research has been conducted on ctenophores in the region (Dunbar 1942; Andersen 1974; Frank 1986; Milne and Corey 1986; Suthers and Frank 1990; Archambault et al. 2010; Klug et al. 2021). With the onset of taxonomic (WoRMS, <https://www.marine-species.org/>) and open-source data portals for biodiversity (e.g., Global Biodiversity Information Facility (GBIF), <https://www.gbif.org/> and Ocean Biodiversity Information System (OBIS), <https://obis.org/>), community science online observation platforms such as iNaturalist® (<https://www.inaturalist.org/>) and social media data mining (e.g., Ringvold et al. 2020; Nascimento et al. 2024), new tools to study a vast area like AC to inform and include the wider public have emerged.

This study aims to present an up-to-date inventory of ctenophore species from Atlantic Canadian territorial shelf waters, as well as to synthesize available regional information to improve our understanding of their seasonal population dynamics, spatial distributions, and trophic interactions.

Materials and methods

Study area

Atlantic Canada (AC) traditionally refers to the land with provinces of New Brunswick, Newfoundland and Labrador, Nova Scotia, and Prince Edward Island (Fig. 1), and is the easternmost region of Canada situated on the Atlantic coast. While traditionally excluding the province of Quebec, we chose an inclusive approach that considered its Atlantic coastal waters (ecological connectivity), including the Gulf of St. Lawrence. According to the Wild Species 2020 report (<https://www.wildspecies.ca/reports>), the territorial shelf waters of AC stretch from the Canadian–US border in the south to the entrance of the Hudson Bay in the north, excluding the French possession of Saint-Pierre and Miquelon (Fig. 1).

Data acquisition

A literature search in the Web of Science, Google Scholar, and the Biodiversity Heritage Library using the search keywords “ctenophore”, “comb jelly”, “Ctenophora”, “Canada”, “New Brunswick”, “Newfoundland and Labrador”, “Nova Scotia”, “Prince Edward Island”, and “Quebec” was performed. Although all pertinent literature accessed during this search was included, some articles (likely early studies) found only in print and not yet digitized may have been unavailable to the search engines. Only 10 studies (Stimpson 1854; Bigelow 1909; Mayer 1912; Dunbar 1942; Anderson 1974; Frank 1986;

Milne and Corey 1986; Suthers and Frank 1990; Podar et al. 2001; Klug et al. 2021) reporting species-specific information from AC (not considering other Canadian waters) were found and used. In addition, we included records with photographic evidence and geographic coordinates available on platforms such as iNaturalist®, the GBIF, and the OBIS as well as from a personal collection (H. Stevens) of observations and photographs acquired over 5 years of scuba diving and snorkeling on the coasts of Nova Scotia. Records published in iNaturalist® can be (but are not always) verified by an independent expert. All search efforts were conducted in July and August 2024. Therefore, records uploaded afterwards are not considered.

A search of occurrences on GBIF was performed for Scientific Name = Ctenophora, Country = Canada, limited to the Atlantic with a search box area of POLYGON (−70.063, 40.262; −47.902, 40.262; −47.902, 57.727; −70.063, 57.727; −70.063, 40.262) (<https://doi.org/10.15468/dl.y6zqcy>). Another data search was conducted on OBIS for areas such as the Gulf of St. Lawrence, Bay of Fundy, Scotian Shelf, and Labrador and Newfoundland (query performed on 26 August 2024). An additional search in SeaLifeBase carried out on 29 July 2024 revealed no further information.

