

Response of Arctic biodiversity and ecosystem to environmental changes: Findings from the ArCS project

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ABSTRACT

Arctic ecosystems are altered profoundly by climate changes. However, the responses of Arctic marine and terrestrial ecosystems as well as their biodiversity to global warming remain largely unknown. This article provides comprehensive insights into the results and major findings from the Arctic Challenge for Sustainability (ArCS) Project – an Arctic region research program initiated in Japan, which aims to address and advance our understanding of these uncertainties. Marine ecosystem studies have identified several biogeochemical processes that are associated with sea ice decline and northward transport and shift of marine species across multiple trophic levels over the Bering and Chukchi Sea shelves. Studies of the terrestrial ecosystem have identified factors that are important for the understanding of terrestrial biodiversity and ecosystems, including Arctic lakes, under the presence of global warming. Novel fungal species from the Arctic terrestrial ecosystem have also been isolated and described. Overall, these results could contribute to the conservation and sustainable management of the Arctic ecosystem services.

1. Introduction

Arctic surface air temperature has increased considerably in response to global warming; the rate of temperature increase over the Arctic is 2.4 times the rate of increase over the northern hemisphere (Box et al., 2019) and 3 times that of the global average warming rate for the past 100 years (Overland et al., 2017; Steele et al., 2008). Abrupt reduction of Arctic sea ice (Comiso, 2006) is a clear impact of Arctic warming; the rate of sea ice decline is higher than the rates that have been forecast by numerical simulations and reported in the Intergovernmental Panel on Climate Change Fourth Assessment Report (IPCC AR4) (Stroeve et al.,

2007). These rapid climate changes and their concomitant effects are definitely impacting Arctic marine and terrestrial ecosystems, including habitats, diversity, growth phenology, and other elements (AMAP, 2019). In addition to climate-related stressors, human-induced ecosystem impacts are also becoming a major concern in the region.

The Arctic marine ecosystem needs sea ice, which serves as a platform for marine life and plays a crucial role in controlling physical and chemical processes that affect biological activity. Therefore, sea ice reduction, its timing, and accompanying ocean temperature increase alter marine environments, inducing changes in primary production (Arrigo et al., 2008; Hirawake et al., 2012), benthic biomass and

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diversity (Grebmeier et al., 2006a, 2006b; Grebmeier, 2012), fish abundance (Stevenson and Lauth, 2012) and regional distributions of plankton (Matsuno et al., 2011, 2014) and fishes (Fossheim et al., 2015). Shifts in habitat of marine living resources are an important focus for scientific research but also raise concerns for global food security and sustainability of industrial fisheries in Arctic countries (Christiansen et al., 2014). In addition, human impact such as bycatch (Davis et al., 2013) and contaminant accumulation in marine food webs (Wania and Mackay, 1996) are posing increasing threats to the Arctic marine ecosystem. Whereas uncertainties in the mechanisms and processes of biogeochemical cycles are being steadily addressed, our knowledge of the marine ecosystem and food web dynamics remains limited. Thus, one of the impelling goals of international scientific community is to advance our understanding of these uncertainties in the Arctic Ocean and adjacent seas to ensure sustainability of marine biological resources and conservation of marine biodiversity.

One of the characteristics of Arctic terrestrial ecosystems and biodiversity is spatial and temporal heterogeneity (e.g. Elmendorf et al., 2012). A variety of terrestrial abiotic and biotic factors co-interact with each other to support and form the Arctic ecosystem and these interactions are changing under the effects of climate change. This renders the understanding of Arctic terrestrial biodiversity and ecosystem changes a complex and difficult task (Callaghan and Jonasson, 1995).

Vegetation is one of the fundamental biotic parts of ecosystems as it affects both the atmosphere and biosphere. In recent decades, tundra shrub cover and growth in Eurasian Arctic have increased (Macias-Fauria et al., 2012) but a lack of adaptation to environmental conditions that are not directly associated with climates, such as photoperiod, biotic interactions or edaphic conditions, would make adaptation much more difficult for Arctic plants in addition to the stress of climate change (Bjorkman et al., 2016).

