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Possible spreading of toxic *Alexandrium tamarense* blooms on the Chukchi Sea shelf with the inflow of Pacific summer water due to climatic warming

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ABSTRACT

A high abundance of resting cysts of the toxic dinoflagellate *Alexandrium tamarense* was recently reported in the vast continental shelf of the Chukchi Sea in the Arctic Ocean, suggesting that the species is widespread in the shelf. Nevertheless, little is known about the occurrence of *A. tamarense* vegetative cells in the water column of the arctic. Sea ice reduction and the inflow of Pacific summer water (PSW) through the Bering Strait have recently increased owing to warming in the shelf. To determine the spatial and temporal distributions of *A. tamarense* in the Chukchi Sea shelf and their relationship to the inflow of PSW, field samplings were conducted in the Chukchi Sea and north Bering Sea shelves three times during the summer of 2013 from July to October. Vegetative cells of *A. tamarense* was detected in both shelves at all sampling periods with a maximum density of 3.55×10^3 cells L^{-1}. This species was also observed at the station at 73°N, indicating the northernmost record of this species to date. The center of the *A. tamarense* distribution was between the north Bering and south Chukchi Sea shelf during the first collection period, and spread to the north Chukchi Sea shelf during the second and third collection periods. The species occurrences were mainly observed at stations affected by the PSW, especially Bering shelf water. Water structure of PSW was characterized by warmer surface and bottom water temperatures, and increased temperatures may have promoted the cell growth and cyst germination of *A. tamarense*. Therefore, it is suggested that an increase in the PSW inflow owing to warming promotes toxic *A. tamarense* occurrences on the Chukchi Sea shelf.

1. Introduction

The toxic dinoflagellate *Alexandrium tamarense* (Lebour) Balech is mainly distributed in temperate and subarctic coastal waters (Steidinger and Tangen, 1997; Lilly et al., 2007). The species, however, has recently been detected in colder arctic regions. Its resting cysts and vegetative cells are found in the coastal areas of the western Bering Sea (Selina et al., 2006; Orlova et al., 2013). Baggesen et al. (2012) and Burrell et al. (2013) first reported the contamination of scallops and mussels with *A. tamarense* from the west coast of Greenland and Iceland. Furthermore, abundant *A. tamarense* resting cysts have been found in the bottom sediment surfaces from the vast continental shelves of the eastern Bering Sea and Chukchi Sea (Gu et al., 2013; Natsuike et al., 2013). These observations suggest frequent bloom occurrences of *A. tamarense* in the arctic region.

Chukchi Sea is a marginal sea of the Arctic Ocean with a continental shelf in which the water depth is less than 50 m; it connects to the north Bering Sea through the Bering Strait (Fig. 1). The occurrence of *A. tamarense* in this area was originally reported in the coastal area near Point Barrow in the Chukchi Sea during the summer (Bursa, 1963). Since then, observations have been quite limited in the Arctic Ocean, including the Chukchi Sea. Neither Horner (1984) nor Okolodkov and Dodge (1996) reported species occurrences in the Beaufort Sea and larger areas in the Arctic Ocean during the summer. The dominance of *Alexandrium* sp., however, was recently reported on the slope of the north Chukchi Sea shelf

