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COMMUNAUTÉS DE DINOFLAGELLÉS DANS LES PORTS À PLUS HAUT RISQUE D'INVASION DE L'ARCTIQUE CANADIEN

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PAR

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RÉSUMÉ

L'augmentation du trafic maritime dans l'Arctique canadien due aux changements globaux, à la diminution de la couverture de glace de mer et au développement économique va accroître les risques potentiels d'introduction d'espèces non indigènes (ENI) en augmentant les rejets d'eau et de sédiments de ballast et l'encrassement sur les coques des navires. De plus, les conditions environnementales dans certains ports de l'Arctique sont de plus en plus similaires à celles des ports d'origine des navires provenant des régions tempérées, réduisant ainsi les barrières environnementales et augmentant les risques d'introduction et de propagation d'ENI. Une fois établies, les ENI sont difficiles ou pratiquement impossible à éradiquer. La détection hâtive est donc essentielle pour diminuer les risques d'invasion. Le groupe des dinoflagellés compte parmi les organismes qui peuvent être introduits et peuvent causer des effets indésirables à l'écosystème. Cependant, le manque d'information sur les espèces indigènes peut être un obstacle pour la détection de nouvelles espèces, ce qui est le cas dans l'Arctique canadien. Dans ce contexte, ce projet vise à déterminer les communautés de dinoflagellés dans les ports à plus haut risque d'invasions de l'Arctique canadien dans le but d'établir une base de données et de détecter l'arrivée éventuelle d'ENI. Au total nous avons identifié 40 taxa appartenant à 8 familles dans les ports de Churchill (MB), Baie Déception (QC), Iqaluit et Milne Inlet (NU), dont 7 taxa qui produisent des toxines, provoquant des intoxications par phycotoxines paralysantes (IPP), par phycotoxines amnestiques (ASP) et par phycotoxines diarrhétiques (IDM). Les communautés de dinoflagellés étaient significativement différentes entre les quatre ports et dans le port de Churchill entre 2007 et 2015. Plusieurs facteurs peuvent influencer la composition de la communauté, tels que la profondeur et la période d'échantillonnage par rapport à la fonte de la glace de mer. La comparaison entre les communautés de dinoflagellés observées dans les eaux de ballast à celles des ports a montré que *Peridinium aciculiferum, Phalacroma ovatum, Gonyaulax* cf. *alaskensis, Ensiculifera mexicana, Oblea rotundata, Fragilidium subglobosum, Protoperidinium marielebourae, Protoperidinium* cf. *grenlandicum, Protoperidinium excentricum, Ceratium tripos* (observés dans les eaux de ballast rejetées par les navires à Baie Déception), *Gyrodinium* aff. *metum* (observés dans les eaux de ballast rejetées par les navires à Churchill*)* et *Tripos furca* (observés dans les eaux de ballast rejetées par les navires à Churchill et Baie Déception) sont des espèces potentiellement non indigènes, ce qui confirme le potentiel d'introduction de nouvelles espèces dans l'Arctique canadien. Cette situation risque de s'aggraver dans un avenir proche en raison des changements climatiques qui prolongent la période libre de glace. L'effort de monitorage doit donc continuer pour la détection hâtive d'ENI et d'autres mesures sont nécessaires pour limiter l'introduction et la propagation.

Mots clés : Dinoflagellés ; Arctique canadien ; Eaux de ballast ; Espèces non indigènes ; Espèces toxiques ; Churchill ; Baie Déception ; Iqaluit ; Milne Inlet

ABSTRACT

The expected increase of shipping activities in the Canadian Arctic due to global warming, the reduction of the sea ice cover and the economic development of the north, may increase potential introductions of non indigenous species (NIS) via increased propagule supply from ballast water and sediments and biofouling vectors. At the same time, environmental conditions in some Arctic ports are becoming more similar to their connected source ports in temperate regions, reducing environmental barriers and increasing introduction risks. Once established, NIS are very difficult or nearly impossible to eradicate. Therefore, prevention and early detection are important in managing risk. Dinoflagellate species are among the taxa that can have important ecological and economic impacts once released in a new environment. However, the lack of information about native species represents an obstacle in detecting the arrival of new ones. Therefore, it is paramount to obtain detailed knowledge on their current distribution and ecology, which is limited in the Canadian Arctic. In this context, the main objective of this study is to characterize dinoflagellate communities in high risk Canadian Arctic ports to provide baseline data and detect the presence of potential NIS. In total, we identified 40 dinoflagellate taxa from 8 families in the ports of Churchill, Deception Bay, Iqaluit and Milne Inlet, including 7 taxa known to be toxin producers, causing Paralytic Shellfish Poisoning (PSP), Amnesic Shellfish Poisoning (ASP) and Diarrhetic Shellfish Poisoning (DSP). Dinoflagellate communities were significantly different between ports, between all pairs of ports and in the most heavily used port of Churchill between 2007 and 2015. Several factors may influence the community composition, such as sampling depth and sampling timing relative to the melting of sea ice. The comparison between dinoflagellate communities found in the ports and those present in ballast water showed that *Peridinium aciculiferum, Phalacroma ovatum, Gonyaulax* cf. *alaskensis, Ensiculifera mexicana, Oblea rotundata, Fragilidium subglobosum, Protoperidinium marielebourae, Protoperidinium* cf. *grenlandicum, Protoperidinium excentricum, Ceratium tripos* (found in ballast water of vessels discharging in Deception Bay), *Gyrodinium* aff. *Metum* (found in ballast water of vessels discharging in Churchill) and *Tripos furca* (found in ballast water of vessels discharging in Churchill and Deception Bay) are potential NIS, confirming the potential for introducing new species in the Canadian Arctic. This may be exacerbated in the near future as a result of extended ice-free conditions due to global warming. Monitoring efforts must be continued to improve early detection of potential NIS and other mitigative measures are needed to limit introductions or spread.

Keywords: Dinoflagellates; Canadian Arctic; Ballast water; Non indigenous species; Toxic species; Churchill; Deception Bay; Iqaluit; Milne Inlet

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DSIMS   Days between sea ice melt and sampling

NIS   Non indigenous species

SEM   Scanning electron microscopy

INTRODUCTION GÉNÉRALE

Arctique canadien

L'une des conséquences des changements globaux, est l'augmentation de la température de l'air et des océans sans précèdent depuis les trente dernières années dans l'hémisphère Nord depuis 1400 ans (Pachauri and Meyer, 2014).

Au cours des années 1950, la température en Arctique a augmenté plus rapidement et d'une manière plus sévère qu'ailleurs sur la planète. En effet, des hausses de la température moyenne annuelle de 2°C ont été observées à travers l'Arctique (McBean *et al.*, 2005). La fonte des glaciers, de la glace de mer, et l'augmentation de la température du pergélisol sont des évidences du réchauffement (Loeng *et al.*, 2005). En outre, sur une période de 10 ans entre 2000 et 2010, il y a eu une diminution de l'étendue de glace annuelle de 12.4% (Stroeve *et al.*, 2012). D'ici 2080, les changements climatiques dans l'Arctique canadien devraient s'accélérer, avec une augmentation prévue de température de 4 à 5°C (Loeng *et al.*, 2005).

L'Arctique canadien constitue 75% des côtes canadiennes. Il comprend plusieurs ressources qui jouent un rôle important dans l'économie du Canada, telles le pétrole, le gaz et les minéraux. Le nombre de projets de développement des ressources est à la hausse et on s'attend que d'ici 2020, plus de 25 projets seront opérationnels dont certains utiliseront la voie maritime pour le transport de marchandises (Gavrilchuk and Lesage, 2014). En effet, le trafic maritime est en train de s'intensifier rapidement (Miller and Ruiz, 2014). Entre 2005 et 2014, le nombre de navires traversant l'Arctique canadien a plus que doublé, passant de 121 à 302 respectivement (Guy and Lasserre, 2016b), et avec les projets en cours de développement, on s'attend à 433 expéditions additionnelles par année (Chan *et al.*, 2013; Chan *et al.*, 2015). De plus, l'Arctique devient une destination touristique, avec un nombre de visiteurs qui ne cesse d'augmenter. Les touristes voyagent

en voiliers, bateaux de plaisance ou de croisière pour découvrir des endroits qui étaient autrefois inaccessibles (Arctic-Council, 2009; Miller and Ruiz, 2014). Le réchauffement climatique et la diminution de la couverture de glace de mer permettront de rallonger la saison de navigation (Lemmen *et al.*, 2008; Pizzolato *et al.*, 2014). En effet, des prédictions ont montré qu'il y aura une diminution de la durée de la glace de mer de 10 jours d'ici 2020, de 15 à 20 jours d'ici 2050 et de 20 à 30 jours d'ici 2080 (Loeng *et al.*, 2005). Par ailleurs, on prévoit que d'ici le milieu du 21ième siècle, le passage du Nord-Ouest reliant l'océan Atlantique au Pacifique, et qui traverse l'Arctique Canadien, sera plus propice à la navigation (Smith and Stephenson, 2013). Cette nouvelle dynamique favorise l'augmentation du trafic maritime en augmentant le nombre de voyages et de navires tout en diminuant la durée de ces voyages. Tous ces changements vont aggraver les risques potentiels d'introduction d'espèces non indigènes via les eaux de ballast ou l'encrassement sur les coques des navires (Chan *et al.*, 2015)

Les invasions biologiques

Les espèces non indigènes (ENI), sont des espèces qui se retrouvent en dehors de leurs aires de répartition en empruntant des vecteurs d'introduction naturels ou anthropiques (Carlton, 1987; Casas-Monroy *et al.*, 2014). Le transport d'organismes par les navires (eau et sédiments de ballast et encrassements sur la coque des navires) est reconnu comme un important vecteur d'introduction (Gollasch, 2002; MPO, 2014). La libération depuis les cages d'aquaculture, l'aquariophilie et le transport d'appâts vivants sont aussi des vecteurs d'introductions considérables (Godwin, 2003).

Avant de s'établir, les organismes doivent passer par une série d'étapes : ils doivent tout d'abord se trouver dans un vecteur d'introduction et survivre aux conditions du transport (Figure 1). Une fois relâchés, ils doivent survivre aux conditions du nouvel environnement, se reproduire et s'établir (Casas-Monroy *et al.*, 2014). Le succès d'invasion dépend aussi des conditions physico-chimiques du milieu récepteur, de l'interaction biologique entre les espèces indigènes et non-indigènes, de la pression de colonisation (nombre d'espèces relâchées dans une région réceptrice) et de la pression de propagule. La pression de propagule est elle-même fonction du nombre d'évènements d'introduction (par exemple, un déversement d'eau de ballast) et du nombre d'individus

relâchés par évènement d'introduction (Lockwood *et al.*, 2005; Lockwood *et al.*, 2009; Simard *et al.*, 2017). Les contraintes biotiques (prédation, déficit dans les ressources alimentaires) ou abiotiques (température, salinité, type du substrat) peuvent entraver le succès de l'invasion (Lockwood *et al.*, 2005; Lockwood *et al.*, 2009; Simard *et al.*, 2017). Les ENI établies peuvent subir un transport secondaire vers un autre milieu, se propager et s'établir (Floerl *et al.*, 2009; Casas-Monroy *et al.*, 2014).

L'introduction d'ENI peut avoir des impacts positifs dans le cas où l'espèce introduite a une valeur commerciale et que son exploitation apporte des gains économiques (Bax *et al.*, 2003). Cependant, les impacts négatifs des ENI sont généralement plus importants. En effet, les ENI ont causé des dommages irréversibles au niveau des ressources naturelles et des écosystèmes terrestres et aquatiques (Vilà *et al.*, 2011; Simberloff *et al.*, 2012). Elles peuvent entrer en compétition avec les espèces indigènes au niveau des ressources alimentaires et de l'habitat, ce qui peut engendrer la perturbation du réseau trophique (Ricciardi *et al.*, 2013), ainsi que le changement de la niche écologique par la modification de la composition et du fonctionnement de l'écosystème en modifiant la biodiversité (Reaser *et al.*, 2007).

L'eau et les sédiments de ballast transportent une panoplie d'organismes de tailles variables allant du microscopique, comme les bactéries, le phytoplancton et certains organismes zooplanctoniques, jusqu'au macroscopique comme les crabes, moules et poissons (MIT Sea Grant, 2006). Ces organismes doivent survivre aux conditions difficiles dans les ballasts avant d'arriver au port receveur, telles que la prédation, l'obscurité et le manque d'oxygène, en plus du nombre de survivants dans les ballasts qui diminue en fonction de la durée du voyage (Simard *et al.*, 2011; Casas-Monroy *et al.*, 2014; Miller and Ruiz, 2014).

L'Arctique canadien a été classé parmi les écosystèmes les moins affectés par la bio-invasion (Chan *et al.*, 2012; Chan *et al.*, 2015). Cependant, il est l'océan le moins échantillonné au monde (Arctic-Council, 2009) et la non-détection d'ENI transportées par les navires ne doit pas être prise comme une évidence de leur absence dans l'environnement (Niimi, 2004). La température et la salinité de l'eau de surface dans certain ports arctiques sont de plus en plus similaires à celles des ports à proximité, constat

à mettre en rapport avec le réchauffement global. La diminution des barrières environnementales et l'augmentation anticipée du trafic maritime, et potentiellement une hausse de la pression de propagules qui y est associée, augmenteront les risques d'introduction et de propagation d'ENI (Casas-Monroy *et al.*, 2014). Suite à ces changements, l'Arctique deviendra plus vulnérable aux invasions futures (Chan *et al.*, 2012). Le groupe des dinoflagellés compte parmi les organismes qui peuvent être introduits via les eaux de ballast et causer ainsi des effets indésirables à l'écosystème.
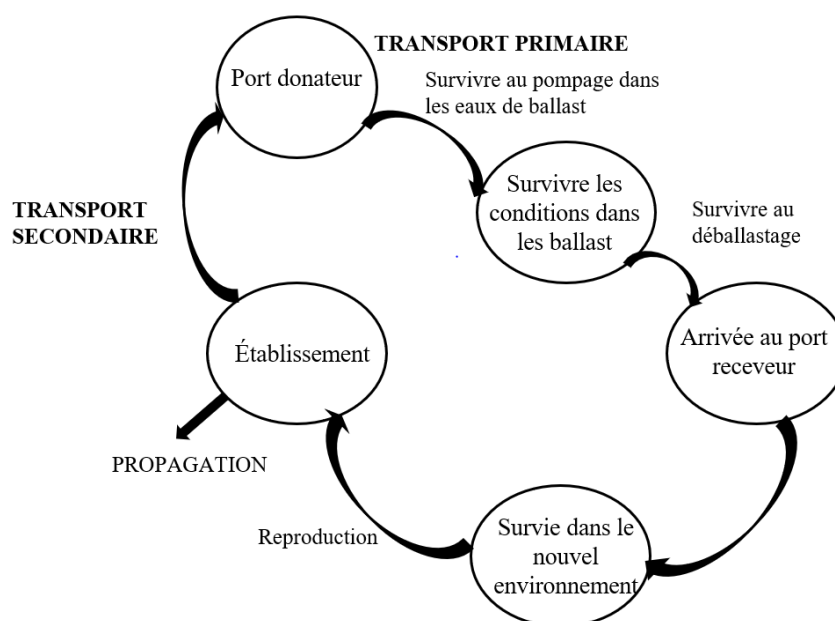
Figure 1: Les étapes de l'invasion biologique par les eaux de ballast (Hallegraeff, 1998; Casas-Monroy et al., 2014).

Les dinoflagellés

Les dinoflagellés sont des microorganismes à deux flagelles se situant à la base de la chaîne alimentaire. Ils sont observés aussi bien en eau douce (10% des espèces connues) qu'en milieu océanique ouvert (90% des espèces connues) (Taylor *et al.*, 2008). Ils ont une grande diversité et une vaste distribution géographique. Ils peuvent se trouver dans les eaux tropicales et polaires, la glace de mer et certains sont même cosmopolites.

Les dinoflagellés ont différentes stratégies alimentaires : 50% sont autotrophes et mixotrophes et 50% sont hétérotrophes ou parasitiques des invertébrés, vertébrés et protistes (Cachon, 1987). Les dinoflagellés hétérotrophes sont des prédateurs de divers

groupes taxonomiques de différentes tailles (3-400 μm) tels que les bactéries, le phytoplancton (ex : diatomées), le zooplancton et même d'autres dinoflagellés. Leur consommation des stades nauplius et œufs de copépodes peut avoir une influence sur les populations de zooplancton. Les multiples modes d'alimentations par engloutissement, déploiement d'un pallium ou pédoncule, permettent aux dinoflagellés d'ingérer des cellules plus petites ou plus grandes qu'eux. Certains sont sélectifs pour le choix de leurs proies. Par exemple, la plupart des espèces du genre *Protoperidinium* se nourrissent exclusivement de diatomées (Jacobson and Anderson, 1986; Jeong, 1999; Jeong *et al.*, 2010).

Le cycle de vie des dinoflagellés comprend une phase haploïde ou végétative et une phase diploïde. Durant la phase haploïde, les cellules se divisent par mitose (reproduction asexuée) pour donner deux cellules filles identiques. Ce mode de division aboutit à la formation de blooms en réponse à un stimulus environnemental. Durant la phase diploïde, les gamètes fusionnent pour donner naissance à un planozygote à 2n mobile (reproduction sexuée), à l'intérieur duquel va se former le kyste chez ~15% des espèces connues. Cette cellule va perdre sa mobilité quand elle se disloque et l'hypnozygote sédimente dans la colonne d'eau et se dépose à la surface du sédiment. La période durant laquelle la cellule reste enkystée dépend de l'espèce et des conditions environnementales. Lorsque ces dernières sont favorables, la cellule exkyste et une nouvelle cellule sort de l'ouverture du kyste (l'archéopyle) et se divise par méiose pour donner naissance à 4 cellules haploïdes (Evitt, 1985; Fensome, 1993). Quand les conditions sont défavorables, la cellule peut demeurer enkystée pendant une longue période. La résistance de la membrane du kyste formée de dinosporine, lui permet de se préserver dans les sédiments. Les kystes fossiles préservés dans les sédiments permettent de retracer l'évolution des conditions océaniques du passé (de Vernal *et al.*, 2001; Richerol *et al.*, 2008; Versteegh *et al.*, 2012).

Certains dinoflagellés produisent des toxines, et représentent 75% de tout le plancton nuisible (Smayda, 1997). Les toxines produites peuvent provoquer plusieurs types d'intoxications et des mortalités chez les humains dans 15% des cas (Hallegraeff, 2003), via la consommation de produits de la mer (par exemple : les mollusques ou les poissons), ayant bioaccumulé une certaine concentration de ces toxines. Les intoxications peuvent être de plusieurs types, mais elles agissent toutes par la modification de la fonctionnalité

d'un organe ou d'un tissu par les toxines. Ces dernières perturbent la communication entre les nerfs et les muscles, inhibent des processus physiologiques et perturbent la conduction nerveuse. Elles peuvent même engendrer des modifications permanentes dans les cellules (Anderson *et al.*, 1993). L'intoxication paralysante (IPP), l'intoxication amnestique (IAM) et l'intoxication diarrhéique (IDM) sont provoquées par la consommation de mollusques contaminés. L'intoxication par phycotoxine paralysante (IPP) est principalement causée par la saxitoxine et ses dérivés. Celle-ci est principalement produite par les taxa du genre *Alexandrium*. La IPP a été documentée pour la première fois en 1793 par le capitaine George Vancouver lorsqu'un matelot est tombé malade suite à un repas de moules pêchées au bras Théodosia (Theodosia Inlet) en Colombie Britannique (Taylor and Harrison, 2002). Intoxication par phycotoxine amnestique (IAM) est principalement causée par l'acide domoïque produite par certaines espèces de diatomées. Les symptômes apparaissent entre 30 minutes et 6h après l'ingestion et sont de type gastrointestinal et nerveux. La première éclosion de cette toxine survenue au Canada était en novembre 1987 et a provoqué la mort de trois personnes lors d'un bloom de *Nitzschia pungens* (Perl *et al.,* 1990). L'intoxication par phycotoxine diarrhéique (IDM) est causée par l'acide okadaïque et ses dérivés. Les symptômes sont de type gastrointestinal et apparaissent généralement entre 30 minutes à quelques heures après la consommation de moules, palourdes et pétoncles. Cette toxine est principalement produite par les espèces des genres *Dinophysis* et *Prorocentrum* (Yasumoto et al., 1980; Yasumoto et al., 1985). Au Canada, la IDM a été détectée pour la première fois en 1990 à Mahone Bay en Nouvelle-Écosse (Quilliam *et al.*, 1993). L'intoxication ciguatérique est un syndrome observé chez les humains, via la consommation de poissons ayant bioaccumulé une certaine concentration de toxines dans les muscles, la peau et les viscères (Halstead, 1964; Lehane and Lewis, 2000). Les premiers symptômes sont de type gastrointestinal, et peuvent durer de quelques heures à quelques semaines. A un stade plus avancé, les symptômes deviennent neurologiques et peuvent s'étendre au cours d'une période allant de quelques semaines à quelques mois. Deux types de toxines sont impliquées dans l'intoxication dont la ciguatoxine (liposoluble) et maitotoxine (soluble dans l'eau) (Bomber and Aikman, 1989; Miller, 1989; Anderson *et al.*, 1993).