To date, there is very limited information on microbes in the Arctic terrestrial ecosystem due to the lack of a comprehensive survey. This is because a large part of the Arctic region remains inaccessible and microbes exhibit highly variable spatial and temporal heterogeneity (e.g. Campbell et al., 2010; CAFF, 2013). Therefore, the research on microbes—their diversity and ecophysiological characteristics—needs to be continued and expanded as information and research on the microbial diversity would greatly improve our understanding of microbial composition and function in the Arctic ecosystem.

Arctic lakes are an important aspect of spatial heterogeneity of the Arctic tundra ecosystem (Kling, 1995). Approximately 18–20% of the land area in the Canadian Arctic (north of 60°N) is covered by freshwater (Prowse and Ommanney, 1990). Global warming has impacted Arctic lakes through the loss of ice cover or increased duration of ice-free

conditions causing the lake ecosystems to enter into a state of rapid transition (Vincent et al., 2008, 2012; Mueller et al., 2009; Prowse et al., 2011). Therefore it is vital to monitor the lake ecosystems and understand their mechanisms in response to climate change for the purposes of scientific research and conservation of Arctic ecosystems.

The goal of the Arctic Challenge for Sustainability (ArCS) Project—an Arctic region research project initiated in Japan—is to elucidate Arctic ecosystem responses and biodiversity alterations under current environmental change. We conducted oceanographic and marine ecological surveys in the northern Bering Sea, the southern Chukchi Sea and on St. Lawrence Island, as well as terrestrial ecosystem and biodiversity investigations in the Canadian High Arctic (Fig. 1). This paper provides a synthesis of the results and new findings on the Arctic ecosystem and biodiversity that have emerged from the ArCS project.

2. Marine ecosystem

2.1. Heat flux, nutrient supply and dissolved organic matter

Rich nutrients in the Anadyr Water and Bering Shelf Water support high primary production in the northern Bering and southern Chukchi seas (Fig. 1) (e.g. Springer and McRoy, 1993; Grebmeier et al., 1988, 2006b). In contrast, Alaskan Coastal Water is poor in nutrients and transports heat from south to north and huge amounts of organic matter from the Yukon River (e.g. Walsh et al., 1989; Eisner et al., 2013). As a result of these recent changes in the Arctic, there is a need to have a better understanding of the processes of nutrient supply, water mass structure and heat flux in the Arctic.

Tsukada et al. (2018) showed that solar heating on the Chukchi shelf and heat flux from the Bering Strait may contribute to interannual variations in heat transport from the shelf to the western Arctic Basin. Therefore, monitoring of solar heating over the Chukchi shelf is key to understanding the summer sea ice retreat in the western Arctic Basin. Moreover, sea ice production and melt play important roles in the biogeochemical cycles. Evans and Nishioka (2018) reported that micronutrients and trace metals, such as iron, from shelf sediments were transported northward through accumulation in sea ice and subsequent melting. Evans and Nishioka (2019) also reported that sea ice formation, chemical reduction and brine injection were the processes driving accumulation and release of iron and other trace metals in Arctic sea ice. These results are important for understanding responses of phytoplankton photosynthesis in response to the reduction of Arctic sea ice.

Volatile organic iodine compounds (VOIs) contribute to ozone depletion in the lower troposphere. Ooki et al. (2015, 2016) conducted a series of unique studies on VOIs to examine their impacts on primary

