Occurrence of toxin-producing marine algae in the Canadian Arctic and adjacent waters

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CANADIAN MANUSCRIPT REPORT

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2019

OCCURRENCE OF TOXIN-PRODUCING MARINE ALGAE IN THE CANADIAN ARCTIC AND ADJACENT WATERS

by

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Abstract

Traditionally, the Arctic has been considered to present unfavorable conditions for toxin-producing marine harmful algal blooms (HABs) to occur. However, it has recently been postulated that: 1) marine algae may, in fact, be producing phycotoxins in the Arctic based on studies in the Alaskan and Greenlandic sector, and 2) global climate change-related impacts in the Arctic may present toxin-producing algae with a new set of environmental conditions favoring their growth. As a result, the importance of research and monitoring of arctic marine toxin-producing algae is gaining significant attention. Here, we present an in-depth literature review of the occurrence of toxin-producing marine algal species in the Canadian Arctic within its five Biogeographic Regions (eastern Canadian Arctic, western Canadian Arctic, Canadian Arctic Basin, and Hudson Bay Complex) and in adjacent waters of western Greenland, northern Alaska and the Chukchi Sea. We show that almost 70% of species globally considered toxic are already present across various habitats of the Canadian Arctic and adjacent waters. Further, we present maps of their reported occurrence. The most prevalent taxonomic classes belonged to Dinophyceae and Bacillariophyceae, followed by Haptophyceae and Raphidophyceae. There are a few published studies documenting presence of marine phycotoxins in the Alaskan and Greenlandic sectors of the Arctic Ocean, but not in the Canadian sector as yet. Finally, we discuss implications of toxin-producing species presence in the Canadian Arctic and identify the most pressing scientific questions that need to be addressed.

Résumé

Par le passé, l’Arctique était considéré comme présentant des conditions défavorables à la prolifération d’algues marines nuisibles productrices de toxines. Toutefois, les hypothèses suivantes ont récemment été émises : 1) les algues marines peuvent, en fait, produire des phycotoxines dans l’Arctique d’après des études menées dans le secteur de l’Alaska et du Groenland, et 2) les répercussions liées aux changements climatiques mondiaux dans l’Arctique peuvent présenter un nouvel ensemble de conditions environnementales qui favorisent la croissance des algues produisant des toxines. Par conséquent, la recherche et la surveillance des algues marines arctiques productrices de toxines gagnent en importance. Nous présentons ici une analyse documentaire approfondie de la présence d’espèces d’algues marines productrices de toxines dans l’Arctique canadien dans ses cinq régions biogéographiques (est de l’Arctique canadien, ouest de l’Arctique canadien, bassin de l’Arctique canadien, complexe de la baie d’Hudson) et dans les eaux adjacentes de l’ouest du Groenland, du nord de l’Alaska et de la mer des Tchouktches. Nous démontrons que près de 70 % des espèces considérées comme toxiques à l’échelle mondiale sont déjà présentes dans divers habitats de l’Arctique canadien et des eaux adjacentes. De plus, nous présentons des cartes de leur occurrence signalée. Les classes taxonomiques les plus répandues appartenaient aux Dinophycées et aux Bacillariophycées, suivies des Haptophycées et des Raphidophycées. Quelques études publiées font état de la présence de phycotoxines marines dans les secteurs de l’Alaska et du Groenland de l’océan Arctique, mais pas encore dans le secteur canadien. Enfin, nous discutons des répercussions de la présence d’espèces productrices de toxines dans l’Arctique canadien et définissons les questions scientifiques les plus urgentes qui doivent être abordées.

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1. Introduction

Worldwide, there are about 40 known marine phytoplankton species that can produce marine toxins (Gerssen et al. 2010). Most toxin-producing marine algal species belong to taxonomic classes Dinophyceae or Bacillariophyceae (Smayda 1997). Toxin-producing phytoplankton cells are usually present in marine waters in concentrations low enough not to cause acute effects on the health of other marine organisms or humans. However, under favorable climatic and hydrographic conditions, toxin-producing algae may proliferate forming dense aggregations of cells classified under the broad term of harmful algal blooms (HABs) (Van Dolah 2000). The HAB designation is a societal concept rather than a scientific definition. Blooms are considered to fit the HAB criterion if they cause injury to human health, components of aquatic ecosystems, or to socio-economic interests (Anderson et al. 2012).

Marine toxins are classified into several classes based on their chemical structure and the syndromes they cause in contaminated shellfish, and include domoic acid (DA), saxitoxins (STX), brevotoxins, okadaic acid, yessotoxins, azaspiracids, and cyclic imine toxins (Gerssen et al. 2010). All of these groups of toxins, and various analogues identified within these groups, have different physical-chemical properties which will ultimately determine their distinct environmental behavior and toxico-kinetics such as water solubility, bioavailability, bioaccumulation potential, or retention/excretion rates by biota. The most prevalent and ubiquitous marine toxins are DA and STX with >10 and >58 analogues, respectively (Vilariño et al. 2018). These are also the most hydrophilic of all marine algal toxins with relatively high water solubility, high bioconcentration and low bioaccumulation potential, low bioavailability, and short half-life in most tissues due to high elimination rates from most organisms (Vilariño et al. 2018). Neurological syndromes caused by DA and STX are referred to as Amnesic Shellfish Poisoning (ASP) syndrome and Paralytic Shellfish Poisoning (PSP) syndrome, respectively.

Marine toxins can bioaccumulate in various marine species such as fish, crustaceans (e.g., crabs) or filter-feeding bivalves (shellfish) including mussels, oysters, scallops and clams. In shellfish, marine toxins accumulate primarily in digestive glands and usually do not cause acute effects. However, they can cause acute adverse effects including severe intoxication and death when contaminated shellfish are ingested by consumers such as fish, whales, birds or humans (Gerssen et al. 2010). Health effects of chronic exposure to low levels of marine toxins are very poorly understood (Vilariño et al. 2018). Traditionally, health effects of sub-acute doses of marine toxins, particularly those from hydrophilic groups, were believed to be temporary and fully reversible. However, some recent studies suggest that chronic exposure to lower concentrations of marine toxins can, in fact, have long-lasting effects on human health including decreased toxin sensitivity or permanent memory decline (EFSA 2009; Grattan et al. 2018).

Most occurrences of HABs have been reported in temperate and tropical regions, and have been on the rise with regards to frequency, intensity, and geographical expansion over the past few decades (Hallegraef 1993; Van Dolah 2000). On a global scale, a few thousand cases of human poisoning (~15% mortality rate) with marine algal toxins after consumption of contaminated shellfish or fish are being reported each year; most of them a result of DA and STX toxicity (Hallegraef 1993). The marine Arctic has traditionally been considered to present highly unfavorable conditions for HABs to develop. A few studies have linked the presence of marine algal species or marine toxins to aquaculture mortality in the Arctic (Skreslet et al. 1993; Baggesen et al. 2012). However, after recent publication of a study documenting presence of DA and STX in tissues of arctic and sub-arctic marine mammals from Alaska in concentrations that could potentially impact their health, the issue of HABs in the Arctic gained significant attention in the scientific community (Lefebvre et al. 2016). Questions of whether toxin-producing species are present in the Arctic, which habitats favor their growth, and if HABs are extremely rare or are present but simply remain under-documented in remote Arctic regions had now become of high relevance.

On-going global climate change-related shifts, in particular the reduction in sea ice extent and thickness, the increase of water temperatures, and changes in water stratification, have all been postulated to increase the probability of HABs in the Arctic (Lefebvre et al. 2016). The Canadian Arctic is experiencing profound changes caused by climate change including sea ice reduction, temperature increases, water stratification and circulation shifts, and increase in shipping (Michel 2013, Michel et al. 2015). As a result, this region can potentially become more vulnerable to HABs and their effects on marine wildlife and humans, in particular when paired with relatively strong dependence of Canadian Northern communities on traditional diets (Wesche and Chan 2010).