Les blooms produits par les dinoflagellés peuvent avoir des impacts économiques. Ils sont responsables de la perte de revenus des produits de la mer. En effet, en cas de bloom, il y aura fermeture des centres de cueillette de bivalves ainsi que des fermes d'aquaculture (Hallegraeff, 2003). Les poissons d'aquaculture sont plus affectés que les poissons sauvages puisqu'ils sont gardés dans des cages et ne sont donc plus capables de fuir les effets du bloom (Taylor and Harrison, 2002). En Nouvelle-Écosse, une mortalité massive dans les cages de saumons a été observée en 2000 à cause d'un bloom de l'espèce *Alexandrium tamarense (*Cembella *et al., 2002)*. En Colombie Britannique, les blooms toxiques sont la cause la plus importante de mortalité des saumons d'aquaculture (Haigh and Esenkulova, 2014). La mortalité peut survenir à la suite d'un dommage physique ou d'une irritation du tissu branchial, d'une réaction aux agents ichtyotoxiques ou d'une hypoxie due à un appauvrissement en oxygène (Rensel and Whyte, 2003). Les blooms peuvent aussi affecter le tourisme, par la fermeture des restaurants, des centres de plongée, des attractions touristiques, et par la diminution de la clientèle dans les hôtels (Steidinger and Baden, 1984).

Le transport de dinoflagellés via les ballasts peut contribuer à la propagation d'espèces toxiques et à l'augmentation de leur aire de distribution géographique, ainsi que la fréquence et l'intensité des blooms toxiques (Hallegraeff, 1998). Les dinoflagellés mobiles mixotrophes et hétérotrophes peuvent survivre aux conditions environnementales dans les ballasts, contrairement aux organismes strictement autotrophes qui ont tendance à mourir 1 à 3 jours après le ballastage (Hallegraeff, 1998). Plusieurs espèces de kystes de dinoflagellés, dont certains sont nuisibles ou toxiques, ont été introduites dans de nouveaux environnements via les sédiments de ballasts (Casas-Monroy *et al.*, 2011). Des kystes se sont accumulés pendant 12 ans dans les sédiments de ballast d'un vraquier et ont exkysté moins d'une heure après avoir été remis en présence de lumière et de nutriments (Rochon *et al.*, 2012)**.**

Le changement des eaux de ballast diminue les risques d'introduction et de propagation des ENI. Cependant, cette mesure n'élimine pas complètement les organismes pompés dans les réservoirs de ballast. Plusieurs facteurs comme les caractéristiques du navire, la méthode et le lieu d'échange utilisés, et le groupe taxonomique peuvent jouer un rôle dans

l'efficacité des échanges de ballast (Wonham *et al.*, 2001; McCollin *et al.*, 2007; McCollin *et al.*, 2008; Simard *et al.*, 2011). Des méthodes de traitement peuvent aussi être utilisées afin de limiter la propagation d'ENI et de dinoflagellés par les ballasts des navires. Cependant, il a été démontré qu'aucune d'entre elles n'est efficace à 100% pour éliminer tous les organismes qui se trouvent dans les eaux de ballasts. Parmi les différentes techniques qui existent, les traitements chimiques avec biocides oxydants peuvent former des substances toxiques par une réaction chimique avec l'eau de mer et être néfastes dans l'environnement où ils sont déchargés (Chase *et al.*, 2001; Tsolaki and Diamadopoulos, 2010). La désoxygénation des ballasts des navires était efficace à plus de 99% pour éliminer le zooplancton, cependant elle n'est pas efficace sur les kystes de dinoflagellés et sur certain organismes benthiques (Hallegraeff, 1998; Tsolaki and Diamadopoulos, 2010). Les traitements par ultraviolets sont aussi sans succès sur les kystes, quand ces derniers se trouvent dans une eau turbide et riche en matière organique. Des kystes peuvent germer même après une exposition de 2h au rayonnement ultraviolet (Montani *et al.*, 1995; Hallegraeff, 1998). Le chauffage des eaux de ballast est une solution non coûteuse, non nuisible à l'environnement et efficace contre les kystes de dinoflagellés. Il a été démontré qu'une courte exposition à une température de 40°C était efficace pour tuer les kystes de dinoflagellés de *Gymnodinium catenatum* et *Alexandrium tamarense* (Bolch and Hallegraeff, 1993; Raaymakers, 2003). Cependant, elle peut engendrer la croissance de bactéries pathogènes (Raaymakers, 2003). Le traitement des dinoflagellés non indigènes dans les ballasts des navires pose un véritable défi (Casas-Monroy *et al.*, 2016). Cependant, une combinaison de plusieurs traitements pourrait être plus efficace (Tsolaki and Diamadopoulos, 2010). Tel que mentionné précédemment, les changements climatiques et le développement économique dans l'Arctique canadien vont probablement contribuer à l'accroissement du trafic maritime, ce qui aura pour conséquence d'augmenter les risques potentiels d'introduction d'espèces non indigènes (Niimi, 2004; Chan *et al.*, 2012; Miller and Ruiz, 2014). Une fois établies, les ENI sont difficiles, voire même impossibles à éradiquer (Hallegraeff, 1998; Andersen *et al.*, 2004; Casas-Monroy *et al.*, 2014). Pour cette raison, il est important d'insister sur la prévention et la détection hâtive (Ware *et al.*, 2014). Cependant, le manque d'information sur les espèces indigènes de l'Arctique canadien pose un problème pour la détection des ENI.

Dans ce contexte, ce projet de maîtrise vise à déterminer les communautés de dinoflagellés présentes dans les ports à plus haut risque d'invasion de l'Arctique canadien dans le but d'établir une base de données et de détecter l'arrivée éventuelle d'espèces non indigènes.

Objectifs spécifiques :

Les ports étudiés sont Churchill (Manitoba), Baie Déception (Québec), Iqaluit et Milne Inlet (Nunavut) (Figure 2). Ces ports reçoivent annuellement les plus grands volumes de déversement d'eau de ballast (Chan *et al.*, 2012). Le port de Churchill était le seul port international de l'Arctique canadien, sa position stratégique lui permettant d'encourager le commerce mondial au nord du Manitoba et d'affirmer la position du Canada dans l'Arctique (Gavrilchuk and Lesage, 2014). Ce port a aussi reçu le plus grand nombre de navires marchands internationaux entre 2005 et 2008 (moyenne de 17.75 ± 1.65 par an), avec un volume moyen de décharge d'eau de ballast de 157,675 ± 19,409 m^3 par année (Chan *et al.*, 2012). Avec le transport de concentré de nickel comme principale activité, le port de Baie Déception figurait parmi les trois ports les plus actifs de l'Arctique entre 2005 et 2008, et les volumes moyens annuels d'eau de ballast déversées par les navires internationaux et domestiques y étaient respectivement de 8,069 ± 4,020 m^3 et 60,144 ± 11,852 m^3 (Chan *et al.*, 2012). Au cours de la même période, le port d'Iqaluit occupait la troisième position, après Churchill et Baie Déception, pour le volume d'eau de ballast déversé par les navires marchands domestiques (1,536 ± 896 m^3) (Chan *et al.*, 2012). Pour le port de Milne Inlet, il occupait la deuxième position après Churchill pour le déversement d'eau de ballast par les navires marchands internationaux (6,959 ± 6,959 m^3) (Chan *et al.*, 2012).

Le volume élevé d'eau de ballast déversée dans les zones côtières ne fait qu'augmenter le risque d'introduction et d'établissement de dinoflagellés non indigènes dans ces régions où les communautés autochtones dépendent fortement de la chasse et de la pêche pour leur subsistance.

Les objectifs de cette étude sont :

Objectif 1: Déterminer l'abondance, la richesse et la diversité des communautés de dinoflagellés dans les ports à plus haut risque d'invasion de l'Arctique canadien;

Objectif 2: Comparer les communautés de dinoflagellés entre les ports et expliquer les variations en relation avec les paramètres environnementaux;

Objectif 3: Comparer les communautés de dinoflagellés échantillonnées en 2007 et 2015 dans le port de Churchill. Les taxa retrouvés en 2015 et non en 2007 pourraient être potentiellement non indigènes dans le cas où ils n'auraient pas été observés en Arctique selon la littérature. Le cas échéant, l'échantillonnage de 2015 sera considéré comme complémentaire à l'étude de 2007 dans un environnement changeant.

Objectif 4: Comparer les communautés de dinoflagellés retrouvées dans les eaux de ballasts et dans les ports où elles sont déversées. Les données de 2014 et 2015 des dinoflagellés retrouvés dans les eaux de ballast des navires domestiques et internationaux de Churchill et de Baie Déception seront comparées à celles du présent travail. Les taxa n'ayant pas été observés dans ces ports, ni dans l'Arctique canadien selon la littérature pourraient être de potentiels ENI, ce qui confirmerait le risque d'invasion lié aux eaux de ballast.

CHAPTER 1

DINOFLAGELLATE COMMUNITIES IN HIGH RISK CANADIAN ARCTIC PORTS

INTRODUCTION

Economic development and tourism in the Arctic coupled with climate change have led to an increase in maritime traffic, with an approximate doubling over the past decade (Arctic-Council, 2009; Miller and Ruiz, 2014; Guy and Lasserre, 2016a; Dawson *et al.*, 2018). Temperatures in the Arctic have increased at an unprecedented rate, leading to the melting of sea ice (Loeng *et al.*, 2005). The continuation of this trend is predicted to facilitate Arctic marine shipping activities due to longer seasons of navigation and the opening of new waterways and shipping routes (Arctic-Council, 2009; Smith and Stephenson, 2013). As a result, the introduction of non indigenous species (NIS) in the Arctic is expected to increase through ballast water discharge and biofouling (Chan *et al.*, 2012). Ballast water exchange regulations were created to limit the risk of introduction of NIS in Canadian waters by international vessels. However, this method is not 100% efficient and many factors, such as the exchange technique, the location of exchange, and the taxonomic group, influence the effectiveness of this method (Wonham *et al.*, 2001; McCollin *et al.*, 2007; McCollin *et al.*, 2008; Simard *et al.*, 2011). Moreover, NIS can still be introduced via domestic vessels, which are exempted from ballast exchange. The new ballast water regulations require from all Canadian vessels anywhere in the world and vessels navigating under the Canadian water jurisdiction to develop a ballast water management plan. These measures would limit the introduction of NIS by 2024. However, the ballast water management systems would be more effective when

implemented with a water treatment (Transport-Canada, 2019; DFO, 2019c). Various organisms are pumped into tanks together with re-suspended sediments and the associated biota, thus facilitating their transport from donor to recipient ports where they may be released into new environments (Casas-Monroy *et al.*, 2014). Individuals (propagules) must survive conditions in the ballast tanks (darkness, predation, lack of oxygen and voyage length) and in the new environment (abiotic similarities and community interactions) for successful establishment (Simard *et al.*, 2011; Casas-Monroy *et al.*, 2014). With climate warming, water temperature and salinity conditions in Arctic ports are becoming more similar to those of non-arctic ports abroad. These are expected to reduce environmental barriers and increase the risk of invasion if propagule supply increases (Casas-Monroy *et al.*, 2014). Non indigenous species have been involved in a variety of impacts in receiving environments through competition with indigenous species for resources and changes in food web structure resulting in loss of biodiversity and extinction, and or decline in abundances of species including those that are commercially important (Shea and Chesson, 2002; Casas-Monroy *et al.*, 2016).

The Canadian Arctic has been described as one of the least affected ecosystems by biological invasions (Chan *et al.*, 2012; Chan *et al.*, 2015). However, it is also the least sampled of the world's oceans (Arctic-Council, 2009), thus, the lack of known ship-mediated NIS should not be taken as evidence of their absence, but could be due to the lack of surveys, research effort and information about indigenous species in this region, limiting abilities to detect invasions (Niimi, 2004; Goldsmit *et al.*, 2014). Native species constitute a "black box", which can be an obstacle for the detection of NIS (Chan *et al.*, 2012).

Dinoflagellates are a group of unicellular biflagellate protists at the base of the food chain and are among a large suite of organisms that can be introduced through transport of ballast water (Taylor *et al.*, 2008). Some produce toxins that can be accumulated in filter feeders and fishes, and then transferred through the food chain, causing several diseases including: paralytic, neurotoxic, diarrhetic shellfish poisoning (PSP, NSP, DSP) and ciguatera fish poisoning (CFP), which can be lethal to marine fauna and humans in 15% of cases (Steidinger and Baden, 1984; Anderson, 1995). Dinoflagellates can also be responsible for changes in water quality by producing harmful blooms and creating

hypoxia in surface waters, leading to fish mortalities and income losses to the aquaculture industry (Hallegraeff, 2003). They also cause negative impacts on business directly or indirectly associated with shellfish production and sale, due to presence of toxins in the tissues, which make them unsafe for consumption (Steidinger and Baden, 1984). Non indigenous dinoflagellates can cause important ecological and economic impacts to new environments, especially toxic species (Hallegraeff, 2003). Some autotrophic dinoflagellates may not survive travelling conditions in the ballast tanks. However, most dinoflagellates are mixotrophic and heterotrophic, and can prey on other organisms in the ballast, and tend to have good survival (Hallegraeff, 1998). About 13 to 16% of dinoflagellates taxa produce cysts (dinocyst) as part of their life cycle (Head, 1996), which are very resistant to extreme conditions, like those found in ballast tanks. Ballast water exchange may also introduce new motile non indigenous dinoflagellates and the associated import of oxygen in the ballast tanks may promote survival of cells remaining in the ballast. Moreover, dinoflagellate cysts are exposed to oxygen-rich conditions when they are pumped with water and sediments during ballasting, which may induce excystment within the ballast tanks. Once released in a new environment, freshly hatched motile cells or soon to be hatched cysts may become available to invade the new environment (Simard *et al.*, 2011; Casas-Monroy *et al.*, 2016).

As explained previously, the lack of information about native species composition may act as a barrier to NIS detection. There have been limited biological invasions in the Arctic to date (Chan *et al.*, 2019), and there is a need to explore this phenomenon in more detail (Chan *et al.*, 2012). Particular attention is required to better understand native biodiversity in order to prepare for expected future increases in the rate of invasions for this region (Ware *et al.*, 2014). In this context, the main objective of this study was to characterize the abundance, richness and diversity of dinoflagellate communities in Canadian Arctic ports with current, or expected future, high risk for invasion to provide baseline data and detect the presence of potential NIS. The specific objectives were to: 1) compare dinoflagellates communities within and among ports and explain variations in relation to environmental factors; 2) determine changes in community composition in Churchill between 2007 and 2015, the most heavily used port in the Arctic and test for

links to temporal variation in abiotic parameters; 3) examine correspondence between dinoflagellate communities found in ballast water of arriving vessels to those found in corresponding ports.

METHODS:

Study area:

Four high risk ports were selected based on their having the highest volume of ballast discharge between 2005 and 2008 (Chan *et al.*, 2012); Churchill (Manitoba), Deception Bay (Quebec), Iqaluit (Nunavut), Milne Inlet (Nunavut), or because they were expected to have substantial future increases in shipping and associated ballast discharge (DFO, 2014; NIRB, 2014; BIMC, 2018; Goldsmit *et al.*, 2019b).

The study ports are in Baffin Bay and Hudson Bay, which are directly under the influence of surface currents of the Eastern Canadian Arctic (Stewart *et al.*, 2015). The water in Hudson Bay is almost entirely from Pacific origin, while in Baffin Bay, Pacific water is found mainly along the western side of the bay. The eastern side of Baffin Bay is composed mainly of Atlantic water (Jones et al. 2003; McLaughlin *et al.*, 2006; Stewart *et al.*, 2015). The flow through Hudson Bay and Hudson Strait mixes with freshwater discharges from Baffin Island before reaching the Labrador Sea. Water in Baffin Bay also has a small Atlantic component that flows through Nares Strait, but most of it enters via the West Greenland Current (Münchow *et al.*, 2011; Stewart *et al.*, 2015; Goldsmit *et al.*, 2019a).

The study area is characterised by thick first-year ice during winter (Stewart *et al.*, 2015), which melts completely during summer. However, the ice-free periods vary between regions due to differences in climate and currents.

Deception Bay (62º10'N, 74º45'W) is characterized by a polar semi-arid climate (Gerardin and McKenney, 2001). Its mean annual surface water temperature and salinity vary from -1.57 to 3.23 ºC and 31 to 33 psu respectively, with the tidal amplitude varying between 6 and 8 m (Stewart *et al.*, 2015). The main activity at the port of Deception Bay is the shipping of nickel concentrate to the port of Quebec City and small quantities of

fuel and supplies on its return voyage (Arctic-Council, 2009). In 2005-2014, Deception Bay was among the top three most active ports in the Arctic. It had the highest activities for international and domestic vessels, with a corrected ballast water discharge of 401 808 metric tons annually for those two types of vessels. The correction in the volume of ballast tanks was made to estimate the propagule supply and consists in applying a factor of 0.1 for ships coming from marine water and 0.01 for ships coming from freshwater to the reported volumes of exchanged ballast water (Chan *et al.*, 2012; Goldsmit *et al.*, 2019b). For the non-icebreaking ships, this region is only accessible for five months, between July 2nd and December 4th (Genivar, 2012). Shipping activities increased substantially in Deception Bay between 2011-2015 compared to 1990-2000, by 1050 to 4100 kilometers traveled by ship per year from homeport to Deception Bay (Dawson *et al.*, 2018). The port of Deception Bay has a high environmental similarity (temperature and salinity) with non-Arctic Canadian ports connected via ballast water, such as Belledune and Saint John (NB), and NIS originating from these two ports have the highest probabilities of survival if introduced to Deception Bay (Chan *et al.*, 2012).

Churchill (58°46′ 09″N, 94°10′ 09″W) is located on the south west coast of Hudson Bay and is characterized by a cold temperate climate, with a mean annual water temperature and salinity of 4.3 ℃ and 26.3 psu respectively (Chan *et al.*, 2015). Churchill was the only international Arctic seaport when it closed in 2016, but it subsequently reopened in 2018 (CBC, 2018). Its strategic position allows reducing shipping distances to Europe and Africa for the transport of grain (Gavrilchuk and Lesage, 2014; Chan *et al.*, 2015).

During the period 2005-2008, Churchill was the Arctic port with the highest risk of invasion from international merchant vessels. The annual number of arrivals (±SE) was 17.75 (± 1.65) and vessels discharged an estimated 157,675 (±19,409) m^3 $year^{-1}$ of untreated ballast water (Chan *et al.*, 2012). During 2005-2014, the number of arrivals to Churchill slightly decreased, but it still received the highest number of international vessels annually (mean of 16.1), with a corrected ballast water discharge of 115,643 million tons annually (Goldsmit *et al.*, 2019b). In addition, 29 connected ports were found to have environmental similarities with this region; NIS introduced from some of these ports have higher probabilities of survival in Churchill, with Port Alfred (QC) being the most important potential source of NIS (Chan *et al.*, 2012).

Iqaluit (63º45′ N, 68º33′ W) is the capital of Nunavut, the territory with the longest coastline of Canada. It is located on Baffin Island in the Eastern Arctic and characterized by a tundra climate with an annual surface water temperature and salinity between -1.57 to 3.23 ºC and 31 to 33 psu respectively (Stewart *et al.*, 2015). Since 1980, the population of Iqaluit has grown considerably, as well as the annual volume of shipped dry goods, tourism and offshore fishing (Aarluk *et al.*, 2005). The port of Iqaluit has a high tidal amplitude, between 10 to 12 m (Stewart *et al.*, 2015), hence the need for a deep-water port, which will be completed in November 2019 (Aarluk *et al.*, 2005; Courtney, 2018). Mean values of arrivals of coastal domestic merchant vessels, international non-merchant and merchant vessels were 15.00 ± 1.87; 9.25 ± 1.60 and 12.00 ± 1.08 respectively between 2005 and 2008 (Chan *et al.*, 2012), which is considered high compared to other Arctic ports, and the total corrected ballast water discharged for domestic vessels were 18,057 million tons between 2005-2014 (Goldsmit *et al.*, 2019b). Further, shipping activities in Iqaluit increased in 2011- 2015 by 1050 to 4100 kilometers traveled by ship per year from homeport to Iqaluit compared to 1990-2000 (Dawson *et al.*, 2018). Vessels arriving from the ports of Kangiqsujuaq (Quebec) and Killinek (Nunavut), have the highest probability of survival of NIS when discharging their ballast water in Iqaluit, due to the high environmental similarities (temperature, salinity) between these three connected ports (Chan *et al.*, 2012).

Milne Inlet (72 °15′N 080 °30′W) is located on northern Baffin Island. This port is at the northernmost latitude compared to the other three ports. Its mean annual surface water temperature vary between -2 to 1 ºC, while salinity is 23 psu at the surface and 32 psu at depth (Ikeda *et al.*, 2018; DFO, 2019a). The ice-free period lasts approximately 3 months (Stewart *et al.*, 2015), between August and early October. The port of Milne Inlet was among the top three ports receiving the largest corrected volume of discharged ballast water, $6,959 \pm 6,959$ m^3 year^{-1}, from international merchant vessels between 2005 and 2008 (Chan *et al.*, 2012). The export of iron ore from the Mary River Iron Mine to Europe, United Kingdom, Taiwan and Japan has risen to 5.1 Mt annually since commencing in 2015 (BIMC, 2018). It is expected to increase to 12 Mt per year as a result of adding 45 days to the shipping season, using larger ore carriers and constructing a second ore dock (DFO, 2019a). With these increased exports, ballast water discharge at the port is

predicted to increase by 662,000 to 812,625 tonnes annually during the shipping season (BIMC, 2018; DFO, 2019a), making Milne Inlet the top Arctic port with high risk of invasion by both ballast water and sediments and biofouling vectors and the fourth highest port in Canada in terms of total annual discharge (DFO, 2014, 2019b).