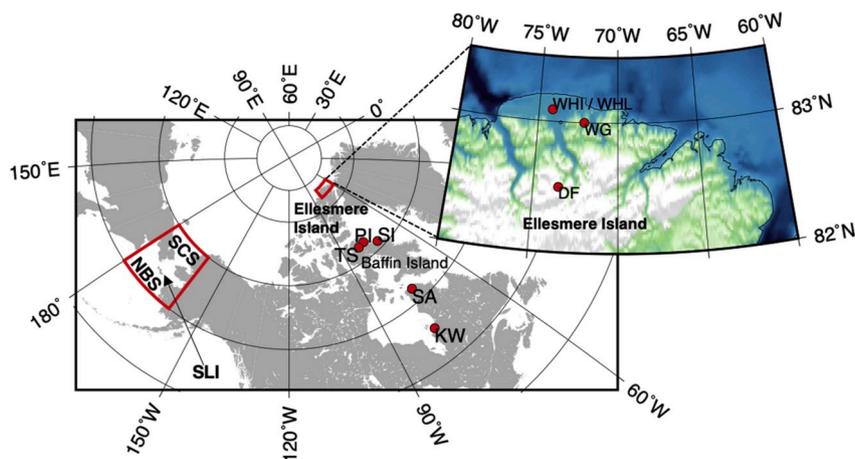


Fig. 1. Maps showing the locations of the study sites for the ArCS project. SCS: Southern Chukchi Sea, NBS: Northern Bering Sea, SLI: St. Lawrence Island, KW: Kuujuarapik-Whapmagoostui, SA: Salluit, TS: Tremblay Sound, PI: Pond Inlet, SI: Scott Inlet, WHI/WHL: Ward Hunt Island/Lake, WG: Walker Glacier, DF: Disraeli Fjord.

production. Their results showed that the Arctic Ocean actively emits VOIs to the atmosphere and the concentrations are high in the bottom water. This suggests that the degradation of organic matter in sediments substantially contributes to the production of VOIs in the Chukchi Sea shelf. Tanaka et al. (2016) and Yamashita et al. (2019) further found evidence that the dissolved organic matter (DOM) in the Bering and Chukchi Sea waters during early summer is conservative and controlled mainly by the mixing of water masses. They used DOM availability and optical parameters to understand the complex water mass distribution in the region. They developed a more precise method to distinguish water masses, using the data from a fluorescent DOM (FDOM) sensor mounted on a conductivity, temperature, depth (CTD) device and combined with conventional approach of temperature-salinity analysis. This improved method is useful for understanding the formation and mixing processes of nutrient-rich water masses such as Anadyr Water.

Abe et al. (2019) deployed a mooring system with an Acoustic Doppler Current Profiler (ADCP) and chlorophyll fluorescence–turbidity sensor at a station in the Bering Strait to examine the impact of locally-enhanced currents to particle transport. Their mooring data captured a clear signal of sediment resuspension where strong local currents exceeded 100 cm s^{-1} . Resuspension occurred when the strong wind-induced barotropic currents exceeded 50 cm s^{-1} . While suspended matter potentially contains phytoplankton in autumn, it is unlikely in winter, suggesting the degradation of phytoplankton in the sediments during sea ice season. These physio-biological processes may play a role in the supply of organic materials to downstream regions and should be taken into account when estimating carbon and nutrient fluxes from the Bering Sea to the Arctic Ocean, especially in response to recent changes in heat flux and sea ice extent.

2.2. Plankton and impact on higher trophic levels

Marine ecosystems on the Bering and Chukchi Sea shelves are characterized by strong pelagic–benthic coupling (Grebmeier et al., 1988) because of elevated primary production of large diatoms (ice algae and phytoplankton) and low zooplankton grazing pressure. Both processes are considerably affected by sea ice extent and timing of sea ice retreat (Grebmeier, 2012; Hunt et al., 2002). Parts of this process were clearly identified by Waga et al. (2019) in their analysis of satellite and long-term monitoring data of benthic biomass. They compared optically retrieved phytoplankton size with benthic macrofaunal biomass, and found a large northward shift in biomass and a strong positive correlation between phytoplankton size and sediment chlorophyll *a* concentration, indicating the availability of food for the benthic community.

Increase in the number of cyclones (McCabe et al., 2001) may also impact this coupling process. Yokoi et al. (2016) reported that abundances of 11 micro-sized phytoplankton species (diatoms, dinoflagellates and ciliates) at a fixed station on the Chukchi Sea shelf increased considerably after a strong wind event in September. More cyclones in the future could transport nutrients from deeper layers to the surface and enhance microplankton blooms in autumn.

Resting stage cells of diatoms in sediments have been considered to be a seed population for the spring phytoplankton bloom (e.g. Garrison, 1984). However, little is known about these cells in the Arctic Ocean. Tsukazaki et al. (2018) reported high densities of viable resting stage cells of typical Arctic diatom species in sediment samples from the Chukchi Sea. However, after being stored for 6 months in the dark, only cells in water samples remained viable, implying that the cells in the water samples could be potential seeds for ice algae and phytoplankton blooms. Fukai et al. (2019) reported fluctuations in density and species composition of resting cells. In 2018, they found that the number of germinating cells in sediments from the northern Bering Sea was 10–100 times that in 2017; phytoplankton and ice algae species were dominant in 2017 and 2018, respectively. These results suggest that community composition and abundance of resting stage cells are highly affected by

sea ice conditions.