The objectives of this report are to: 1) summarize the current state of knowledge on the presence of marine toxin-producing algae in the Canadian Arctic waters and adjacent marine regions (Chukchi Sea, Northern Alaska and the Western Greenland), and 2) to identify scientific gaps that need to be addressed in order to understand the probability of occurrence and risks associated with HABs in the Canadian Arctic in the future.

2. Methods

The literature review was carried out following a step-wise strategy. First, a literature search was carried out using the Search Engines Web of Science (Institute for Scientific Information), Google Scholar (Google) and ResearchGate scientific social network. The following words, and their combinations, were searched for: algae, Arctic, bloom, community, harmful, harmful algal bloom, phytoplankton, plankton, polar, protists, sea ice, toxic, toxin. Geographic regions of interest comprised the Canadian Arctic Biogeographic Regions (eastern Canadian Arctic, western Canadian Arctic, Canadian Arctic Basin, and Hudson Bay Complex) (DFO 2009) and adjacent waters of western Greenland, northern Alaska and the Chukchi Sea (Figure 1). Latin and vernacular names of toxic algae listed in Poulin et al. (2011) for the Arctic were also included in the literature search. The references gathered by the initial search were analyzed for relevance and cited studies were also assessed. Authors' searches expanded the list of references from authors of relevant studies. We reviewed studies reporting composition of phytoplankton and ice algae communities in the Canadian Arctic and adjacent waters for the presence of toxin-producing algae. Species listed in Lassus et al. (2016), AlgaeBase (Guiry and Guiry 2018) and the IOC-UNESCO list of harmful microalgae (Moestrup et al. 2018) were specifically searched for.

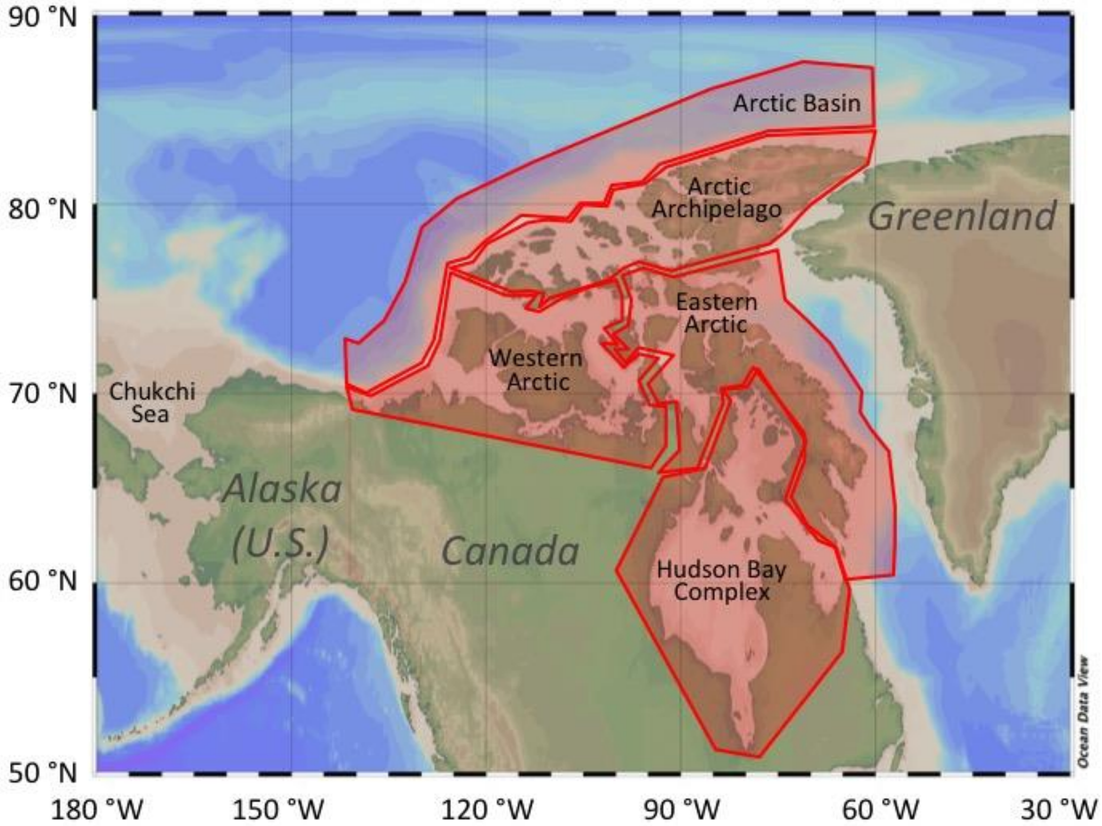

Figure 1. Canadian Arctic Biogeographic Regions for which the review of marine toxin-producing algae occurrence was carried out. Regions defined after DFO (2009).

In this document, we refer to algae species that are known to produce toxins under some circumstances as "toxin-producing". The following two conditions needed to be fulfilled for a species to be included in the list of toxin-producing algae reported herein: 1) at least one report documenting the species to produce toxins, not limited to Arctic regions, and 2) at least one report documenting the presence of the species in the Canadian Arctic and/or adjacent waters. All toxic algae included in tables and figures of this report were identified to species level by means of traditional taxonomy (inverted microscopy) or molecular taxonomy, i.e., environmental DNA methods. Some studies referenced herein report potentially toxic algae identified only to genus level (Table 2), and these are included in the maps depicting toxin-producing algae occurrence in the Canadian Arctic and adjacent waters across 4 reported taxonomic classes (Figures 2-5). The focus of this review is on toxin-producing marine algae and as such, does not include cyanobacteria and non-toxic harmful algae such as *Phaeocystis pouchetii*, a species responsible for clogging of fishing nets and accumulation of foam due to formation of mucilaginous aggregations.

3. Results and Discussion

There are 27 species of marine toxin-producing algae reported for the Canadian Arctic and adjacent waters, the majority belonging to taxonomic classes Dinophyceae (18 species) and Bacillariophyceae (8 species) (Table 1). In addition to reports of toxin-producing algae identified to species level, there are numerous studies documenting the presence of four algae genera that present challenges in identification to species level (Gymnodinium spp./Gyrodinium spp. complex, Cochlodinium spp. and Chrysochromulina spp.) but are well known to contain at least one toxin-producing species (Table 2). The most ubiquitous genera and species with regards to geographic occurrence were Gymnodinium spp./Gyrodinium spp. complex (Dinophyceae) and two species of potentially toxic Bacillariophyceae: *Pseudo-nitzschia delicatissima and Pseudo-nitzschia seriata* (Tables 2 and 3). They were present in each of the Canadian Arctic Biogeographic Regions as well as in the adjacent waters of western Greenland, northern Alaska and the Chukchi Sea. Toxin-producing species were recorded across various marine habitats such as sea ice, water column or sediment (Table 4). Species belonging to Bacillariophyceae were commonly present in both sea ice and pelagic habitats, while Dinophyceae and Raphidophyceae tend to be pelagic.

Table 1. List of toxin-producing species of marine algae reported in the Canadian Arctic and adjacent waters.