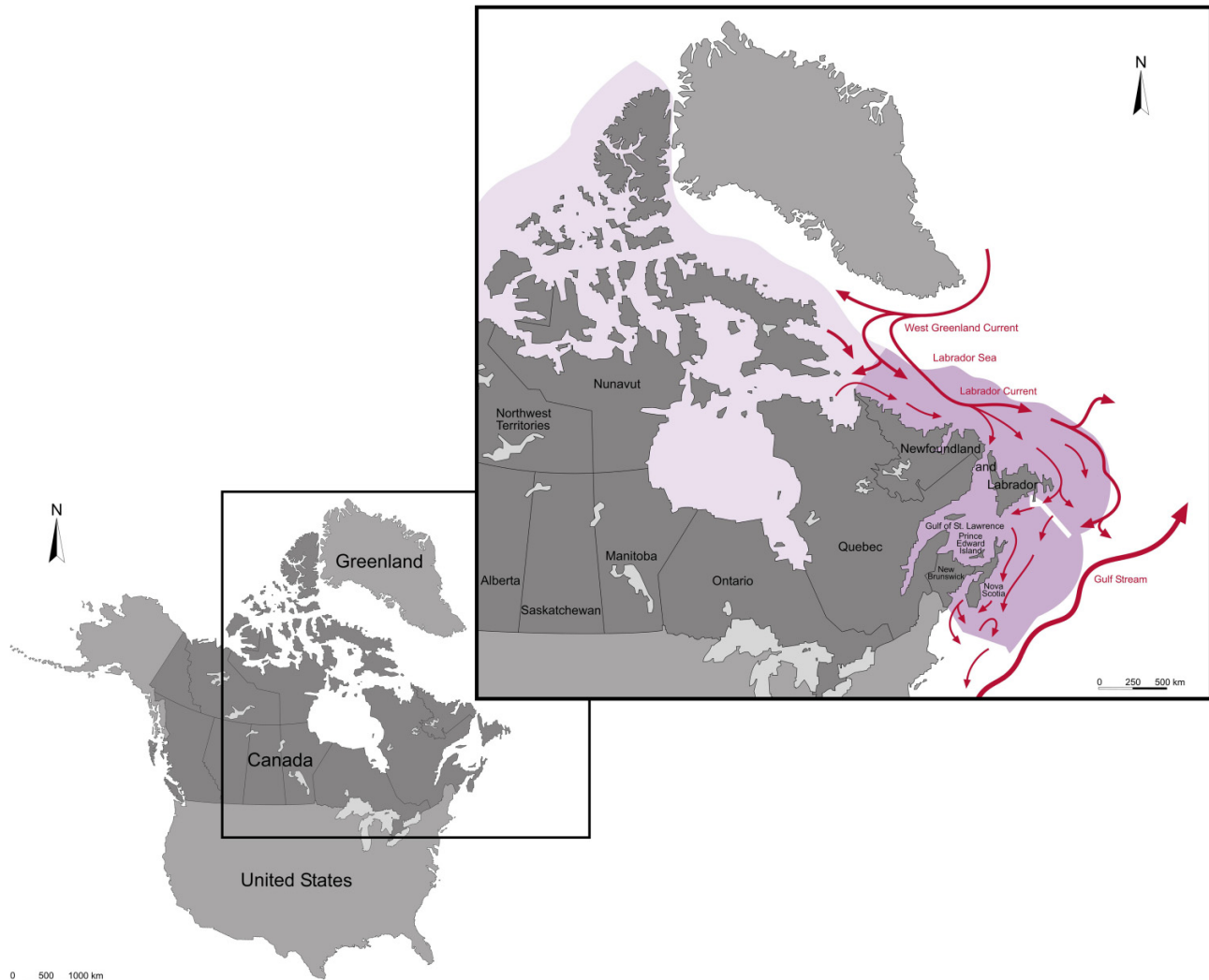
Results

Ctenophore species records in literature and biodiversity repositories

Species richness in literature and open-source biodiversity repositories in Atlantic Canadian (AC) territorial shelf waters is moderately low. There are up to 13 species of ctenophores (potentially four Nuda, five Cydippida, three Lobata, and one prehistoric species; Fig. 2 and Table 1) recorded. Their abundance, phenology, and distribution patterns vary vastly. Because of this, we will synthesize available knowledge from peer-reviewed literature and open-source biodiversity repositories separately by species. In general, all ctenophore species in AC are holoplanktonic. No benthic ctenophores have been reported yet. Broadly speaking, in Nova Scotia (and presumably other AC provinces), ctenophore blooms occur semi-annually in coastal habitats—one in the spring/early summer (April–June) and another one in the fall/early winter (October–December; H. Stevens, pers. obs.; Archambault et al. 2010).