Toxic algae, which could germinate on the surface of sediments, were also found in waters of the Chukchi and Bering Sea shelves. Natsuike et al. (2017a) detected vegetative cells of *Alexandrium tamarense* on the shelves in summer; high densities were found mainly in warmer waters such as in Bering Shelf Water. Densities far exceeded those indicating risks of paralytic shellfish poisoning (PSP), and exhibited a significant positive correlation with water temperature (Natsuike et al., 2017b). Thus, recent and future increases in water temperature could enhance toxic algal blooms, which, in turn, bring severe negative effects on the various plankton feeders and higher trophic level predators, including humans.

Zooplankton advection is one of the potential mechanisms that could also change pelagic–benthic coupling. Amano et al. (2019) examined spatial distributions of chaetognath abundance and community structure in 1991 and 2007 and found that *Eukrohnia hamata* was only recorded in the southern Chukchi Sea in 2007. They also reported that the water mass in the southern Chukchi Sea in 2007 was warmer than that in 1991 and identified this warm water mass as Alaskan Coastal Water, based on the criteria from Danielson et al. (2017). This provides evidence of the transport of *E. hamata* with Pacific water through the Bering Strait. Landeira et al. (2018) reported the foremost documented northward expansion of the planktonic larvae of the commercially important tanner crab *Chionoecetes bairdi* to the Chukchi Sea in summer of 1992. In an earlier study, Landeira et al. (2017), reported that in 2007 and 2008, *C. bairdi* larvae were only distributed in the southern Bering Sea and their presence had strong correlation with that of their adult populations. Populations transported from the Bering Sea or Pacific Ocean into the Arctic Ocean would have difficulty surviving and reproducing under the current climate conditions. Nonetheless, they may become viable under future ocean warming. Matsuno et al. (2016), for instance, showed that warm water temperature had a clear positive effect on the growth of the dominant zooplankton species (*Calanus glacialis*) in the area. Landeira et al. (2018) further concluded that on the Chukchi Sea shelf, water temperature that is a few degrees higher than the current level would lead to eventual recruitment of *C. bairdi* postlarvae.

Maekakuchi et al. (2018) compared the body size and population density of the appendicularian species *Oikopleura vanhoeffeni* in summers of 2007 and 1983–1996. Their analyses showed an overall decrease in the species' body size and population density in 2007 relative to 1983–1996, potentially from an earlier spawning event due to early sea ice retreat in 2007. Nakano et al. (2016) examined the stomach contents of polar cod caught in the northern Bering and southern Chukchi seas in summer of 2013 and revealed that appendicularian was the most dominant prey item in the polar cod's diet. This highlights the trophic importance of gelatinous zooplankton and necessitates the further monitoring of seasonal and interannual changes in their abundance and distribution.

Zooplankton distribution and abundance may be closely linked to the seasonal migration of seabirds. In particular, the short-tailed shearwater *Andenna tenuirostris*, an abundant marine top predator in the Pacific, was also seen in the Bering Sea in spring and summer and the Chukchi Sea in autumn. Nishizawa et al. (2017) reported that *A. tenuirostris* distributions were concentrated in the waters where large-sized krill were more abundant, suggesting that the changes in the zooplankton advection and size are crucial determinants of shearwaters' distribution. Sea ice in the northern Bering Sea exhibited an anomalously early retreat in the winter of 2017/2018 (Stabeno and Bell, 2019), and crested and least auklets (*Aethia cristatella* and *A. pusilla*) in St. Lawrence Island, which are also zooplankton feeders, failed to fledge their chicks during the summer of 2018 (Will et al. personal comm.).