Class	Species or genus
Bacillariophyceae	*Halamphora cf. coffeaformis var. borealis* (Agardh) Levkov 2009 *Pseudo-nitzschia delicatissima* (Cleve) Heiden 1928 *Pseudo-nitzschia granii* (Hasle) Hasle 1974 *Pseudo-nitzschia obtusa* (Cleve) Hasle and Lundholm 2005 *Pseudo-nitzschia pseudodelicatissima* (Hasle) Hasle 1993 *Pseudo-nitzschia pungens* (Grunow ex Cleve) Hasle 1993 *Pseudo-nitzschia seriata* (Cleve) Peragallo 1899 *Pseudo-nitzschia turgidula* (Hustedt) Hasle 1993
Dinophyceae	*Alexandrium tamarense* (Lebour 1925) Balech 1995 *Alexandrium fundyense* Balech 1985 *Alexandrium ostenfeldii* (Paulsen 1904) Balech and Tangen 1985 *Amphidinium aff. carterae* Hulburt 1957 *Amphidinium operculatum* Claparède and Lachmann 1859 *Amphidinium gibbosum* (Maranda and Shimizu) Jørgensen and Murray 2004 *Dinophysis acuminata* Claparède and Lachmann 1859 *Dinophysis acuta* Ehrenberg 1839 *Dinophysis norvegica* Claparède and Lachmann 1859 *Gonyaulax cf. spinifera* (Claparède and Lachmann) Diesing 1866 *Karenia brevis* (Davis) G. Hansen and Moestrup 2000 *Karlodinium veneficum* (Ballantine) J. Larsen 2000 *Margalefidinium polykroides* (Margalef) Gómez, Richlen and Anderson 2017 *Phalacroma rotundatum* (Claparède and Lachmann) Kofoid and Michener 1911 *Prorocentrum cordatum* (Ostenfeld) Dodge 1975 *Prorocentrum lima* (Ehrenberg) Stein 1878 *Protoceratium reticulatum* (Claparède and Lachmann) Bütschli 1885 *Protoperidinium crassipes* (Kofoid) Balech 1974
Raphidophyceae	*Heterosigma cf. akashiwo* (Hada) Hara and Chihara 1987

Table 2. Presence/absence of toxin-producing marine algae identified to genera level in the Canadian Arctic and adjacent waters. × indicates that the genus was reported at least once within the region: AB – Arctic Basin, W – Western Arctic, AR – Arctic Archipelago, E – Eastern Arctic, HB – Hudson Bay Complex, CS – Chukchi Sea, NA – Northern Alaska, WG – Western Greenland (see Figure 1 for geographic boundaries of the Canadian Arctic regions).

Class	**Genus**	**Canadian Arctic**					**Adjacent waters**			**References**
		AB	W	AR	E	HB	CS	NA	WG	
Dinophyceae	Gymnodinium spp./Gyrodinium spp. complex	×	×	×	×	×	×	×	×	Bursa 1961; Elferink et al. 2017; Horner and Schrader 1982; Hsiao 1979a; Hsiao and Pinkewycz 1985; Lapoussière et al. 2009; Michel and Lessard unpublished data; Mikkelsen et al. 2008; Monier et al. 2014; Quillfeldt et al. 2003; Riedel et al. 2003; Różańska et al. 2009
	Cochlodinium spp.		×							Michel and Lessard unpublished data
Haptophyceae	Chrysochromulina spp.		×		×	×			×	Lapoussière et al. 2009; Lovejoy et al. 2002; Michel and Lessard unpublished data; Mikkelsen et al. 2008; Mundy et al. 2011; Terrado et al. 2011

Table 3. Presence/absence of toxin-producing marine algae species in the Canadian Arctic and adjacent waters. ✕ indicates that the species was reported at least once within the region: AB – Arctic Basin, W – Western Arctic, AR – Arctic Archipelago, E – Eastern Arctic, HB – Hudson Bay Complex, CS – Chukchi Sea, NA – Northern Alaska, WG – Western Greenland (see Figure 1 for geographic boundaries of the Canadian Arctic regions).

Class	**Species**	**Canadian Arctic**					**Adjacent waters**			**References**
		AB	W	AR	E	HB	CS	NA	WG	
Bacillariophyceae	*Halamphora cf. coffeaformis var. borealis*						✕			Quillfeldt et al. 2003
	Pseudo-nitzschia delicatissima	✕	✕	✕	✕	✕	✕	✕	✕	Anderson and Roff 1981; Booth 1984; Borstad and Gower 1984; Bursa 1963; Campbell et al. 2018; Cross 1982; Hasle 2002; Horner and Schrader 1982; Hsiao 1979a; Hsiao and Pinkewycz 1985; Lapoussière et al. 2009; Lovejoy et al. 2002; Melnikov et al. 2002; Philippe 2013; Poulin et al. 1983; Quillfeldt et al. 2003; Riedel et al. 2003; Różańska et al. 2009; Smith et al. 1993, 1997
	Pseudo-nitzschia granii		✕		✕		✕			Balzano et al. 2017; Lovejoy et al. 2002; et al. 2003
	Pseudo-nitzschia obtusa		✕		✕	✕	✕	✕	✕	Campbell et al. 2018; Harðardóttir et al. 2015; Hasle 2002; Hasle and Lundholm 2005; Michel and Lessard unpublished data; Quillfeldt et al. 2003
	Pseudo-nitzschia pseudodelicatissima		✕		✕		✕			Michel and Wiktor unpublished data; Hasle 2002; Mundy et al. 2011; Philippe 2013; Quillfeldt et al. 2003; Różańska et al. 2008; Różańska et al. 2009; Simard 2003
	Pseudo-nitzschia		✕			✕	✕	✕		Bursa 1961; Quillfeldt et al. 2003; Różańska et al.

	pungens									2009; Sukhanova et al. 2009
	Pseudo-nitzschia seriata	×	×	×	×	×	×	×	×	Anderson and Roff 1981; Booth 1984; Borstad and Gower 1984; Bursa 1961, 1963; Campbell et al. 2018; Cross 1982; Foy and Hsiao 1976; Harðardóttir et al. 2015; Hasle 2002; Horner and Schrader 1982; Hsiao 1976, 1979b, 1980; Hsiao and Pinkewycz 1985; Hsiao et al. 1978; Lapoussière et al. 2009; Melnikov et al. 2002; Michel and Wiktor unpublished data; Miesner et al. 2016; Onodera et al. 2015; Philippe 2013; Quillfeldt et al. 2003; Różańska et al. 2009; Rüsz Hansen et al. 2011; Smith et al. 1994, 1995; Stapleford and Smith 1996; Tammilehto et al. 2012, 2015
	Pseudo-nitzschia turgidula		×							Różańska et al. 2009
Dinophyceae	*Alexandrium tamarense*		×	×	×	×	×	×		Bursa 1961, 1963; Hsiao and Pinkewycz 1985; Matsuno et al. 2014; Natsuike et al. 2017a; Niemi et al. 2011; Riedel et al. 2003; Różańska 2009
	Alexandrium fundyense						×		×	Baggesen et al. 2012; Gu et al. 2013; Natsuike et al. 2013, 2017a; Richlen et al. 2016; Tillmann et al. 2016
	Alexandrium ostenfeldii					×	×		×	Bursa 1961; Natsuike et al. 2017b; Tillmann et al. 2014
	Amphidinium aff. carterae				×					Lovejoy et al. 2002
	Amphidinium operculatum							×		Bursa 1963
	Amphidinium gibbosum							×		Bursa 1963
	Dinophysis acuminata	×	×		×	×		×		Anderson and Roff 1981; Bursa 1963; Hsiao 1976; Hsiao and Pinkewycz 1985; Lapoussière et al. 2009; Melnikov et al. 2002; Różańska 2009; Różańska et al. 2008