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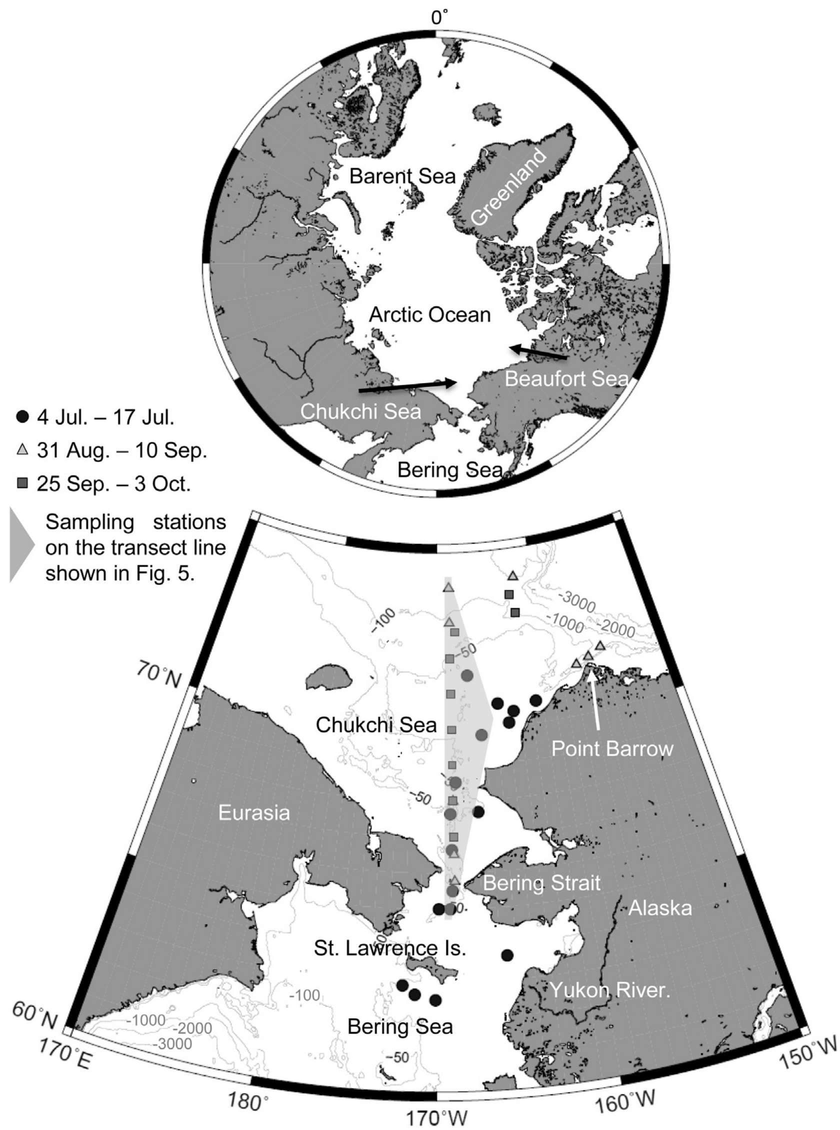

Fig. 1. Locations of sampling stations in the north Bering Sea and Chukchi Sea shelves during the summer of 2013. Black circles (●) indicate the stations included during the first period (July 4–Jul 17). The grey triangles (▲) and squares (■) indicate stations included during the second sampling period (August 31–September 10) and third sampling period (September 25–October 3), respectively.

during the summer of 2002, yet the precise species was unknown (Sukhanova et al., 2009). Furthermore, the occurrence of *A. tamarense* was noted in the Chukchi Sea shelf during the summers of 2002 and 2003 (Walsh et al., 2011), and abundant depositions of *A. tamarense* resting cysts were found in the bottom sediment surfaces from the continental shelves of the eastern Bering Sea and Chukchi Sea (Gu et al., 2013; Natsuike et al., 2013). Thus, the occurrence of *A. tamarense* vegetative cells in the coastal areas of Chukchi Sea and abundant deposition of *A. tamarense* cysts in sediment of Chukchi Sea shelf have been confirmed (Bursa, 1963; Gu et al., 2013; Natsuike et al., 2013). Nevertheless, the temporal and spatial distributions of the *A. tamarense* vegetative cells in water column are yet unclear in the Chukchi Sea shelf.

Recently, increasing inflows of Pacific water from the Bering Strait to the Chukchi Sea shelf have been observed during the summer, along with drastic reductions in sea ice owing to warming; these inflows increase the water temperature in the shelf (Shimada et al., 2006). Thus, recent drastic sea ice reductions by warming are suspected to affect *A. tamarense* occurrences in the shelf. Nevertheless, little is known about the relationship between *A. tamarense* populations and the inflow of Pacific summer water (PSW). In the present study, field observations were conducted to clarify the temporal and spatial distributions of *A. tamarense* vegetative cells on the Chukchi Sea shelf during the summer and examined the relationships between species occurrences and PSW inflow.