In the peer-reviewed literature, only six species (*Beroe cucumis*, *Bolinopsis infundibulum*, *Daihuoides jakobvinteri*† Klug et al. 2021, *Dryodora glandiformis* (Mertens, 1833), *Mertensia ovum*, and *Pleurobrachia pileus*) were reported (Table 1). Four of the five living species (except *D. glandiformis*) are common cold-water species found across the boreal/sub-arctic North Atlantic. OBIS recorded three common taxa and three uncertain ones, with most records not being identified beyond Ctenophora (1451 of 2381 records). The identified taxa were *Bolinopsis infundibulum* (2 checklist records only), *Beroe ovata* (1 record in 1976), *Hormiphora cucumis* (Mertens, 1833) (120 records with 4 records being *Hormiphora plumosa* as synonym), *M. ovum* (64 records), *Mnemiopsis leidyi* (2 records in 2009), and *Pleurobrachia pileus*. GBIF revealed 10 taxa (882 records),

Fig. 1. Extent of the Canadian territorial shelf waters with focus (highlighted in red) on the Atlantic portion (provinces New Brunswick, Newfoundland and Labrador, Nova Scotia, Prince Edward Island, and parts of Quebec). Major ocean currents in the region are indicated. Base maps, Map data © 2024 Google (Canada), were edited in FreeHand MX® software.



the vast majority being *P. pileus*, and some uncertain ones (Table 1). As with OBIS, some entries did not specify beyond Ctenophora, and a few *Pleurobrachia* and *Beroe* records were assigned to *P. pileus* and *B. cucumis*, respectively. In addition, iNaturalist® lists records of *Beroe abyssicola* Mortensen, 1927, *Beroe gracilis* Künne, 1939, *Bolinopsis microptera* (A. Agassiz, 1865), *D. glandiformis*, *Euplokamis dunlapae* Mills, 1987, and *M. leidy* (Table 1). Two of these records were confirmed by pictures taken by one of the paper's authors (HS), i.e., *D. glandiformis* and *E. dunlapae* (Table 1).

Species- and region-specific profiles

Beroe cucumis, the common northern comb jelly, is a predator of other ctenophores; these tend to appear around a week after the start of ctenophore blooms and then persist for a couple more weeks after the prey numbers dwindle (H. Stevens, pers. obs.; Figs. 2A–2C). This beroid ctenophore species occurs commonly in late May to June, but also appears within the fall bloom in lower numbers (H. Stevens, pers. obs. from Nova Scotia), and generally in areas of deeper

water (as seen in the Bay of Fundy; Milne and Corey 1986). This species may be absent from the zooplankton between October and December in Nova Scotian bays, but remains off Newfoundland (Bigelow 1909). Common prey of *Beroe cucumis* in AC territorial shelf waters is the tentaculate species *Pleurobrachia pileus* (Fig. 2B).

Individuals of the lobate *Bolinopsis infundibulum*, like *Beroe cucumis*, tend to become large and obvious later in the spring and into early summer (H. Stevens, pers. obs.; Figs. 2D and 2E). These also appear in the fall in Nova Scotia and were named “exceedingly abundant” off the coast of Newfoundland in summer (Mayer 1912). *Bolinopsis infundibulum* are crustacean predators that swim while feeding. *Mertensia ovum*, the Arctic comb jelly, appears infrequently during the winter months, but becomes more common in Nova Scotia in April and May, and some specimens may persist into June (H. Stevens, pers. obs.; Figs. 2F and 2G), and may grow up to 10 cm oral–aboral length. However, its “true home” was named to be off the coast of Labrador (Mayer 1912), where they also occur later in the season (Bigelow 1909).