	Dinophysis acuta	×	×			×	×		Anderson and Roff 1981; Bursa 1961, 1963; Matsuno et al. 2014; Melnikov et al. 2002
	Dinophysis norvegica	×	×			×	×		Anderson and Roff 1981; Bursa 1961, 1963; Lapoussière et al. 2009; Matsuno et al. 2014; Melnikov et al. 2002
	Gonyaulax spinifera	×			×	×			Heikkilä et al. 2016; Lovejoy et al. 2002; Melnikov et al. 2002
	Karenia brevis					×			Roff and Legendre 1986
	Karlodinium veneficum				×				Terrado et al. 2011
	Margalefidinium polykroides				×				Terrado et al. 2011
	Phalacroma rotundatum	×				×			Anderson and Roff 1981; Melnikov et al. 2002
	Prorocentrum cordatum		×		×				Matsuno et al. 2014; Michel and Lessard unpublished data
	Prorocentrum lima		×						Niemi et al. 2011
	Protoceratium reticulatum				×	×	×	×	Bursa 1961, 1963; Heikkilä et al. 2016; Lovejoy et al. 2002; Sala-Pérez et al. 2016; Tillmann et al. 2014; Mertens et al. 2018
	Protoperidinium crassipes	×							Melnikov et al. 2002
Raphidophyceae	*Heterosigma cf. akashiwo*		×	×	×	×			Michel and Lessard unpublished data; Riedel et al. 2003

Table 4. Presence/absence of toxin-producing marine algae species in different types of habitat (ice, water column, sediment) in the Canadian Arctic and adjacent waters. × indicates that the species was reported at least once within the habitat.

Class	**Species**	**Habitat type**		
		Ice	Water	Sediment
Bacillariophyceae	*Halamphora cf. coffeaformis var. borealis*	×		
	Pseudo-nitzschia delicatissima	×	×	
	Pseudo-nitzschia granii	×	×	
	Pseudo-nitzschia obtusa	×	×	
	Pseudo-nitzschia pseudodelicatissima	×	×	×
	Pseudo-nitzschia pungens	×	×	×
	Pseudo-nitzschia seriata	×	×	×
	Pseudo-nitzschia turgidula	×		
Dinophyceae	*Alexandrium tamarense*	×	×	×
	Alexandrium fundyense		×	×
	Alexandrium ostenfeldii		×	
	Amphidinium aff. carterae		×	
	Amphidinium gibbosum		×	
	Dinophysis acuminata	×	×	
	Dinophysis acuta		×	
	Dinophysis norvegica		×	
	Gonyaulax spinifera		×	×
	Karenia brevis		×	
	Karlodinium veneficum		×	
	Margalefidinium polykroides		×	
	Phalacroma rotundatum		×	
	Prorocentrum cordatum		×	
	Prorocentrum lima	×	×	
	Prorocentrum minimum		×	
	Protoceratium reticulatum		×	×
	Protoperidinium crassipes		×	
Raphidophyceae	*Heterosigma cf. akashiwo*		×	

Maps of reported occurrence of toxin-producing Bacillariophyceae, Dinophyceae, Haptophyceae, and Radiophyceae are presented in Figures 2-5. These figures indicate a widespread occurrence of Bacillariophyceae and Dinophyceae throughout the Canadian Arctic and adjacent waters, and more local occurrence of species belonging to Haptophyceae and Radiophyceae classes. Notably, these occurrence maps should be looked at as depiction of recorded occurrence rather than true geographic distributions. First, many publications did not provide exact geographic sampling coordinates, and thus, could not be included in Figures 2-5. Second, vast areas of the Canadian Arctic and adjacent waters are not sampled or analyzed for marine algal species biodiversity. Therefore, the lack of species in certain areas may simply indicate lack of data rather than actual absence of species.

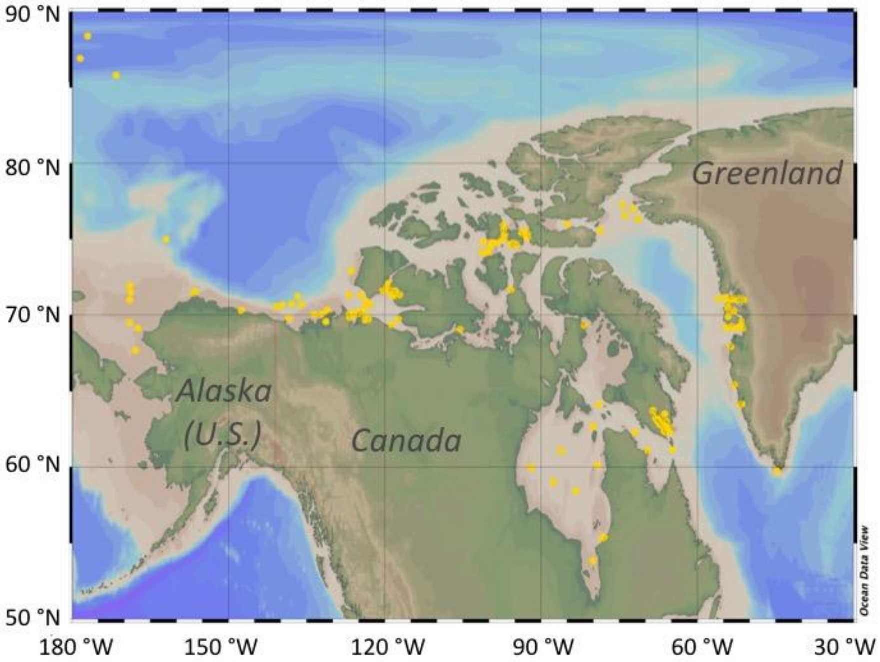

Figure 2. Occurrence of toxin-producing Bacillariophyceae in the Canadian Arctic and adjacent waters; includes Bacillariophyceae identified to at least genus level where exact sampling coordinates were available.

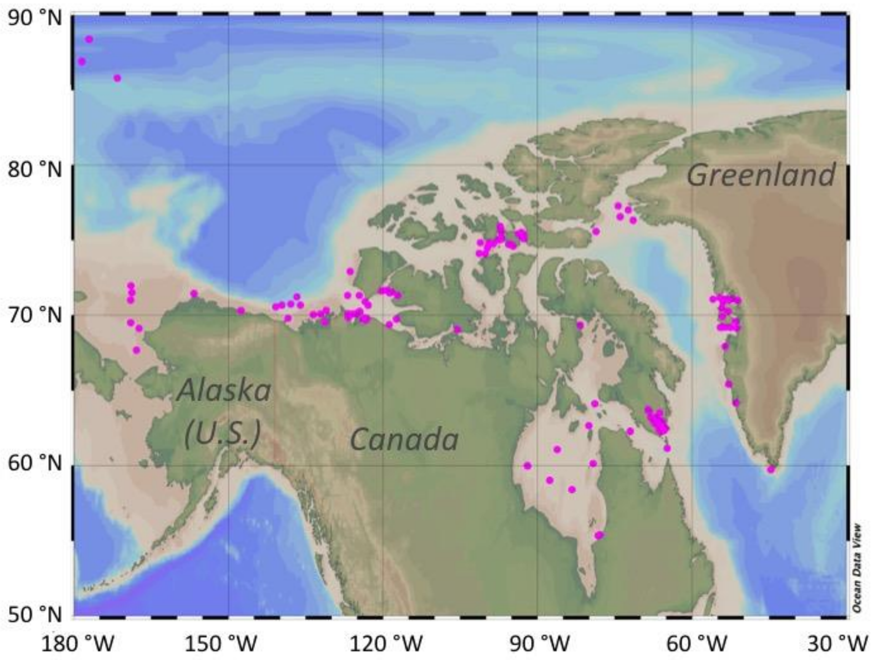

Figure 3. Occurrence of toxin-producing Dinophyceae in the Canadian Arctic and adjacent waters; includes Dinophyceae identified to at least genus level where exact sampling coordinates were available.