2. Materials and methods

Field observations in the north Bering Sea to the Chukchi Sea were conducted to track sea ice melting during three periods in the summer of 2013. During the first observation period from July 4 to July 17, the T/S *Oshoro-Maru* was used at 17 stations from the north Bering Sea, including the station located south of the St. Lawrence Island, to south of the Chukchi Sea shelf (Fig. 1). South of St. Lawrence Island is known as a polynya, which is an open water area that is surrounded by sea ice during the winter. The second (from August 31 to September 10) and the third (September 25–October 3) observations were performed using the R/V *Mirai* at 10 and 9 stations in the Chukchi Sea shelf and slope, respectively (Fig. 1). Vertical profiles of the water temperature and salinity were obtained using a CTD, and seawater samples were collected at depths of 0, 5, 10, 20, and 30 m using a Niskin water sampler with the CTD and a plastic bucket (for 0-m samples).

One liter of each seawater sample was fixed with glutaraldehyde at a final concentration of 1% immediately after collections were obtained on the ship. Fixed samples were concentrated approximately 50–100-fold using the settling method (Utermöhl, 1958). To stain the thecal plates of *A. tamarense* vegetative cells, a fluorescent dye (Calcofluor-white M2R) was added to the concentrated seawater samples (Fritz and Triemer, 1985). Subsamples (1–2 mL) were mounted on a glass slide and observed using an inverted epifluorescence microscope (Eclipse TE200) under UV light excitation (365 nm) for morphological species identification and enumeration of *A. tamarense* vegetative cells. All *Alexandrium* vegetative cells found with microscopic observation were identified following their morphological features. In this study, *A. tamarense* and *A. ostenfeldii* vegetative cells were found, and their typical thecal plates found in a seawater sample are presented in Fig. 2. The vegetative cells of *A. tamarense* were identified from shapes of ventral pore and the 1′ plate (Fig. 2A), apical pore plate (Fig. 2B), and sulcal plate (Fig. 2C) (Fukuyo, 1985; Tomas, 1997). The vegetative cells of *A. ostenfeldii* were identified from the shapes of a 1′ plate and a ventral pore on 1′ plate. (Fig. 2D) (Tomas, 1997).

3. Results

At all collection periods, *A. tamarense* (Fig. 2A–C) and *A. ostenfeldii* (Fig. 2D) were detected as the genus of *Alexandrium*. In the detected *Alexandrium* species, *A. tamarense* was dominant, while *A. ostenfeldii* was rare with a density of less than 1.7×10^2 cells L^{-1}. Fig. 3 shows the spatial distribution of *A. tamarense* cells. During the first collection period, *A. tamarense* was primarily distributed from the north Bering Sea to the south Chukchi Sea shelf near the Bering Strait, between 65° and 68°30′N, with a maximum density of 3.55×10^3 cells L^{-1}. Vegetative cell of *A. tamarense* was also observed from the Chukchi Sea shelf to 70°N at much lower densities (i.e., less than 10 cells L^{-1}). The species was not detected at stations near the Yukon River and St. Lawrence Island. During the second period, *A. tamarense* was mainly observed at the south Chukchi Sea shelf (66°30′–68°30′N), with a maximum density reaching 3.06×10^3 cells L^{-1}, and at much lower densities in the north Chukchi Sea shelf and near Point Barrow, ranging from under the detection limit (<10 cells L^{-1}) to 1.90×10^2 cells L^{-1}. In the third period, *A. tamarense* was not detected in the south Chukchi Sea shelf (67–69°N), but was mainly detected in the north Chukchi Sea shelf (70–73°N). The maximum cell densities decreased to below those of the first and second periods, that is, 9.2×10^2 cells L^{-1}.