Sampling for this study took place over the course of several years near the ports and in the surrounding areas of Churchill, Deception Bay, Iqaluit and Milne Inlet (Figure 2; Table 1). Additional data for Wager Bay (Ukkusiksalik National Park), located on the northwest coast of Hudson Bay, were added to the study through an opportunistic collaboration between Parks Canada and Fisheries and Oceans Canada. This region is one of the least known and understudied areas of Nunavut and is of particular interest/concern due to its mineral exploitation and tourism potential (Wodicka *et al.*, 2017). Correspondingly, it has high probabilities for increasing future shipping activities. The addition of this area to the studied ports was meant as a measure to facilitate detection of future invasions by dinoflagellates from ballast water. However, due to the low number of samples and the differences in the sampling methods compared to other ports, the dinoflagellate communities found in this area in August 2016 were examined with presence/absence only (data listed in Annexe 1).

Figure 2: Map of sampled areas (MB: Manitoba, QC: Quebec, NU: Nunavut). Pink stars indicate the port locations; Arrows indicate surface currents; Yellow dots indicate sampling locations in Churchill and Iqaluit (2015), Deception Bay (2016) and Milne Inlet (2017) and red dots indicate sampling locations in Churchill (2007).

Table 1: Sampling information

Ports	Years of sampling	Dates	Samples (#)	CTD
Churchill	2007	16-21 August	15	Eureka
	2015	11-14 August	10	Seabird SBE19plus
Iqaluit	2015	18-20 August	10	Seabird SBE19plus
Deception Bay	2016	19-26 August	11	Seabird SBE19plus
Wager Bay	2016	15-25 August	7	Idronaut/ Minos-X
Milne Inlet	2017	12-20 August	11	Castaway

Dinoflagellate sampling

Dinoflagellate samples were collected from 10-15 random sites, located within a 6 km radius of each port in nearshore waters ranging from 10-20 m depth at chart datum (N=57

sites; Figure 2) using a 20 µm plankton net (30 cm diameter). At each site, a heavy lead weight was fixed to the net, which was then lowered vertically to within 1 m of the bottom with a measured rope. After a couple of seconds, it was hauled back at a constant speed of 1 m s^{-1}. The net was rinsed from its opening to the codend with filtered water from the site to ensure maximum recovery of the sample in the net codend. The concentrated organisms were transferred into a 250 ml plastic jar and preserved with 4% formaldehyde solution and refrigerated in the dark. Additional samples collected from ballast tanks of vessels arriving at two of the ports (Churchill and Deception Bay) were also available from an earlier study that examined plankton communities in ballast water of arriving vessels. In Deception Bay 2016, samples were collected in ballast tanks from the same vessel but filled in different exchange locations (Jacques Cartier Strait and the Strait of Belle Isle in the Gulf of Saint Lawrence) and over successive trips. Detailed methodology for ballast sampling in Deception Bay 2016 is provided in Laget (2017). Ballast samples in Deception Bay 2014 and Churchill (2014 and 2015) were collected with a Niskin bottle at 3 depths, mixed, and preserved with a Lugol solution (Howland and Simard, unpublished data). The inclusion of these samples allowed for comparisons of dinoflagellates in the port environment to those transported in the ballast of vessels for these two locations.

Environmental data

The sampling depth was recorded with a calibrated rope. The euphotic depth was estimated with a Secchi disk (average based on 3 measurements). Temperature and salinity were measured in situ by vertical profiling with a CTD and using a Multi-Parameter Water Quality Meter (YSI ProDSS) on water samples from three Niskin bottles taken at 1 m below surface, halfway between the surface and maximal depth and at the euphotic depth (Table 1).

Microscopic investigation

Dinoflagellates were identified and counted using an inverted microscope (Nikon Eclipse TE-2000-U) at 200 X magnification. Samples were prepared using the Utermöhl method (Utermöhl, 1958; Edler and Elbrächter, 2010). Jars were mixed by overturning 200 times to obtain a homogeneous cell distribution, and a subsample of 2.973 ml was poured in a

sedimentation chamber. In some cases, the samples were diluted because of the high cell density. After 24h of sedimentation, between 300-500 cells, with and without cellular content, were counted and identified. Dinoflagellate cysts were not taken into consideration in this study. Specimen identifications were done using several identification keys with clear illustrations, including: (Schiller, 1937; Bérard-Therriault *et al.*, 1999; Horner, 2002). The species lists of Gómez (2012, 2013) were used for updates of dinoflagellate taxonomy.

To confirm the identification of some taxa, specimens were examined with a scanning electron microscope (JEOL JSM-6460 LV SEM). For SEM observation, a subsample was rinsed profusely with distilled water, cells were individually picked with a glass micropipette and transferred in a sample carrier on an 8 mm Nucleopore polycarbonate membrane with 8μm pore size. This subsample was dehydrated in a graded series of ethanol concentrations (10%, 20%… 100%) for 10 min at each step. Samples were critical point-dried in liquid CO_2 using a critical point-dryer (Polaron E-3000 and E4800 Series Chiller Recirculator). Finally, the membranes were mounted on aluminum stubs (Cambridge), and sputter-coated (SC7640 High Resolution Sputter Coater) with gold-palladium.

Statistical analyses

Relative abundance and diversity of dinoflagellate communities were calculated on untransformed data. The Shannon-Wiener index was used for the diversity because it covers species richness and evenness. To determine if there were differences among ports and between port pairs for each of these indices, we used one-way type III ANOVA and post-hoc pair-wise Tukey tests, respectively on the factor port and the dependant variables diversity and relative abundance. To compare dinoflagellate communities between ports and explain variations in relation to environmental variables, we used several statistical analyses using the software R version 3.5.0. We used PERMANOVA with post-hoc pair-wise adonis comparisons to determine if there were significant differences in the community composition using transformed square root abundances between ports. This was complemented by SIMPER analyses to determine the taxa that contributed the most to the dissimilarity between each pair of ports and by non-metric multidimensional

scaling based on Bray-Curtis dissimilarity for visual analyses. For the latter, the distance between samples in the plots represent their degree of similarity, whereby the closer the points are, the more similar they are. The residual sums of squares is represented by the stress value. When the MDS fits with stress values closer to zero, the relationship between dissimilarities and the distance is in perfect invariability (Kruskal, 1964). To explain the variations in the community composition in relation to environmental factors, a redundancy analyses (RDA) was performed between ports (Churchill 2015, Iqaluit 2015, Deception Bay 2016 and Milne Inlet 2017). Churchill 2007 was not included in this analysis because of the lack of environmental data compared to the other ports. The environmental variables in the RDA were standardised and selected using the BIO-ENV test (Clarke, 1993), coupled with the use of a variance inflation factor to avoid collinearity between environmental factors. An ANOVA with port as factor was performed on each explanatory environmental variable to test if they explained a significant portion of the variation in community composition. Similarly, an ANOVA was performed for the axes of the RDA to test which axes were significant (Legendre and Legendre, 2012). Finally, a partial RDA was performed to determine the contribution of each environmental variable to the community composition. The community composition was compared between 2007 and 2015 in Churchill using NMDS, PERMANOVA and a similarity Percentage analysis (SIMPER) to identify the taxa that contributed the most to the dissimilarity among years. Non-metric multidimensional scaling (MDS) plots on transformed square root dinoflagellate abundances and hierarchical clustering using average link on Bray Curtis dissimilarity were performed for the dinoflagellate communities of Churchill, Iqaluit, Deception Bay and Milne Inlet in order to represent the relationships between samples in a multidimensional space. Average linkage hierarchical clustering was performed inside each port followed by PERMANOVA on transformed square root abundances to test if there were significant differences in the community composition among the group of samples generated by the cluster within the port of Churchill and Iqaluit. For the PERMANOVA, the Non-metric multidimensional scaling (MDS) and the canonical analyses of redundancy (RDA), transformed square root abundances were used to give greater importance to rare species. For the MDS and the RDA, a dummy species with an abundance of 1 was added to deal with plots with zero

abundances. A randomized taxa accumulation curve with standard deviation was performed for individual ports and for the 2 sampling years of Churchill combined to characterize if the sampling was sufficient to estimate the biodiversity of these areas. Ballast and port communities were compared by developing a table to compare dinoflagellate taxa found in ballast water, including potential NIS, from domestic and international vessels that visited Churchill and Deception Bay ports in 2013 and 2014, with dinoflagellates found at sites within and around the ports of Churchill and Deception Bay.

RESULTS

Objective 1: Comparison of dinoflagellate communities between the sampled ports

Abundance, richness and diversity of dinoflagellate communities

We identified 40 dinoflagellate taxa from 8 families in the ports of Churchill, Deception Bay, Iqaluit and Milne Inlet (Figure 4: Mean dinoflagellate abundance and Shannon-Wiener index (±SE) of sampled ports. Bars with different letters are significantly different at p < 0.05.; Annexe 1): 30 taxa in Churchill 2007 and 2015, from which 26 were present in both years; 5 taxa in Iqaluit; 37 taxa in Deception Bay; 22 taxa in Milne Inlet (Figure 4: Mean dinoflagellate abundance and Shannon-Wiener index (±SE) of sampled ports. Bars with different letters are significantly different at p < 0.05.). The majority of these taxa have previously been observed in the Arctic. Naked dinoflagellates from the family Gymnodiniaceae were not identified from these ports due to preservation issues with formaldehyde. In Wager Bay, 32 taxa were identified, including 19 from the Gymnodiniaceae and 5 toxin producers (Annexe 1). Gymnodiniacea specimens are fragile and easily loose their structure, which makes their identification difficult. However the use of a Niskin bottle for sampling and Lugol solution for fixation as in Wager Bay preserves their structure better (Gómez, 2007).
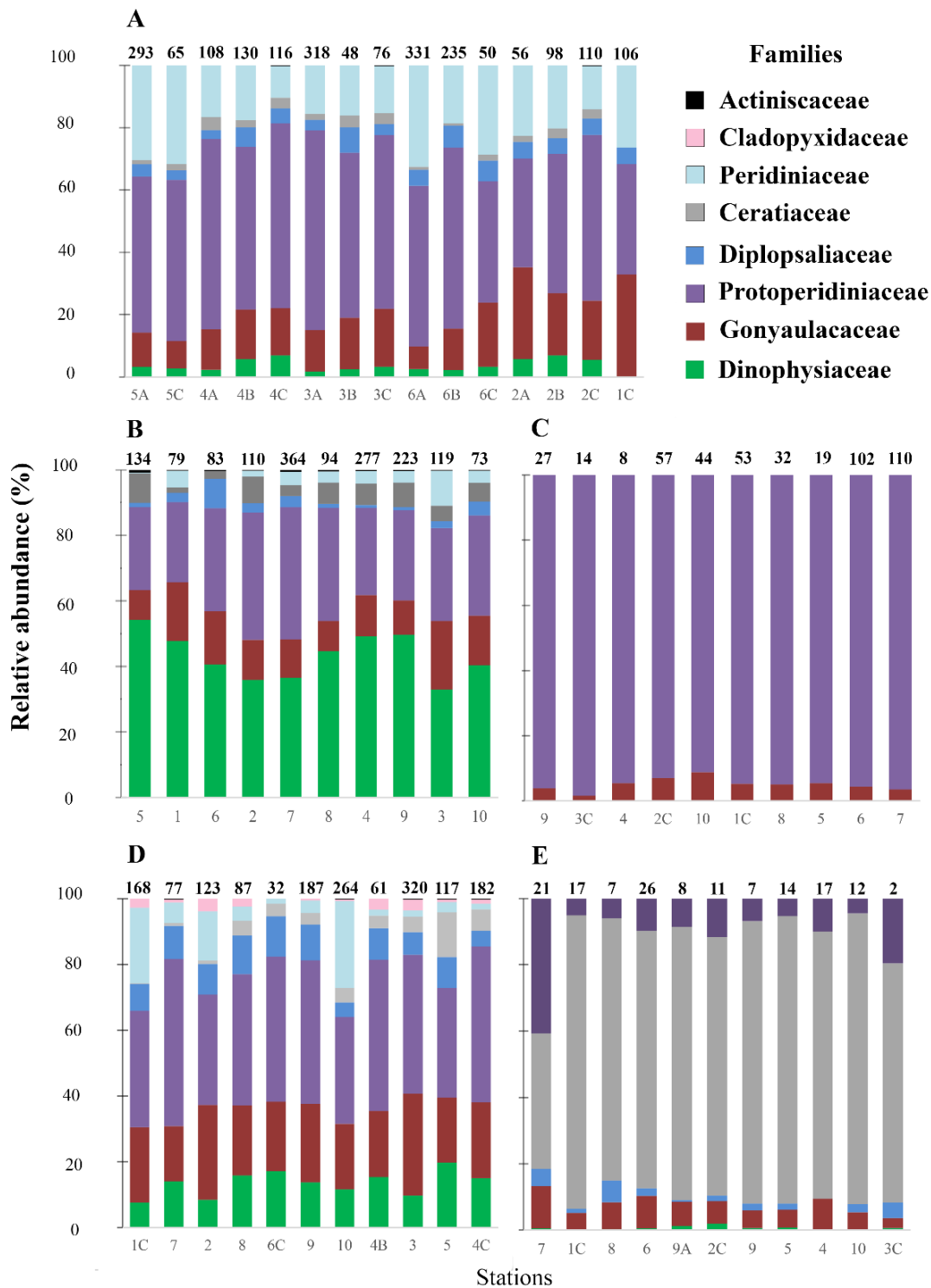
Figure 3: Relative abundances of dinoflagellate families in A) Churchill 2007, B) Churchill 2015, C) Iqaluit, D) Deception Bay and E) Milne Inlet. Values at the top of each bar are the abundances (cells L-1) at each station.

Abundances were significantly different among ports (ANOVA, p < 0.0001; Table 2) with the highest mean abundances in the ports of Churchill (155 cells L^{-1} in 2015 and 143 cells L^{-1} in 2007) and Deception Bay (147 cells L^{-1}) followed by Iqaluit and Milne Inlet (46 cells L^{-1} and 13 cells L^{-1} respectively) (Figure 4: Mean dinoflagellate abundance and Shannon-Wiener index (±SE) of sampled ports. Bars with different letters are significantly different at p < 0.05.), Dinoflagellate abundances inside each port varied from 48 to 331 cells L^{-1} in Churchill 2007, 73 to 364 cells L^{-1} in Churchill 2015, 8 to 110 cells L^{-1} in Iqaluit, 32 to 320 cells L^{-1} in Deception Bay, and from 2 cells L^{-1} outside the port area to 26 cells L^{-1} in the middle of the bay in Milne Inlet (Figure 3). Post-hoc pairwise comparisons indicated that the lower latitude ports of Deception Bay and Churchill (2007 and 2015) were not significantly different from each other in their abundance and likewise for the higher latitude ports of Iqaluit and Milne Inlet (Tukey test, all p > 0.05; Figure 4: Mean dinoflagellate abundance and Shannon-Wiener index (±SE) of sampled ports. Bars with different letters are significantly different at p < 0.05.; Table 2). The Shannon-Wiener index was also significantly different among ports (ANOVA, p < 0.0001), with the highest mean diversity in Deception Bay, followed by Churchill (2015 and 2007), Milne Inlet and Iqaluit (Figure 4: Mean dinoflagellate abundance and Shannon-Wiener index (±SE) of sampled ports. Bars with different letters are significantly different at p < 0.05.). Post-hoc pairwise comparison revealed that diversity was similar among years (2007 and 2015) for Churchill (Tukey test, p = 0.0632; Figure 4).
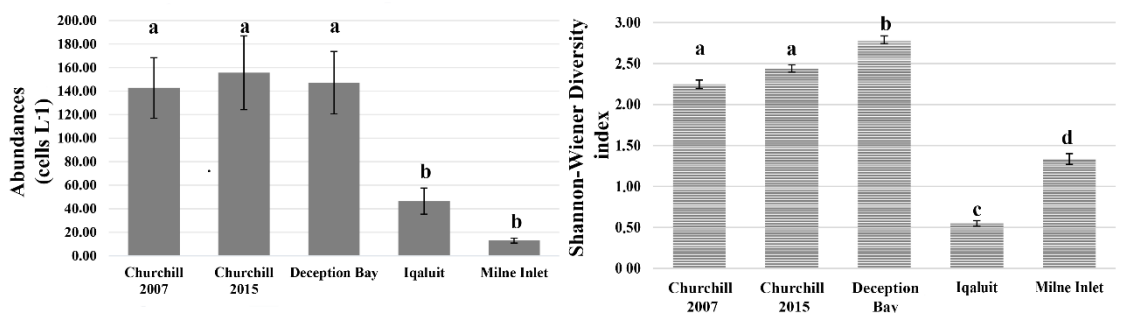
Figure 4: Mean dinoflagellate abundance and Shannon-Wiener index (±SE) of sampled ports. Bars with different letters are significantly different at p < 0.05.

