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Strong regionalism in dinoflagellate cysts in recent sediments from the Chukchi-East Siberian Seas, Arctic Ocean

--Manuscript Draft--

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Abstract:	The Pacific sector of the Arctic Ocean, a region with the fastest sea-ice loss in recent decades, is experiencing unprecedented biological regime shifts in its marine ecosystems today. However, a shelf-wide characterization of marine plankton communities over this region and environmental processes behind it remain largely unresolved, despite phytoplankton phenology is now considered to be an important factor for assessing how Arctic Ocean interacts with global climate change. Here, we present the first detailed description of recent dinoflagellate cyst assemblages in 32 surface sediment samples from the Chukchi–East Siberian Sea shelves, the Pacific Arctic Ocean, to examine their biogeographic patterns and associated environmental forcing factors. We find a strong regionalization in the species composition and distribution along the shallow-shelf cyst accumulation zone; in the Chukchi Sea sector, northward flow of warm-Pacific water along with extreme seasonality, sufficient nutrient supplies and higher light availability leads to a large occupation of cosmopolitan, opportunistic-nature taxa, whilst the East Siberian Sea sector with more extensive sea-ice cover and lower temperatures is primarily dominated by “round brown spiny cyst” taxa that have a strong affinity for cold, polar conditions. Specifically, an exclusive dominance of heterotrophic taxa at the East Siberian Sea region is inferred to be closely tied to Atlantic-origin water intrusions that lift nutrient-rich, cold bottom water up to oligotrophic surface layer to grow diatoms and other prey organisms. The observed contrast in this geographical “hot spot”, where the Pacific- and Atlantic-origin waters face each other, clearly manifests a growing expansion of southern waters into an increasingly ice-free Arctic Ocean that reshapes Arctic Ocean biogeography from the base of marine food chains. Our study highlights considerable potential of

	dinoflagellate cysts as a valuable environmental proxy to indicate complex interactions between ocean physics and marine biology under the rapidly changing Arctic climate system.
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Response to Reviewers:	

COVER LETTER

December 28, 2022

Dear Prof. Enrique Curchitser, Editor-in-Chief, and Referees:

We are sending herewith our revised manuscript, ″Strong regionalism in dinoflagellate cysts in recent sediments from the Chukchi-East Siberian Seas, Arctic Ocean″ [PROOCE-D-22-00155], which we would like to re-submit for publication in Progress in Oceanography.

We appreciate you and the reviewers for careful and thorough reading of our manuscript, and the positive and thoughtful comments that help to improve the quality of this manuscript. The manuscript has been modified according to your comments and suggestions, and detailed corrections are listed below point by point. We hope that all these changes fulfill the requirements to make the manuscript acceptable for publication in Progress in Oceanography.

Thank you again for your time and effort you′ve sent on reviewing our manuscript.

Yours sincerely,

So-Young Kim on behalf of the authors

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AUTHORS' RESPONSE TO DECISION LETTER

Manuscript Number: PROOCE-D-22-00155
Strong regionalism in dinoflagellate cysts in recent sediments from the Chukchi-East Siberian Seas, Arctic Ocean

Editor:

Thank you for submitting your manuscript to Progress in Oceanography. I have received comments from reviewers on your manuscript. Your paper should become acceptable for publication pending suitable minor revision and modification of the article in light of the appended reviewer comments. When resubmitting your manuscript, please carefully consider all issues mentioned in the reviewers' comments, outline every change made point by point, and provide suitable rebuttals for any comments not addressed.

***Associate Editor*:**

Both reviewers appreciated the improvements to the manuscript made in the revision, and both have just a few additional items that would add to the value of the manuscript. I do not think it will take very long to address these.

Authors' response: The authors are very grateful for your and the reviewer's comments, and the positive evaluation of our work. We truly appreciate the feedback which indeed helped us to improve the quality of this manuscript. As required, we have revised the texts and figures according to the referee's critiques. We hope that the revision is satisfactory and the paper would now be found suitable for publication. We address all the reviewer's comments below (the author's responses are in blue fonts).

Reviewer's Responses to Questions:

[Q1] Reviewer 2: The revised MS is much improved relative to the original version. However, I believe a few more areas of the MS may need more revision. The most important is a remaining lack of discussion of sediment age. It is understood that determining the age of the analysed sediments is too much to request for this study. However, the authors could well discuss the potential age ranges based on the estimates for the uppermost sediments (cm scale) in or nearby the study area. There is a number of recent papers that provide relevant data, notably, Cooper & Grebmeier, 2018; Astakhov et al., 2019.

Authors' response: We would like to thank the reviewer's careful reading of the manuscript, and for the additional suggestions for further improvement. We appreciate the reviewer for bringing these papers to our attention. In line with the reviewer suggestion, we have added sentences in the Discussion section as below:

➔ line 465-471) "Despite that information on sedimentation rates are lacking for the study area, there are reports of estimations made at the Chukchi Shelf region – for instance, the southern/central Chukchi Sea (0.03 – 0.37 cm/yr; Cooper and Grebmeier, 2018), the central Chukchi Sea (0.04 – 0.91 cm/yr; Astakhov et al., 2019) and the northern Chukchi Sea (0.09 cm/yr; Kim et al., 2020b). Accordingly, it can be tentatively speculated that the sediment materials under study may represent about 1 – 30 years of sediment accumulation."

[Q2] Regarding the taphonomic issues, the revised version addresses the cyst preservation factor. However, there can be more factors involved, such as dilution by terrigenous sediment, which is closely related to sedimentation rates discussed above.

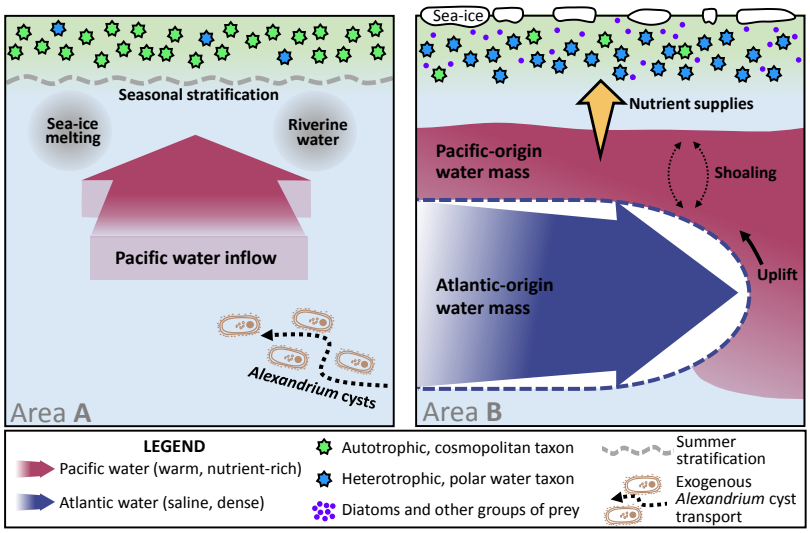
Authors' response: We thank for the reviewer's kind reminders. In line with the reviewer's suggestion, a new sentence has been added to address this point, as follow:

➔ line 473-476) "In particular, magnitudes of terrigenous particulate matter input from nearby continents could have influenced accumulation rates of sediments at varying degrees, which in turn can dilute or enhance the sedimentary dinoflagellate cyst signals."

[Q3] Also, I don't understand what's the problem with fixing Fig. 6. Is it so difficult to swap the panels? Having the first mentioned panel on the right is confusing. And the removal of the panel letters A and B just adds more confusion as it makes more difficult to relate the figure to the text.

Authors' response: We apologize here, as we unfortunately misunderstood the reviewer's previous request. In line with the reviewer's suggestion, we have revised the figure.

➔ Revised Figure 1



➔ line 1149-1164) **Figure 6.** Conceptual overview of mechanisms causing regional contrasts in dinoflagellate cyst distributions between the Chukchi Sea (area A) and the East Siberian Sea (area B) under the current Arctic warming trend. Area A (left panel) exemplifies the increasing northward Pacific water flow (red arrow) affecting dinoflagellate production in the Chukchi Sea environment. The warm, nutrient-rich Pacific water inflow not only supplies enough nutrients for dinoflagellate population growth, but also increases freshwater input by melting sea-ice and delivering riverine waters (gray shaded circles) that generate more open water habitat with strong seasonal stratification (gray dotted line) favored by autotrophic and opportunistic dinoflagellate taxa (green stars). The black dashed arrow indicates a possible transport of PSP-causative *Alexandrium* cysts from the Alaskan Arctic cyst deposits by local hydrodynamics and wind-induced currents. Area B (right panel) illustrates an intensification of the Atlantic-origin water intrusion (blue arrow) to the East

Siberian Sea. The increased saline, dense Atlantic-origin water mass lifts the overlying nutrient-rich Pacific-origin waters up to the oligotrophic surface water, which boosts high production of photosynthesizing primary producers (purple dots) and ensuing heterotrophic, polar water dinoflagellate taxa (blue stars).

Response to Reviewer 1's comments:

Thanks for taking into consideration my comments and suggestions. The paper improved a lot and I enjoyed reading it. I only have a few minor comments:

Authors' response: We are grateful for the positive and kind comments. The reviewer's suggestions are helpful for us to refine this paper. Our responses to your comments are given in a point-by-point manner below.