2.3. Fishery resources

Understanding responses of the distribution of fishery resources to

climate change is important for conservation and sustainable management of marine species for future food supply and security (Hollowed et al., 2013). While marine species generally exhibit climate-driven range shifts in response to changes in water temperature (Burrows et al., 2019), potential differences in their response could also be attributed to non-climatic factors that are related to species-specific sensitivity and exposure to climate regimes. Alabia et al. (2018) analyzed distribution shifts of major marine fish and invertebrate taxa collected from bottom trawl surveys in the Bering shelf region during local climate regime shifts (cool to warm and warm to cold transitions). Using multi-model ensemble outputs, they showed that observed and modeled rates of distribution shifts in marine taxa were poorly correlated with the rate of climate change. Their results add to the increasing evidence on the shift of marine resources and raise concerns about future availability of marine living resources for commercial fisheries. Distribution shifts of most target species trail behind climate regime shifts, suggesting that these taxa will be unable to remain in their preferred climatic envelopes; thus, underpins the possibility of regional species loss in a rapidly warming ocean.

Bycatch from fishing activities also poses a serious threat to marine life, such as the Greenland shark *Somniosus microcephalus*, which is a large shark that is up to 6 m in total length and can exceed 1000 kg in body mass. It lives in the North Atlantic and Arctic Oceans, and forages on a variety of fish, invertebrates (e.g., squid), and marine mammals (e.g., seal). It is considered as an apex predator in the Arctic, assuming vital ecological roles (MacNeil et al., 2012). Greenland sharks have been massively harvested in the past, primarily for their liver oil. Although Greenland shark fisheries have declined dramatically since the mid-1900s, a number of sharks are still caught as bycatch in fisheries targeting other species. As part of the ArCS project, Barkley et al. (2020) attached sensors on the heads of Greenland sharks to investigate swimming behavior around Baffin Island. Most tagged sharks recovered from capture stress and behaved normally within a day, and no individuals died following release. These results suggest that Greenland sharks are not especially vulnerable to capture stress, if handled appropriately when caught by long-line fisheries as bycatch (e.g. cutting a branch of the long line to release the shark quickly), and most of them that are released back to the sea may eventually survive.

3. Terrestrial ecosystem

3.1. Microbial diversity in the Canadian Arctic

3.1.1. Fungal diversity in the Canadian High Arctic

The Pan-Arctic checklist of lichens and lichenicolous fungi compiled by the Conservation of Arctic Flora and Fauna (CAFF) (Kristionsson et al., 2010) includes over 1000 species of lichens and lichenicolous fungi from the Canadian High Arctic, of which, approximately 400 species can be found on Ellesmere Island alone. Recently, as many as 25 novel fungal taxa have been isolated from mosses collected from Oobloyah Bay on Ellesmere Island (Osono et al., 2012). Despite this progress, the information about fungal diversity in the Canadian High Arctic still remains very fragmentary and limited.

In order to fill in the research gap on fungal diversity in the High Arctic, we conducted a microbiological survey out at Ward Hunt Island (83.0 °N, 74.1 °W) in the northern Ellesmere region (Fig. 1), with the aim to discover and isolate novel fungal species. Benthic microbial mats in a meltwater pool on an ice island in Disraeli Fjord (82.5 °N, 73.5 °W) were sampled. Maps and further details about the sampling site are described in Vincent et al. (2011). A total of 76 different fungal strains were isolated from five different microbial mat samples and their DNA were sequenced. On the basis of the sequences of the ITS region and the D1/D2 domain of the LSU rDNA gene, these strains were classified into 11 ascomycetous genera, 10 basidiomycetous genera and 1 zygomycetous genus. Dominant fungi from the sampling site mostly belonged to the genera *Vishniacozyma* (approximately 38%), *Preussia* (approximately

16%), *Cladosporium* (approximately 11%), and *Mrakia* (approximately 11%). Additionally, two novel yeast species from the sampling site were isolated and described as *Gelidatrema psychrophila* and *Mrakia arctica* (Tsuji et al., 2018a, 2018b).

We also conducted studies in the area of Walker Glacier (unofficial name) (83.0 °N, 72.1 °W; Fig. 1) on the northern coast of Ellesmere Island. Fungi were isolated from the melting glacier surface and the soil exposed by glacier retreat. We sequenced the DNA of 275 fungal strains; 51 strains were classified to the genus *Vishniacozyma* while two strains were identified as members of a novel species with the proposed name, *Vishniacozyma ellesmerensis* (Tsuji et al., 2019a). The ITS and D1/D2 domain sequences of 4 out of 111 *Mrakia* strains showed low similarity to other members of known species from this genus. We subsequently described and named these four strains as the new species, *Mrakia hoshinonis* (Tsuji et al., 2019b). In summary, a total of four novel fungal species were isolated and described from this microbial survey at Ellesmere Island.