We observed 8 dinoflagellate families in Churchill and Deception Bay, 2 families in Iqaluit, and 5 families in Milne Inlet (Figure 3). Their relative abundances were similar between sampling sites inside each port except for the site situated in the mouth of the river in Milne Inlet (station 7, Figure 2). This site had more Protoperidiniaceae than the other sites due to the predominance of *Protoperidinium brevipes*. Species in the family Protoperidiniaceae were the most dominant in the ports of Iqaluit, Churchill 2007 and Deception Bay, with a relative abundance of 95%, 53% and 40% respectively (Figure 3). In Churchill 2015 and Milne Inlet, species from the families Dinophysiaceae and Ceratiaceae were the most common, with a relative abundance of 43% and 76% respectively (Figure 3). The dominant species in the studied ports were *Pentapharsodinium dalei*, *Dinophysis acuminata*, *P. bipes, P. brevipes* and *Tripos arcticus* with a collective mean relative abundance of 22%, 29%, 85%, 14% and 61% for Churchill 2007 and 2015, Deception Bay, Iqaluit and Milne Inlet respectively (Figure 5). From the 40 taxa identified, 7 are known to be toxin producers, and they collectively represented 17%, 54%, 5%, 33% and 8% of the relative abundance of Churchill 2007, 2015, Iqaluit, Deception Bay and Milne Inlet respectively (Figure 6; Figure 7).
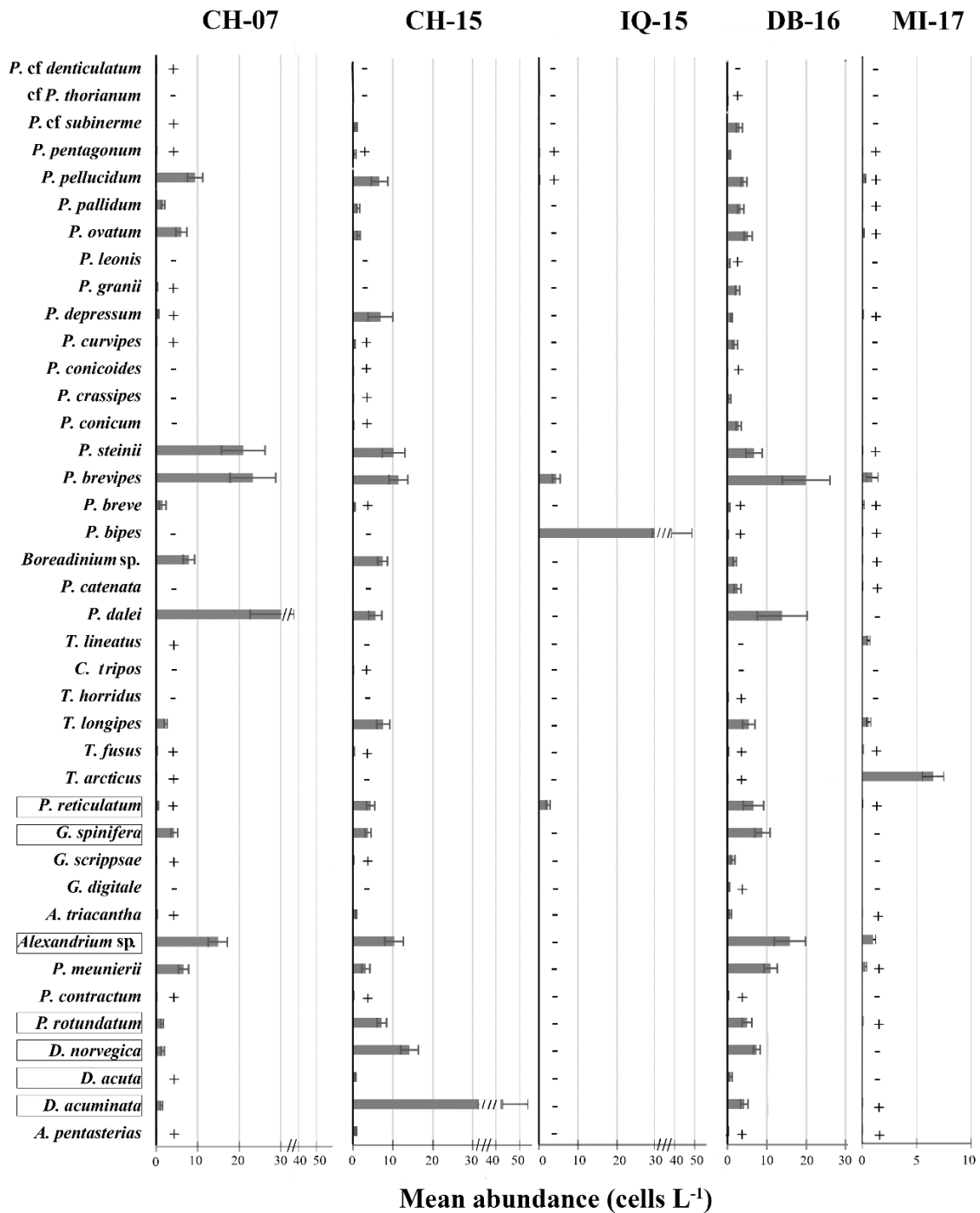
Figure 5: Mean dinoflagellate abundance (cells L^{-1}) (± standard error) of taxa found in CH-07 = Churchill 2007, CH-15 = Churchill 2015, IQ-15 = Iqaluit 2015, DB-16 = Deception Bay 2016, MI-17 = Milne Inlet 2017; Toxin producers' taxa are framed. ('+': taxa present with a mean abundance less than 0.5 cells L^{-1}, '-': taxa absent). Note that scales for DB-16 and MI17 are different from other ports.
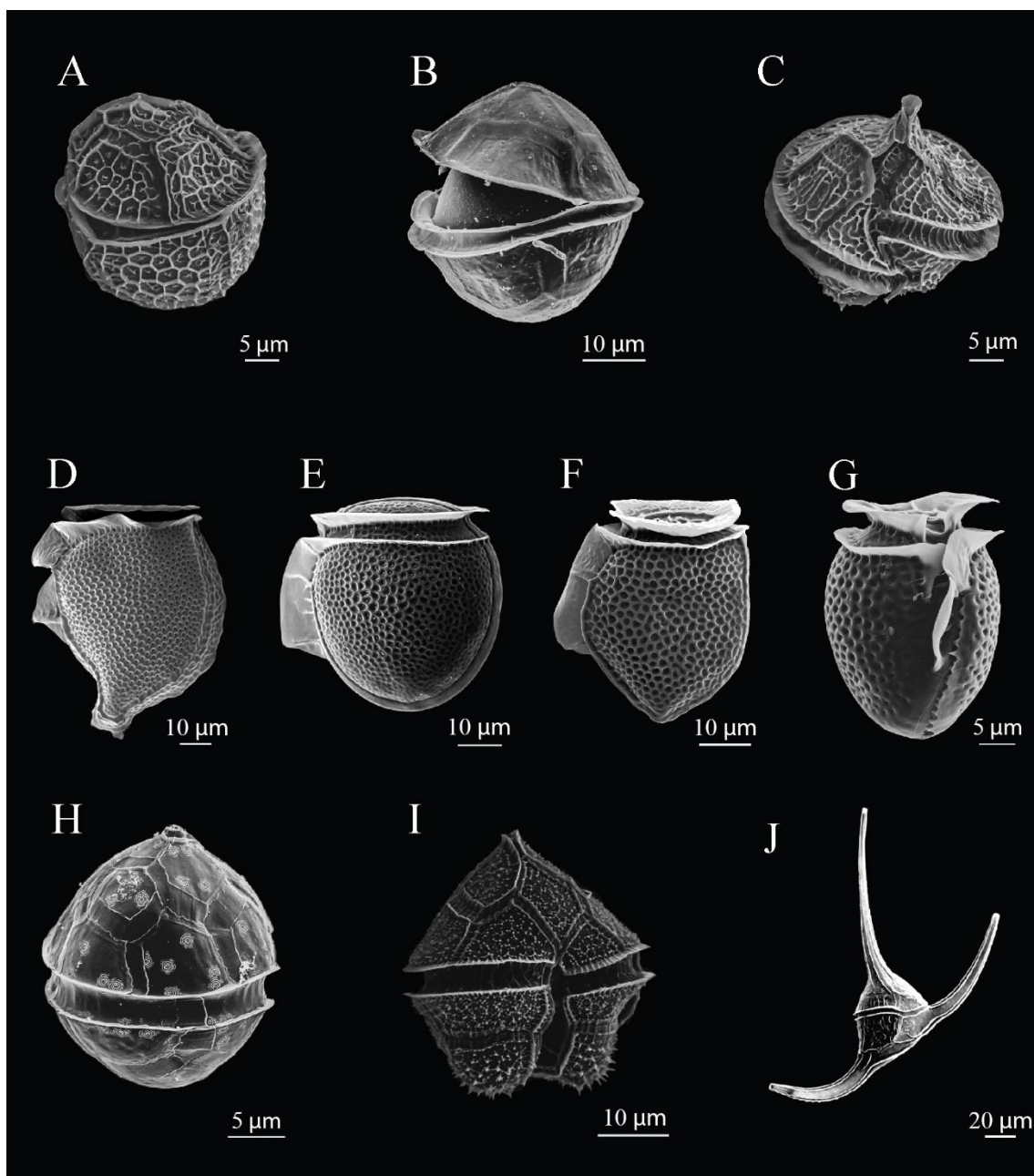
Figure 6: SEM micrographs of harmful (A-G) and most abundant dinoflagellates taxa in the studied ports; A) *Protoceratium reticulatum* B) *Alexandrium* sp. C) *Gonyaulax spinifera* D) *Dinophysis norvegica* (picture: A. Rochon) E) *Phalacroma rotundatum* F) *Dinophysis acuta* G) *Dinophysis acuminata* H) *Pentapharsodinium dalei* I) *Protoperidinium brevipes* J) *Tripos arcticus*.
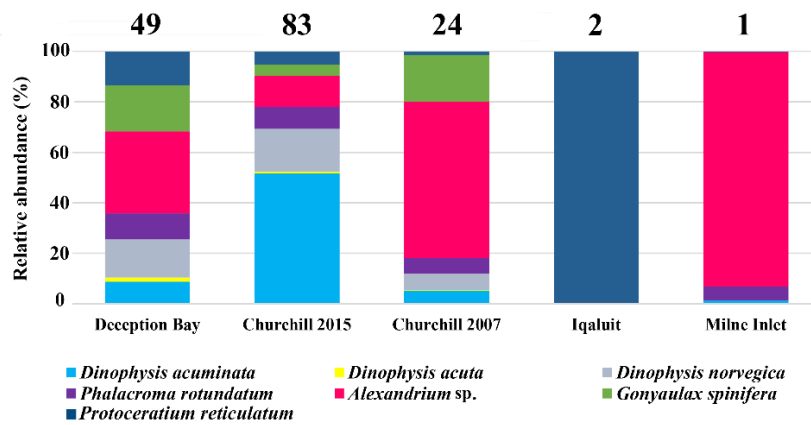
Figure 7: Relative contribution (% based on number of cells L^{-1}) of each toxin producer taxa to the total toxin producers. Bold numbers at the top of each bar represent mean abundances (cells L^{-1}) of the toxin producers found in each port.

Table 2: Results of ANOVA (III) and Pair-wise test of abundances

ANOVA (III) for transformed square root abundances				
	Sum Sq	Df	F-value	Pr (>F)
(Intercept)	242322	1	39.8272	**6.196e-08 ***
Port1	193978	4	7.9704	**4.340e-05 ***
Residuals	316386	52		

Pair-wise Tukey test for transformed square root abundances					
Contrast	Estimate	SE	Df	t-ratio	p-value
CH15 - CH07	12.929057	31.84425	52	0.406	0.9941
CH15 - DB	8.419889	34.08160	52	0.247	0.9991
CH15 - IQ	109.138882	34.88363	52	3.129	**0.0230**
CH15 - MI	142.706536	34.08160	52	4.187	**0.0010**
CH07 - DB	-4.509168	30.96359	52	-0.146	0.9999
CH07 - IQ	96.209824	31.84425	52	3.021	**0.0306**
CH07 - MI	129.777478	30.96359	52	4.191	**0.0010**
DB - IQ	100.718992	34.08160	52	2.955	**0.0362**
DB - MI	134.286646	33.26023	52	4.037	**0.0016**
IQ - MI	33.567654	34.08160	52	0.985	0.8609

Sum Sqs= Sum of Squares; Df = Degrees of freedom. Values in bold indicate significant differences (p < 0.05). CH07 = Churchill 2007, CH15 = Churchill 2015, DB = Deception Bay, IQ = Iqaluit, MI = Milne Inlet.

Table 3: Results of ANOVA (III) and Pair-wise test for Shannon-Wiener index

ANOVA (III) Shannon-Wiener index (non-transformed data)				
	Sum Sqs	Df	F-value	Pr (>F)
(Intercept)	59.559	1	1972.49	**< 2.2e-16 ***
Port1	35.196	4	291.41	**< 2.2e-16 ***
Residuals	1.570	52		

Pair-wise Tukey test for Shannon-Wiener index (non-transformed data)					
Contrast	Estimate	SE	Df	t-ratio	p-value
CH15 - CH07	0.1935796	0.07094007	52	2.729	0.0632
CH15 - DB	-0.3494145	0.07592425	52	-4.602	**0.0003**
CH15 - IQ	1.8916262	0.07771095	52	24.342	**<.0001**
CH15 - MI	1.1054218	0.07592425	52	14.560	**<.0001**
CH07 - DB	-0.5429941	0.06897821	52	-7.872	**<.0001**
CH07 - IQ	1.6980466	0.07094007	52	23.936	**<.0001**
CH07 - MI	0.9118423	0.06897821	52	13.219	**<.0001**
DB - IQ	2.2410406	0.07592425	52	29.517	**<.0001**
DB - MI	1.4548363	0.07409448	52	19.635	**<.0001**
IQ - MI	-0.7862043	0.07592425	52	-10.355	**<.0001**

Sum Sqs= Sums of Squares; Df = Degrees of freedom. Values in bold indicate significant differences (p<0.05). CH07= Churchill 2007, CH15= Churchill 2015, DB= Deception Bay, IQ= Iqaluit, MI= Milne Inlet.

Non-metric multidimensional scaling (NMDS) on transformed square root abundance of dinoflagellates revealed 5 groups with distinct taxonomic composition representing the community of each port (Figure 8). Dinoflagellate communities were significantly different among all ports (PERMANVOVA, p = 0.001; perm = 999; t-test: all adjusted p < 0.01; Table 4), however, the communities in Churchill and Deception Bay were grouped more closely on the NMDS compared to the communities in Iqaluit and Milne Inlet, with Milne Inlet being most distinct. The species that contributed the most to the difference between Churchill 2015 and the other ports was *D. acuminata. Protoperidinium bipes*, contributed the most to the difference between Iqaluit and Churchill 2007 (14%), Deception Bay (11%) and Milne Inlet (36%); *Pentapharsodinium dalei* contributed the most to the difference between Churchill 2007 with Deception Bay (8%) and Milne Inlet

(13%); and *P. brevipes* contributed the most to the difference between Deception Bay and Milne Inlet (6%) (Figure 5, Annexe 6).

Table 4: Results of PERMANOVA and Pair-wise test for transformed square root dinoflagellate communities

PERMANOVA for transformed square root abundances						
	Df	Sum Sqs	Mean Sqs	F-Model	R^2	Pr(>F)
Port	4	10.6953	2.67383	59.83	0.8215	**0.001 *****
Residuals	52	2.3239	0.04469	0.1785		
Total	56	13.0192	1.0000			

Pair-wise Adonis test for transformed square root abundances				
Pairs	F-Model	R^2	p-value	p-adjusted
DB vs CH15	8.68448	0.3136949	0.001	**0.01**
DB vs CH07	10.86636	0.3116575	0.001	**0.01**
DB vs IQ	78.17297	0.8044724	0.001	**0.01**
DB vs MI	64.92468	0.7644972	0.001	**0.01**
CH15 vs CH07	14.35847	0.3843430	0.001	**0.01**
CH15 vs IQ	95.37139	0.8412298	0.001	**0.01**
CH15 vs MI	76.18151	0.8003814	0.001	**0.01**
CH07 vs IQ	101.71433	0.8155785	0.001	**0.01**
CH07 vs MI	77.10422	0.7626212	0.001	**0.01**
IQ vs MI	86.84017	0.8204840	0.001	**0.01**

Df = Degrees of freedom, Sum Sqs= Sum of Squares; Mean Sqs = Mean of Squares. Values in bold indicate significant differences (p = 0.01). CH07 = Churchill 2007, CH15 = Churchill 2015, DB = Deception Bay, IQ = Iqaluit, MI = Milne inlet.
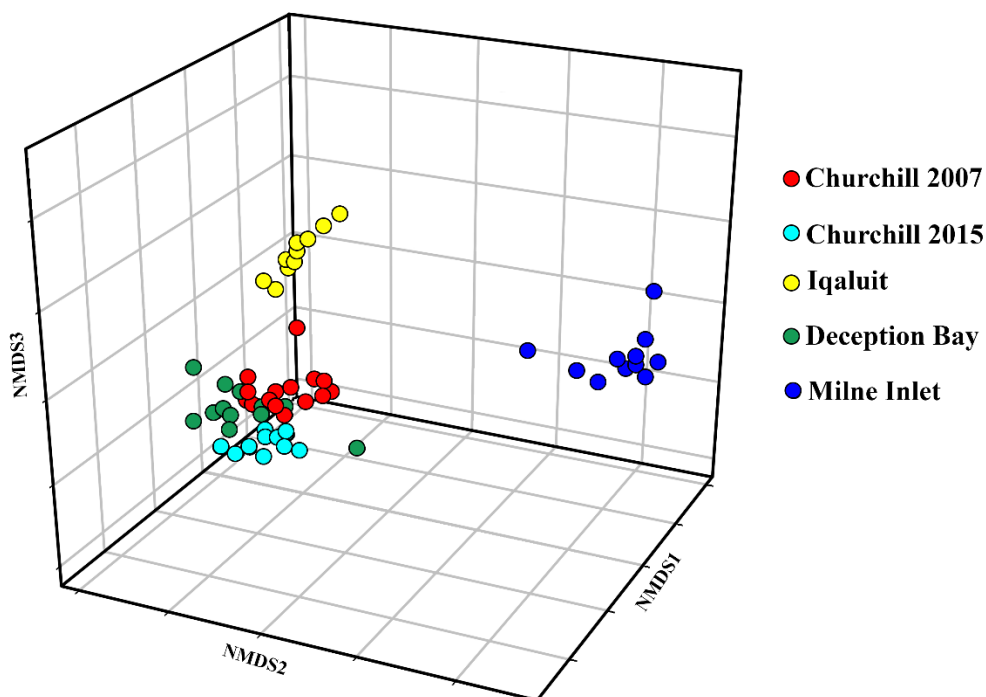
Figure 8: Non-metric multidimensional scaling (NMDS) plot of Bray-Curtis dissimilarity on transformed dinoflagellate abundances (3 dimensions, stress = 3%).

Variations of dinoflagellate communities in relation to environmental factors

Among the environmental variables considered for the RDA analysis, surface temperature (TSurf), days between sea ice melt and sampling (DSIMS), bottom salinity (Sbot) and water depth were most important in explaining variations in dinoflagellate communities and retained after forward selection (Figure 9). These variables explained 21% (adjusted $R^2 = 0.21$) of the total dinoflagellate variability (Annex 4). The first axis was positively correlated with depth ($r = 0.41$) and Sbot ($r = 0.034$), and negatively correlated with TSurf ($r = -0.74$) and DSIMS ($r = -0.97$), while the second axis was positively correlated with TSurf ($r = 0.64$) and DSIMS ($r = 0.19$) and negatively correlated with depth ($r = -0.63$) and Sbot ($r = -0.55$). The DSIMS was the environmental variable that contributed the most to the variability of dinoflagellate communities by 14%, followed by TSurf, by 2% dividing ports into two main groups: the higher latitude ports of Iqaluit and Milne Inlet, and the lower latitude ports of Deception Bay and Churchill (adjusted $R^2 = 0.14$, 0.02 respectively). In fact, sampling in Deception Bay and Churchill took place more than 6 weeks after the melting of the sea ice, whereas it was only

conducted after 10-20 days in Iqaluit and Milne Inlet ports. Indeed, a substantial gradient of surface water temperature at time of sampling was observed between Churchill (12.6 ºC ± 0.6) and Iqaluit (0.6 ºC ± 0.12). Most of the dinoflagellate taxa showed a positive relationship with the DSIMS and TSurf, except for *P. bipes*, *T. arcticus* and *T. lineatus* (Figure 9). Interestingly, *P. bipes* and *T. arcticus* were the most abundant taxa in Iqaluit (84%) and Milne Inlet (54 %) respectively, while *T. lineatus* was relatively abundant in Milne Inlet and was absent in all the other ports except for a single occurrence in Churchill in 2007 (Figure 5, Figure 9).
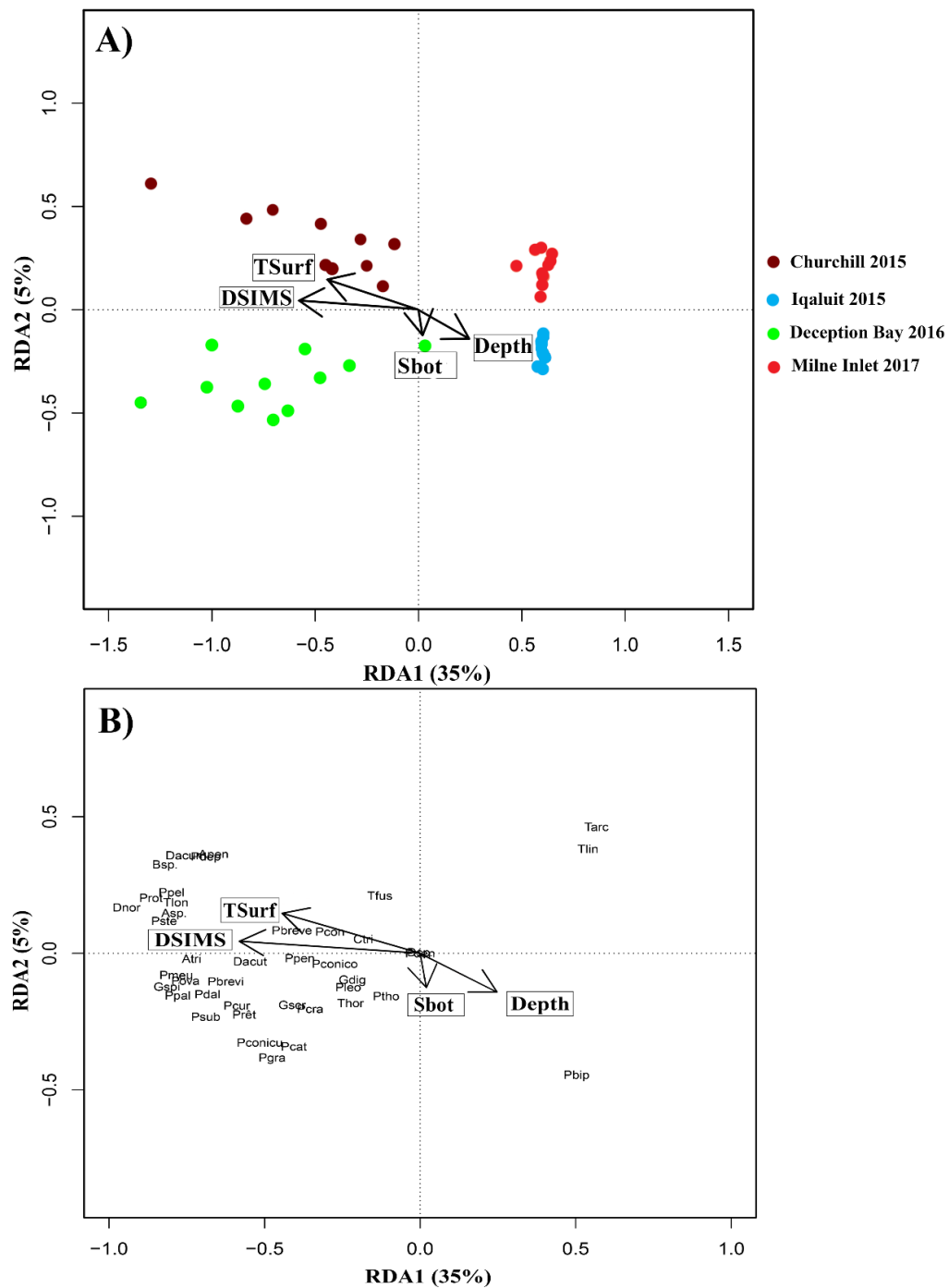
Figure 9: Redundancy analysis (RDA) ordinates by sampling station (A) and dinoflagellate taxa (B) in relation to statically significant environmental variables (p < 0.05); DSIMS: Days between sea ice melt and sampling day; TSurf: Surface temperature Sbot: Bottom salinity and Depth. Full names of taxa are listed in Annex 1. Axes 1 and 2 (significant at p < 0.05). Percent of total explained variance for each axis indicated in brackets.