[Q4] Line 408: The ? is missing on *Islandinium cezare* -> *Islandinium? cezare*
Also, table 3: *Islandinium cezare* sensu lato -> *Islandinium? cezare* sensu lato

Authors' response: We corrected the text.

➔ line 409) "... *E. karaense, I.*? *cezare* s.l. and..."

➔ Table 3

Islandinium? *cezare*	Unknown	Icez	H	0–3.3
Islandinium? *cezare* sensu lato – Morphotype 1 (Head et al., 2001)	Unknown	Icez M1	H	0–12.9

[Q5] I have one small concern about the use of "marine phytoplankton", as I said in the first review, dinoflagellates are phototroph and heterotroph, so it may be better to say marine plankton -> Lines 27 & 85

Authors' response: We changed the text as suggested.

➔ line 27) "a shelf-wide characterization of marine plankton communities over this region and... "

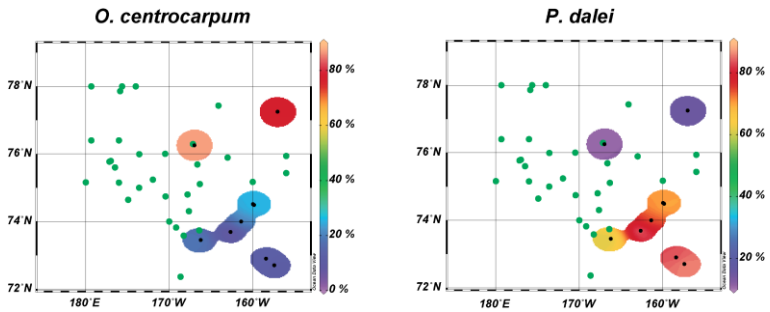
➔ line 85) "However, understanding marine plankton characteristics in... "

[Q6] Line 576 "Our study highlights considerable potential of dinoflagellate cysts as a valuable proxy for changes in hydrographic conditions and phytoplankton communities in the Arctic marine ecosystem." -> plankton communities

Authors' response: We have changed the text as suggested.

➔ line 585) "…hydrographic conditions and plankton communities in the Arctic marine ecosystem."

[Q7] Last concern: In de Vernal et al., 2020, and in Marret et al., 2020, when you look at the distribution of the sites from the same coordinate as yours, from 72 to 78°N and from 166°W to 156°E. There are 8 sites (see map below). You have to acknowledge those sites somewhere. In fact, they actually record the same pattern as yours; a dominance of *P. dalei* and *O. centrocarpum*. You may just write:
Line 222: "overwhelming dominance of autotrophic taxa cysts of P. dalei (max. 5505 cysts/g, 79%) and O. centrocarpum s.l. (max. 2687 cysts/g, 51%), as previously reported by Radi et al. (2001)." -> as previously reported by Radi et al. (2001) and found in the 8 samples of the 1968 database (de Vernal et al., 2020). Or introduce them somewhere else.



Authors' response: We agree with the reviewer's suggestion and have modified the sentence.

➔ line 222-223) "Samples from the Chukchi Sea shelf sites are characterized by an overwhelming dominance of autotrophic taxa cysts of *P. dalei* (max. 5505 cysts/g, 79%) and *O. centrocarpum* s.l. (max. 2687 cysts/g, 51%), as previously reported by Radi et al. (2001) <u>and found in the 8 samples of the 1968 database (de Vernal et al., 2020).</u>"

Highlights

• Biogeography of dinoflagellate cysts in the Pacific Arctic Ocean were investigated.

• Strong regionality infers a growing impact of southern waters on warming Arctic Ocean.

• Toxic-*Alexandrium* cyst accumulations point to potential bloom initiation in Arctic Ocean.

• Dinoflagellate cysts are useful indicators of Arctic marine conditions under global warming.

Strong regionalism in dinoflagellate cysts in recent sediments from the Chukchi-East Siberian Seas, Arctic Ocean

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Abstract

The Pacific sector of the Arctic Ocean, a region with the fastest sea-ice loss in recent decades, is experiencing unprecedented biological regime shifts in its marine ecosystems today. However, a shelf-wide characterization of marine plankton communities over this region and environmental processes behind it remain largely unresolved, despite phytoplankton phenology is now considered to be an important factor for assessing how Arctic Ocean interacts with global climate change. Here, we present the first detailed description of recent dinoflagellate cyst assemblages in 32 surface sediment samples from the Chukchi–East Siberian Sea shelves, the Pacific Arctic Ocean, to examine their biogeographic patterns and associated environmental forcing factors. We find a strong regionalization in the species composition and distribution along the shallow-shelf cyst accumulation zone; in the Chukchi Sea sector, northward flow of warm-Pacific water along with extreme seasonality, sufficient nutrient supplies and higher light availability leads to a large occupation of cosmopolitan, opportunistic-nature taxa, whilst the East Siberian Sea sector with more extensive sea-ice cover and lower temperatures is primarily dominated by "round brown spiny cyst" taxa that have a strong affinity for cold, polar conditions. Specifically, an exclusive dominance of heterotrophic taxa at the East Siberian Sea region is inferred to be closely tied to Atlantic-origin water intrusions that lift nutrient-rich, cold bottom water up to oligotrophic surface layer to grow diatoms and other prey organisms. The observed contrast in this geographical "hot spot", where the Pacific- and Atlantic-origin waters face each other, clearly manifests a growing expansion of southern waters into an increasingly ice-free Arctic Ocean that reshapes Arctic Ocean biogeography from the base of marine food chains. Our study highlights considerable potential of dinoflagellate cysts as a valuable environmental proxy to indicate complex interactions between ocean physics and marine biology under the rapidly changing Arctic climate system.

Keywords: Dinoflagellate cysts, Sediments, Arctic Ocean, Climate warming

1. Introduction

In recent years, extreme climatic events have increased across the Northern Hemisphere mid-latitudes – e.g., unusual heatwaves, rainfall and severe winter weather in Eurasia and North America (Trenberth, 2011; Rahmstorf and Coumou, 2011; Coumou and Rahmstorf, 2012; Gallant et al., 2014; Donat et al., 2016). The increasing frequency of such mid-latitude weather extremes is currently ascribed to the Arctic's rapid warming (Honda et al., 2009; Francis and Vavrus, 2012; Tang et al., 2013; Kim et al., 2014; Cohen et al., 2014, 2018; Blackport and Screen, 2020), which is most notably manifested as a drastic shrinkage of the summer Arctic sea-ice cover (Stroeve et al., 2012a; Zhang et al., 2013; Gascard et al., 2019). The warming-induced Arctic sea-ice loss is predicted to be accelerated over the coming decades (Stroeve et al. 2012b; Overland and Wang, 2013; Wang and Overland, 2015), tentatively fueling knock-on effects for the lower latitude continental weather. This new climatic status settling over the Arctic Ocean, shifting from a frozen region with heavily ice-covered environments to a warmer, increasingly ice-free condition, is closely linked to anomalous Atlantic- and Pacific-origin water advections from lower latitudes – commonly referred to as borealization (Polyakov et al., 2017, 2018, 2020; Woodgate et al., 2012; Woodgate, 2018; Tsubouchi et al., 2021). Its impacts are most clearly observed in significant biogeographical shifts in Arctic marine ecosystems, such as alterations in species distribution and composition of biological communities across all trophic levels (Questel et al., 2013; Fossheim et al., 2015; Gall et al., 2016; Pinchuk and Eisner, 2017; Vihtakari et al., 2018; Møller and Nielsen, 2020).

In this respect, the Pacific sector of the Arctic Ocean (i.e., the Chukchi and East Siberian seas) is a geographical focus for climate studies today, because this region has experienced the most rapid decline in sea-ice cover over the recent decades (Shimada et al., 2006; Steele et al., 2008; Stroeve et al., 2012a, b; Frey et al., 2015). In the Chukchi Sea, one of the most productive regions in the Arctic Ocean, the drastic sea-ice loss and associated hydrographic changes have induced a significant regime shift in its biological communities and productivity across the whole marine food web (e.g., Jin et al., 2009; Grebmeier, 2012; Ershova et al., 2015). Particularly, given the emerging biogeophysical significance of marine phytoplankton in amplifying surface warming of the Arctic Ocean (e.g., Lim et al. 2019a,b; Park et al., 2015, 2020; Pefanis et al., 2020), phenological variability of dominant phytoplankton community members over this region can carry vital information about the

complex interactions between biological system and the current Arctic warming trend. However, understanding marine plankton characteristics in a rapidly changing Arctic Ocean, particularly for the Pacific sector of the Arctic Ocean, has yet remained important but largely unexploited.