All four novel fungal species are basidiomycetous yeasts. They are characterized by growth at sub-zero temperatures and in vitamin-free and amino acids-free media. These characteristics allow these species to survive and grow in perennially cold, oligotrophic habitats in the High Arctic. The genus *Vishniacozyma* accounted for around 40% of culturable fungi in the ice island melt pool and 19% of fungal strains isolated from the area of Walker Glacier. Around 11% of culturable fungi from the ice island and 40% from Walker Glacier sites belonged to the genus *Mrakia*. These two genera appear to be the major mycoflora representatives in this region. Extracellular enzyme tests indicate that the novel fungal species isolated from the northern part of Ellesmere Island were able to decompose a variety of organic materials even at subzero temperature, suggesting that they might play an important role in the biogeochemical cycles of the ecosystems of the Canadian High Arctic. According to the information on sequence similarity available in the DNA Databank, these four taxa are unique species and their distribution is highly localized. Under the current trajectory of climate change, these cold-dwelling fungi are highly vulnerable to habitat loss and may become endangered. Therefore, to conserve the fungi native to the Canadian High Arctic, large-scale microbial investigations should continue, and a Red List of Arctic fungi should be prepared.

3.1.2. Plant pathogenic fungi in the Canadian sub-Arctic

Phytopathogenic fungi and fungal-like microbes have been found in plants in cold regions (Hoshino et al., 2009; Tojo and Newsham, 2012). Some of them can act as snow rot pathogens, which causes cryophilic fungal diseases (Hoshino et al., 2009) in many wild plants. However, the information on snow rot pathogens in natural, cold environments is very limited. Therefore, it is important to understand the characteristics of these pathogenic fungi, including their effects on plants (Matsumoto and Hsiang, 2016).

We collected snow rot pathogens from a forest tundra in Kuujuarapik-Whapmagoostui (KW), Quebec, Canada (55 °N). From our samples, we found snow molds (*Typhula* spp.) that can typically be found as far north as the Arctic and as far south as snowy regions in the temperate zone. In the Arctic, *Typhula* spp. are typically found in continental rather than maritime climates (Hoshino et al., 2009) while none was found on the Arctic coastal plants (Connors, 1967). Our study was the first to record the distribution of *Typhula* sp. on coastal plants in the sub-Arctic region. We also found sclerotia forming on the surface of dead sea peas (*Lathyrus japonicus*) leaves at the banks of the Great Whale River where humidity is relatively high. Mycelia with clamp connection were isolated from these sclerotia, and their optimal growth temperature was found to be around 10–15 °C. When cultured on potato dextrose agar plates at 10 °C, they easily lost most of their sclerotium-forming ability.

Globisporangium spp., which was previously a member of the genus *Pythium*, are fungal-like microbes and are widely distributed in soil and water (van der Plaats-Niterink, 1981). Natural *Globisporangium* infection in mosses in the polar regions had been recorded (Hoshino et al., 2009;

Tojo et al., 2012) as some cold environment species from this genus can behave as snow rot pathogens (Tojo, 2019). We conducted a moss survey in the forests of KW, Quebec, Canada in 2016, and isolated an unknown *Globisporangium* species from our samples. We tentatively named it *Globisporangium* sp. strain KW5. Based on the molecular phylogenetic identity, strain KW5 is most closely related to *G. okanoganense*, a well-known snow rot pathogen in Japan (Takamatsu, 1989; Takamatsu and Takenaka, 2001) and USA (Lipps and Bruehl, 1978, 1980). Strain KW5, therefore, has the potential to behave as a snow rot fungus.