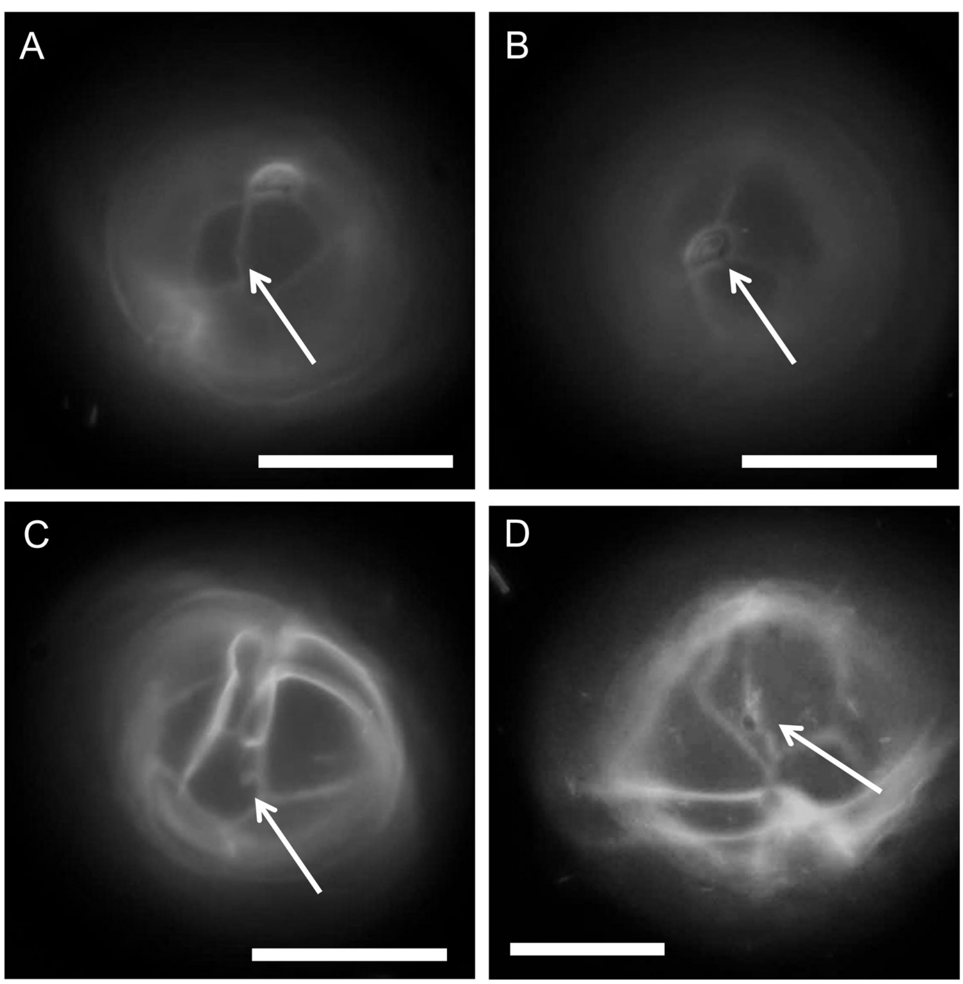

Fig. 2. Microphotographs of *Alexandrium tamarense* and *A. ostenfeldii* vegetative cells found at stations in the Chukchi Sea shelf. A–C show the same cells from different angles. White arrows indicate a ventral pore between the 1′ and 4′ plates (A), apical pore complex (B), sulcal plate (C), and a ventral pore between the 1′ and 4′ plates of *A. ostenfeldii* (D). Scale bars = 20 μm.