Dinoflagellates are highly diverse unicellular eukaryotic organisms in a wide range of aquatic environments, representing one of the major marine plankton groups along with diatoms and coccolithophores (Taylor, 1987; Falkowski et al., 2004; Delwiche, 2007). Approximately 20% of living dinoflagellate species are known to produce resting cysts, a benthic dormant stage, mainly composed of a complex biomacromolecule substance and highly resistant to physical, chemical and biological degradation (e.g., Dale, 1983; Versteegh and Blokker, 2004). Therefore, they have a strong preservation potential in sediments deposited under various environmental settings, even where other siliceous and calcareous microphytoplankton groups are subject to dissolution problems (e.g., Williams, 1990; de Vernal et al., 1992). These characteristics make sedimentary dinoflagellate cysts can serve as a useful indicator of present and past marine productivity in the photic zone. The reliability of dinoflagellate cyst signals depends on a sound understanding of their spatial distributions in relation to environmental parameters, which can be region-specific. Notwithstanding of numerous studies dedicated to develop a global biogeographic database of dinoflagellate cysts and their environmental correlates (e.g., de Vernal et al., 2001; Marret and Zonneveld, 2003; Zonneveld et al., 2013; Marret et al., 2020), the Pacific sector of the Arctic Ocean is still poorly documented. Thus, biogeographic information on dinoflagellate cysts in this region is pertinent to fill the gap in the current reference database, and also to identify its possible correlation with crucial environmental factors. Moreover, recent studies drew attention to cyst accumulations of *Alexandrium*, a major producer of paralytic shellfish poisoning (PSP)-associated neurotoxin, in seafloor sediments at the Chukchi Sea region (Natsuike et al., 2013; Anderson et al., 2021; Obrezkova et al., 2022). Because the Arctic waters were previously believed to be safe from such high levels of this algal toxin due to unfavorable habitat conditions limiting general phytoplankton growth, such unprecedented phenomenon signifies a substantial transformation occurring in the environments.

Here, we report on the distribution of dinoflagellate cysts from 32 surface sediments collected from the Pacific sector of the Arctic Ocean, encompassing the area from the Chukchi shelf to the northeastern part of the East Siberian Sea. Influenced by combined

effects of rapidly changing sea-ice conditions and contrasting water masses of different origins, the study area shows great gradients in sea-surface environmental variables (Wassmann et al., 2015; Wang et al., 2021), and is expected to have a tangible effect on the dinoflagellates and their cyst distributions at the region. The ultimate goals of this study are: (1) to provide information, for the first time concerning this data-sparse region, about the spatial distribution and abundance of dinoflagellate cyst assemblages; and (2) to identify dominant forcing factors driving their distributional patterns.

2. Materials and methods

2.1. Sample collection, laboratory treatments and cyst identification

A total of 32 surface sediment samples were collected from the Pacific sector of the Arctic Ocean with a box corer and a multiple corer during several research cruises of the R/V ARAON from 2011 to 2018 (Fig. 1). The sampling locations are distributed from 72 to 78°N and from 166°W to 156°E, within water depths of 43–3084 m across the Chukchi Sea and East Siberian Sea shelves including the Chukchi Plateau and Mendeleyev Ridge (Table 1). Dinoflagellate cyst analysis was performed on the uppermost sediment layers (~1 cm) with an undisturbed sediment/water interface and no sign of bioturbation. Each sub-sample of the surface sediments was processed, following the standard palynological preparation procedure described by Marret and Zonneveld, 2003. Approximately 10–30 g of wet sediment per sample were oven-dried at 60°C for 24 hours and weighted. After adding a *Lycopodium clavatum* spore tablet of batch #1031 (X = 20,848 per tablet, σ = ±1546, University of Lund) to each sample, they were treated with 20 mL of cold 10% hydrochloric acid (HCl) for the removal of calcium carbonate. After 20 min, the residue was rinsed with distilled water, and 20 mL of cold 40% hydrofluoric acid (HF) was added and left for 20 min to remove silicates. The HCl and HF steps were repeated 2–3 times. Afterwards, the cold HF was added to the residue, and after resting overnight and decantation, the cold HCl was added for 20 min. The final residues were washed with distilled water to neutralize the pH. To shorten settling time and avoid losing the residue, centrifugation was used at each step of decanting at 3000 r min−1 for 10 min. Then samples were passed through a 10-μm pore-sized mesh sieve and the residue was preserved in a 10-mL vessel with two to three drops of phenol added. Dinoflagellate cysts were counted with an Axio Imager A2 microscope (Carl Zeiss Microscopy GmbH) at 400× and 1,000× magnification. Dinoflagellate cyst identification

follows published morphological descriptions (Rochon et al., 1999; Head et al., 2001; Radi et al., 2001; Radi and de Vernal, 2004; Radi et al., 2013; Potvin et al., 2018). Most dinoflagellate cyst types were identified at the species level except for *Brigantedinium*, round brown cysts, which often did not allow clear observation of the archeopyle due to the orientation or folding of the cyst. These cysts were grouped as *Brigantedinium* spp without further identification. Another exception is the cysts produced by *Alexandrium*, which are also difficult to assign to species morphologically using microscopy. Therefore, these cysts with ellipsoidal and transparent wall surrounded by a mucous layer are counted as cysts of *Alexandrium* spp (Fig. 2a). We distinguished *Operculodinium centrocarpum* sensu Wall and Dale (1966) with long, fully developed processes and *O. centrocapum* characterized by short, poorly developed processes ("Arctic morphotype"), following Rochon et al. (1999), de Vernal et al. (2001) and Radi et al. (2001) – both morphotypes are assigned to *O. centrocarpum* sensu lato (s.l.) (Fig. 2d, e).

Where possible, at least 300 specimens of dinoflagellate cysts were counted per sample. Concentrations of each dinoflagellate cyst sum counted are expressed as concentrations of dinoflagellate cysts per weight of dry sediment. The concentration of palynomorphs was calculated as follows (Benninghoff, 1962):

$$c \text{ (dinoflagellate cysts g}-1 \text{ dry sediment)} = \frac{g_c \times L_t \times t}{L_c \times w}$$

where c is the concentration = number of dinoflagellate cysts per gram of dry sediment, g_c is the number of counted dinoflagellate cysts, Lt is the number of *Lycopodium* spores/tablet, t is the number of tablets added to the sample, Lc is the number of counted *Lycopodium* spores, and w is the weight of dried sediment (g).

[Insert Figure 1]

[Insert Table 1]

[Insert Figure 2]

2.2. Statistical treatments

Ordination techniques based on multivariate analyses were carried out to identify patterns in the distribution of species and assemblages and to attempt to relate them to environmental factors. We used the software PRIMER v7 (Clarke and Gorley, 2015) as it offers a large range of statistical functions to analyse abiotic and biotic datasets. For the dinoflagellate cyst assemblages, we performed a non-metric multidimensional scaling (nMDS) analysis on standardized and square-root transformed dinocyst raw data. All species were included in this analysis. For the examination of the distribution and importance of abiotic (environmental) parameters, a covariance based principal component analysis (PCA) was carried out, as recommended by Clarke and Gorley (2015). Environmental parameters were normalised as they can have a large range of measurement scales. We selected a number of surface environmental conditions that we know to influence dinoflagellate cyst distribution (e.g., de Vernal et al., 2020) (Table 2).

[Insert Table 2]

3. Results

3.1. Dinoflagellate cyst assemblages and abundance

Twenty-eight dinoflagellate cyst taxa were identified from the 32 study sites, excluding unidentifiable round brown spiny cyst (RBSC) type (Table 3). Dinoflagellate cysts were observed in all the sediment samples, and species richness at any single sample ranged between 2 (site 20) and 20 (site 1), with an average of 11 taxa per site. Total dinoflagellate cyst concentrations at each sampling site are shown in Table 1 and Fig. 3. The concentrations per sample ranged from 104 to 10179 cysts/g (1737 cysts/g on average). In general, higher concentrations are observed in the shallow shelf locations: sites 1–9 in the Chukchi Sea (981–10179 cysts/g, 3977 cysts/g on average) and sites 24–32 in the East Siberian Sea (522–4512 cysts/g, 1642 cysts/g). Samples from ice-covered/higher-latitude regions have lower concentrations (sites 10–23; 104–1029 cysts/g, 383 cysts/g on average).

[Insert Table 3]

[Insert Figure 3]

Overall, dinoflagellate cyst assemblages are dominated by cysts of *P. dalei*, *O. centrocarpum*, *O. centrocarpum*-arctic morphotype, *I. minutum*, *I. minutum* subsp. *barbatum* and *E. karaense*. Other taxa that have relatively high abundance include *S. elongatus*, *Brigantedinium* spp., *Islandinium*? *cezare* morphotype 1 (M1; Head et al. 2001) and *I. brevispinosum*. Composition of the cyst assemblages shows some significant spatial patterns within the shallow shelf sites, particularly distinguished by their trophic preferences (nutritional strategy): either "autotrophs" that are photosynthesizing primary producers, or "heterotrophs" feeding on light-dependent organisms such as diatoms (Jacobson and Anderson, 1986; Smayda and Reynolds, 2003). Samples from the Chukchi Sea shelf sites are characterized by an overwhelming dominance of autotrophic taxa cysts of *P. dalei* (max. 5505 cysts/g, 79%) and *O. centrocarpum* s.l. (max. 2687 cysts/g, 51%), as previously reported by Radi et al. (2001) and found in the 8 samples of the 1968 database (de Vernal et al., 2020). In contrast, the East Siberian Sea shelf samples are largely occupied by heterotrophs *I. minutum* (max. 1867 cysts/g, 58%), *I. minutum* subsp. *barbatum* (max. 957 cysts/g, 30%) and *E. karaense* (max. 523 cysts/g, 13%), although at some sites, the cyst of *P. dalei* is present in significant amounts.