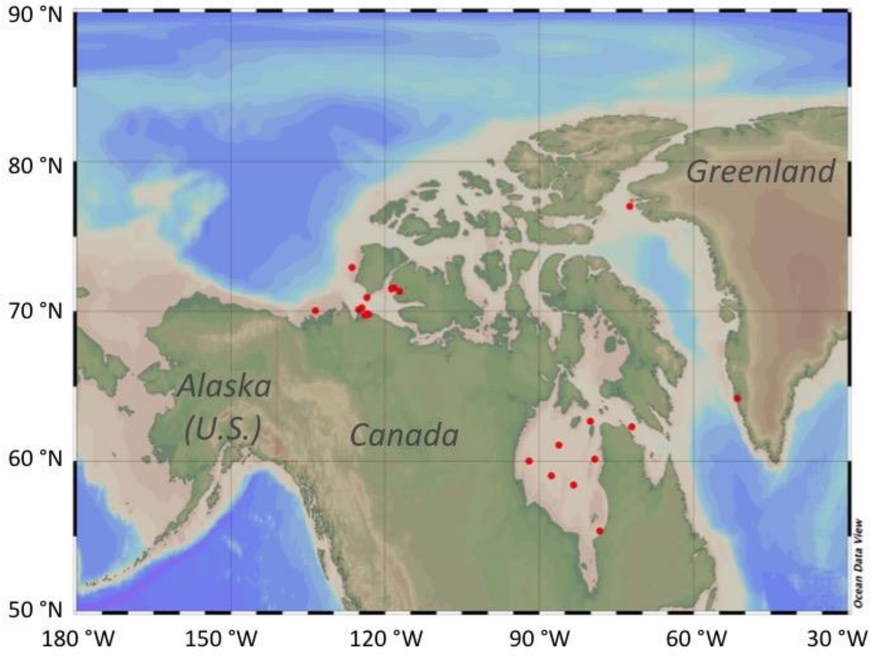

Figure 4. Occurrence of toxin-producing Haptophyceae in the Canadian Arctic and adjacent waters; includes Haptophyceae identified to at least genus level where exact sampling coordinates were available.

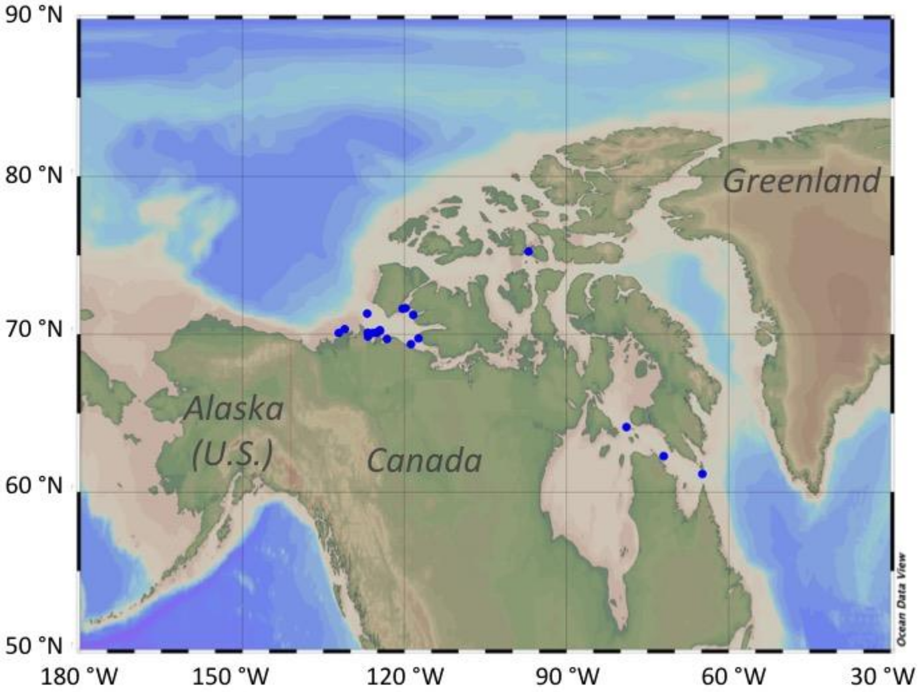

Figure 5. Occurrence of toxin-producing Raphidophyceae in the Canadian Arctic and adjacent waters; includes Raphidophyceae identified to at least genus level where exact sampling coordinates were available.

Production of toxins is a complex process with multiple modes of regulation which are believed to be not only species-specific but also life-stage and region-specific, and remain greatly under-studied (Granéli and Flynn 2006). While many isolates of the same species display qualitatively similar toxin profiles, they are commonly able to turn off/on toxin production as well as alter its intensity. Virtually all the information available on the mechanisms of marine toxin production and its regulation originates from outside of the polar regions. Factors suggested as toxigenicity regulators include physiological parameters such as life stage, cell size, proliferation rate, and environmental controls such as micro- and macro-nutrient concentrations, irradiance, temperature, salinity-induced hypoosmotic stress, hydrodynamics, and abundance of certain free-living or epibiont bacteria (Cusack et al. 2002; Errera and Campbell 2011; Fawcett et al. 2007; Hold et al. 2001; Navarro et al. 2006). Widespread presence of toxin-producing marine algal species in the Canadian Arctic does not mean that these species actually produce toxins in their Arctic habitat. It does indicate, however, that the potential for toxigenicity exists. In the waters of western Greenland and the Chukchi Sea, *Psedo-nitzschia* spp., *Alexandrium* spp. and *Protoceratium* sp. have been shown to produce domoic acid, saxitoxins and spirolides, and yessotoxins, respectively (Baggesen et al. 2012; Gu et al. 2013; Harðardóttir et al. 2015; Miesner et al. 2016; Natsuike et al. 2017a; Rüsz Hansen et al. 2011; Sala-Pérez et al. 2016; Tammilehto et al. 2012, 2015; Tillmann et al. 2014, 2016) (Table 5).

The Arctic presents species with a set of distinctively different environmental conditions from temperate and tropical regions. The presence of sea ice, cold temperatures, pronounced water column stratification, and polar day/night cycle provide for pronounced uniqueness of this region. As a result, toxin production rates and their regulatory mechanisms and pathways, toxin half-lives as well as bioaccumulation and depuration rates of arctic organisms are likely to be much different from those established in other regions. Our significantly limited understanding of toxigenic marine algae responses to multifactorial drivers of toxin production and toxicokinetics in arctic settings calls for urgent attention. Moreover, the relatively high rate at which the Arctic and the Canadian Arctic are experiencing global climate-change related change presents us with a set of additionally pressing questions associated with whether the changing arctic environment may become more favorable for toxic HABs to occur. We have evidence that diverse toxigenic algal communities are already present across various marine habitats of the Canadian Arctic. An important knowledge gap pertains to whether these communities are producing toxins, and whether these toxins make their way to the arctic food web.

4. Conclusions

The Arctic has been traditionally considered to present unfavorable conditions for toxin-producing HABs to occur. However, recent studies in the Alaskan sector present strong evidence that arctic marine algae are producing phycotoxins, and that those toxins make their way into the arctic food web (Lefebvre et al. 2016). Here, we show that almost 70% of species globally considered toxic are already present across various habitats of the Canadian Arctic and adjacent waters. The most prevalent taxonomic classes belong to Dinophyceae and Bacillariophyceae, followed by Haptophyceae and Raphidophyceae. Since this diverse toxigenic algal community is present in the Canadian Arctic, a real potential of phycotoxins production and bioaccumulation by higher trophic levels including commercially and subsistence harvested species exists. It is of pressing importance to establish whether potentially-toxic marine algae are producing phycotoxins in the Canadian sector of the Arctic, and if so, whether these toxins are present in the Canadian arctic food chain.