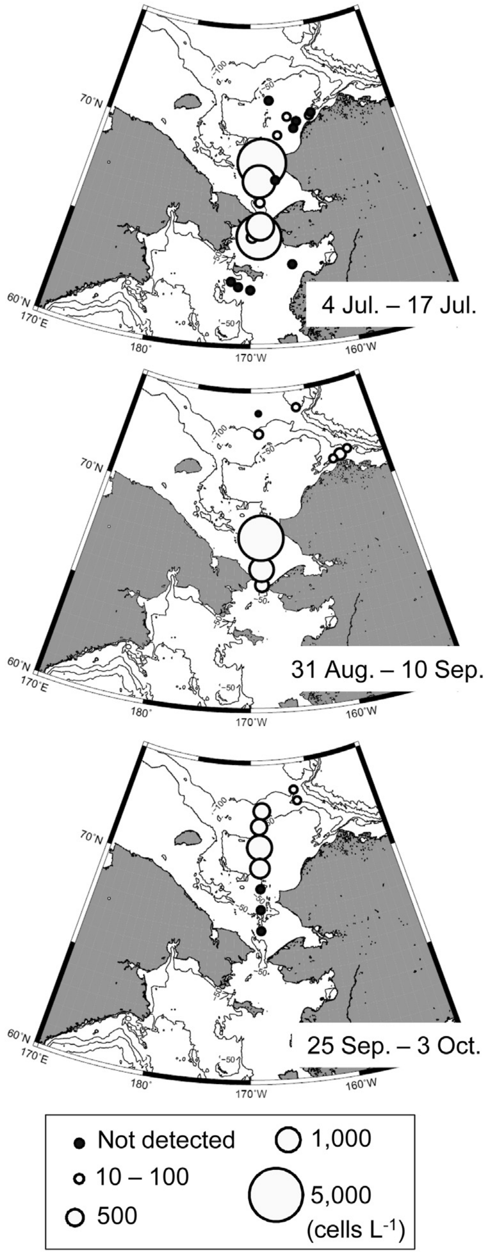

Fig. 3. Spatial distributions of *Alexandrium tamarense* in the Chukchi Sea and north Bering Sea shelves during the first (July 4–July 17; A), second (August 31–September 10; B), and third (September 25–October 3; C) periods. Bubbles indicate the maximum cell densities from depths of 0 or 5 m at the sampling stations.

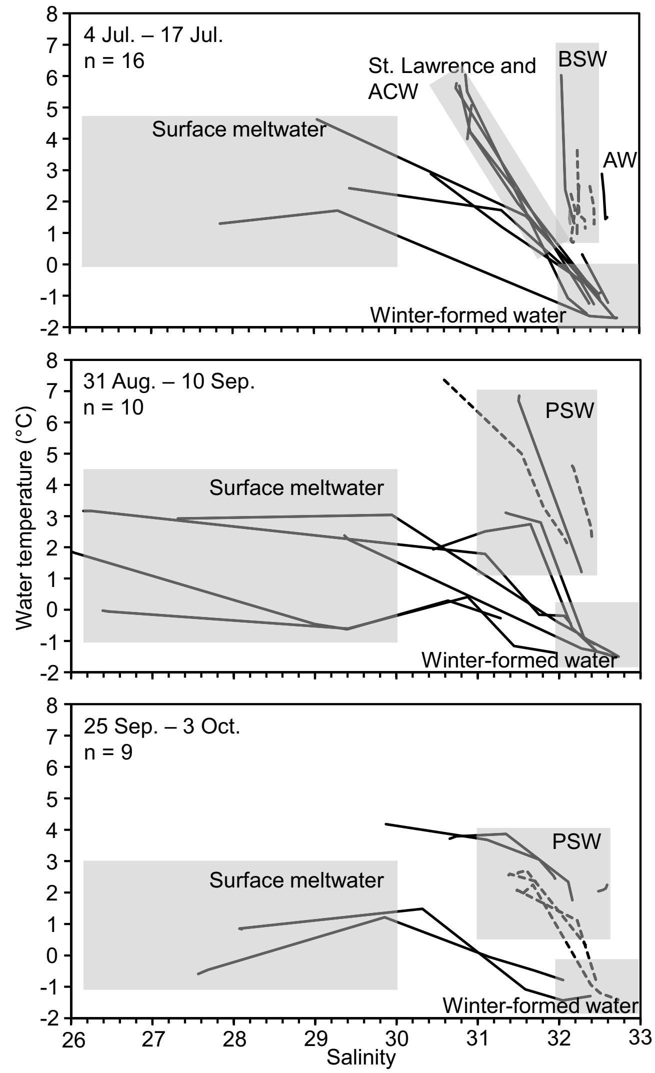

Fig. 4. Temperature-salinity diagrams of the sampling stations in the Chukchi Sea and north Bering Sea shelves during the first (July 4–July 17; A), second (August 31–September 10; B), and third (September 25–October 3; C) periods. Solid lines suggest the t-s diagram of the stations where *A. tamarense* occurred at relatively lower densities (<300 cells L^{-1}). Dashed line suggest the stations where *A. tamarnese* occurred at higher densities (>300 cells L^{-1}). The abbreviations of ACW, BSW, AW, and PSW indicate Alaska coastal water, Bering Shelf water, Anadyr water, and Pacific summer water, respectively.

Fig. 4 shows the temperature-salinity diagrams for all sampling stations. In the first and second periods, the bottom temperatures and salinities were higher at the stations with higher densities of *A. tamarense*. In contrast, *A. tamarense* was rarely detected at stations with low surface salinities and bottom temperatures. During the third period, lower bottom temperatures and higher salinities were observed at the stations with higher densities of *A. tamarense*. In contrast, *A. tamarense* was rarely detected at stations with lower surface salinities and bottom temperatures, and at higher surface and bottom temperatures.