I. minutum subsp. *barbatum* tends to be exclusively restricted to the shallow East Siberian Sea shelf (sites 24–31; 76–957 cysts/g, 7–30%), whereas only a few are found in the Chukchi Sea samples (except for site 2). Cysts of *Alexandrium* species also show a very restricted distribution, only being found at sites very close to the Bering Strait (sites 1–3; up to 325 cysts/g, 3.8%), while other samples turned out to be almost barren (Fig. 3).

3.2. Statistical analysis

The nMDS carried out on the dataset shows some significant patterns. The ordination of species (Fig. 4a) clearly highlights the grouping of species according to the trophic aspect; interestingly, the species *Trinovantedinium applanatum* appeared within the autotrophic cluster.

The covariance based PCA on environmental parameters (Fig. 4b) shows that the ordination of samples is mostly explained by summer productivity along the first axis (40.2%) and summer SST and sea ice along the second axis (23.6%). Other factors seem to have some influence of the samples' ordination, with a third PC dimension explaining 17.5% of the variation. The nMDS (Fig. 4c) shows a clear grouping of dinoflagellate cyst assemblages and

could be associated with dominating environmental factors (stress is 0.08), notably the assemblages from the East Siberian Sea (summer productivity and silicate).

[Insert Figure 4]

4. Discussion

In general, dinoflagellate cysts were well preserved in the investigated materials and their numbers are highly variable. Two distinctive features can be identified in the dinoflagellate cyst data and provide insight on the nature of dinoflagellate cyst assemblages and their distributional patterns. First, the dinoflagellate cyst data show high accumulations at locations of lower latitude, shallow-shelf environments. Second, there is a strong spatial disparity in the assemblage compositions and abundances at the cyst accumulation zone – geographically divided into two areas: sites 1–9 on the northern Chukchi Sea shelf (A) and sites 24–32 (B) on the East Siberian Sea shelf (Figs. 1 and 5).

4.1. Dinoflagellate cyst assemblages and their general trends

There are few published works focused on species-specific characteristics of organic-walled dinoflagellate cysts in the Chukchi Sea and East Siberian Sea shelf sediments (e.g., Natsuike et al., 2013, 2017; Potvin et al., 2018; Anderson et al., 2021). With the exception of Radi et al. (2001), we find no studies of spatial variability in species composition and assemblages of dinoflagellate cysts in the region. Therefore, comparisons of dinoflagellate cyst distribution patterns observed in the present study are geographically limited. Our study shows dinoflagellate cyst concentrations in the investigated area are generally high (104–10,179 cysts/g), and are in the same order of magnitude as those reported from other regions of the Arctic Ocean such as the northeastern Chukchi Sea (2000–25,000 cysts/cm^3; Radi et al., 2001), western Svalbard (88–33,234 cysts/g; Grøsfjeld et al., 2009) and West Greenland margin (> 10,000 cysts/g; Allan et al., 2020). It is known that species diversity of dinoflagellate cysts in sub-Arctic and Arctic environments generally constitutes ~ 20 species (e.g., de Vernal et al., 2001; Radi et al., 2001; Matthiessen et al., 2005; Grøsfjeld et al., 2009; Solignac et al., 2009; Allan et al., 2020; Marret et al., 2020), and this is well consistent with our study (6–20 cyst types per sample; Table 3). The dinoflagellate cyst assemblages in the present study include cosmopolitan taxa that are tolerant to a wide range of hydrographical

conditions (e.g., *O. centrocarpum*, *Brigantedinium* spp. and *Spiniferites* group). Typical cold polar water taxa – such as the Arctic morphotype of *Polykrikos* sp. (Potvin et al., 2018), *Islandinium*? *cezare* s.l. (i.e., *Islandinium*? *cezare* and *Islandinium minutum* subsp. *barbatum*; see Van Nieuwenhove et al., 2020), *Echinidinium karaense* and *Impagidinium pallidum* – were also the main components of the assemblages and generally well conform to those characterizing the Arctic type environment (e.g., Head et al., 2001; de Vernal et al., 2001; Radi et al., 2001; Potvin et al., 2018).

Notably, the dinoflagellate cyst concentrations show a clear latitudinal trend, characterized by high concentrations between 72°N and 75°N that gradually decrease towards the central Arctic Ocean (Fig. 3). Before interpreting such patterns and associated environmental factors in detail, it is important to discuss a possible effect of lateral transport. Because dinoflagellate cysts are generally about 15–100 µm in diameter behaving like silt particles in the water column, they can be transported over large distances by ocean currents or resuspended by bottom currents before their settling down to the sea floor (de Vernal., 2009; Dale, 1996; Mudie and Harland, 1996; Nooteboom et al., 2019, 2020). This implies that the dinoflagellate cysts accumulated at 72°N–75°N may have been formed elsewhere, not necessarily representing higher production of dinoflagellates above the sediment sampling site. Given that the depositional environment in the Chukchi Sea is strongly affected by the Pacific water inflows carrying fine particles via the Bering Strait throughflow (Barnes and Reimnitz, 1974; Viscosi-Shirley et al., 2003; Mathis et al., 2007; Kadko et al., 2008), long-range transportation of dinoflagellate cysts from the northern Bering Sea is possible. However, considering the circulation pattern of Pacific-origin water that is generally deflected eastwards after passing the Bering Strait and does not seem to extend far beyond the northern Chukchi shelf margin (Weingartner et al., 2005; Danielson et al., 2014, 2020), its influence delivering particle materials on the collection sites is unlikely significant. We also note that several studies on the dinoflagellate cyst assemblages in surface sediments from the Bering Sea region have reported a predomination of *O. centrocarpum* (e.g., Radi et al., 2001; Radi and de Vernal, 2004; Bonnet et al., 2012; Orlova and Morozova, 2013) – which disagrees with the present study that shows the highest abundance and percentage of cysts of *P. dalei* at the closest locations from the Strait (sites 1–3; Figs. 1 and 3). Such a clear disparity in the dinoflagellate cyst compositions between the Arctic- and Pacific sides of the Strait seems to infer that the dinoflagellate cyst assemblages in the study area were primarily

determined by *in-situ* ecological mechanisms, rather than long-range transport processes.

The dinoflagellate cyst accumulations that are almost exclusive to the shallow shelf locations (mostly < 130 m deep) may indicate a number of environmental factors that afford such large dinoflagellate production. Primarily, it can be explained by the ecological preference of dinoflagellates for neritic environments where a major part of marine phytoplankton communities originates from (Dale and Fjellså, 1994; Dale, 1996; Marret and Zonneveld, 2003). Another explanation would be that, in contrast to the higher latitude locations where heavy sea-ice cover blocks light and associated photosynthetic activities in the upper waters, seasonally ice-free conditions at these shelf sites would ensure more light availability for phytoplankton growth (de Vernal et al., 2001; Matthiessen et al., 2005). Further, a continuously reducing summer sea-ice extent in this region owing to an intensification of the warm Pacific water inflow in recent years may provide more open-water habitat for phytoplankton population therein (Woodgate et al., 2010, 2012; Woodgate, 2018). Another important factor to consider is a sufficient nutrient supply from the northern Bering Sea and/or adjacent large rivers such as Yukon and Anadyr rivers that appear to play a significant role in supporting higher primary productivity in the shallow Chukchi Shelf sites (Walsh and Dieterle, 1994; Grebmeier et al., 1995; Viscosi-Shirley et al., 2003; Naidu et al., 2003; Carmack et al., 2006).

4.2. Strong regional contrasts in the cross-shelf dinoflagellate cyst distributions

As previously described, surface sediments from the Chukchi-East Siberian seas show an important dinoflagellate cyst accumulation at the shallow-shelf locations subject to a longer open-water season with sufficient nutrient supplies, which may create favorable conditions for overall phytoplankton production. It is intriguing to note that there are site-specific patterns in the cyst assemblage compositions that divide the cyst accumulation zone into two spatial domains: the Chukchi shelf (A; sites 1–9) and the East Siberian shelf (B; sites 24–32) (Figs. 3, 4c and 5). Area A is characterized by a predominance of *P. dalei* cysts with the most intense accumulation at sites 1–4 (2622–5505 cysts/g, 46–67%) and, to a lesser extent, *O. centrocarpum* s.l. (307–2687 cysts/g, 12–51%). A particular note is for the exclusive occurrence of autotrophs including *Spiniferites* group, cysts of *Alexandrium*, *B. tepikiense* and *Impagidinium* species, which are virtually barren in area B. By contrast, area B is dominated by heterotrophic taxa, notably *I. minutum* (72–1867 cysts/g, 8–58%) and "round

brown spiny" cyst group including *I. minutum* subsp. *barbatum*, *E. karaense*, *I.*? *cezare* s.l. and *I. brevispinosum*. Our study questions whether the recognized heterogeneous patterns in the species compositions reflect different environmental forcing factors that separate the assemblages. Results from the nMDS analysis do highlight a relatively strong link between surface parameters and taxa distribution, particularly in relation to surface productivity and nutrients.