Table 5. List of toxin-producing species for which toxins were detected and identified in waters adjacent to the Canadian Arctic. CS – Chukchi Sea, WG – Western Greenland.

Class	**Species**	**Region**		**Toxin detected**		**References**
		CS	WG	Class	Analogues	
Bacillariophyceae	*Pseudo-nitzschia obtusa*		×	Domoic Acid	NA	Harðardóttir et al. 2015
	Pseudo-nitzschia seriata		×	Domoic Acid	DA, Isomer IA, Isomer IB	Harðardóttir et al. 2015; Miesner et al. 2016; Rüsz Hansen et al. 2011; Tammilehto et al. 2012, 2015
Dinophyceae	*Alexandrium fundyense*	×	×	Saxitoxins	STX, neoSTX, GTX1, GTX2, GTX3, GTX4, C2	Baggesen et al. 2012; Gu et al. 2013; Natsuike et al. 2017a; Tillmann et al. 2016
	Alexandrium ostenfeldii	×	×	Spirolides	SPX-1, Spirolide C, Spirolide H, 20-meG, Cp 1, Cp 2, Cp 3, Cp 4, Cp 5, Cp 6, Cp 7, Cp 8	Tillmann et al. 2014
	Protoceratium reticulatum	×	×	Yessotoxins	YTX	Sala-Pérez et al. 2016

NA – not available

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6. References

Anderson, D.M., Cembella, A.D., and Hallegraeff, G.M. 2012. Progress in understanding harmful algal blooms (HABs): Paradigm shifts and new technologies for research, monitoring and management. Ann. Rev. Mar. Sci. 4: 143-176.

Anderson, J.T., and Roff, J.C. 1981. The diatoms and dinoflagellates of Hudson Bay. Can. J. Bot. 59: 1793-1810.

Baggesen, C., Moestrup, O., Daugbjerg, N., Krock, B., Cembella, A.D., and Madsen, S. 2012. Molecular phylogeny and toxin profiles of *Alexandrium tamarense* (Lebour) Balech (Dinophyceae) from the west coast of Greenland. Harmful Algae 19: 108-116.

Balzano S., Percopo, I., Siano, R., Gourvil, P., Chanoine, M., Marie, D., Vaulot, D., and Sarno, D. 2017. Morhological and genetic diversity of Beaufort Sea diatoms with high contributions from the *Chaetoceros neogracilis* species complex. J. Phycol. 53: 161-187.

Booth, J.A. 1984. The epontic algal community of the ice edge zone and its significance to the Davis Strait ecosystem. Arctic 37: 234-243.

Borstad, G.A., and Gower, J.F.R. 1984. Phytoplankton chlorophyll distribution in the Eastern Canadian Arctic. Arctic 37: 224-233.

Bursa, A.S. 1961. The annual oceanographic cycle at Igloolik in the Canadian Arctic II. The phytoplankton. J. Fish. Res. Bd. Canada 18: 563-615.

Bursa, A.S. 1963. Phytoplankton in coastal waters of the Arctic Ocean at Point Barrow, Alaska. Arctic 16: 239-262.

Campbell, K., Mundy, C.J., Belzile, C., Delaforge, A., and Rysgaard, S. 2018. Seasonal dynamics of algal and bacterial communities in Arctic sea ice under variable snow cover. Polar Biol. 41: 41-58.

Cross, W.E. 1982. Under-ice biota of the Pond Inlet ice edge and in adjacent fast ice areas during spring. Arctic 35: 13-27.

Cusack, C.K., Bates, S.S., Quilliam, M.A., Patching, J.W., and Raine, R. 2002. Confirmation of domoic acid production by *Pseudo-nitzschia australis* (Bacillariophyceae) isolated from Irish waters. J. Phycol. 38: 1106-1112.

DFO, 2009. Development of a framework and principles for the biogeographic classification of Canadian Marine Areas. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2009/056.

Elferink, S., Neuhaus, S., Wohlrab, S., Toebe, K., Voss, D., Gottschling, M., Lundholm, N., Krock, B., Koch, B.P., Zielinski, O., Cembella, A., and John, U. 2017. Molecular diversity patterns among various phytoplankton size-fractions in West Greenland in late summer. Deep-Sea Res. I 121: 54-69.

Errera, R.M., and Campbell, L. 2011. Osmotic stress triggers toxin production by the dinoflagellate *Karenia brevis*. PNAS 108: 10597-10601.

European Food Safety Authority (EFSA). 2009. Scientific opinion of the Panel of Contaminants in the Food Chain on a request from the European Commission on Marine biotoxins in shellfish-saxitoxin group. EFSA J. 1019: 1-76.

Fawcett A., Pitcher G.C., Bernard, S., Cembella, A.D., and Kudela, R.M. 2007. Contrasting wind patterns and toxigenic phytoplankton in the southern Benguela upwelling system. Mar. Ecol. Prog. Ser. 348: 19-31.

Foy, M.G., and Hsiao, S.I.C. 1976. Phytoplankton data from James Bay, 1974. Fish. Mar. Serv. Tech. Rep. No. 617: 44 p.

Gerssen, A., Pol-Hofstad, I.E., Poelman, M., Mulder, P.P.J., van den Top, H.J., and de Boer, J. 2010. Marine toxins: Chemistry, toxicity, occurrence and detection, with special reference to the Dutch situation. Toxins 2: 878-904.

Granéli, E., and Flynn, K. 2006. Chemical and Physical Factors influencing Toxin Content. In : Granéli, E., and Turner, J.T. (Eds.) Ecology of Harmful Algae. Ecological Studies (Analysis and Synthesis), vol. 189, Berlin. pp. 229-241.

Grattan, L.M., Boushey, C.J., Liang, Y., Lefebvre, K.A., Castellon, L.J., Roberts, K.A., Toben, A.C., and Morris, J.G. 2018. Repeated dietary exposure to low levels of domoic acid and problems with everyday memory: Research to public health outreach. Toxins 10: 103.

Gu, H., Zeng, N., Xie, Z., Wang, D., Wang, W., and Yang W. 2013. Morphology, phylogeny, and toxicity of *Atama* complex (Dinophyceae) from the Chukchi Sea. Polar Biol. 36: 427-436.

Guiry, M.D., and Guiry, G.M. 2018. AlgaeBase [Online]. Available from http://www.algaebase.org [accessed on 25 March 2018].

Hallegraeff, G.M. 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32: 79-99.

Harðardóttir, S., Pančić, M., Tammilehto, A., Krock, B., Møller, E.F., Nielsen, T.G., and Lundholm, N. 2015. Dangerous relations in the Arctic marine food web: Interactions between toxin producing *Pseudo-nitzschia* diatoms and *Calanus* copepodites. Mar. Drugs 13: 3809-3835.

Hasle, G.R. 2002. Are most of the domoic acid-producing species of the diatom genus *Pseudo-nitzschia* cosmopolites? Harmful Algae 1: 137-146.

Hasle, G.R., and Lundholm, N. 2005. *Pseudo-nitzschia seriata f. obtuse* (Bacillariophyceae) raised in rank based on morphological, phylogenetic and distributional data. Phycologia 44: 608-619.

Heikkilä, M., Pospelova, V., Forest, A., Stern, G.A., Fortier, L., and Macdonald, R.W. 2016. Dinoflagellate cyst production over an annual cycle in seasonally ice-covered Hudson Bay. Mar. Micropaleontol. 125: 1-24.