Fig. 5 describes the spatial changes in *A. tamarense* cell densities and physical factors (water temperature, salinity) along the transect line from 65°N to 74°N during the three periods. The distribution *A. tamarense* shifted from the south (68°N) to the north (71°N) of the shelf as time elapsed. A low salinity at the surface layer (<31 psu) and low temperature at the bottom layer (<1 °C) were observed south of the shelf (69°N) during the first period, and the water mass structure moved to above 70°N during the second period. The colder bottom water was hardly detectable at the shelf during the third period. Warmer water with a higher salinity (>2 °C, >31 psu) spread from the south to the north of the shelf during the study period.

4. Discussion

In the Chukchi Sea shelf, *A. tamarense* was initially observed in the coastal areas (71°20′–71°23′N) near Point Barrow (Bursa, 1963). Reports of its occurrence have since been limited to coastal areas (approximately 3 km offshore). The present study confirmed that *A. tamarense* vegetative cell occurs in larger areas of the Chukchi Sea and northern Bering Sea shelves, and the center of the species distribution exhibited a dynamic shift from the south part to the north part of the Chukchi Sea shelf during the early summer to

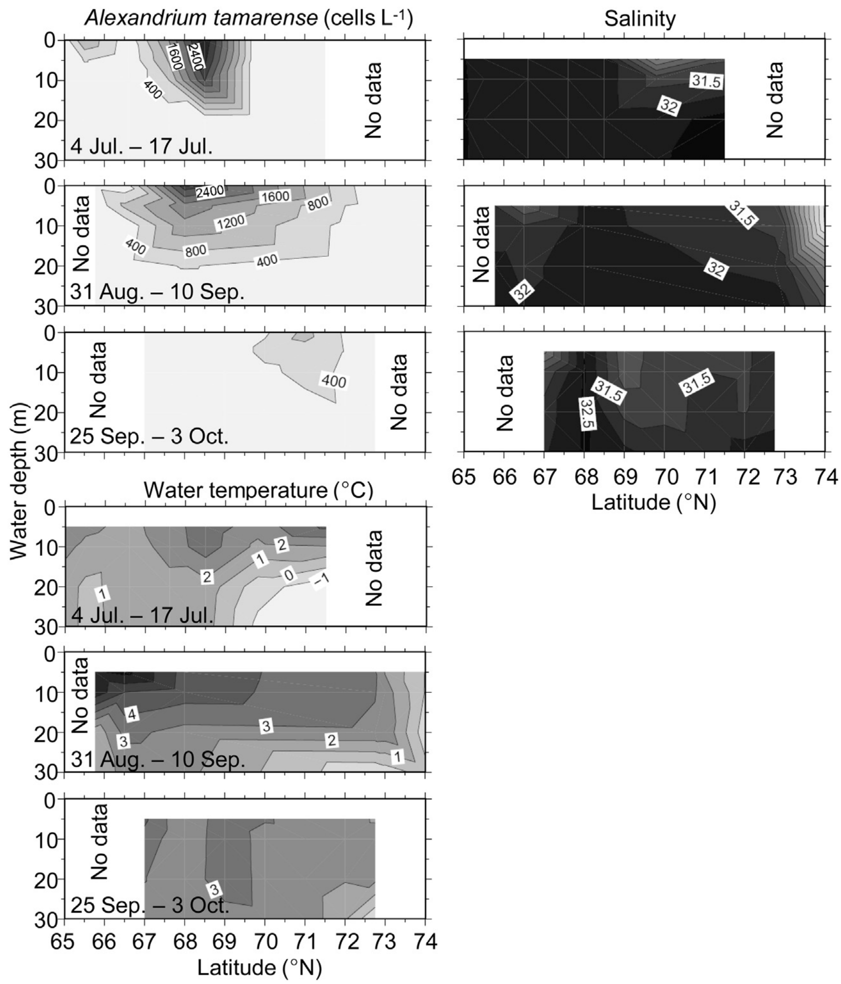

Fig. 5. Temporal changes in *Alexandrium tamarense* cell density, salinity, and water temperature from 0 to 30 m along the transect line from 65 (north Bering Sea shelf) to 74°N (north Chukchi Sea shelf) through the Bering Strait.