[Insert Figure 5]

In general, dinoflagellate cyst assemblages in Arctic environments are reported to be dominated by heterotrophic taxa such as *I. minutum* and *Brigantedinium* spp. (e.g., de Vernal et al., 1997; Rochon et al., 1999; Head et al., 2001; Radi et al., 2001; Grøsfjeld et al., 2009). Therefore, the co-predominance of *P. dalei* cysts and *O. centrocarpum*, which all relate to an autotrophic production, in the A region is noteworthy. A particular note is for the multifold-higher abundance of *P. dalei* cysts in area A, compared with all other specimens (Figs. 3 and 5a). The cyst of *P. dalei*, a cosmopolitan taxon tolerating large temperature and salinity ranges, is commonly observed in sub-Arctic sea sediments (e.g., de Vernal et al. 2001; Mudie and Rochon 2001; Marret et al., 2004; Grøsfjeld et al., 2009; Solignac et al., 2009). In particular, this taxon has a strong affinity for highly stratified and relatively productive waters at a distance from the multiyear sea-ice zone (Radi et al., 2001; Radi et al., 2007; Solignac et al., 2009; Milzer et al., 2013). We note that area A is located among the regions of the low-salinity surface layer where receives large inputs of freshwater from sea-ice melting and river outflow, fueled by increasing northward flow of the warm-Pacific water today (Carmack et al., 2006; Markus et al., 2009; Woodgate et al., 2012; Codispoti et al., 2013; Jung et al., 2021a). This is in accordance with the notion that the dominance of *P. dalei* cysts is resulted from an intense seasonal surface layer stratification led by the massive freshwater supplies, along with a lengthening of summer open-water season (e.g. Grøsfjeld et al., 2009; Heikkilä et al. 2014). It is also noteworthy to mention that *O. centrocarpum*, another cosmopolitan species with large environmental tolerances (Marret and Zonneveld, 2003; Zonneveld et al., 2013; Marret et al., 2020), co-dominates with *P. dalei* cysts at the southernmost Chukchi shelf samples (Figs. 3 and 5b). As this taxon is known to favor unstable water conditions associated with high turbidity, the neritic/oceanic transition and dynamic frontal systems

(Dale, 1996; Dale et al., 2002; Marret and Scourse, 2002), its high occurrence may indicate rather deteriorated water column stability, possibly induced by large temperature-salinity gradients and seasonally fluctuating stratification. This speculation gains further support from higher concentrations of the Arctic morphotype of *O. centrocarpum* in this area, because its morphological variation bearing poorly developed processes is resulted from phenotypic adaptation to rapidly changing salinity environments (e.g., de Vernal et al., 1989; Mertens et al., 2011). All of these seem to confirm a pivotal impact of the Pacific water inflow on the exclusive occupation of these opportunistic-nature taxa in area A; by not only rendering ample supplies of nutrient-rich water and increased light availability during open-water season (Walsh et al., 1989; Grebmeier et al., 1995; Naidu et al., 2003; Codispoti et al., 2005; Lee et al., 2012; Zhuang et al., 2016; Jin et al., 2017), but also creating extreme seasonality and associated environmental stress that are rather too harsh for most other species to thrive (Fig. 6).

[Insert Figure 6]

By contrast, the dinoflagellate cyst assemblage in area B is preferentially occupied by "round brown spiny cyst" taxa (collectively *I. minutum* subsp. *barbatum*, *E. karaense*, *I.*? *cezare* s.l. and *I. brevispinosum*) (Fig. 3). They generally characterize cold polar to subpolar waters of the high northern latitudes, particularly abundant to dominant in regions with an extensive seasonal sea-ice cover, and summer temperatures below 7°C (Rochon et al., 1999; de Vernal et al., 2001; Head et al., 2001). We find that the strong regionalism of this cyst group is well match with a spatial disparity in sea-ice conditions between the areas A and B (Fig. 1d). According to observational studies on the relative change of the sea-ice extent (e.g., Rigor and Wallace, 2004; Rodrigues, 2008), the East Siberian Sea shelf shows more extensive, thick sea-ice cover during the summer months when compared with the Chukchi Sea sector. This may explain the high abundance of *I. minutum* (~ 58%) in area B (Figs. 3 and 5d), as this taxon is known to have an affinity to cold (–2°C), longer sea-ice cover times (up to 12 months per year) (Harland and Pudsey, 1999; Head et al., 2001; Marret and Zonneveld, 2003; Grosfjeld et al., 2009). However, it should be noted that a number of recent studies report no statistical relationship between their occurrences and sea-ice conditions (e.g., Heikkilä et al., 2014, 2016; Allan et al., 2020; de Vernal et al., 2020) and thus, the controls on

their distribution require further investigation. Noteworthy is an exclusive occurrence of *I. minutum* subsp. *barbatum* at this area (Figs. 3 and 5e). Given its more robust geographical restriction than other round brown spiny cysts, we are tempted to suggest this cyst type as a more sensitive indicator of cold, sea-ice covered environments.

It should be noted, however, that cold polar conditions are not necessarily the sole explanation of their abundance in area B. As shown in Figs. 3 and 5, area B exhibits almost selective occupation of *I. minutum*, *I. minutum* subsp. *barbatum*, *E. karaense*, *I.*? *cezare* s.l. and *I. brevispinosm* that are all related to a heterotrophic behavior, compared with area A where their occurrences are overwhelmed by a strong domination of autotrophs (e.g., cysts of *P. dalei*, *O. centrocarpum* s.l. and *Spiniferites* species). This feature may reflect different trophic mode and nutritional environments in area B, which seem to play as a deterministic factor to foster heterotrophic dinoflagellate population therein. Heterotrophic dinoflagellates typically feed on other light-dependent organisms and therefore, their abundance and biomass strongly depend on production of diatoms and other prey groups such as bacteria, nanoflagellates, hapto- and prasinophytes or other dinoflagellate species (Matsuoka, 1999; Godhe and McQuoid, 2003; Kim et al., 2009; Jeong et al., 2010). Indeed, observation data – e.g., chlorophyll-a concentrations, phytoplankton photophysiological properties and microplankton communities – reported remarkably high marine productivity at area B (e.g., Yun et al., 2015a; Ko et al., 2020; Kim et al., 2021; Fig. 1d). In this respect, regardless of the favorable cold, polar conditions aforementioned above, the dominant prevalence of heterotrophic dinoflagellate cysts may strongly relate to such excessive marine primary production and ensuing prey availability. Effects of different nutritional structures and biochemical compositions of photosynthetic organisms on the grazing activity of heterotrophic dinoflagellates are possible (Lee et al., 2009; Yun et al., 2015b; Mills et al., 2018), but these ecophysiological processes are beyond the scope of this study and further in-depth investigations are needed to better understand trophic interactions in this marine ecosystem. Interestingly, our nMDS analysis on cyst taxa (Fig. 3a) highlighted an interesting feature, with the ordination of *T. applanatum* within the autotrophic species. A recent study on the chemical composition of the cyst wall indicates presence of sporopollenin, as well as the occurrence of nitrogen-containing functional groups (Gurdebeke et al., 2020). It is, therefore, possible that the trophic strategy of this species may favor nutrient-rich waters rather than productive waters. However, because there is only limited knowledge of nutrient

environments at the sites, our data cannot provide conclusive evidence and more research with *in-situ* observation data through monitoring schemes is needed to assess this question.

But what can drive such high primary productivity and ensuing opportunity for heterotrophic dinoflagellate population in area B? We tentatively link this feature to a very specific oceanographical phenomenon, the so-called "Atlantification"– i.e., growing intrusions of Atlantic water into the interior of the Arctic Basin as the Arctic becomes increasingly ice-free. It seems now evident that continuing sea-ice loss on the Atlantic side of the Arctic Ocean triggers a weakening of the ocean's cold layering system that blocks Atlantic inflows, and subsequently leads to a warmer, denser Atlantic water spreading toward the eastern Eurasian Basin (Polyakov et al., 2017, 2018, 2020; Bertosio et al., 2022). This notion gains further support from a recent work of Jung et al. (2021b). They observed an intrusion of Atlantic-origin water into the weakened halocline boundary between Pacific and Atlantic-origin waters at a site located in area B (Fig. 1; yellow star). That cold, saline water mass lifts the overlying nutrient-rich Pacific-origin waters up to the upper euphotic zone and consequently boosts anomalously high surface phytoplankton blooms in the area – where otherwise shows highly oligotrophic surface waters during summer (Carmack and Chapman, 2003; Tremblay et al., 2011; Williams and Carmack, 2015). Therefore, it appears conceivable that the heterotrophic dinoflagellate cyst accumulations in area B could be affected by a growing intrusion of the Atlantic-origin water spreading into the East Siberian Sea shelf waters during the time of the cyst production – being an ultimate driver of nutrient-rich, cold bottom water supplies to the surface layer and high level of biological productivity therein (Fig. 6). Considering relatively thicker, stronger summer sea-ice condition in the East Siberian Sea region, the phytoplankton bloom development in area B is likely to be led by photosynthetic ice algae rather than pelagic phytoplankton communities (Hill and Cota, 2005; Wassmann and Reigstad, 2011; Leu et al., 2015). We tentatively suggest that, in addition to the pivotal role of nutrient supply, sea-ice on light regime may act as a unique habitat for ice algae growth and ensuing dominance of heterotrophic dinoflagellates due to its ability to survive in the dark, harsh arctic environments with longer sea-ice cover times (Harland and Pudsey, 1999; Rochon et al., 1999).