3.2. Terrestrial biodiversity and ecosystem functions in the Arctic

Global warming is expected to influence biodiversity and community structure. It could introduce substantial alterations in fundamental ecosystem functions such as primary productivity and nutrient cycling, which are currently supported by different biota (Walker et al., 2005; Bhatt et al., 2010; Reynolds et al., 2012; Scheffer et al., 2012; CAFF, 2013; Ims et al., 2013). Local studies have shown that vegetation type results from local environmental factors such as soil fertility and moisture availability, which can determine interactions among plant species. That vegetation structure could, in turn, lead to differences in the function of the ecosystem (Billings, 1973; de Molenaar, 1987; Walker et al., 1994; Tilman et al., 1996, 2014; Grime, 1998). Understanding how these local processes affect and determine the structure and functionality of ecological communities is urgently required. This is particularly true, given the likelihood of substantial changes in carbon dynamics in the region that can further alter climate systems through the feedback loop between vegetation and climate. Therefore, we first aim to gain local empirical knowledge on how biological or physiochemical processes can shape the ecological communities and then understand how these species assemblages can support the ecosystem functions.

Vegetational shifts are increasing in the Arctic regions due to anthropogenic climate change. For instance, studies have consistently reported that global warming could lead to shrub expansion to the tundra vegetation, which would, in turn, lead to a short-term decline in vascular plant diversity (Myers-Smith et al., 2011). However, another global analysis suggested that the forest-tundra transitions are more likely to be controlled by non-linear (tipping-point) processes (Scheffer et al., 2012) because tundra vegetation shift depends on local factors (e.g. soil nutrient, biological interactions) as well as global or regional factors (e.g. atmospheric heating, surface albedo). Compared with regional climate changes, local factors or processes often have greater influences on vegetation composition (Dearborn and Danby, 2017; Nabe-Nielsen et al., 2017). We investigated vascular plant composition and abiotic environments in the tundra–boreal forest ecotone (KW on Fig. 1) in summer of 2016 to clarify local factors promoting shrub expansion. The investigation revealed a positive colonizing relationship between shrub species, suggesting that such local biotic interaction could provide positive feedback to shrub expansion (Kitagawa et al., 2020).

Local factors greatly influence the relationship between biotic properties, such as biodiversity and ecosystem functions. The impact of local factors is particularly important in the Arctic ecosystem, which is characterized by the predominance of abiotic factors such as low temperature and limited moisture availability that can limit the activities of biotic organisms. To fill this knowledge gap, we identified the potential mechanisms and functional contribution of vascular plant diversity in determining the soil properties in the High Arctic tundra ecosystem (Mori et al., 2017). We specifically attempted to clarify the causal relationships between species assemblages and environmental properties, with a focus on seral changes in species/functional diversity of vascular plants in tundra ecosystems of the High Arctic. We found that, although species richness was influenced by soil properties in the earlier stages of primary succession, the causalities were reversed in the later stages due to the increase in positive interactions (facilitation) (Mori et al., 2017). These feedbacks and interactions were important in shaping the plant

assemblages in the Arctic (Svoboda and Henry, 1987; Callaway and Walker, 1997). Although further studies are needed to study the relationships between biodiversity and ecosystem functions in tundra ecosystems (Zhu et al., 2016; Mori et al., 2017; Wang et al., 2018), the knowledge gained here acts as an important foundation and ground-based evidence proving that plant communities can be substantial in determining the fundamental functions of terrestrial ecosystems such as carbon dynamics. Climate change can change this ecosystem balance through feedback loops between species assemblages and their contributions towards climate stabilization.

In addition to plant diversity, we also need to shed light on other facets of diversity such as animals, fungi and bacteria, to know how they are related to ecosystem functions. Life history strategies vary, but nutrient and energy cycling as a result of decomposition, and interactions between trophic levels may provide important contributions to ecosystem functioning (Wallenstein et al., 2007). For example, plant-based food web studies show that geese grazing pressure or pathogenic damage could affect the carbon balance of the ecosystem or result in vegetation degradation (Milakovic and Jefferies, 2003; Olofsson et al., 2011). Similar dynamics have also been observed and reported in the Arctic tundra (Masumoto et al., 2018). Trophic interactions between elements above and below ground may also vary on different spatial scales, resulting in different responses in the ecosystem towards global warming.