Fig. 2. Some of the ctenophore species reported for Atlantic Canada. (A–C) = *Beroe cucumis* (B = *B. cucumis* has ingested a *Pleurobrachia pileus* specimen), (D and E) = *Bolinopsis infundibulum*, (F and G) = *Mertensia ovum*, (H) = *Dryodora glandiformis*, (I) = *Euplokamis dunlapae*, (J and K) = *P. pileus*. No size measurements were taken during the dives. All photos were taken by HS.

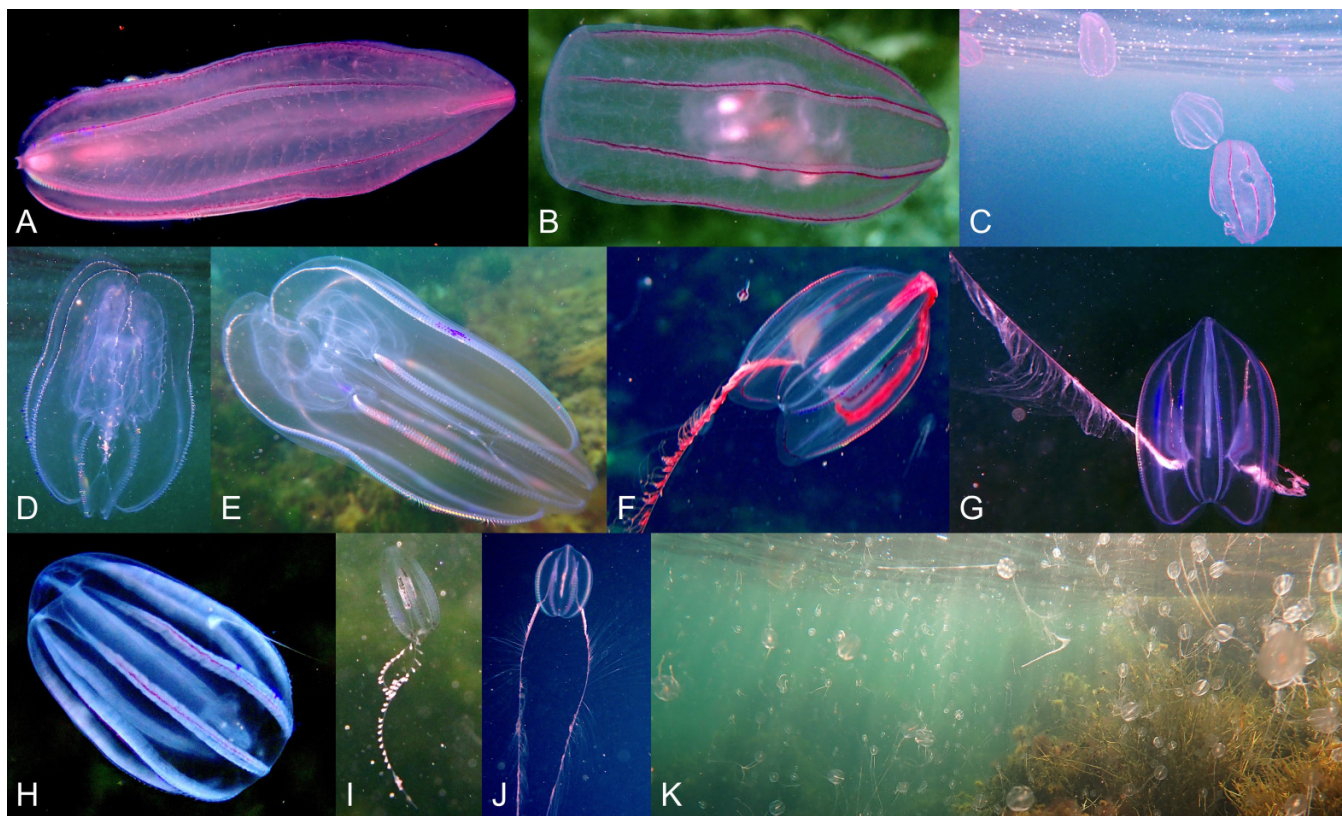


Table 1. List of ctenophore species recorded in Atlantic Canada territorial shelf waters.