autumn (Fig. 3). This study also revealed seasonal changes in *A. tamarense* populations, where they increased and peaked during summer, and decreased during late summer. The vegetative cells of *A. tamarense* was detected at northern stations (i.e., north of 73°N) during the third period (Fig. 3), which is the northernmost record of the species to date. On the other hand, the sampling stations of this study were not same in the three successive periods (Fig. 1), due to time limitation and difficulty to invade to northern area by sea ice coverage. Thus, the present study could not fully reveal northern distribution of *A. tamarense* during first and third sampling periods (>72°N) in the Chukchi Sea and the distribution of *A. tamarense* in the northern Bering Sea shelf during second and third periods (<67°N; Fig. 5). In addition, a large gap between the stations on the transect line exists during second period (69–71°N; Fig. 3). Therefore, observation for *A. tamarense* collection in continuous stations during successive periods are still required to fully understand their distributions in the northern Bering Sea and Chukchi Sea shelves.

The contamination of shellfish, such as mussels on the seashore and scallops on the sea bed, with toxins exceeding regulatory levels is typically observed when *A. tamarense* densities are greater than 100–1000 cells L^{-1} in western Canada and northern Japan, located in a subarctic climate (Blasco et al., 2003; Shimada et al., 2012). In this study, the density of *A. tamarense* was highest at 3.55×10^3 cells L^{-1} in the Chukchi Sea self (68°30′N) and at 3.01×10^3 cells L^{-1} in the northern Bering Sea shelf (65°N). These densities were much higher than the alert level for shellfish contamination. Moreover, *A. tamarense* was continuously detected at densities of greater than 100 cells L^{-1} from the stations in the Chukchi Sea and north Bering shelves from 65°N to 72°45′N throughout the sampling periods. In addition, the dominant toxin of the *A. tamarense* strains isolated from the sediments of the Chukchi Sea shelf is saxitoxin (Natsuike et al., submitting), which is one of the most toxic paralytic shellfish poisons (PSPs), while the dominant toxins of other reported *A. tamarense* strains are C2, GTX3, and GTX4 (Natsuike et al., submitting). Therefore, high PSP toxin contamination of shellfish is strongly suspected to occur with the range of *A. tamarense*, with particularly high toxicity in the Chukchi Sea and north Bering Sea shelves during the summer.

These results suggested that water masses greatly affected the occurrence of *A. tamarense* in the Chukchi Sea and north Bering Sea shelves (Fig. 4). Pacific summer waters from the north Bering Sea into the Chukchi Sea shelf during the summer vary with respect to salinity. Anadyr Water (AW) is highly saline (>32.5 psu) and nutrient-rich, and flows to the west of the strait. Alaska Coastal Water (ACW) is fresher (<31.8) and nutrient-limited, and flows to the east of the strait. The salinity of Bering Shelf Water (BSW) is intermediate (31.8–32.5) between AW and ACW (Coachman et al., 1975; Grebmeier et al., 2006). In addition, surface meltwater with a low salinity (<30) and winter bottomwater with a high salinity and cold temperatures originally spread to the Chukchi Sea shelf (Weingartner et al., 2013). During the first observation period in this study, *A. tamarense* was abundant near the Bering Strait (Figs. 3 and 5); these sampling stations appeared to be occupied by BSW

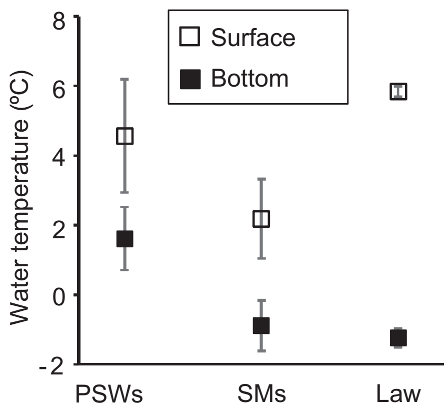

Fig. 6. Variation in *Alexandrium tamarense* cell density, water temperature, and salinity of surface and bottom waters in the Pacific summer waters (PSWs), surface melt, and bottom winter-formed waters in the Chukchi Sea shelf (SMs), and polynya water in the St. Lawrence Island during the first and second periods (Law). Open symbols indicate measured values and the error bars show the standard deviation on the fitted mean.