3.3. Arctic lakes

Global warming also affects the Arctic lakes resulting in losses of lake ice, glaciers, ground ice and summer snow cover (Derksen et al., 2012). Until recently, many lakes in the High Arctic have been covered by thick perennial ice, and their water columns have had little exchange with the atmosphere. Over past decades, several deep lakes in the Canadian High Arctic have lost their perennial ice cover (Mueller et al., 2009; Veillette et al., 2010), but little attention has been paid on the seasonal changes in the High Arctic lakes. Therefore, we carried out a study to investigate the seasonal and interannual variations between abiotic and biotic elements in the northernmost lake in the Canadian High Arctic.

In 2016, 2018, joint Canada–Japan field expeditions were carried out at Ward Hunt Lake on Ward Hunt Island (WHI; Fig. 1). In July 2016, we installed a mooring system at the lake to monitor its environmental conditions with high temporal resolution throughout the year and repeated the operation in July 2018. In July 2016, samples were collected from the orange-pigmented microbial mat that covers the bottom of the lake, and the microbial mat was found to be dominated by Cyanobacteria (Mohit et al., 2017). We also identified seven other species from the mat that belonged to Basidiomycota and Ascomycota and some species have never been recorded at the lake.

We also made the first-ever seasonal measurements of abiotic and biotic parameters at Ward Hunt Lake. In mid-August in 2016, almost all of the ice on the surface of the lake has melted causing the lake water to be mixed by strong winds, and water temperature in the upper layer to decrease rapidly. We found that water temperature during the following autumn, winter and spring affected water temperature during the summer in 2016 and the oxygen concentration was also affected by the melting of the ice cover (Bégin et al., accepted). Continuous time-series data of chlorophyll *a* concentration showed that phytoplankton blooms formed from the end of August to early September in 2016 and during the summer in 2017. The maximum chlorophyll *a* concentration, which is an index of phytoplankton biomass, was higher in 2016 than in 2017. Higher chlorophyll *a* concentration of 2016 may have been caused by vertical mixing of the water column and the greater availability of light associated with the melting of the ice cover. Vertical mixing could supply the whole water column with nutrients that have been accumulated at the bottom of the oligotrophic lake, triggering phytoplankton blooms. Moreover, we found that chlorophyll *a* concentration began to increase in April 2017 when light intensity in the lake was still very low

(Bégin et al., accepted).

Year-round monitoring data from Ward Hunt Lake provided us with new information on the environmental conditions at the lake during autumn, winter and spring. We also found that seasonal environmental conditions are affected by the summer ice cover. Data are needed to improve our understanding of the mechanisms that could result in pronounced ecological shifts in the High Arctic lakes under global warming, and as some of these mechanisms could be difficult to predict, continuous monitoring should be conducted.

4. Summary and perspectives

As part of the ArCS project, we have successfully identified oceanographic features including water mass structure, northward transport of particulate matter and processes of nutrient supply of the northern Bering and southern Chukchi seas. We also reported on northward transports or shifts and considerable interannual differences in plankton, benthos, fish and seabirds, encompassing most trophic levels. Most of these changes were related to the decline of sea ice and associated warming in the study area over the past decades. However, an anomalously early sea ice retreat abruptly occurred in the northern Bering Sea in winter 2017/2018, underpinning the need to further analyze data collected from the 2017 and 2018 ArCS research cruises to better understand short-term responses of ocean and marine ecology.

This paper is the first review of studies of Arctic biodiversity under the ArCS project. We found novel fungal species and a novel plant pathogenic fungus in the sub-Arctic. We also clarified the biodiversity and ecosystem function on a local scale using data from three sites between the sub-Arctic and the High Arctic. Our preliminary results at KW highlight the importance of studies on local scales to evaluate and predict the effects of global warming at Arctic tundra ecosystems.

The northernmost site in the ArCS project was set up at Ward Hunt Lake in the Canadian High Arctic. Using a mooring system, we started monitoring the lake, which is beginning to experience major environmental changes, to understand variations in environmental conditions throughout the year. The data will be very important for understanding High Arctic limnology and for contributing to other international projects such as Terrestrial Multidisciplinary distributed Observatories for the Study of Arctic Connections (T-MOSAIC, 2018) and, Sentinel North.

Our results from the ArCS project as summarized in this paper provide important knowledge on present states and recent changes in the Arctic ecosystem and biodiversity. These results contribute to the conservation and sustainable management of Arctic ecosystem services and support the decision-making process of stakeholders in Arctic countries. Further collaboration studies with social scientists are also needed.

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