Class	Order	Species	Literature	OBIS	GBIF	iNaturalist®	Personal collection	
Nuda	Beroida	<i>Daihuoides jakobvintheri</i> [†] Klug et al. 2021	×					
		<i>Beroe abyssicola</i> Mortensen, 1927*			×	×		
		<i>Beroe cucumis</i> Fabricius, 1780	×		×	×	×	
		<i>Beroe gracilis</i> Künne, 1939*					×	
		<i>Beroe ovata</i> Bruguière, 1789*		×	×			
Tentaculata	Cydippida	<i>Dryodora glandiformis</i> (Mertens, 1833)	×		×	×	×	
		<i>Euplokamis dunlapae</i> Mills, 1987			×	×	×	
		<i>Hormiphora cucumis</i> (Mertens, 1833)*		×	×			
		<i>Mertensia ovum</i> (Fabricius, 1780)	×	×	×	×	×	
		<i>Pleurobrachia pileus</i> (O.F. Müller, 1776)	×	×	×	×	×	
		Lobata	<i>Bolinopsis infundibulum</i> (O.F. Müller, 1776)	×	×	×	×	×
			<i>Bolinopsis microptera</i> (A. Agassiz, 1865)*					×
			<i>Mnemiopsis leidyi</i> A. Agassiz, 1865*		×	×	×	×
Σ		6	6	10	10	6		

Note: Sources: literature = see reference details in the text, OBIS = Ocean Biodiversity Information System, GBIF = Global Biodiversity Information Facility, iNaturalist®, and personal photo collection by HS. Doubtful species are indicated with an asterisk.

Dryodora glandiformis is a rare cydippid species in Nova Scotia even during the spring and fall bloom times (H. Stevens, pers. obs.; Fig. 2H). This record is one of the few from eastern North America. Please note that one of two type locations (Gulf of St. Lawrence) is located inside the study area. *Euplokamis dunlapae*, another cydippid species that is presum-

ably polar (holotype from Friday Harbor, Salish Sea, WA; C.E. Mills, pers. comm.), generally co-occur with *M. ovum* before disappearance (H. Stevens, pers. obs.; Fig. 2I).

Pleurobrachia pileus, commonly called sea gooseberry, is by far the most common ctenophore species in AC territorial shelf waters (H. Stevens, pers. obs.; Stimpson 1854; Bigelow

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1909; Suthers and Frank 1990; Figs. 2J and 2K). The highest abundance appears in May and later in the summer/fall (Fig. 2K), though individuals can be found year-round (F. Luskow and H. Stevens, pers. obs. from Nova Scotia). It is also the most abundant species in both the spring and fall blooms. In the Bay of Fundy, one study showed that small *P. pileus* specimens were abundant in summer and fall, whereas larger specimens were found in spring (Milne and Corey 1986). *Pleurobrachia pileus* occurs in coastal and open waters, such as Browns Bank, SW Nova Scotian shelf, though with higher abundances nearshore. In open waters, *P. pileus* competes with planktivorous fish (larvae) like haddock (*Melanogrammus aeglefinus* (Linnaeus, 1758)) and cod (*Gadus morhua* Linnaeus, 1758), and its predation impact can be considerable (Frank 1986; Suthers and Frank 1990). Like most ctenophore species occurring in AC waters, *P. pileus* is a vivid ambush predator of crustaceans, mostly copepods. To this day, diel vertical migration has not been documented for any of the ctenophores occurring in AC waters.