If correct, our data may provide sedimentary evidence of the persistence of the aforementioned oceanographic phenomenon on a regional scale. Despite that information on sedimentation rates are lacking for the study area, there are reports of estimations made at the

Chukchi Shelf region – for instance, the southern/central Chukchi Sea (0.03 – 0.37 cm/yr; Cooper and Grebmeier, 2018), the central Chukchi Sea (0.04 – 0.91 cm/yr; Astakhov et al., 2019) and the northern Chukchi Sea (0.09 cm/yr; Kim et al., 2020a). Accordingly, it can be tentatively speculated that the sediment materials under study may represent about 1 – 30 years of sediment accumulation. We clearly stress that different depositional environments and taphonomic processes may have affected the dinoflagellate cyst concentration and hence, we cannot exclude the probability of aliasing errors in the interpretation of our data. In particular, magnitudes of terrigenous particulate matter input from nearby continents could have influenced accumulation rates of sediments at varying degrees, which in turn can dilute or enhance the sedimentary dinoflagellate cyst signals. Nevertheless, given that organic-walled dinoflagellate cysts are composed of refractory organic matter, a complex polymer similar to the sporopollenin (Dale, 1983; Versteegh and Blokker, 2004), the observed distribution patterns of dinoflagellate cysts don't seem to be severely biased by post-depositional degradation. In order to assess how accurately our data represent the originally deposited dinoflagellate cyst assemblages, further studies are needed to characterize various oceanographic and depositional environments (e.g., sedimentation rate, hydrodynamics and topography) in such a complex area.

4.3. Further implications

Our results show a strong regional contrast in patterns of the dinoflagellate cyst distributions across the Chukchi–East Siberian Sea shelves. This is the region where currently experiences drastic changes in hydrographic environments due to increasing advections of southern waters on the Pacific and Atlantic sides of the Arctic Ocean, along with greater areas of open water (e.g., Woodgate et al., 2010, 2012, 2018; Polyakov et al., 2017, 2018, 2020). Tentatively, we speculate that the distinct geographic contrasts observed in our dinoflagellate cyst data can be a result of species-specific responses to such prominent regional oceanographic characteristics, probably affected by the growing intrusions of the Atlantic- and Pacific-origin water on both sides of the Arctic Ocean. This notion is in line with recent observations of widespread structural changes in species distribution and biological community of Arctic marine environments, triggered by a poleward expansion of warm currents from lower latitudes (e.g., Fossheim et al., 2015; Frainer et al., 2017; Lewis et al., 2020).

From a climatic point of view, our data may also have implications for a potential impact of the current Arctic warming trend on phytoplankton community changes through biological-physical coupling processes. Recent climate model studies highlight a certain role of marine phytoplankton biomass in modifying physical properties of the ocean and thereby affecting the global climate system (e.g., Manizza et al., 2005; Anderson et al., 2009; Lengaigne et al., 2009; Jochum et al., 2010; Patara et al., 2012). This biogeophysical feedback appears to significantly influence the Arctic climate – i.e., higher phytoplankton biomass increases phytoplankton pigments in the ocean that are related to more light absorption and ocean surface warming, which in turn lead to higher phytoplankton growth (Park et al., 2015; Lim et al., 2019a,b). Current climate models forecast greater areas of open water in the Arctic Ocean following an increase in water temperature and loss of sea-ice in the coming decades (e.g., Wang and Overland, 2009; Stroeve et al., 2012b; Stocker et al., 2013; Casas-Prat and Wang, 2020; Wang, 2021). Therefore, it seems evident that, if the regional contrasts identified in our dinoflagellate cyst data indeed are the result of a poleward expansion of southern waters into the warming Arctic Ocean, the sharp biogeographic divide is expected to only intensify into the future. This raises important questions regarding a potential impact of such on-going structural changes of the marine phytoplankton community on the Arctic climate, particularly in light of its phenological significance. It should be noted that there is uncertainty associated with different depositional environments and taphonomic processes – obviously, this is an important factor limiting our interpretation of the dinoflagellate cyst distribution at specific sites and their linkages to the prevailing conditions at those sites. What becomes apparent is that sediment cores will be one of the most important sources of information about long-term changes in the aforementioned biological and oceanographical coupling processes in the context of recent climate warming, for which our study can be based.

4.4. *Alexandrium* cyst accumulations

Although limited in numbers, our data show preferential accumulations of *Alexandrium* cysts at the southeastern location (sites 1–4; Figs. 3 and 5). Given that these cysts mostly occur in coastal sediments of temperate regions with mesotrophic and eutrophic settings (e.g., Anderson et al., 2005a,b; Zonneveld et al., 2013; Kim et al., 2018), the *Alexandrium* cysts found in the sites under study are likely to have exogenous origin rather than *in-situ*

production under site-specific favorable habitat conditions. It is interesting to consider these findings in the light of a recent study by Anderson et al. (2021) that reported massive *Alexandrium* cyst deposits in the Alaskan Arctic sediments; hypothetically being formed via a long-range transportation from the north Pacific region by the Bering Strait throughflow, or *in-situ* germination from the cyst bed originally existed in the region. This indicates a high probability of its delivery to the aforementioned location (sites 1–4, this study) from the Alaskan Arctic cyst deposits, potentially facilitated by local hydrodynamics and wind-induced currents causing cyst dispersal in the sedimentary regime. It should be noted that the distribution and concentrations of *Alexandrium* cysts in the present study can be underestimated, because they are difficult to detect at light microscopy. Thus, regardless of the transporting mechanisms, our data infer that the *Alexandrium* cysts may distribute over a considerable stretch of this shelf region that extend well beyond the Alaskan Arctic area. However, this remains speculative until further data on the presence and magnitude of their distribution becomes available. Other questions also remain whether the continual sedimentary accumulations of cysts of *Alexandrium*, the dinoflagellate genus that produce paralytic shellfish poisoning toxins, have a potential risk to the Arctic's marine ecosystems; given the increasing probability for rapid cyst germination and ensuing *Alexandrium* bloom initiation in response to habitat amelioration led by further Arctic warming (Anderson et al., 2021). However, our data cannot provide conclusive evaluations and more investigations are needed to assess these issues.

5. Conclusions

This study provides the first detailed description of recent dinoflagellate cyst assemblages from 32 surface sediment samples distributed in the Chukchi and East Siberian Sea shelves, the Pacific sector of the Arctic Ocean. In this region, increasing Pacific water inflows through the Bering Strait play as a major factor determining its hydrographic characteristics and a wide range of variations in oceanic temperature, salinity and seasonal sea-ice cover. Our data document an intense dinoflagellate cyst accumulation at the shallow-shelf sites, owing to a longer open-water season and sufficient nutrient supplies that provide favorable habitat conditions for overall dinoflagellate population growth therein. The most prominent feature is a strong geographic pattern of the dinoflagellate cyst species composition and distribution, which separate the cyst accumulation zone into two spatial

domains: the Chukchi Sea shelf and the East Siberian Sea shelf. The Chukchi Sea shelf sediments exhibit an exclusive occupation of cosmopolitan, opportunistic-nature taxa (*P. dalei* cysts and *O. centrocarpum*), induced by warm-Pacific water inflows that may have caused not only extreme seasonality and unstable water conditions but also sufficient nutrient supplies and higher light availability. By contrast, the East Siberian Sea shelf sites with more extensive sea-ice cover and lower temperatures is primarily occupied by "round brown spiny cyst" taxa (e.g., *I. minutum* subsp. *barbatum*, *E. karaense*, *I.*? *cezare* s.l. and *I. brevispinosum*) that have a strong affinity for cold, polar conditions. We speculate that such strong occupation of heterotrophic dinoflagellate population is primarily linked to Atlantic-origin water intrusions into the East Siberian Sea shelf, by way of uplifting nutrient-rich, cold bottom water to oligotrophic surface layer for the growth of primary producers. The robust regionalism reflected in our dinoflagellate cyst data signifies a growing impact of southern waters flooding on the Arctic Ocean, which seems to exert a determinant role on restructuring hydrographic conditions and associated phytoplankton communities therein. In light of emerging climate amelioration for Arctic phytoplankton habitats, the unique assemblage structure of dinoflagellate cyst distributions in the present study may infer substantial shifts in the Arctic phytoplankton phenology and associated biogeophysical feedback, possibly prompting further climate impacts in the future. Further, cyst accumulations of toxin-producing dinoflagellate *Alexandrium* at the Chukchi Sea shelf may signal the urgency for in-depth investigations on their distributions and dispersal dynamics in the Arctic Ocean, as well as their potential for rapid germination and ensuing bloom initiation under the current warming trends. Our study highlights considerable potential of dinoflagellate cysts as a valuable proxy for changes in hydrographic conditions and plankton communities in the Arctic marine ecosystem. For longer-term perspectives, especially whether the postulated dinoflagellate cyst signals are indeed a response to climate-driven environmental perturbations, a promising approach is to reconstruct dinoflagellate cyst proxy time-series from sediment cores, along with a robust chronological framework at time-scales relevant for climate studies. Such information will be essential to provide insights into how Arctic marine ecosystems with greater areas of open water will potentially react to a future climate change.