Hold, G.L., Smith, E.A., Rappé, M.S., Maas, E.W., Moore, E.R.B., Stroempl, C., Stephen, J.R., Prosser, J.I., Birkbeck, T.H., and Gallacher, S. 2001. Characterisation of bacterial communities associated with toxic and non-toxic dinoflagellates: *Alexandrium* spp. and *Scrippsiella trochoidea*. FEMS Microbiol. Ecol. 37: 161-173.

Horner, R., and Schrader, G.C. 1982. Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. Arctic 35: 485-503.

Hsiao, S.I.C. 1976. Biological productivity of the Southern Beaufort Sea: phytoplankton and seaweed studies. Beaufort Sea Tech. Rep. No. 12c: 99 p.

Hsiao, S.I.C. 1979a. Sea ice microalgal data from the Eskimo Lakes, 1972 to 1974. Fish. Mar. Serv. Data Rep. No. 146: 43 p.

Hsiao, S.I.C. 1979b. Sea ice microalgal data from Eclipse Sound, 1976 and 1977. Fish. Mar. Serv. Data Rep. No. 131: 34 p.

Hsiao, S.I.C. 1980. Quantitative composition, distribution, community structure and standing stock of sea ice microalgae in the Canadian Arctic. Arctic 33: 768-793.

Hsiao, S.I.C., and Pinkewycz, N. 1985. Phytoplankton data from a 1976 cruise in Frobisher Bay. Can. Data Rep. Fish. Aquat. Sci. No. 575: 212 p.

Hsiao, S.I.C., Kittle, D.W., and Foy, M.G. 1978. Effects of crude oils and the oil dispersant Corexit on primary production of Arctic marine phytoplankton and seaweed. Environ. Pollut. 15: 209-221.

Lapoussière, A., Michel, C., Gosselin, M., and Poulin, M. 2009. Spatial variability in organic material sinking export in the Hudson Bay system, Canada, during fall. Cont. Shelf Res. 29: 1276-1288.

Lassus, P., Chomérat, N., Hess, P., and Nézan, E. 2016. Toxic and Harmful Microalgae of the World Ocean – Micro-algues Toxiques et Nuisibles de l'Océan Mondial. International Society for the Study of Harmful Algae – Intergovernmental Oceanographic Commission of UNESCO. IOC Manuals and Guides, Copenhagen (Denmark).

Lefebvre, K.A., Quakenbush, L., Frame, E., Huntington, K.B., Sheffield, G., Stimmelmayr, R., Bryan, A., Kendrick, P., Ziel, H., Goldstein, T., Snyder, J.A., Gelatt, T., Gulland, F., Dickerson, B., and Gill, V. 2016. Prevalence of algal toxins in Alaskan marine mammals foraging in a changing arctic and subarctic environment. Harmful Algae 55: 13-24.

Lovejoy, C., Legendre, L., Martineau, M.-J., Bâcle, J., and Quillfeldt, C.H.V. 2002. Distribution of phytoplankton and other protists in the North Water. Deep-Sea Res. II 49: 5027-5047.

Lovejoy, C., Legendre, L., Martineau, M.-J., Bâcle, J., and Quillfeldt, C.H.V. 2003. Erratum to "Distribution of phytoplankton and other protists in the North Water". Deep-Sea Res. II 50: 1053.

Matsuno, K., Ichinomiya, M., Yamaguchi, A., Ichiro, I. and Takashi, K. 2014. Horizontal distribution of microprotist community structure in the western Arctic Ocean during late summer and early fall of 2010. Polar Biol. 37: 1185-1195.

Mertens, K.N., Carbonell-Moore, M.C., Pospelova, V., Head, M.J., Highfield, A., Schroeder, D., Gu, H., Andree, K.B., Fernandez, M., Yamaguchi, A., Takano, Y., Matsuoka, K., Nézan, E., Bilien, G., Okolodkov, Y., Koike, K., Hoppenrath, M., Pfaff, M., Pitcher, G., Al-Muftah, A., Rochon, A., Lim, P.T., Leaw, C.P., Lim, Z.F. and M. Ellegaard. 2018.

Pentaplacodinium saltonense gen. et sp. nov. (Dinophyceae) and its relationship to the cyst-defined genus *Operculodinium* and yessotoxin-producing *Protoceratium reticulatum*. Harmful Algae 71: 57-77.

Melnikov, I.A., Kolosova, E.G., Welch, H.E., and Zhitina, L.S. 2002. Sea ice biological communities and nutrient dynamics in the Canada Basin of the Arctic Ocean. Deep-Sea Res. I 49: 1623-1649.

Michel, C. 2013. Marine ecosystems. *In:* Arctic biodiversity assessment. Status and trends in Arctic biodiversity., Meltofte, H. (Ed.), Conservation of Arctic Flora and Fauna. Akureyri, pp. 487-527.

Michel, C., Hamilton, J., Hansen, E., Barber, D., Reigstad, M., Iacozza, J., Seuthe, L., and Niemi, A. 2015. Arctic Ocean outflow shelves in the changing Arctic: A review and perspectives. Prog. Oceanogr. 139: 10.1016/j.pocean.2015.08.007.

Miesner, A.K., Lundholm, N., Krock, B., and Nielsen, T.G. 2016. The effect of *Pseudo-nitzschia seriata* on grazing and fecundity of *Calanus finmarchus* and *Calanus glacialis*. J. Plankton Res. 38: 564-574.

Mikkelsen, D.M., Rysgaard, S., and Glud, R.N. 2008. Microalgal composition and primary production in Arctic sea ice: a seasonal study from Kobbefjord (Kangerluarsunnguaq), West Greenland. Mar. Ecol. Prog. Ser. 368: 65-74.

Moestrup, Ø., Akselmann, R., Fraga, S., Hoppenrath, M., Iwataki, M., Komárek, J., Larsen, J., Lundholm, N. and Zingone, A. 2018. IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae [Online]. Available from http://www.marinespecies.org/hab [accessed on 25 March 2018].

Monier, A., Findlay, H.S., Charvet, S., and Lovejoy, C. 2014. Late winter under ice pelagic microbial communities in the high Arctic Ocean and the impact of short-term exposure to elevated CO2 levels. Front. Microbiol. 5: 490.

Mundy, C.J., Gosselin, M., Ehn, J.K., Belzile, C., Poulin, M., Alou, E., Roy, S., Hop, H., Lessard, S., Papakyriakou, T.N., Barber, D.G., and Stewart, J. 2011. Characteristics of two distinct high-light acclimated algal communities during advanced stages of sea ice melt. Polar Biol. 34: 1869-1886.

Natsuike, M., Nagai, S., Matsuno, K., Saito, R., Tsukazaki, C., Yamaguchi, A., and Imai, I. 2013. Abundance and distribution of toxic *Alexandrium tamarense* resting cysts in the sediments of the Chukchi Sea and the eastern Bering Sea. Harmful Algae 27: 52-59.

Natsuike, M., Matsuno, K., Hirawake, T., Yamaguchi, A., Nishino, S., and Imai, I. 2017a. Possible spreading of toxic *Alexandrium tamarense* blooms on the Chukchi Sea shelf with the inflow of Pacific summer water due to climatic warming. Harmful Algae 61: 80-86.

Natsuike, M., Oikawa, H., Matsuno, K., Yamaguchi, A., and Imai, I. 2017b. The physiological adaptations and toxin profiles of the toxic *Alexandrium fundyense* on the eastern Bering Sea and Chukchi Sea shelves. Harmful Algae 63: 13-22.