Objective 2: Comparison of dinoflagellate communities within each port

NMDS plots of abundance based on taxonomic composition of stations within ports revealed that there were some stations that grouped together more closely inside each port (Figure 10). Although, these groups did not differ based on their taxonomic composition, some differed with respect to relative abundances. In Churchill, stations were separated into two groups, the first with lowest abundances (sites 7, 4, 9) and the second with abundances higher than 134 cells L^{-1} (sites 5, 3, 2, 8, 10, 1C). In Iqaluit, there was some separation into two groups along axis 1: the first with stations having abundances less than 40 cells L^{-1} (sites 3C, 4, 5, 8, 9) and the second including those with abundances higher than 40 cells L^{-1} (sites 1C, 2C, 6, 7, 10). In Deception Bay, all stations were grouped together except for 6C, which had the lowest abundance. In Milne Inlet, stations were also grouped together with the exception of one site outside the bay (3C) and the one in the mouth of the river (7). With the exception of Milne Inlet port, none of the RDAs examining the composition of the dinoflagellate communities in relation environmental variables were significant at p < 0.05. In the case of Milne Inlet, TSurf, Teuph (Temperature in the euphotic zone) and SSurf were found to be the most important variables based on forward selection (Figure 11) and together they explained 23% (adjusted R^2 = 0.23, Annexe 6) of the dinoflagellate community variability in this port. The first axis was positively correlated with TSurf and Teuph (r = 0.75 and 0.44 respectively), and negatively correlated with SSurf (r = -0.95). The second axis was positively correlated with Teuph and SSurf (r = 0.81 and 0.30 respectively), and negatively correlated with TSurf (r = - 0.47). Temperature in the euphotic zone (Teuph) explained the majority of the variability of the dinoflagellate communities (adjusted R^2 = 14%) with a negative temperature gradient from the mouth of the river to the outside of the bay (Figure 11).
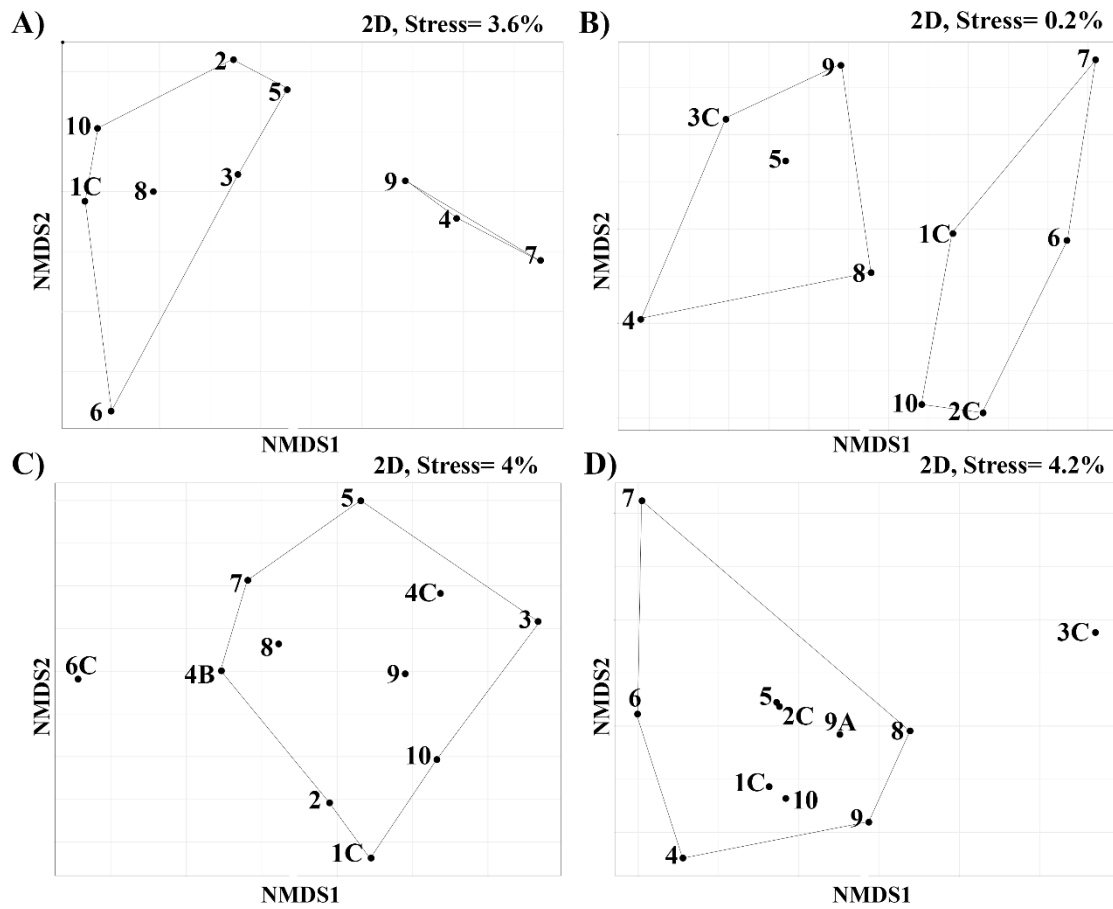
Figure 10: Non-metric multidimensional scaling (NMDS) plot of Bray-Curtis dissimilarity and hierarchical clustering analyses on transformed square root dinoflagellate abundances in A) Churchill B) Iqaluit, C) Deception Bay and D) Milne Inlet. The letters and numbers refer to the sample stations.
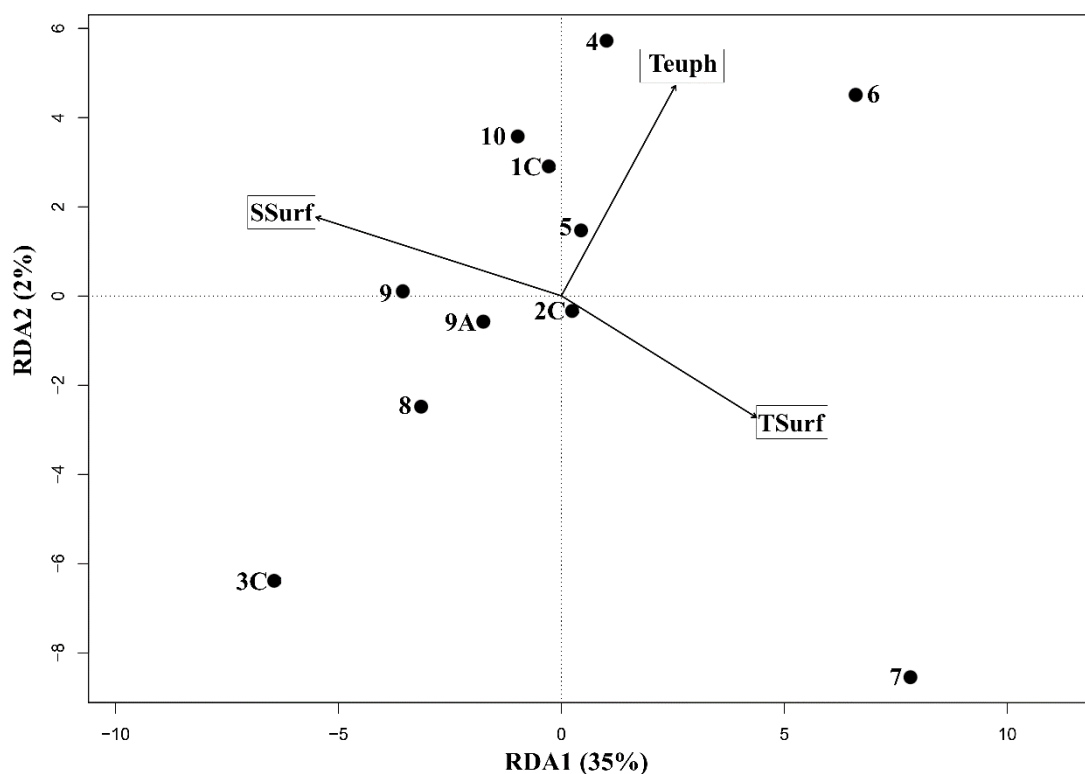
Figure 11: RDA ordination on stations with significant explanatory variables in Milne Inlet (TSurf: Surface temperature, Teuph: Temperature in the euphotic zone, SSurf: Surface salinity), RDA I, TSurf and Teuph are significant ($p < 0.05$). Percent of variance explained by axes are indicated in brackets.

Objective 3: Determine changes in community composition between 2007 and 2015 in the most heavily used port of Churchill

Differences in dinoflagellate communities in the port of Churchill 2007 and 2015

Dinoflagellate communities were significantly different in Churchill between 2007 and 2015 (PERMANOVA; $p = 0.001$; perm = 999; Table 5). This was also evident from the NMDS plot (Figure 12), which showed that stations clustered together by year. SIMPER analysis indicated that three taxa contributed the most to explaining 32% of the dissimilarity between Churchill 2007 and 2015 (Table 6): *P. dalei* was dominant in 2007 (21% of the community), *D. acuminata* (toxin-producer) was dominant in 2015 (28% of the community), and *D. norvegica* (toxin-producer) was more abundant in 2015 (9% *vs.* 1% in 2007). Toxin producer taxa were generally more abundant in Churchill in 2015 than in 2007, except for the two taxa cf. *Alexandrium* sp. and *G. spinifera* (Figure 5).

Table 5: Results of PERMANOVA on transformed square root abundance data for Churchill dinoflagellate communities in 2007 and 2015

PERMANOVA for transformed square root abundances						
	Df	Sum Sqs	Mean Sqs	F.Model	R^2	Pr (>F)
Port	1	0.58018	0.58018	14.358	0.38434	**0.001 *****
Residuals	23	0.92936	0.04041	0.61566		
Total	24	1.50953	1.00000			

Df = Degrees of freedom, Sum Sqs= Sum of Squares; Mean Sqs= Mean of Squares. Values in bold indicate significant differences (p = 0.001).
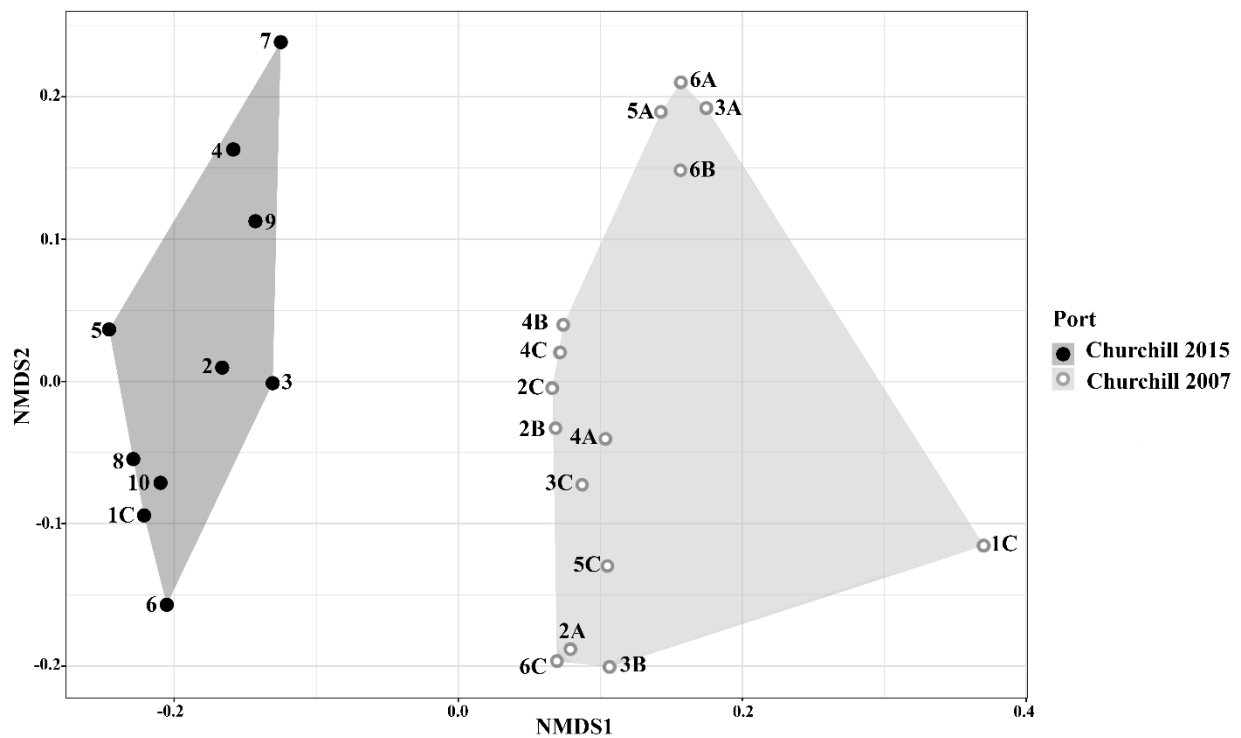
Figure 12: Results of non-metric multidimensional scaling ordination (NMDS) plot and hierarchical clustering analysis of transformed square root abundance dinoflagellate abundances at Churchill in 2007 and 2015, 2 dimensions, stress= 7%.

Table 6: SIMPER results for the taxa that contribute 94% of the dissimilarity

	Average dissimilarity (%)	Diss/sd	Individual contribution (%)	Cumulative contribution (%)
Dinophysis acuminata	6.1	**2.7744**	15%	15%
Pentapharsodinium dalei	3.6	**1.4268**	9%	24%
Dinophysis norvegica	3.1	**2.4700**	8%	32%
Protoperidinium steinii	2.4	**1.3437**	6%	38%
Protoperidinium brevipes	2.3	**1.3759**	6%	44%
Protoperidinium depressum	2.2	**1.5396**	5%	49%
Protoceratium reticulatum	1.9	**2.2437**	4%	54%
Phalacroma rotundatum	1.8	**1.7646**	4%	58%
Alexandrium **sp.**	1.6	**1.2902**	4%	62%
Tripos longipes	1.6	**1.4978**	4%	66%
Protoperidinium pellucidum	1.5	**1.4476**	4%	70%
Protoperidinium ovatum	1.4	**1.4203**	3%	73%
Boreadinium **sp.**	1.2	**1.3708**	3%	76%
Preperidinium meunieri	1.1	**1.3911**	3%	79%
Gonyaulax spinifera	1.1	**1.3902**	3%	82%
Protoperidinium pallidum	0.9	**1.5255**	2%	84%
Protoperidinium breve	0.9	**1.0898**	2%	86%
Protoperidinium **cf** *subinerme*	0.8	**1.4893**	2%	88%
Actiniscus pentasterias	0.8	**2.0282**	2%	90%
Amylax triacantha	0.7	**1.4528**	2%	92%
Dinophysis acuta	0.5	0.9005	1%	93%
Protoperidinium curvipes/subcurvipes	0.5	**1.2883**	1%	94%

Diss/sd= average dissimilarity/ standard deviation. Values of Diss/sd $\geq$ 1 are in bold and represent taxa which consistently contributed to the observed community change. Mean abundance of each taxa is presented in Figure 5.

Comparison of dinoflagellate communities between 2007 and 2015 according to physical and chemical parameters in the port of Churchill:

An RDA on dinoflagellate taxonomic composition (using transformed square root abundances) with forward selection showed that Depth, TSurf and DSIMS were the most important variables and collectively explained 24% (adjusted R^2 = 0.24, Annexe 5) of the dinoflagellate variability among years at the port of Churchill. The first axis (RDA1), which explained the majority of the variation among years was positively correlated with DSIMS (r = 0.57) and TSurf (r = 0.19), and negatively correlated with Depth (r = -0.88) (Figure 13). Sampling in 2015 was done at a greater depth than in 2007 (mean of 6.5 m in 2007 and 12.3 m in 2015).
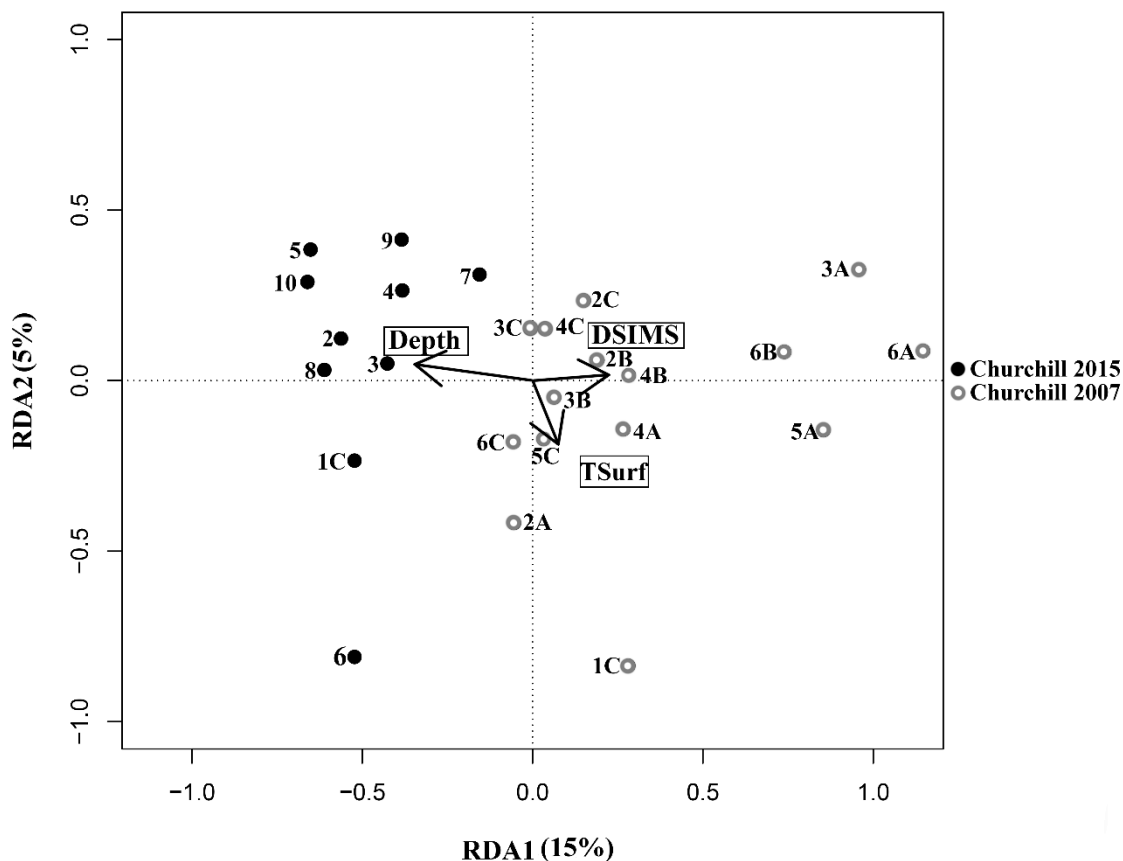
Figure 13: RDA ordination by stations showing main explanatory variables: DSIMS: Days between sea ice melt and sampling, TSurf: Surface temperature and Depth. Depth and RDA1 are significant (p < 0.05). Percent of variance explained by axes are indicated in brackets.

Objective 4: Comparison of dinoflagellate communities found in ballast water versus communities found in the ports of Deception Bay and Churchill

A comparison of the dinoflagellate community in the port of Deception Bay in 2016, with the communities found in 7 ballast tanks of domestic vessels in 2014 and in 8 tanks in 2015, showed that 75 marine dinoflagellate taxa were present in ballast tanks, of which 27 taxa were also present in the port (Table 7). Two freshwater taxa were observed in the ballast tanks: *Amphidinium kesslitzii* and a potential NIS *Peridinium aciculiferum*. Two toxin producer taxa were also observed in ballast tanks but not in the port: *Amphidinium* aff. *carterae and Alexandrium ostenfeldii.* However, these taxa have been observed in other regions of the Canadian Arctic so are not considered to be NIS. Among all taxa present in ballast tanks in Deception Bay, 10 species: (*P. aciculiferum, Phalacroma ovatum, Gonyaulax* cf. *alaskensis, Ensiculifera. mexicana, Oblea rotundata, Fragilidium subglobosum, Protoperidinium marielebourae, Protoperidinium* cf. *grenlandicum, Protoperidinium excentricum, Ceratium tripos)* have never been observed in the Canadian Arctic and are considered as potential NIS. Another species, *Tripos furca* has been only once reported as far North as northern Labrador Sea in 2008 (Rochon unpublished data). These species should be considered as NIS to the Arctic (Annexe 2).

A similar comparison was made between dinoflagellate communities in the port of Churchill to those from ballast tanks of 11 international and domestic vessels sampled in 2014, and from ballast tanks of 4 international vessels sampled in 2015. Among the 48 dinoflagellate taxa identified in the ballast tanks, 10 were also present in the port. The freshwater species *A. kesslitzii* and the toxin producer species *Prorocentrum minimum* were both present in the ballast tanks, but not in the port. Among all the taxa present in ballast tanks in Churchill, two species, *Gyrodinium* aff. *metum,* and *T. furca,* also found in the ballast of vessels arriving to Deception Bay, were considered to be NIS to the Canadian Arctic. As mentioned above, there is only one case of this species being identified in a plankton sample and was from the northern Labrador Sea (Rochon, unpublished data; Table 7).