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Figure captions

Figure 1. Map of the study area illustrating locations of sampling sites and main oceanographic features. a) Surface sediment samples used in our study are indicated by their

numbers (black dots; details in Table 1). Arrows indicate major ocean current patterns (red=Pacific-origin and blue=Atlantic-origin): the upper right map visualizes the two dominant ocean current systems in the Arctic Ocean (after Hunt et al., 2013; Polyakov et al., 2020). Dashed white line represents sea-ice extent during August in 2017, obtained from the National Snow and Ice Data Center (drawn following Kim et al., 2020b). The yellow star marks location of the study site of Jung et al. (2021) mentioned in the text. b, c) The mean summer sea-surface temperature and salinity distributions obtained from sites nearby the sediment sampling location during the ARAON cruises in 2015–2017 (from the KOPRI data server; https://kpdc.kopri.re.kr/search/80785502-2cb4-4146-a799-b7c76d65f47c). d) The GlobColour-merged chlorophyll-a concentration (mg/m^3) derived from satellite observation during the summers of 2015–2017. e) The mean satellite-observed sea-ice concentrations during the summers of 2015–2017 retrieved from NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration. Geographic locations are divided into two major regions: the Chukchi Sea (sites 1-9; area A) and the East Siberian Sea (sites 24-32; area B).

Figure 2. Photomicrographs of selected dinoflagellate cysts collected in surface sediments from the Chukchi–East Siberian Seas (Scale bar = 20 μm). a) *Alexandrium* species. b) Cyst of *Pentapharsodinium dalei*. c) *Trinovantedinium applanatum*. d) *Operculodinium centrocarpum*. e) *Operculodinium centrocarpum*–Arctic morphotype, with incompletely developed and sparsely distributed processes (red box). f) *Islandinium brevispinosum*. g) *Islandinium minutum*. h) *Echinidinium karaense*. i) *Islandinium*? *cezare* with smooth process, stems of uniform thickness and tips minutely expanded distally with recurved margins (red box). j) *Islandinium minutum* subsp. *barbatum* with process stems that are tapered and bear unusual barbs on (red box).

Figure 3. Total cyst concentrations (cysts/g; curve) and relative abundances of selected cyst taxa (contributing >1%; bar) in surface sediment samples (autotrophic taxa=green and heterotrophic taxa=blue). Spatial domains of areas A (sites 1-9) and B (sites 24-32) are denoted on the top of the diagram (shaded in grey).

Figure 4. a) non-metric multidimensional scaling (nMDS) plot of the 28 cyst taxa. Green dot represents autotrophic species and brown inverted triangle, heterotrophic ones. b) Covariance

based principal component analysis on normalised abiotic parameters. Blue dots are samples from the Chukchi Sea (A), red inverted triangles are samples from the East Siberian Sea (B), and green squares are the other samples (OS). c) nMDS plot of the 32 dinoflagellate cyst assemblages with multiple regression vectors for environmental parameters (stress of 0.08, indicative of a good fit).

Figure 5. Distributions of key dinoflagellate cyst taxa and groups, expressed as percentages and concentrations (cysts/g). a) *Pentapharsodinium dalei*. b) *Operculodinium centrocarpum*. c) Autotrophs. d) *Islandinium minutum*. e) *I. minutum* subsp. *barbatum*. f) Heterotrophs. g) *Alexandrium* cysts.

Figure 6. Conceptual overview of mechanisms causing regional contrasts in dinoflagellate cyst distributions between the Chukchi Sea (area A) and the East Siberian Sea (area B) under the current Arctic warming trend. Area A (left panel) exemplifies the increasing northward Pacific water flow (red arrow) affecting dinoflagellate production in the Chukchi Sea environment. The warm, nutrient-rich Pacific water inflow not only supplies enough nutrients for dinoflagellate population growth, but also increases freshwater input by melting sea-ice and delivering riverine waters (gray shaded circles) that generate more open water habitat with strong seasonal stratification (gray dotted line) favored by autotrophic and opportunistic dinoflagellate taxa (green stars). The black dashed arrow indicates a possible transport of PSP-causative *Alexandrium* cysts from the Alaskan Arctic cyst deposits by local hydrodynamics and wind-induced currents. Area B (right panel) illustrates an intensification of the Atlantic-origin water intrusion (blue arrow) to the East Siberian Sea. The increased saline, dense Atlantic-origin water mass lifts the overlying nutrient-rich Pacific-origin waters up to the oligotrophic surface water, which boosts high production of photosynthesizing primary producers (purple dots) and ensuing heterotrophic, polar water dinoflagellate taxa (blue stars).

Table 1. Sediment sampling site number, geographical coordinates, water depth and total dinoflagellate cyst concentrations of analyzed samples.

Site No.	Cruise	Gear	Latitude	Longitude	Water depth (m)	Total dinoflagellate cyst concentrations (cysts/g)
1	ARA08	Box corer	72.36°N	168.67°W	59	10179
2	ARA08	Box corer	73.58°N	168.28°W	125	5762
3	ARA09	Box corer	73.74°N	166.42°W	126	8512
4	ARA02	Multi corer	74.3°N	167.65°W	244	4583
5	ARA07	Box corer	74.80°N	167.81°W	223	981
6	ARA02	Multi corer	75.11°N	166.34°W	442	2531
7	ARA09	Box corer	75.69°N	166.64°W	290	1124
8	ARA09	Box corer	75.24°N	171.97°W	495	1097
9	ARA07	Box corer	75.15°N	176.03°W	350	1019
10	ARA07	Box corer	75.79°N	176.99°W	1278	518
11	ARA07	Box corer	76.00°N	170.5°W	1319	327
12	ARA01	Multi corer	75.17°N	160.00°W	1962	853
13	ARA01	Multi corer	75.43°N	156.01°W	3084	593
14	ARA01	Multi corer	75.94°N	156.02°W	1207	159
15	ARA01	Multi corer	75.89°N	163.01°W	2064	1029
16	ARA02	Multi corer	76.29°N	167.16°W	395	485
17	ARA07	Box corer	77.43°N	164.12°W	325	145
18	ARA07	Box corer	77.86°N	175.88°W	1613	104
19	ARA02	Multi corer	78.00°N	175.66°W	1595	142
20	ARA02	Multi corer	78.00°N	179.33°W	1567	200
21	ARA02	Multi corer	78.00°N	174.00°E	1332	152
22	ARA02	Multi corer	76.40°N	176.03°W	1920	178
23	ARA02	Multi corer	76.40°N	179.33°W	1002	114
24	ARA08	Box corer	75.16°N	179.99°W	591	1583
25	ARA08	Box corer	75.77°N	177.16°E	582	522
26	ARA09	Box corer	75.60°N	176.50°E	340	1334
27	ARA09	Box corer	75.99°N	173.58°E	265	954
28	ARA08	Box corer	75.00°N	173.60°E	107	1932
29	ARA09	Box corer	74.64°N	174.92°E	70	4512
30	ARA07	Box corer	74.74°N	170.46°E	59	1098
31	ARA08	Box corer	74.00°N	170.00°E	46	1770
32	ARA07	Box corer	73.82°N	169.19°E	43	1075

Table 2. Selected sea-surface environmental variables and sources.

Abiotic parameters	Code used for multivariate analysis	Sources
% Sea ice: Annual average for the period 1955-2012	SICE	http://nsidc.org/data/G10010
Dissolved oxygen (ml/l)	DOxy	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Nitrates (µmol/l)	Nitr	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Phosphates (µmol/l)	Phos	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Silicates (µmol/l)	Sili	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Salinity Summer Winter	SSUM SWIN	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Temperature (°C) Summer Winter	TSUM TWIN	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Productivity (mgC/m²/day) July August September	PJul PAug PSep	Standard VGPM Monthly files from MODIS R2018 Data http://orca.science.oregonstate.edu/2160.by.4320.monthly.xyz.vgpm.m.chl.m.sst.php

Table 3. List of dinoflagellate cyst taxa identified in the investigated sediments, trophic type and relative abundance of cyst species (%).

Taxa name	Motile affinity	Code	Trophic mode	Percentage range (%)
Cyst of *Alexandrium* species	*Alexandrium* species	Alex	A	0–3.8
Cyst of *Pentapharsodinium dalei*	*Pentapharsodinium dalei*	Pdal	A	1.1–78.6
Operculodinium centrocarpum sensu Wall and Dale 1966	*Protoceratium reticulatum*	Ocen	A	0.7–72.4
Operculodinium centrocarpum–Arctic morphotype	Unknown	OceA	A	0–13.3
Bitectatodinium tepikiense	*Gonyaulax digitale*	Btep	A	0–5.9
Spiniferites bentorii	*Gonyaulax digitale*	Sben	A	0–0.7
Spiniferites elongatus	*Gonyaulax elongata*	Selo	A	0–7.5
Spiniferites mirabilis	*Gonyaulax spinifera*	Smir	A	0–0.4
Spiniferites membranaceus	*Gonyaulax membranacea*	Sme m	A	0–1.3
Spiniferites spp.	Unknown	Sspp	A	0–2.1
Nematosphaeropsis labyrinthus	Unknown	Nlab	A	0–0.5
Impagidinium sphaericum	Unknown	Isph	A	0–0.9
Impagidinium pallidum	Unknown	Ipal	A	0–3.5
Impagidinium spp.	Unknown	Ispp	A	0–1.4
Brigantedinium spp.	*Protoperidinium* spp.	Bspp	H	0–23.2
Echinidinium karaense	Unknown	Ekar	H	0–45.6
Islandinium brevispinosum	*Protoperidinium haizhouense*	Ibre	H	0–12.9
Islandinium? *cezare*	Unknown	Icez	H	0–3.3
Islandinium? *cezare* sensu lato – Morphotype 1 (Head et al., 2001)	Unknown	Icez M1	H	0–12.9
Islandinium minutum	*Islandinium minutum*	Imin	H	0–58.4
Islandinium minutum subsp. *barbatum*	Unknown	Ibar	H	0–30.3
Cyst of *Polykrikos* sp.–Arctic morphotype	Unknown	Parc	H	0–2.8
Cyst of *Polykrikos kofoidii*	*Polykrikos kofoidii*	Pkof	H	0–0.3
Cyst of *Polykrikos schwartzii*	*Polykrikos schwartzii*	Psch	H	0–2.4
Cyst of *Protoperidinium americanum*	*Protoperidinium americanum*	Pame	H	0–0.8
Selenopemphix quanta	*Protoperidinium conicum*	Squa	H	0–0.8
Selenopemphix nephroides	*Protoperidinium subinerme*	Snep	H	0–0.7
Trinovantedinium applanatum	*Protoperidinium shanghaiense*	Tapp	H	0–1.4