Navarro, J.M., Muñoz, M.G., and Contreras, A.M. 2006. Temperature as a factor regulating growth and toxin content in the dinoflagellate *Alexandrium catenella*. Harmful Algae 5 : 762-769.

Niemi, A., Michel, C., Hille, K., and Poulin, M. 2011. Protist assemblages in winter sea ice: setting the stage for the spring ice algal bloom. Polar Biol. 34: 1803-1817.

Onodera, J., Watanabe, E., Harada, N., and Honda, M.C. 2015. Diatom flux reflects water-mass conditions on the southern Northwind Abyssal Plain, Arctic Ocean. Biogeosciences 12: 1373-1385.

Philippe, B. 2013. Changements récents dans la dynamique des algues de glace dans le secteur canadien de la mer de Beaufort. MSc Thesis, Université du Québec à Rimouski, Rimouski (Québec).

Poulin, M., Cardinal, A., and Legendre, L. 1983. Réponse d'une communauté de diatomées de glace à un gradient de salinité (baie d'Hudson). Mar. Biol. 76: 191-202.

Poulin, M., Daugbjerg, N., Gradinger, R., Ilyash, L., Ratkova, T., and von Quillfeldt, C. 2011. The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: a first-attempt assessment. Mar. Biodiv. 41: 13-28.

Quillfeldt, C.H.V., Ambrose Jr, W.G., and Clough, L.M. 2003. High number of diatom species in first-year ice from the Chukchi Sea. Polar Biol. 26: 806-818.

Richlen, M.L., Zielinsky, O., Holinde, L., Tillmann, U., Cembella, A., Lyu, Y., and Anderson, D.M. 2016. Distribution of *Alexandrium fundyense* (Dinophyceae) cysts in

Greenland and Iceland, with an emphasis on viability and growth in the Arctic. Mar. Ecol. Prog. Ser. 547:33-46.

Riedel, A., Michel, C., Poulin, M., and Lessard, S. 2003. Taxonomy and abundance of microalgae and protists at a first-year sea ice station near Resolute Bay, Nunavut, spring to early summer 2001. Can. Data Rep. Hydrogr. Ocean Sci. No. 159: 54 p.

Roff, J.C., and Legendre, L. 1986. Physico-chemical and biological oceanography of Hudson Bay. *In* Canadian Inland Seas. Martini, I.P. (Ed.). Elsevier Oceanography Series, Amsterdam, The Netherlands, pp. 265-291.

Różańska, M. 2009. Influence des facteurs du milieu sur la composition taxonomique et le développement des algues et autres protistes de la glace de mer dans le secteur canadien de la mer de Beaufort. PhD Thesis, Université du Québec à Rimouski, Rimouski (Québec).

Różańska, M., Gosselin, M., Poulin, M., Wiktor, J.M., and Michel, C. 2009. Influence of environmental factors on the development of bottom ice protest communities during the winter-spring transition. Mar. Ecol. Prog. Ser. 386: 43-59.

Różańska, M., Poulin, M., and Gosselin, M. 2008. Protist entrapment in newly formed sea ice in the coastal Arctic Ocean. J. Mar. Syst. 74: 887-901.

Rüsz Hansen, L., Soylu, S.Í., Kotaki, Y., Moestrup, Ø., and Lunholm, N. 2011. Toxin production and temperature-induced morphological variation of the diatom *Pseudo-nitzschia seriata* from the Arctic. Harmful Algae 10: 689-696.

Sala-Pérez, M. Alpermann, T.J., Krock, B., and Tillmann, U. 2016. Growth and bioactive secondary metabolites of arctic *Protoceratium reticulatum* (Dinophyceae). Harmful Algae 55: 85-96.

Simard, M. 2003. Influence des facteurs du milieu sur la dynamique printanière des microalgues de glace de la région des eaux du nord (Baie de Baffin). MSc Thesis, Université du Québec à Rimouski, Rimouski (Québec).

Skreslet, S., Heidal, K., and Mohus, A. 1993. Hindsight on Arctic toxic bloom. Harmful Algae News 7: 7-9.

Smayda, T.J. 1997. Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea. Limnol. Oceanogr. 42: 1137-1153.

Smith, R.E.H., Cavaletto, J.F., Eadie, B.J., and Gardner, W.S. 1993. Growth and lipid composition of high Arctic ice algae during the spring bloom at Resolute, Northwest Territories, Canada. Mar. Ecol. Prog. Ser. 97: 19-29.

Smith, R.E.H., Stapleford, L.C., and Ridings, R.S. 1994. The acclimated response of growth, photosynthesis, composition, and carbon balance to temperature in the psychrophilic ice diatom *Nitzschia seriata*. J. Phycol. 30: 8-16.

Smith, R.E.H., Demers, S., Hattori, H., Kudoh, S., Legendre, L., Michel, C., Gosselin, M., Robineau, B., Suzuki, S., Takahashi, M., Therriault, J.-C., Juniper, S.K., and Sime-Ngando, T. 1995. Biological and chemical investigations of the Saroma-Resolute project in ice-covered Resolute Passage, 1992. Can. Data Rep. Hydrogr. Ocean Sci. No. 137: 19 p.

Smith, R.E.H., Gosselin, M., and Taguchi, S. 1997. The influence of major inorganic nutrients on the growth and physiology of high arctic ice algae. J. Mar. Syst. 11: 63-70.

Stapleford, L.C., and Smith, R.E.H. 1996. The interactive effects of temperature and silicon limitation on the psychrophilic ice diatom *Pseudonitzschia seriata*. Polar Biol. 16: 589-594.

Sukhanova, I.N., Flint, M.V., Pautova, L.A., Stockwell, D.A., Grebmeier, J.M., and Sergeeva, V.M. 2009. Phytoplankton of the western Arctic in the spring and summer 2002: Structure and seasonal changes. Deep-Sea Res. II 56: 1223-1236.

Tammilehto, A., Nielsen, T.G., Krock, B., Møller, E.F., and Lundholm, N. 2012. *Calanus* spp.–Vectors for the biotoxin, domoic acid, in the Arctic marine ecosystem? Harmful Algae 20: 165-174.

Tammilehto, A., Nielsen, T.G., Krock, B., Møller, E.F., and Lundholm, N. 2015. Induction of domoic acid production in the toxic diatom *Pseudo-nitzschia seriata* by calanoid copepods. Aquat. Toxicol. 159: 52-61.

Terrado, R., Medrinal, E., Dasilva, C., Thaler, M., Vincent, W.F., and Lovejoy, C. 2011. Protist community composition during spring in an Arctic flaw lead polynya. Polar Biol. 34: 1901-1914.

Tillmann, U., Kremp, A., Tahvanainen, P., and Krock, B. 2014. Characterization of spirolide producing *Alexandrium ostenfeldii* (Dinophyceae) from the western Arctic. Harmful Algae 39: 259-270.

Tillmann, U., Krock, B., Alpermann, T.J., and Cembella, A. 2016. Bioactive compounds of marine dinoflagellate isolates from western Greenland and their phylogenetic association within the genus *Alexandrium*. Harmful Algae 51: 67-80.

Van Dolah, F.M. 2000. Marine algal toxins: Origins, health effects, and their increased occurrence. Environ. Health Perspect. 108 (suppl 1): 133-141.

Vilariño, N., Louzao, M.C., Abal, P., Carrera, C., Vieytes, M.R., and Botana, L.M. 2018. Human poisoning from marine toxins: Unknowns for optimal consumer protection. Toxins 10: 324.

Wesche, S.D., and Chan, H.M. 2010. Adapting to the impacts of climate change on food security among Inuit in the Western Canadian Arctic. EcoHealth 7: 361-373.