Doubtful taxa

Limited information and questionable records in OBIS, GBIF, and iNaturalist® exist on several ctenophore species (Table 1). As we do not have strong evidence against the report's correctness, we briefly list them here: *Beroe abyssicola*, *Beroe gracilis*, *Beroe ovata*, *Hormiphora cucumis*, *Bolinopsis microptera*, and *Mnemiopsis leidy*. However, as some of these species are known to prefer warm waters (e.g., *Beroe ovata*) or have recently been delineated from a previous species complex (e.g., *Bolinopsis microptera*), these records may be treated with caution. In the absence of more conclusive evidence from expert-verified barcoding efforts, underwater footage, or zooplankton samples, we refer to them as “Schrödinger’s comb jellies”, i.e., these ctenophore species may or may not be present in AC territorial shelf waters.

Discussion

In Atlantic Canada (AC), historically, four ctenophore species are known: *Beroe cucumis*, *Bolinopsis infundibulum*, *Mertensia ovum*, and *Pleurobrachia pileus* (e.g., Mayer 1912; Dunbar 1942; Frank 1986; Suthers and Frank 1990; Archambault et al. 2010). The prehistoric ctenophore species *Daihuoides jakobvinteri*[†] is only known from one fossil record in eastern Quebec (Klug et al. 2021). While regional peer-reviewed literature is sparse, open-source data portals for biodiversity (e.g., GBIF and OBIS) and community science observation platforms such as iNaturalist® can act to complement species inventories and distribution maps. Using the latter approaches, we were able to double with certainty (and triple with precautions) the species number (Table 1). In vast regions with limited scientific oversight and funding availability, online biodiversity repositories can be vital for increasing our knowledge, but require expert verification (e.g., Nascimento et al. 2024). AC has annual cross-regional zooplankton surveys (Atlantic Zone Monitoring Program, <https://www.dfo-mpo.gc.ca/science/data-donnees/azmp-pmza/index-eng.html>). However, nearshore/coastal observations by divers are strongly biased towards the Halifax metro

region and other parts of Nova Scotia (C. Nozères, pers. comm.). Picture evidence deposited on social media platforms such as Facebook® or Instagram® may prove to be a silver bullet in data-limited regions such as AC (e.g., Ringvold et al. 2020; Nascimento et al. 2024). A major caveat of the present (and similar style previous species inventories) is the lack of open-ocean and deep-water observations. These can only be obtained with professional cost-intensive equipment (e.g., remotely operated vehicles, research vessels, metazoan-including long-term open-ocean biodiversity monitoring programs) that is available in AC. However, it seems that ctenophores are part of an overlooked share of the deep-water fauna.

One puzzling case is the identity of the *Beroe* species. The precise taxonomic position of AC *Beroes* is yet to be confirmed. Recently, Johansson et al. (2018) and Shiganova and Abyzova (2022) questioned the traditionally believed global biogeography. While historically, *Beroe cucumis* is thought to inhabit the regional AC waters and a vast part of the Arctic, future phylogeographic studies will need to investigate its validity. The inclusion of provisionally labelled *Beroe abyssicola* is recommended because online biodiversity repository entries of this species are mostly based on its intense coloration and may be incorrect.

Another intriguing case is *Euplokamis dunlapae*, which is noteworthy reported here for the first time in the Northwest Atlantic. Specimens of *E. dunlapae* were studied by divers in a submersible at about 250 m depth. These were identified morphologically, but till today, no specimens have been sequenced. *Euplokamis* specimens from Norway were studied morpho- and molecularly, and matched with specimens from the type location at Friday Harbor, WA (Majaneva et al. 2021). Specimens photographed in Nova Scotia and reported in iNaturalist® can be identified with certainty as *E. dunlapae* (C.E. Mills, pers. comm.). As showcased with *Beroe cucumis* and *E. dunlapae*, as well as *M. ovum* (Podar et al. 2001), incorporating ctenophores in regional/global phylogenetic studies is lacking and remains for future generations.