Table 7: Comparison of dinoflagellate communities in ballast waters (international and domestic) in 2014 and 2015 versus communities in the ports of Churchill and Deception Bay identified during this study in samples from 2015 and 2016. Taxa in bold are toxin producers (IOC-UNESCO, 2018)

| Dinoflagellates taxa | Deception Bay | | | Churchill | | | | Canadian Arctic (Y/NIS) | References |
| | | Domestic | | | Domestic | International | | | |
	Port 2016	7 ballast tanks 2014 [1]	8 ballast tanks 2015 [2]	Port 2015	2 ballast tanks 2014 [1]	9 ballast tanks 2014 [1]	4 ballast tanks 2015 [1]		
Amphidinium aff. *carterae*		X						Y	(Poulin *et al.*, 2011)
Alexandrium ostenfeldii		X						Y	(Poulin *et al.*, 2011)
Amphidinium crassum		X				X		Y	(Riedel *et al.*, 2003)
*Amphidinium kesslitzii**		X			X	X	X	Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Amphidinium sphenoides					X	X	X	Y	(Riedel *et al.*, 2003)
Amphidoma acuminata				X	X	X		Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Amylax triacantha	X		X					Y	(Pinkewycz and Hsiao, 1987)
Ceratium furca (Neoceratium furca) (Tripos furca)			X		X			P.NIS	Rochon, unpublished data
Ceratium fusus (Neoceratium fusus) (Tripos fusus)	X	X	X	X		X		Y	(Laget, 2017); Rochon, unpublished data
Ceratium lineatum (Neoceratium lineatum) (Tripos lineatus)		X	X				X	Y	(Lovejoy *et al.*, 2002)
Ceratium tripos		X		X				P.NIS	
Dinophysis acuminata = D. skagii	X	X	X	X	X		X	Y	(Percy, 1992; Poulin *et al.*, 2011)
Dinophysis acuta = D. dens	X		X					Y	(Percy, 1992; Poulin *et al.*, 2011)
Dinophysis caudata			X					Y	(Poulin *et al.*, 2011)
Dinophysis norvegica	X	X	X				X	Y	(Poulin *et al.*, 2011)
Dinophysis ovatum (Phalacroma ovatum)			X					P.NIS	

Species								Status	Reference
Dinophysis rotundata (Phalacroma rotundatum)	X	X	X	X			X		Y	(Percy, 1992; Poulin *et al.*, 2011)
Ensiculifera carinata			X						Y	Rochon, unpublished data
Ensiculifera mexicana			X						P.NIS	
Fragilidium subglobosum			X						P.NIS	
Gonyaulax cf. *alaskensis*			X						P.NIS	
Gonyaulax cf. *scrippsae*	X		X						Y	(Hsiao and Pinkewyc, 1985)
Gonyaulax digitale	X	X							Y	Rochon, unpublished data
Gonyaulax gracilis		X				X	X		Y	(Riedel *et al.*, 2003)
Gonyaulax spinifera	X	X	X						Y	(Poulin *et al.*, 2011)
Gymnodinium aff. *gracilentum*[+]		X				X			Y	(Riedel *et al.*, 2003)
Gymnodinium aff. *parvum*					X	X			Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Gymnodinium aff. *subroseum*[+]		X			X	X	X		Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Gymnodinium elongatum					X	X	X		Y	(Simo-Matchim *et al.*, 2017)
Gymnodinium galeatum		X			X	X	X		Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Gymnodinium mikimotoi (Karenia mikimotoi)							X		Y	(Poulin *et al.*, 2011)
Gymnodinium simplex		X			X	X	X		Y	(Percy, 1992)
Gymnodinium verruculosum[+]		X					X		Y	(Riedel *et al.*, 2003)
Gyrodinium aff. *grave*							X		Y	(Riedel *et al.*, 2003)
Gyrodinium aff. *guttula*		X			X	X	X		Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Gyrodinium aff. *Gyrodinium aciculatum*			X						Y	(Simo-Matchim *et al.*, 2017)
Gyrodinium aff. *metum*						X	X		P.NIS	
Gyrodinium flagellare		X			X	X	X		Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Gyrodinium formosum[+]		X			X	X	X		Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Gyrodinium fusiforme							X		Y	(Riedel *et al.*, 2003)
Gyrodinium pepo					X				Y	(Riedel *et al.*, 2003)

Species								Status	Reference
Gyrodinium pingue						X		Y	(Percy, 1992)
Gyrodinium spirale		X				X		Y	(Percy, 1992)
Heterocapsa rotundata		X			X	X	X	Y	(Riedel *et al.*, 2003)
Heterocapsa triquetra			X					Y	(Lovejoy *et al.*, 2002)
Katodinium glaucum		X			X	X	X	Y	(Riedel *et al.*, 2003)
Mesoporos perforatus		X				X		Y	(Lovejoy *et al.*, 2002)
Micracanthodinium claytonii						X		Y	(Lovejoy *et al.*, 2002)
Oblea rotunda (Oblea rotundata)		X	X					P.NIS	
Oxytoxum gracile (Oxytoxum variabile)						X	X	Y	(Lovejoy *et al.*, 2002)
Peridiniella catenata	X		X					Y	(Percy, 1992)
Peridiniella danica		X	X		X	X	X	Y	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Peridiniopsis cf. *quadridens (Peridinium aciculiferum)* *+			X					P.NIS	
Podolampas palmipes			X					Y	Rochon, unpublished data
Preperidinium meunieri	X		X					Y	Rochon, unpublished data
Pronoctiluca pelagica					X	X	X	Y	(Riedel *et al.*, 2003)
Prorocentrum minimum						X	X	Y	(Poulin *et al.*, 2011; Simo-Matchim *et al.*, 2017)
Protherythropsis vigilans (Nematopsides vigilans)					X	X	X	Y	(Lovejoy *et al.*, 2002)
Protoceratium reticulatum	X			X			X	Y	(Poulin *et al.*, 2011)
Protoperidinium americanum		X						Y	(Simo-Matchim *et al.*, 2017); Rochon, unpublished data
Protoperidinium arcticum			X					Y	Rochon, unpublished data
Protoperidinium bipes	X				X		X	Y	(Percy, 1992; Riedel *et al.*, 2003)
Protoperidinium breve (Protoperidinium pyriforme)	X		X					Y	(Bursa, 1961); Rochon, unpublished data
Protoperidinium brevipes	X	X	X	X		X		Y	(Riedel *et al.*, 2003)
Protoperidinium cerasus		X	X				X	Y	(Percy, 1992)
Protoperidinium cf. *grenlandicum*			X					P.NIS	
Protoperidinium conicoides	X		X	X		X		Y	Rochon, unpublished data

Species	1	2	3	4	5	6	7	Status	Reference
Protoperidinium conicum	X			X		X		Y	Rochon, unpublished data
Protoperidinium crassipes	X		X					Y	(Poulin *et al.*, 2011)
Protoperidinium curtipes		X	X					Y	Rochon, unpublished data
Protoperidinium curvipes/ subcurvipes	X		X					Y	Rochon, unpublished data
Protoperidinium depressum	X		X			X		Y	(Percy, 1992)
Protoperidinium divergens			X					Y	Rochon, unpublished data
Protoperidinium excentricum			X					P.NIS	
Protoperidinium globulus var. *quarnerense*			X			X		Y	(Anderson *et al.*, 1981)
Protoperidinium granii	X		X					Y	(Riedel *et al.*, 2003)
Protoperidinium marielebourae			X					P.NIS	
Protoperidinium minutum (Archaeperidinium minutum)		X	X					Y	Rochon, unpublished data
Protoperidinium oblongum			X					Y	Rochon, unpublished data
Protoperidinium obtusum			X					Y	(Hsiao and Pinkewyc, 1985)
Protoperidinium ovatum	X		X					Y	(Percy, 1992)
Protoperidinium pallidum	X	X	X					Y	(Percy, 1992)
Protoperidinium pellucidum	X		X	X	X			Y	(Percy, 1992)
Protoperidinium pentagonum	X		X					Y	Rochon, unpublished data
Protoperidinium quarnerense			X					Y	Rochon, unpublished data
Protoperidinium steinii	X	X	X	X	X			Y	Rochon, unpublished data
Protoperidinium subinerme	X		X					Y	(Laget, 2017); Rochon, unpublished data
Protoperidinium thorianum	X		X					Y	(Lovejoy *et al.*, 2002)
Scrippsiella trochoidea (Scrippsiella acuminata)		X	X					Y	(Riedel *et al.*, 2003)
Torodinium robustum		X				X	X	Y	(Riedel *et al.*, 2003)
Tripos articus	X		X					Y	(Percy, 1992)
Tripos longipes	X		X					Y	(Percy, 1992)

[+] brackish taxa; * freshwater taxa; [(1)] Niskin, [(2)] phytoplankton net (20 µm); P.NIS: potential Non indigenous species

DISCUSSION

Abundance and diversity of dinoflagellate species

In this study, we provided the first baseline data for dinoflagellate communities in the ports of Churchill, Deception Bay, Iqaluit, Milne Inlet and Wager Bay. All the taxa found in these ports have previously been observed elsewhere in the Arctic. However, some were new for the Canadian Arctic or within the ecoregions where they were observed (Annex 1).

The Arctic was divided into 19 ecoregions, which are defined as areas with a relatively uniform community composition that differs from other adjacent or outside areas (Spalding *et al.*, 2007). The ports included in this study were within the Hudson Complex ecoregion (Deception Bay and Churchill), Northern Labrador ecoregion (Iqaluit) and Baffin Bay ecoregion (Milne Inlet). Seven taxa were considered as new records in the ecoregions where they were found (Annex 1). *Ceratium tripos* and *Tripos horridus* were not recorded in the Canadian Arctic according to the literature but were present in the Barents Sea (*T. horridus*) and in southern Labrador-Grand Banks and Kara and Barents Seas (*C. tripos*), and thus could be considered as a potential NIS. However, they were present in low abundance in Deception Bay and Churchill respectively (mean less than of 0.5 cells L^{-1}) during this study. The five other taxa (*P. contractum*, *G. digitale*, *G. scrippsae*, *T. lineatus*, *P. leonis*) are not suspected as NIS due to their presence in neighboring ecoregions including the studied ecoregion and relatively widespread distribution in the Arctic (Annex 1). The prior absence of these taxa in a given port could be explained by methodological aspects, such as sampling effort, timing of sampling, or type of gear used to collect samples. Their presence in this study could also be evidence of the increasing number of surveys in the Canadian Arctic.

This study is a valuable contribution toward assessing the taxonomic richness of each sampled area. However, with the exception of the port of Deception Bay, the taxa accumulation curve did not reach an asymptote for the ports of Churchill, Iqaluit and Milne Inlet, suggesting that sampling was not sufficient to determine the full extent of

biodiversity in these areas (Annex 2, Annex 3). Sampling in the Arctic requires more logistic and effort and is typically limited to a short period of time, during the ice-free season. However, regular sampling across different seasons would provide a better representation of the seasonal variability in the communities of this region and the succession of species during blooms (Annex 2). For example, in Iqaluit, only five dinoflagellate taxa were found, but the complete phytoplankton community analysis (Howland and Simard, unpublished data) revealed a high abundance of diatoms at the time this port was visited. Thus it appears that dinoflagellate sampling in this port was done during a diatom bloom shortly after ice break-up, which usually occurs before the dinoflagellate bloom (Rochon, 2009). Diatoms are the first to bloom after the melting of the sea ice due to their capacity to thrive in areas characterized by high nutrient concentrations (Sarthou et al., 2005). The diatom bloom eventually ends when the upper mixed layer is depleted of nitrate and silica (Tremblay *et al.*, 2002) and is followed by the bloom of dinoflagellates, which do not require silica or high nutrient concentrations to continue developing (Margalef, 1978; Tremblay *et al.*, 2002; Rochon, 2009).

Mean dinoflagellate abundances measured in this study were lower than those from previous studies conducted in the same regions; for example previous studies found they ranged from 2000 to 125 000 cells L^{-1} in Churchill River out into Hudson Bay, and they were less than 10 000 cells L^{-1} in Hudson Strait (Anderson *et al.*, 1981; Harvey *et al.*, 1997). Biological production in those studies was high in the upper 50 m of the water column where the chlorophyll maximum is widespread below the pycnocline, and where hydrodynamic processes allow the regeneration of nutrients in the mixed layer (Harvey *et al.*, 1997). Sampling depth during this study was limited to the euphotic layer, which varied from 4 to 17 m in Churchill (2015), 9 to 29 m in Iqaluit and 14 to 22 m in Deception Bay. However, the majority of the dinoflagellates are heterotrophic and mixotrophic, hence they are not limited to the euphotic layer. For this reason, abundance of dinoflagellates could be underestimated and species from greater depths could have been missed.

In the ports sampled during this study, dinoflagellate relative abundances decreased with latitude. Pollingher (1990) demonstrated that latitude influence the phytoplankton abundance and composition and that the phytoplankton biomass decreases with latitude. However, the diversity and richness in this study were more variable and lacked a distinct gradient with latitude. The port of Deception Bay had the highest diversity and richness. This could be due to its connection with Hudson Strait, where surface currents from both Baffin Bay and Hudson Bay could transport numerous species (Estrada *et al.*, 2012). The higher abundances in Churchill compared to other ports may be explained by the low stratification, the nitrogen and silicate loading from the river and the organic matter accumulated during the flushing time in the pre-melt period, all of which can promote phytoplankton production by increasing abundances (Kuzyk *et al.*, 2008).

Comparison of dinoflagellate communities between ports

Dinoflagellate communities were significantly different between ports. However, the NMDS plot showed that Churchill and Deception Bay were more similar with respect to community composition compared to Iqaluit and Milne inlet (Figure 8). This is consistent with Churchill and Deception Bay belonging to the same ecoregion (Spalding *et al.*, 2007), and taxa in this zone are made up of a combination of species from the Arctic, boreal and temperate zones (Anderson *et al.*, 1981). Differences in dinoflagellate communities across ports were also partly explained by the DSIMS (Figure 9). This is expected, given that the initiation of the spring bloom is dependent upon the duration of sea ice cover after the winter season, which is variable from place to place and from year to year (Bursa, 1961). A sufficient nutrient supply and optimal light availability (both dependent on timing of ice break-up) will favor the growth of autotrophic dinoflagellates (Tremblay *et al.*, 2002), providing the prey needed for growth of heterotrophic species. Further, the richness and abundance of phytoplankton and dinoflagellates increase as the season advances (Bursa, 1961; Hsiao, 1992; Gosselin *et al.*, 1997; Odate *et al.*, 2002), which could explain the low abundances and number of taxa in the dinoflagellate communities of Iqaluit and Milne Inlet, which were sampled earlier relative to break-up. *Protoperidinium bipes* was the most abundant taxon in Iqaluit during the sampling period. This species contributed the

most to the difference between Iqaluit and the ports of Churchill 2007, Deception Bay and Milne Inlet. *Protoperidinium bipes* was present after only a few days following the disappearance of sea ice, consistent with the dominance of this species during the spring diatom bloom previously documented by Jeong et al., (2004). Its high swimming speed and growth rate compared to other *Protoperidinium* species makes it the most successful and abundant in the environment during a diatom bloom (Jeong *et al.*, 2004).

Brackish-marine phytoplankton communities are associated with regions like Churchill, which are influenced by freshwater runoff and river discharge (Harvey *et al.*, 1997). However, our study of the dinoflagellates in the port of Churchill did not reveal the presence of any strictly freshwater species; the only freshwater-tolerant species was *G. spinifera,* which tolerates large salinity variations (Guiry and Guiry, 2019). Studies on phytoplankton in James Bay, characterized by high freshwater runoff, revealed similar results with *G. spinifera* and *Katodinium rotundatum* being the only freshwater-tolerant dinoflagellate species and *Dinobryon balticum*, a brackish-freshwater chrysophyte species, in addition to mainly marine phytoplankton species (Harvey *et al.*, 1997). However, these results diverge from Gerrath et al., (1980), who documented a high relative abundance of typically freshwater plankton species in regions of Hudson Bay influenced by river inputs. Ongoing studies of the larger plankton community, based on Niskin bottle sampling, also documented high relative abundances of freshwater phytoplankton species in the Churchill region, including two brackish and freshwater dinoflagellate species (*Peridinium aciculiferum* and *Peridinium* cf. *umbonatum)* (Howland and Simard., unpublished data).

Dinophysis acuminata was the species that contributed the most to the difference between Churchill (2015) and the other ports. However, this species was also present in low densities in the other ports, with the exception of Iqaluit. *Dinophysis acuminata* is a cosmopolitan species tolerant of a wide range of temperature and salinity, and its relatively high abundance in Churchill may be linked to the organic enrichment from the river and to the weak stratification (Hajdu, 2002; Hajdu and Larsson, 2006; Kuzyk *et al.*, 2008).

Comparison of dinoflagellate communities in Churchill between 2007 and 2015

Monitoring the evolution of the community composition in the same area is an excellent barometer of the variations occurring in a changing environment, especially in a location such as Churchill, which is classified as a high invasion risk port due to the past history of high volumes of ballast water discharged by international merchant vessels and the higher rate of warming in this part of the Arctic (Chan *et al.*, 2012; Goldsmit *et al.*, 2018). Dinoflagellate communities were significantly different in Churchill in 2007 and 2015. Several parameters, independent or combined, could explain changes that occurred in this area. Environmental conditions in Churchill diverge abruptly depending on the presence of river and/or landfast ice, or within the rubble zone (Kuzyk *et al.*, 2008). Different physical forces may act on the surface water temperature, salinity, stratification and mixed layer to modify the nutrient availability and light conditions, and consequently the phytoplankton community over time and space (Harvey *et al.*, 1997). The RDA showed that sampling depth, which was different between the two years (averages of 6.5 m in 2007 and 12.3 m in 2015), explained some of the difference in the community composition between 2007 and 2015 (Figure 13). This suggests that some species could be more abundant at a particular depth, depending on their feeding mode (autotroph or heterotroph). Autotrophic dinoflagellates may be more abundant in the surface layer where the light penetration is suitable for photosynthesis. However, this hypothesis cannot be confirmed in this study, because in both years a vertical plankton net was used to sample the entire water column, including the surface layer, and we did not know the specific sampling depth of each species. The lack of environmental data in 2007 (due to equipment malfunction) was a handicap in assessing the effect of other parameters on differences in the community composition among years. The distribution of dinoflagellate communities depends on temperature, salinity, currents, nutrients, feeding strategies and the distribution of their prey (Rochon, 2009). A change in any one of these parameters could influence the entire community. Furthermore, sampling in 2007 and 2015 in Churchill was carried out in slightly different geographic positions albeit over the same general area (Figure 2). For a better comparison, the sampling should ideally take place

regularly, each year at the same period relative to ice-melting, which was a strong driver of community composition.

We identified taxa in Churchill in 2015 that were previously observed in the Canadian Arctic, but not in 2007 in this location. However, given the limitations mentioned above, it is unclear whether this was due to changes in sampling procedures, increased research effort (with the addition of another survey year), or the presence of new species in the area. Further sampling effort is needed to increase the number of taxa found, as the taxa accumulation curve did not reach an asymptote, even when combining data from both years (Annex 3). This implies that our results on the richness in Churchill are conservative and more species likely remain to be documented in this area. However, patterns among the dominant taxa can still be compared across years. The dominant taxa in both sampling years in Churchill were different (*P. dalei* in 2007 and *D. acuminata* in 2015). Several studies documented the distribution of the cysts from *P. dalei* in sediments, which have been observed from polar regions to the tropics (Godhe *et al.*, 2001; Radi *et al.*, 2001; Marret and Zonneveld, 2003), and it is considered a cosmopolitan species (Marret and Zonneveld, 2003). *Pentapharsodinium dalei* cysts were observed in high abundance in arctic fjords and embayments characterized by high productivity and water column stratification (Howe *et al.*, 2010; Richerol *et al.*, 2012). The presence of dinoflagellate cysts in the sediment implies that vegetative cells were present in the upper water column as demonstrated by the high relative abundances of vegetative cells of *P. dalei* in Churchill. *Dinophysis acuminata* also tolerates a wide temperature gradient (Hajdu and Larsson, 2006), and its growth can be influenced directly or indirectly by the quantity of available nutrients (Tong *et al.*, 2010). Since this species is a mixotroph, it is able to consume inorganic and organic nutrients (Singh *et al.*, 2014; Hattenrath Lehmann and Gobler, 2015) such as its prey, the ciliate *Mesodinium rubrum*, which was present in high abundance in the water samples collected during the same field work (Howland and Simard, unpublished data). Given that the sampling depth in 2015 (12.3m) was greater than in 2007 (6.5m), *D. acuminata* could have been missed in 2007 and higher abundances

of this species would be expected in deeper waters, since this species performs vertical migrations for nutrition (Setälä *et al.*, 2005).

Dinoflagellate communities in ballast water vs ports

The presence of toxin producer taxa in the ballast tanks of ships arriving in the ports of Deception Bay and Churchill confirms that dinoflagellate transport by ships contributes to spreading toxic species (Hallegraeff, 1998). Although most of these taxa have already been observed elsewhere in the Canadian Arctic (Table 7), their presence in the ballast tanks may increase their geographic distribution in new ecoregions of the Arctic. Furthermore, the Arctic could also be a source of toxin-producing NIS to other ports around the world.