(Fig. 4). During the second period, abundant *A. tamarense* was observed at stations in the south Chukchi Sea shelf, and these stations included a mixture of PSW and surface meltwater (Fig. 4). Finally, *A. tamarense* was mainly detected on the northern part of Chukchi Sea shelf during the third period, which was also characterized by the mixture of PSW and surface meltwater (Fig. 4). This species was rarely detected at stations belonging to the ACW, south of St. Lawrence Island, and surface meltwater during the sampling periods. Thus, *A. tamarense* was abundant in areas affected by the PSW, except the ACW, and spread to the north of the Chukchi Sea shelf with the inflow of PSW. Recent climatic warming in the Arctic region has increased the inflow of the PSW in the Chukchi Sea shelf (Shimada et al., 2006; Woodgate et al., 2010). This increase in the PSW likely contributed to the widespread occurrences of *A. tamarense* in the Chukchi Sea shelf. Natsuike et al. (2013) observed abundant *A. tamarense* cysts in sediment samples collected from nearly the entire shelf area in the summers of 2010 and 2012. These results indicate that occurrences of *A. tamarense* in the Chukchi Sea shelf corresponded with a reduction in sea ice and increase in PSW inflow.

Fig. 6 depicts the average surface and bottom water temperatures for each water mass (PSWs, surface melt and winter-formed bottom waters, and polynya water south of St. Lawrence Island) during the first and second periods of the *A. tamarense* expansion phase. The surface water temperature of the PSW was significantly higher than that of the surface meltwater, which originally spread to the Chukchi Sea shelf ($p < 0.01$, one-way ANOVA with Dunnett's multiple comparison post-hoc test), and the bottom water temperature of PSWs was also significantly higher than those of the winter-formed bottom water and polynya water ($p < 0.001$, one-way ANOVA with Dunnett's multiple comparison post-hoc test). Thus, PSWs were characterized by higher surface and bottom water temperatures, which promote the proliferation of *A. tamarense*. The cell growth and cyst germination of *A. tamarense* increase for water temperatures of 1–10 °C and reach an optimum at 10–20 °C (Watras and Chisholm, 1982; Perez et al., 1998; Miyazono, 2002; Natsuike et al., submitting). Therefore, increased surface and bottom water temperatures owing to PSW inflow likely promoted cyst germination and the vigorous growth of *A. tamarense* in the Chukchi Sea shelf. Cysts of *A. tamarense* are thought to germinate less effectively under the lower bottom water temperatures of the polynya (south of St. Lawrence Island) and winter-formed water in the Chukchi Sea shelf. As a result, the occurrence of *A. tamarense* in these water masses was significantly lower than that in PSWs. Increase in water temperature likely promotes cyst germination rate in the Chukchi Sea shelf, based on the results of in vitro cyst germination experiments. Nevertheless, in situ germination rate were not investigated in this study. Recently, some methods to estimate in situ cyst germination flux have been developed (Ishikawa et al., 2007; Natsuike et al., in press), and thus estimation of contribution of *A. tamarense* cysts to occurrence of vegetative cells in water column is considered to be next important issue to understand dynamics of *A. tamarense* vegetative cells in Chukchi Sea shelf.

5. Conclusion

The present study revealed that toxic *A. tamarense* is widely distributed throughout the Chukchi Sea and north Bering Sea shelves during the summer. Moreover, the occurrences of this species most likely spread to the Chukchi Sea shelf in the summer, with the inflow of warmer PSWs from the north Bering Sea. Warmer PSWs likely promoted high rates of cyst germination and cell growth in the species. Thus, occurrence of *A. tamarense* during summer are strongly affected by the reduction in sea ice and increase in PSW inflow owing to warming. This species causes PSP toxin contamination of zooplankton (White, 1981), and feeding on these contaminated animals causes mass mortalities through the food web, including fishes, seabirds, and whales (Armstrong et al., 1978; White, 1981; Geraci et al., 1989; Montoya et al., 1997). Results of the present study inferred that toxic *A. tamarense* blooms potentially occur in response to future warming and accordingly will impact various animal taxa in the Chukchi Sea shelf, as predicted by Walsh et al. (2011).

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