For comparison, the species richness in AC territorial shelf adjacent regions is low, which can be explained by the relatively limited observational effort. In the coastal waters of Iceland, off the Northeast coast of Greenland as well as in the Labrador and Icelandic Seas, there are only three ctenophores reported yet: *Beroe* spp., *Bolinopsis infundibulum*, and *M. ovum* (Licandro et al. 2015; Sigurdsson et al. 2021; Mazanowski et al. 2023). Similarly, the Canadian Arctic (taking the waters off Nunavut as the closest territory) houses *Beroe cucumis*, *Bolinopsis infundibulum*, and *M. ovum* (Dunbar 1942; Grainger et al. 1985; Percy 1989; Siferd and Conover 1992). In contrast, the distant waters off British Columbia (Northeast Pacific Ocean) harbor a distinct species assemblage with some taxa shared with eastern Canada, i.e., *Beroe cucumis*, *Dryodora glandiformis*, and *Euplokamis dunlapae* (Mackie and Mills 1983; Mackie 1985; Larson 1986, 1987; Mills 1987; Purcell 1990; Wrobel and Mills 1998; Mackas et al. 2013; Luskow et al. 2021; Johnson et al. 2022). However, other species such as *Beroe abyssicola*, *Bolinopsis microptera*, *Hormiphora californiensis*, *Pleurobrachia bachei*, and *Thalassocalyce inconstans* are indicators for Pacific and deeper water masses. The abundance of ctenophores (relative to

other gelatinous zooplankton taxa) may considerably vary seasonally (Halsband et al. 2018). Thus, the presented species inventories offer just temporal and spatial snapshots of local gelatinous zooplankton assemblages prone to incompleteness and should be treated with some caution.

Today, no benthic ctenophores (order Platyctenida) are described from AC, and future dedicated investigations may deliver specimens. Mortensen (1910) described the platyctenid species *Tjalfiella tristoma* from the west coast of Greenland. Furthermore, Kramp (1942) sampled it near the type location, and Bezio and Collins (2024) re-described the species from New England and the Northwest Atlantic. While these collections suggest that the genus (or benthic ctenophore in general) could occur in AC waters, there is currently no conclusive evidence.

We need to summarize that historically and recently, not much research attention has been paid to gelatinous zooplankton, and ctenophore species in particular, in AC. This may bring us into a potentially difficult situation as future predictions of population developments, assemblage composition changes, and the introduction/regional extinction of species can only be made upon properly resolved spatiotemporal data (Lüskow 2020). The influence exerted by ctenophores appearing seasonally en masse in both predator and prey contexts is almost certainly vital to the population dynamics of other animal species. Trophic cascades potentially endangering commercially important fauna, such as finfish and shellfish, caused by beyond-seasonal boom and bust dynamics can hardly be understood and mitigated if we do not have a proper inventory of marine species. The low number of ctenophore species in the boreal/sub-arctic North Atlantic may also be indicative of cryptic species. Future molecular studies should investigate this aspect further. This is especially true for benthic ctenophores that are typically not picked up in trawls. As the world's ocean dynamics respond to global climate shifts, we must make efforts to understand the role of each “cog” in the marine ecosystem, and how it fits amongst the others. Generating a modern contemporary inventory of historically overlooked yet critical marine species, such as ctenophores, is the first step in understanding their erratic population dynamics and ecological roles in the rapidly changing waters of AC.

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Data availability

All data used to create the figures can be accessed in the text and table.

Author information

Author ORCIDs

Florian Lüskow <https://orcid.org/0000-0002-2100-7012>

Hunter Stevens <https://orcid.org/0009-0007-2232-8903>

Author contributions

Conceptualization: FL

Data curation: FL

Formal analysis: FL

Investigation: FL, HS

Methodology: FL

Project administration: FL

Resources: FL, HS

Software: FL

Supervision: FL

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