The cumulative number of taxa and NIS found in ballast of vessels arriving in Deception Bay was higher than in Churchill port (10 NIS in Deception Bay vs 2 NIS in Churchill). This could be explained by differences in the typical voyage lengths of vessels in these two ports, which affects survival of entrained species (Chu *et al.*, 1997; Ruiz *et al.*, 1997; Dickman and Zhang, 1999; Gollasch *et al.*, 2000; Verling *et al.*, 2005). Vessels arriving in Deception Bay are mainly domestic, which usually make shorter trips (10-13 days), compared to vessels arriving in Churchill which were primarily international vessels that make longer trips (8-30 days) (Chan *et al.*, 2014; Laget, 2017). The sampling method could also play a role in the number of taxa found in samples from each port. In this case, ballast samples from two different studies utilizing different sampling approaches were combined to make comparisons with port communities. In Deception Bay 2016, samples were collected with a plankton net (entire water column) in several ballast tanks from the same vessel but filled in different exchange locations (Jacques Cartier Strait and the Strait of Belle Isle in the Gulf of Saint Lawrence) and over successive trips. This resulted in samples that spanned across seasons and each given sample was also concentrated from a large volume of water; these two factors would be expected to increase the cumulative number of species detected as well as the probabilities of detecting the large rare dinoflagellate species, since samples are too concentrated to detect small species. Samples collected with a Niskin bottle were preserved with a Lugol's solution, which has the

advantage of better preserving the morphology of species of Gymnodiniaceae, facilitating their recognition and identification (Gómez, 2007), hence the higher number of taxa from this family found in samples preserved with Lugol's compared to the samples preserved with formaldehyde in this study (Table 7). Furthermore, this method is effective in preserving and detecting small species (< 20 μm). However, Lugol's has the disadvantage of coloring the specimens, which makes their identification much more difficult and time consuming.

Eleven taxa in the ballast samples of Deception Bay and Churchill have not previously been observed in the Canadian Arctic (Table 7), and are clearly potential NIS: *P. aciculiferum, P. ovatum, G.* cf. *alaskensis, E. mexicana, O. rotundata, F. subglobosum, P. marielebourae, P.* cf. *grenlandicum, P. excentricum, C. tripos* and *G.* aff. *metum.* However, *T. furca*, which was observed once in northern Labrador Sea in 2008 (Rochon, unpublished data) is also considered as NIS, and its presence in the ballast samples from Churchill and Deception Bay in 2014 and 2015 respectively is evidence of the potential for invasion by this species via ballast waters. Assuming that *T. furca* is not an indigenous species, its invasion could have been limited geographically to the northern Labrador Sea in 2008. However, this species is reported to be cosmopolitan, existing in a wide range of temperatures (2-30 ℃) (Baek *et al.*, 2008b). Its presence in ballast samples from Churchill and Deception Bay, combined with future sampling in the Canadian Arctic could reveal the potential propagation of this species.

Although none of the non indigenous taxa found in ballast tanks are toxin producers, *T. furca* has been recognized as dominant species during a red tide event in the coastal waters of Chesapeake Bay (USA), Sagami Bay (Japan), Pago Pago Harbor (American Samoa) (Smalley and Coats, 2002; Baek *et al.*, 2008a; Morton *et al.*, 2011). These observations of NIS in vessels arriving to the Arctic confirm the importance of establishing baseline data and monitoring programs for early detection of invasions in this region.

CONCLUSIONS

We extended our knowledge on dinoflagellate communities in the most heavily used ports of the Canadian Arctic. Our results indicate that dinoflagellate communities were significantly different between ports, and in Churchill between 2007 and 2015. The differences among years were partly explained by sampling depth and timing relative to the sea ice melting, demonstrating the importance of controlling for these variables in future comparative studies. We highlighted the fact that non indigenous dinoflagellates have the potential for introduction in the Arctic by the presence of eleven potential NIS in ballast tanks sampled in Churchill and Deception Bay, which have never been observed in the Canadian Arctic and an additional species, *T. furca*, which has had only a single occurrence in 2008 in the northern Labrador Sea, suggesting that it has been incidentally present, or arrived in the Arctic in the last 11 years, but has probably not established yet.

Extended ice-free conditions due to global warming may promote the establishment of introduced NIS, and the invasion success of other taxa, including toxin producers. These results show the importance of establishing baseline data for the early detection of NIS, and the priority of pursuing monitoring efforts. Further, other mitigation measures are needed for early detection and limiting the introduction or spread of NIS, such as improving ballast water treatment technology (including for domestic vessels) or increasing sampling frequency and coverage through innovative new techniques, such as environmental RNA and DNA for a rapid detection of NIS in ballast tanks and in coastal waters (Pochon *et al.*, 2017; Lacoursière-Roussel *et al.*, 2018). These measures should help limit the introduction and spread of NIS and toxin producing taxa that could have severe impacts on the environment and human health.

CONCLUSION GÉNÉRALE

Le changement climatique est un phénomène connu et ressenti à l'échelle du globe. La fonte du pergélisol, l'élévation du niveau marin et l'acidification des océans sont des conséquences du réchauffement climatique. En Arctique, on observe une diminution du volume des glaciers, de la couverture de glace de mer et l'augmentation de la période libre de glace (Loeng *et al.*, 2005; Stroeve *et al.*, 2012), ce qui a pour conséquence le rallongement de la saison de navigation. L'augmentation du trafic maritime engendrée par le développement économique en Arctique et une saison de navigation plus longue auront pour conséquence l'amplification du risque d'introduction d'ENI (Chan *et al.*, 2015).

Cette recherche a été motivée par l'augmentation du risque d'introduction d'ENI dans les ports de l'Arctique. Le choix de la zone d'échantillonnage était stratégique et a permis de couvrir les ports avec le plus de déversement d'eau de ballast. Ces eaux sont chargées d'organismes qui peuvent devenir des envahisseurs et provoquer des effets indésirables à l'écosystème.

Cette étude est pionnière dans la création de base de données concernant la communauté de dinoflagellés dans les ports à plus haut risque d'invasion de l'Arctique canadien, à savoir Churchill, Baie Déception, Iqaluit et Milne Inlet (Chan *et al.*, 2012). Cette recherche nous a permis d'obtenir plus d'informations sur la biodiversité dans les régions côtières de l'Arctique et a montré que plus de 17% des espèces identifiées n'avaient pas encore été recensées dans les écorégions de l'Arctique dans lesquelles l'échantillonnage a été réalisé, d'où l'importance de cette étude dans l'augmentation de la surveillance et de l'effort d'échantillonnage. Cette étude a amélioré notre connaissance sur la communauté des dinoflagellés dans ces ports et a confirmé que leur abondance diminuait avec la latitude. Nos travaux ont également montré que les communautés de dinoflagellés étaient différentes entre les écorégions et pour une même écorégion sur différentes années d'échantillonnage. Plusieurs facteurs peuvent influencer la composition de la communauté, comme le nombre de jours écoulés entre la fonte de la glace et l'échantillonnage, ou encore la profondeur d'échantillonnage. Nous avons aussi comparé

les taxa de dinoflagellés retrouvés dans différents ballasts de navires arrivant à Churchill et Baie Déception à ceux retrouvés dans ces ports et dans l'ensemble de l'Arctique canadien. Nous avons détecté la présence de douze espèces qui étaient potentiellement non indigènes, soit *Peridinium aciculiferum, Phalacroma ovatum, Gonyaulax* cf. *alaskensis, Ensiculifera mexicana, Oblea rotundata, Fragilidium subglobosum, Protoperidinium marielebourae, Protoperidinium* cf. *grenlandicum, Protoperidinium excentricum, Ceratium tripos* (ballast de Baie Déception), *Gyrodinium* aff. *metum* (ballasts de Churchill) et *Tripos furca* (ballasts de Churchill et Baie Déception). Ces espèces n'ont jamais été observées dans l'Arctique canadien, ce qui suggère leur potentiel d'invasion, à l'exception d'une seule cellule de *Tripos furca* qui a été observée en 2008 dans le nord de la mer du Labrador (Rochon, unpublished data). Sa présence dans les ballasts en 2014 et 2015 suggère que cette espèce est transportée via les eaux de ballast et déversée dans les ports de l'Arctique canadien depuis plusieurs années, mais qu'elle n'a probablement pas encore rencontré les conditions favorables pour s'établir dans cette région, malgré qu'il s'agisse d'une espèce cosmopolite (Graham, 1941). Les ENI retrouvées dans les ballasts ne sont pas des espèces qui produisent des toxines. Cependant, la présence accrue d'ENI dans les ballasts pourra également contribuer à l'augmentation de la distribution géographique des espèces nocives, et ainsi contribuer à augmenter la fréquence des blooms toxiques, qui auront possiblement des impacts négatifs sur l'économie et la santé humaine (Hallegraeff, 1998). Ces résultats novateurs montrent le potentiel d'invasion de dinoflagellés non indigènes via les eaux de ballasts. Les barrières biotiques et abiotiques et la faible pression de propagules comptent parmi les raisons pouvant expliquer l'absence des ENI dans les ports de l'Arctique (Locke *et al.*, 2007).

Nos travaux permettront de monitorer les changements de communautés des dinoflagellés dans les zones étudiées par la détection rapide de l'arrivée de nouvelles espèces, ce qui facilitera la prise de décision face aux envahisseurs potentiels. Il est impératif de poursuivre le monitorage afin de compléter la base de données dans les ports concernés et dans d'autres ports arctiques. En effet, cette étude a ciblé les ports ayant le maximum de trafic maritime entre 2005 et 2008, mais compte tenu des travaux récents sur

l'augmentation prévue des mouvements de navires d'ici à 2050 (Sardain *et al.*, 2019), d'autres ports pourraient éventuellement être concernés. Cette augmentation de trafic maritime, couplée avec le réchauffement climatique, pourraient favoriser l'établissement de certains taxa (Chan *et al.*, 2012), augmentant ainsi le nombre de zones à risque d'invasion (Sardain *et al.*, 2019), ce qui nécessitera plus de monitorage. Des mesures plus efficaces de traitement d'eau et de sédiments de ballast sont entrées en vigueur le 8 septembre 2017 dans le cadre de la convention internationale pour le contrôle et la gestion des eaux de ballast et sédiments des navires de l'organisation maritime internationale. Depuis que le traité est entré en vigueur, les navires doivent avoir à bord un plan de gestion des eaux de ballast, un registre d'eau de ballast afin de noter toutes les activités relatives aux eaux de ballast ainsi qu'un certificat international de gestion des eaux de ballast (OMI, 2019). Ces mesures vont permettre, entre autres, d'entraver la propagation de dinoflagellés dont les floraisons toxiques peuvent affecter les poissons et les mammifères marins dans des régions où la population locale dépend de la pêche comme principale moyen de subsistance.

Nos travaux ont mis en évidence le potentiel d'invasion des ENI dans l'Arctique canadien par leur présence dans l'eau de ballast. Cependant, afin d'optimiser les résultats, une surveillance accrue des ports à risques est souhaitable. L'identification des dinoflagellés au microscope optique est critique pour certain taxa. Cependant, les similarités morphologiques entre certaines espèces nécessitent souvent l'utilisation de la microscopie électronique à balayage pour confirmer les identifications, ce qui augmente le temps de traitement des échantillons. Le recours aux techniques d'analyse de l'ADN environnemental peut constituer un moyen plus efficace pour limiter le temps de traitement de chaque échantillon et permettre ainsi un suivi rapide (Lacoursière-Roussel *et al.*, 2018; Shaw *et al.*, 2019). L'échantillonnage durant cette étude a été réalisé en une seule campagne d'échantillonnage de deux semaines pendant l'été pour la majorité des ports (Baie Déception, Iqaluit et Milne Inlet). Ceci nous a fourni une image ponctuelle de la communauté à ce moment-là, alors que des turbulences, un ajout en nutriments ou toute autre modification qui pourrait survenir dans l'environnement, pourraient provoquer des

changements dans la communauté (Bursa, 1961). Le nombre limité d'échantillons est relié aux coûts élevés des campagnes d'échantillonnage en Arctique et à l'inaccessibilité de cette région durant la majeure partie de l'année. Cependant, ce projet a permis d'enseigner les méthodes d'échantillonnage à des membres de communautés locales des ports étudiés dans le but éventuel de contribuer à la collecte d'échantillons dans le cadre d'un futur programme de monitorage dans l'Arctique. Ainsi, nous pourrons maintenir une surveillance continue des milieux concernés et appréhender les changements des communautés de dinoflagellés ou les introductions des ENI. Le suivi des paramètres environnementaux et la mesure de paramètres supplémentaires (par ex. nutriments, matière organique) pourraient expliquer les différences de compositions des communautés de dinoflagellés d'une année à l'autre et permettre ainsi d'estimer la chance de survie des ENI introduites.

Les données recueillies durant cette étude sur les communautés de dinoflagellés dans les ports à plus haut risque d'invasion constituent une contribution majeure pour l'amélioration des connaissances des zones côtières de l'Arctique canadien, afin de limiter les invasions et éviter la propagation des espèces productrices de toxine.

ANNEXES

Annex 1: List of dinoflagellate taxa identified in the sampled ports Churchill (C), Deception Bay (D), Iqaluit (IQ), Milne Inlet (M) and Wager Bay (W), and their current distribution in 19 Arctic ecoregions (Spalding *et al.*, 2007). 1. North Greenland; 2. North and East Iceland; 3. East Greenland Shelf; 4. West Greenland Shelf; 5. Northern Grand Banks–Southern Labrador; 6. Northern Labrador; 7. Baffin Bay–Davis Strait; 8. Hudson Complex; 9. Lancaster Sound; 10. High Arctic Archipelago; 11. Beaufort–Amundsen–Viscount Melville–Queen Maud; 12. Beaufort Sea–continental coast and shelf; 13. Chukchi Sea; 14. Eastern Bering Sea; 15. East Siberian Sea; 16. Laptev Sea; 17. Kara Sea; 18. North and East Barents Sea; 19. White Sea

Dinoflagellate taxa	Distribution by ecoregions	C	D	IQ	M	W 1*	References
Actiniscus pentasterias	7-13, 17, 18	I	I		I		(Okolodkov, 1998); Rochon, unpublished data
Alexandrium sp.		X	X		X		
Amphidinium aff. *carterae*	2, 4, 7					I	(Lovejoy *et al.*, 2002; Kubiszyn *et al.*, 2014)
Amphidinium aff. *kesslitzii*	6, 8-10					I	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Amphidinium crassum	6, 8, 9, 13a, 17, 19					I	(Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Amphidinium sphenoides	6, 8, 9, 17-19					I	(Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Amylax triacantha	1-4, 6-8, 12, 14, 16- 18	I	I		I		(Pinkewycz and Hsiao, 1987; Okolodkov and Dodge, 1996; Falk-Petersen *et al.*, 1997; Okolodkov, 2005); Rochon, unpublished data
Boreadinium sp.		X	X		X		
Dinophysis acuminata	3-10, 12, 13, 16, 17	I	I		I	I	(Anderson *et al.*, 1981; Hsiao and Pinkewyc, 1985; Falk-Petersen *et al.*, 1997; Okolodkov, 2005; Rózańska *et al.*, 2009; Poulin *et al.*, 2011)
Dinophysis acuta	3, 4, 6-10, 12, 13, 16, 17	I	I				(Anderson *et al.*, 1981; Okolodkov, 2005; Poulin *et al.*, 2011)
Dinophysis norvegica	1-4, 6-8, 10, 12-15, 17	I	I			I	(Bursa, 1961; Anderson *et al.*, 1981; Okolodkov and Dodge, 1996; Okolodkov, 1998, 2005; Poulin *et al.*, 2011)
Gonyaulax digitale	3, 5, 7, 17, 18		N				(OBIS, 2018); Rochon, unpublished data
Gonyaulax scrippsae	1, 3, 5-7, 10, 11, 17, 18	N	N				(Hsiao and Pinkewyc, 1985; Pinkewycz and Hsiao, 1987; OBIS, 2018); Rochon, unpublished data
Gonyaulax spinifera	3, 4, 6-8, 10-13, 16-18	I	I				(Falk-Petersen *et al.*, 1997; Jensen and Veland, 2006; Poulin *et al.*, 2011)
Gymnodinium aff. *subroseum*	6, 8-10					I	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Gymnodinium galeatum	2, 4, 6-10					I	(Lovejoy *et al.*, 2002; Riedel *et al.*, 2003; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Gymnodinium simplex	4, 6, 8, 9, 18					I	(Lovejoy *et al.*, 2002; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Gymnodinium verruculosum	2, 6, 8-10					I	(Riedel *et al.*, 2003; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Gyrodinium aff. *guttula*	6, 8-10					I	(Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data

Species	Locations						References
Gyrodinium **aff.** *grave*	2, 6, 8-10, 17, 18					I	(Riedel *et al.*, 2003; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Gyrodinium flagellare	2, 6, 8-10					I	(Riedel *et al.*, 2003; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Gyrodinium formosum	2, 8, 10					I	(Riedel *et al.*, 2003; Kubiszyn *et al.*, 2014); Howland and Simard, unpublished data
Gyrodinium fusiforme	6, 8, 10					I	(Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017)
Gyrodinium pepo	4, 7, 8, 10					I	(Lovejoy *et al.*, 2002); Howland and Simard, unpublished data
Gyrodinium spirale	4, 6, 8-10, 13, 18, 19					I	(Okolodkov, 1998; Lovejoy *et al.*, 2002; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Heterocapsa rotundata	2, 6, 8, 9, 18					I	(Okolodkov, 1998; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Katodinium glaucum	4, 6-10, 18					I	(Okolodkov, 1998; Lovejoy *et al.*, 2002; Riedel *et al.*, 2003; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Micracanthodinium claytonii	2, 6-9, 18					I	(Okolodkov, 1998; Lovejoy *et al.*, 2002; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Pentapharsodinium dalei	1, 5, 7, 8, 10, 11, 17, 18	I	I				(Richerol *et al.*, 2012; Heikkilä *et al.*, 2016; OBIS, 2018); Rochon, unpublished data
Peridiniella catenata	1-4, 7, 8, 10, 12-18		I		I		(Bursa, 1961; Okolodkov, 1996; Okolodkov and Dodge, 1996; Falk-Petersen *et al.*, 1997; Okolodkov, 2005; Rozanska *et al.*, 2009)
Peridiniella danica	6-11					I	(Riedel *et al.*, 2003; Laget, 2017; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data; Rochon, unpublished data
Phalacroma contractum	1, 6, 7, 17, 18	N	N				Rochon, unpublished data (as *Dinophysis contracta*)
Phalacroma rotundatum	2-4, 6-8, 10, 12	I	I		I		(Anderson *et al.*, 1981; Falk-Petersen *et al.*, 1997; Okolodkov, 2005; Poulin *et al.*, 2011)
Preperidinium meunieri	4, 7-11, 13, 17-19	I	I		I	I	(Okolodkov, 1998; Jensen and Veland, 2006; Laget, 2017) ; Rochon, unpublished data
Pronoctiluca pelagica	2, 8-10					I	(Riedel *et al.*, 2003; Kubiszyn *et al.*, 2014); Howland and Simard, unpublished data
Prorocentrum minimum	2, 6, 8, 9, 18					I	(Okolodkov, 1998; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Protherythropsis vigilans (*Nematopsides vigilans*)	6, 8, 9					I	(Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Protoceratium reticulatum	1-4, 6-8, 10-13	I	I	I	I	I	(Okolodkov, 2005; Poulin *et al.*, 2011); Rochon, unpublished data
Protoperidinium bipes	1-3, 6-10, 13, 14, 17-19		I	I	I	I	(Anderson *et al.*, 1981; Falk-Petersen *et al.*, 1997; Okolodkov, 1998; Riedel *et al.*, 2003; Kubiszyn *et al.*, 2014; OBIS, 2018); Rochon, unpublished data
Protoperidinium breve	1, 7-10, 17, 18	I	I		I		(Bursa, 1961; Okolodkov, 1998); Rochon, unpublished data
Protoperidinium brevipes	1, 2, 6-13, 16-19	I	I	I	I	I	(Anderson *et al.*, 1981; Booth and Horner, 1997; Falk-Petersen *et al.*, 1997; Okolodkov, 1998; Riedel *et al.*, 2003; Poulin *et al.*, 2011; Kubiszyn *et al.*, 2014); Rochon, unpublished data
Protoperidinium cerasus	2, 8, 12, 13, 16-19					I	(Hsiao, 1976; Kubiszyn *et al.*, 2014; Laget, 2017)
Protoperidinium conicoides	6-11, 13, 15-19	I	I				(Okolodkov, 1998; Jensen and Veland, 2006; Laget, 2017); Rochon, unpublished data
Protoperidinium conicum	8, 13, 16-19	I	I				(Okolodkov, 1998; Laget, 2017)

Taxon	Stations						References
Protoperidinium crassipes	4, 6-8, 12, 13, 15-17	I	I				(Okolodkov, 1998, 2005; Poulin *et al.*, 2011)
Protoperidinium curvipes/subcurvipes	6-11, 13, 16-19	I	I				(Bursa, 1961; Okolodkov, 1998); Rochon, unpublished data
Protoperidinium denticulatum	8, 13, 16, 18	I					(Okolodkov, 1998; Laget, 2017)
Protoperidinium depressum	2, 7-11, 13, 17-19	I	I				(Anderson *et al.*, 1981; Okolodkov, 1998; Kubiszyn *et al.*, 2014); Rochon, unpublished data
Protoperidinium granii	1, 6, 8-11, 13, 16, 18, 19	I	I				(Bursa, 1961, 1971; Okolodkov, 1998; Riedel *et al.*, 2003); Rochon, unpublished data
Protoperidinium leonis	6, 13, 17-19		N				(Dodge, 1994; Okolodkov, 1998); Rochon, unpublished data
Protoperidinium ovatum	1, 2, 4, 6-11, 13, 17-19	I	I		I		(Falk-Petersen *et al.*, 1997; Okolodkov, 1998; Jensen and Veland, 2006; Laget, 2017); Rochon, unpublished data
Protoperidinium pallidum	1, 2, 6-11, 13, 15-19	I	I		I		(Bursa, 1961; Anderson *et al.*, 1981; Falk-Petersen *et al.*, 1997; Okolodkov, 1998); Rochon, unpublished data
Protoperidinium pellucidum	1, 2, 6-13, 15-19	I	I	I	I	I	(Bursa, 1961; Anderson *et al.*, 1981; Booth and Horner, 1997; Falk-Petersen *et al.*, 1997; Poulin *et al.*, 2011); Rochon, unpublished data
Protoperidinium pentagonum	1, 4, 6-11, 13, 17, 18	I	I	I	I		(Okolodkov, 1998; Jensen and Veland, 2006); Rochon, unpublished data
Protoperidinium steinii	1, 2, 4, 6-11, 17-19	I	I		I	I	(Okolodkov, 1998; Jensen and Veland, 2006; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017) ; Rochon, unpublished data
Protoperidinium subinerme	4, 6, 8, 10, 11, 13, 16-19	I	I				(Okolodkov, 1998; Jensen and Veland, 2006; Laget, 2017); Rochon, unpublished data
cf *Protoperidinium thorianum*	7, 8, 13, 17-19		I				(Bursa, 1961; Okolodkov, 1998; Lovejoy *et al.*, 2002)
Torodinium robustum	2, 4, 6-10, 17, 18					I	(Okolodkov, 1998; Lovejoy *et al.*, 2002; Riedel *et al.*, 2003; Kubiszyn *et al.*, 2014; Simo-Matchim *et al.*, 2017); Howland and Simard, unpublished data
Ceratium tripos	3-5, 17, 18	N					(Okolodkov, 1998; OBIS, 2018)
Tripos arcticus	2- 14, 16-18	I	I		I		(Bursa, 1961; Anderson *et al.*, 1981; Okolodkov, 1996; Okolodkov and Dodge, 1996; Falk-Petersen *et al.*, 1997; Okolodkov, 2005)
Tripos fusus	2, 4, 7-9, 13, 17-19	I	I		I		(Okolodkov, 1998; Jensen and Veland, 2006; Kubiszyn *et al.*, 2014; Laget, 2017); Rochon, unpublished data
Tripos horridus	3, 18		N				(Okolodkov, 1996; Okolodkov, 1998)
Tripos lineatus	3- 7, 9, 11, 14, 19	N			I		(Okolodkov, 1996; OBIS, 2018); Rochon, unpublished data
Tripos longipes	2, 4, 6-8, 10, 12-14, 18	I	I		I		(Bursa, 1961; Anderson *et al.*, 1981; Okolodkov, 1996; Okolodkov and Dodge, 1996)

[1] **Niskin bottle samples;** [*] **Only taxa identified to the species level were considered; I= Indigenous, N= Not observed in port ecoregion before**

Annex 2: Sampling effort (+Standard deviation) of dinoflagellate communities in the studied ports
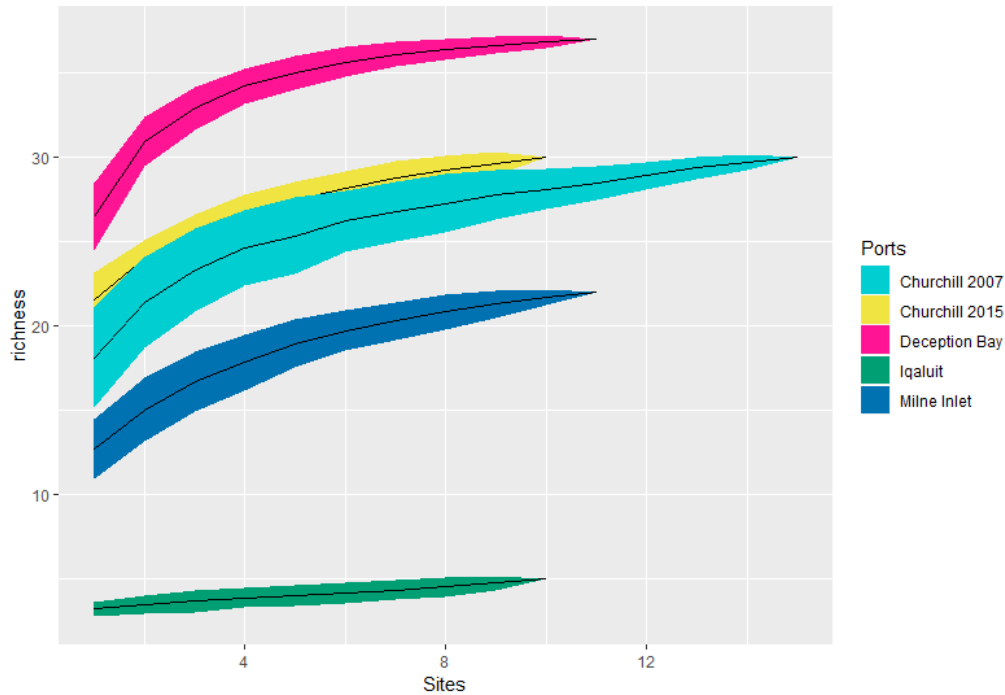
Sampling effort did not reach an asymptote for the sampled ports except for Deception Bay, suggesting that sampling was sufficient to determine the full extent of biodiversity in this particular area.

Annex 3: Sampling effort (+Standard deviation) of dinoflagellate communities in the port of Churchill
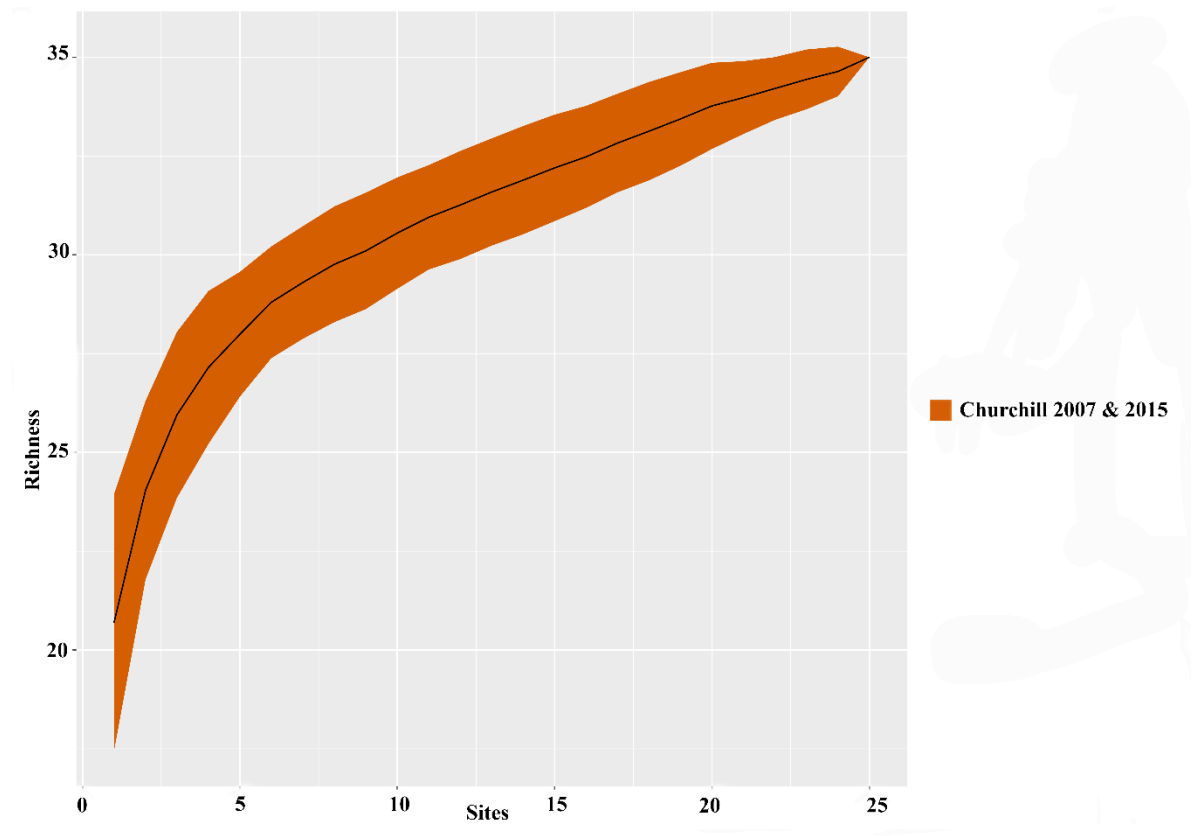
Sampling effort did not reach an asymptote for Churchill when combining data from 2007 and 2015. Further sampling is needed to determine the full extent of biodiversity of this area.

Annex 4: Partition of variance in RDA for all port
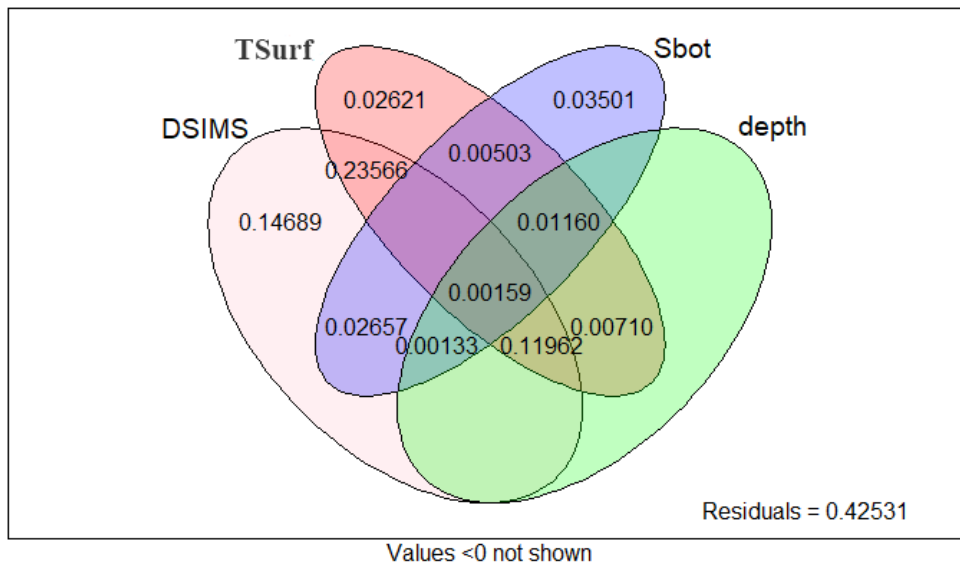
DSIMS, TSurf and Sbot explain respectively 14%, 2.6% and 3% for the dinoflagellate community variabilities.

Annex 5: Partition of variance in RDA for Churchill

Values <0 not shown
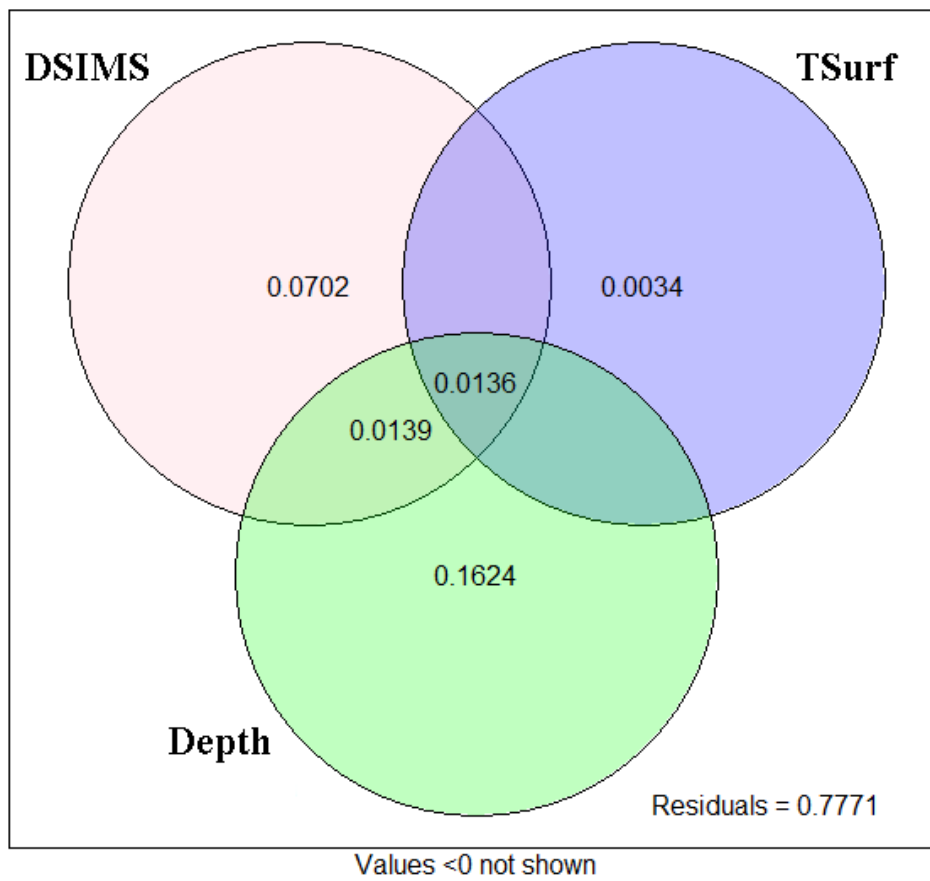
DSIMS, TSurf and Depth explain respectively 7%, 0.34% and 16% for the dinoflagellate community variabilities.

Annex 6: Partition of variance in RDA for Milne Inlet
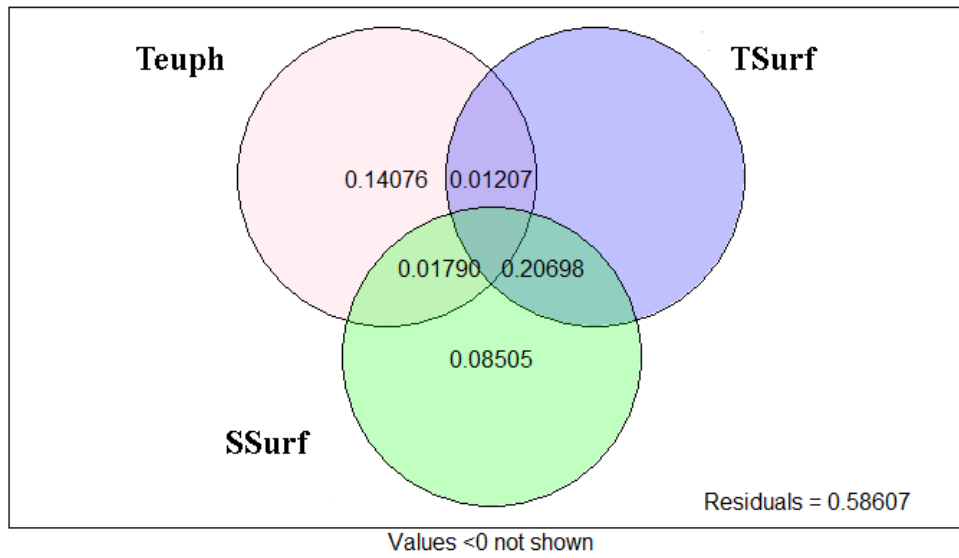
Teuph and SSurf explain respectively 14% and 8% for the dinoflagellate community variabilities.

Annex 6: SIMPER results for the 10 first taxa that contribute the most to the dissimilarity between DB-CH15; DB-CH07; DB- IQ; DB-MI; CH15- IQ; CH15-MI; CH07-IQ; CH07-MI and IQ-MI (transformed square root abundance data)

DB VS CH15	Average dissimilarity (%)	Diss/sd	Individual contribution (%)	Cumulative contribution (%)
D. acuminata	4%	**1.9127**	12%	12%
P. dalei	2%	**1.1047**	5%	17%
P. brevipes	2%	**1.2945**	5%	22%
P. meunieri	2%	**2.239**	4%	26%
P. conicum	2%	**3.2185**	4%	30%
P. granii	2%	**2.601**	4%	34%
Boreadinium **sp.**	2%	**1.46**	4%	38%
P. steinii	2%	**1.3761**	4%	42%
Alexandrium sp.	1%	**1.3709**	4%	46%
Peridiniella catenata	1%	**1.8996**	4%	50%
DB VS CH07				
P. dalei	3%	**1.4945**	8%	8%
P. brevipes	3%	**1.3603**	6%	15%
P. steinii	2%	**1.2225**	6%	21%
Protoceratium reticulatum	2%	**1.5765**	5%	25%
D. norvegica	2%	**1.9026**	5%	30%
Boreadinium **sp.**	2%	**1.2823**	4%	34%
P. conicum	2%	**3.5676**	4%	39%
P. subinerme	2%	**1.7709**	4%	43%
Alexandrium **sp.**	2%	**1.249**	4%	47%
Peridiniella catenata	2%	**1.9068**	4%	51%
DB VS IQ				
P. bipes	10%	**2.0644**	11%	11%
Alexandrium **sp.**	6%	**4.9876**	7%	18%
P. meunieri	5%	**6.6677**	6%	24%
P. dalei	5%	**1.6279**	5%	30%
G. spinifera	5%	**3.5276**	5%	35%
D. norvegica	5%	**6.2936**	5%	40%
P. steinii	4%	**3.7938**	4%	44%
P. ovatum	4%	**3.7698**	4%	48%
P. rotundatum	3%	**2.1569**	4%	52%
P. brevipes	3%	**1.5681**	4%	56%
DB VS MI				

P. brevipes	5%	**2.4054**	6%	6%
P. dalei	5%	**1.6389**	6%	12%
G. spinifera	5%	**3.5851**	6%	18%
P. meunieri	5%	**5.1634**	6%	23%
D. norvegica	5%	**6.4047**	6%	29%
Alexandrium **sp.**	5%	**2.9159**	6%	35%
T. arcticus	4%	**2.5973**	5%	40%
P. steinii	4%	**3.4942**	4%	44%
P. reticulatum	3%	**1.9658**	4%	48%
P. ovatum	3%	**2.99**	4%	52%
CH15 VS IQ				
D. acuminata	11%	**5.2299**	13%	13%
P. bipes	11%	**2.4683**	12%	25%
D. norvegica	7%	**8.0626**	8%	33%
Alexandrium **sp.**	6%	**3.5387**	6%	39%
P. steinii	5%	**3.4759**	6%	45%
Boreadinium **sp.**	5%	**5.0604**	6%	50%
P. rotundatum	5%	**4.6145**	5%	56%
T. longipes	5%	**3.6341**	5%	61%
P. depressum	4%	**2.5497**	5%	66%
P. pellucidum	4%	**3.7441**	5%	71%
CH15 VS MI				
D. acuminata	11%	**5.2953**	14%	14%
D. norvegica	7%	**8.5682**	8%	22%
Boreadinium **sp.**	5%	**5.1857**	6%	28%
P. steinii	5%	**3.3071**	6%	34%
T. arcticus	5%	**3.097**	6%	40%
P. brevipes	5%	**2.8406**	6%	46%
P. rotundatum	5%	**4.262**	5%	51%
Alexandrium **sp.**	4%	**2.1303**	5%	56%
P. depressum	4%	**2.1975**	4%	60%
P. reticulatum	4%	**4.3164**	4%	65%
CH07 VS IQ				
P. bipes	13%	**2.4265**	14%	14%
P. dalei	10%	**4.0434**	12%	26%
P. steinii	8%	**4.2211**	9%	35%
Alexandrium **sp.**	8%	**3.0216**	9%	44%
P. pellucidum	6%	**3.7358**	6%	51%
Boreadinium **sp.**	6%	**2.3721**	6%	57%
P. meunieri	5%	**5.4117**	6%	63%
P. brevipes	5%	**1.6597**	5%	68%
P. ovatum	5%	**4.1389**	5%	73%
G. spinifera	4%	**2.7531**	4%	78%
CH07 VS MI				

P. dalei	11%	**4.1547**	13%	13%
P. steinii	8%	**4.1416**	10%	24%
P. brevipes	7%	**2.4709**	9%	33%
Alexandrium sp.	6%	**2.2025**	8%	41%
Boreadinium sp.	6%	**2.3751**	7%	48%
T. arcticus	6%	**2.8451**	7%	55%
P. pellucidum	5%	**3.1669**	6%	61%
P. meunieri	4%	**3.5134**	5%	66%
P. ovatum	4%	**3.115**	5%	71%
G. spinifera	4%	**2.7872**	5%	76%
IQ VS MI				
P. bipes	32%	**3.7863**	36%	36%
T. arcticus	15%	**3.6552**	16%	52%
P. brevipes	8%	**2.234**	9%	60%
P. reticulatum	8%	**2.9986**	9%	69%
Alexandrium sp.	5%	**2.9637**	6%	75%
T. lineatus	4%	**2.3804**	5%	79%
T. longipes	4%	**1.6347**	4%	84%
P. meunieri	3%	**1.9543**	3%	87%
P. pellucidum	3%	**2.7776**	3%	90%
T. fusus	2%	**3.8663**	2%	92%

CH07= Churchill 2007, CH15= Churchill 2015, IQ= Iqaluit, DB= Deception Bay, MI= Milne Inlet, Diss/sd= average dissimilarity/ standard deviation. Values of Diss/sd ≥ 1 are in bold and represent taxa which consistently contributed to the observed community change. Mean abundance of each taxa is presented in Figure 5.

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