Strong regionalism in dinoflagellate cysts in recent sediments from the Chukchi-East Siberian Seas, Arctic Ocean

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Abstract

The Pacific sector of the Arctic Ocean, a region with the fastest sea-ice loss in recent decades, is experiencing unprecedented biological regime shifts in its marine ecosystems today. However, a shelf-wide characterization of marine plankton communities over this region and environmental processes behind it remain largely unresolved, despite phytoplankton phenology is now considered to be an important factor for assessing how Arctic Ocean interacts with global climate change. Here, we present the first detailed description of recent dinoflagellate cyst assemblages in 32 surface sediment samples from the Chukchi–East Siberian Sea shelves, the Pacific Arctic Ocean, to examine their biogeographic patterns and associated environmental forcing factors. We find a strong regionalization in the species composition and distribution along the shallow-shelf cyst accumulation zone; in the Chukchi Sea sector, northward flow of warm-Pacific water along with extreme seasonality, sufficient nutrient supplies and higher light availability leads to a large occupation of cosmopolitan, opportunistic-nature taxa, whilst the East Siberian Sea sector with more extensive sea-ice cover and lower temperatures is primarily dominated by "round brown spiny cyst" taxa that have a strong affinity for cold, polar conditions. Specifically, an exclusive dominance of heterotrophic taxa at the East Siberian Sea region is inferred to be closely tied to Atlantic-origin water intrusions that lift nutrient-rich, cold bottom water up to oligotrophic surface layer to grow diatoms and other prey organisms. The observed contrast in this geographical "hot spot", where the Pacific- and Atlantic-origin waters face each other, clearly manifests a growing expansion of southern waters into an increasingly ice-free Arctic Ocean that reshapes Arctic Ocean biogeography from the base of marine food chains. Our study highlights considerable potential of dinoflagellate cysts as a valuable environmental proxy to indicate complex interactions between ocean physics and marine biology under the rapidly changing Arctic climate system.

Keywords: Dinoflagellate cysts, Sediments, Arctic Ocean, Climate warming

1. Introduction

In recent years, extreme climatic events have increased across the Northern Hemisphere mid-latitudes – e.g., unusual heatwaves, rainfall and severe winter weather in Eurasia and North America (Trenberth, 2011; Rahmstorf and Coumou, 2011; Coumou and Rahmstorf, 2012; Gallant et al., 2014; Donat et al., 2016). The increasing frequency of such mid-latitude weather extremes is currently ascribed to the Arctic's rapid warming (Honda et al., 2009; Francis and Vavrus, 2012; Tang et al., 2013; Kim et al., 2014; Cohen et al., 2014, 2018; Blackport and Screen, 2020), which is most notably manifested as a drastic shrinkage of the summer Arctic sea-ice cover (Stroeve et al., 2012a; Zhang et al., 2013; Gascard et al., 2019). The warming-induced Arctic sea-ice loss is predicted to be accelerated over the coming decades (Stroeve et al. 2012b; Overland and Wang, 2013; Wang and Overland, 2015), tentatively fueling knock-on effects for the lower latitude continental weather. This new climatic status settling over the Arctic Ocean, shifting from a frozen region with heavily ice-covered environments to a warmer, increasingly ice-free condition, is closely linked to anomalous Atlantic- and Pacific-origin water advections from lower latitudes – commonly referred to as borealization (Polyakov et al., 2017, 2018, 2020; Woodgate et al., 2012; Woodgate, 2018; Tsubouchi et al., 2021). Its impacts are most clearly observed in significant biogeographical shifts in Arctic marine ecosystems, such as alterations in species distribution and composition of biological communities across all trophic levels (Questel et al., 2013; Fossheim et al., 2015; Gall et al., 2016; Pinchuk and Eisner, 2017; Vihtakari et al., 2018; Møller and Nielsen, 2020).

In this respect, the Pacific sector of the Arctic Ocean (i.e., the Chukchi and East Siberian seas) is a geographical focus for climate studies today, because this region has experienced the most rapid decline in sea-ice cover over the recent decades (Shimada et al., 2006; Steele et al., 2008; Stroeve et al., 2012a, b; Frey et al., 2015). In the Chukchi Sea, one of the most productive regions in the Arctic Ocean, the drastic sea-ice loss and associated hydrographic changes have induced a significant regime shift in its biological communities and productivity across the whole marine food web (e.g., Jin et al., 2009; Grebmeier, 2012; Ershova et al., 2015). Particularly, given the emerging biogeophysical significance of marine phytoplankton in amplifying surface warming of the Arctic Ocean (e.g., Lim et al. 2019a,b; Park et al., 2015, 2020; Pefanis et al., 2020), phenological variability of dominant phytoplankton community members over this region can carry vital information about the

complex interactions between biological system and the current Arctic warming trend. However, understanding marine plankton characteristics in a rapidly changing Arctic Ocean, particularly for the Pacific sector of the Arctic Ocean, has yet remained important but largely unexploited.

Dinoflagellates are highly diverse unicellular eukaryotic organisms in a wide range of aquatic environments, representing one of the major marine plankton groups along with diatoms and coccolithophores (Taylor, 1987; Falkowski et al., 2004; Delwiche, 2007). Approximately 20% of living dinoflagellate species are known to produce resting cysts, a benthic dormant stage, mainly composed of a complex biomacromolecule substance and highly resistant to physical, chemical and biological degradation (e.g., Dale, 1983; Versteegh and Blokker, 2004). Therefore, they have a strong preservation potential in sediments deposited under various environmental settings, even where other siliceous and calcareous microphytoplankton groups are subject to dissolution problems (e.g., Williams, 1990; de Vernal et al., 1992). These characteristics make sedimentary dinoflagellate cysts can serve as a useful indicator of present and past marine productivity in the photic zone. The reliability of dinoflagellate cyst signals depends on a sound understanding of their spatial distributions in relation to environmental parameters, which can be region-specific. Notwithstanding of numerous studies dedicated to develop a global biogeographic database of dinoflagellate cysts and their environmental correlates (e.g., de Vernal et al., 2001; Marret and Zonneveld, 2003; Zonneveld et al., 2013; Marret et al., 2020), the Pacific sector of the Arctic Ocean is still poorly documented. Thus, biogeographic information on dinoflagellate cysts in this region is pertinent to fill the gap in the current reference database, and also to identify its possible correlation with crucial environmental factors. Moreover, recent studies drew attention to cyst accumulations of *Alexandrium*, a major producer of paralytic shellfish poisoning (PSP)-associated neurotoxin, in seafloor sediments at the Chukchi Sea region (Natsuike et al., 2013; Anderson et al., 2021; Obrezkova et al., 2022). Because the Arctic waters were previously believed to be safe from such high levels of this algal toxin due to unfavorable habitat conditions limiting general phytoplankton growth, such unprecedented phenomenon signifies a substantial transformation occurring in the environments.

Here, we report on the distribution of dinoflagellate cysts from 32 surface sediments collected from the Pacific sector of the Arctic Ocean, encompassing the area from the Chukchi shelf to the northeastern part of the East Siberian Sea. Influenced by combined

effects of rapidly changing sea-ice conditions and contrasting water masses of different origins, the study area shows great gradients in sea-surface environmental variables (Wassmann et al., 2015; Wang et al., 2021), and is expected to have a tangible effect on the dinoflagellates and their cyst distributions at the region. The ultimate goals of this study are: (1) to provide information, for the first time concerning this data-sparse region, about the spatial distribution and abundance of dinoflagellate cyst assemblages; and (2) to identify dominant forcing factors driving their distributional patterns.

2. Materials and methods

2.1. Sample collection, laboratory treatments and cyst identification

A total of 32 surface sediment samples were collected from the Pacific sector of the Arctic Ocean with a box corer and a multiple corer during several research cruises of the R/V ARAON from 2011 to 2018 (Fig. 1). The sampling locations are distributed from 72 to 78°N and from 166°W to 156°E, within water depths of 43–3084 m across the Chukchi Sea and East Siberian Sea shelves including the Chukchi Plateau and Mendeleyev Ridge (Table 1). Dinoflagellate cyst analysis was performed on the uppermost sediment layers (~1 cm) with an undisturbed sediment/water interface and no sign of bioturbation. Each sub-sample of the surface sediments was processed, following the standard palynological preparation procedure described by Marret and Zonneveld, 2003. Approximately 10–30 g of wet sediment per sample were oven-dried at 60°C for 24 hours and weighted. After adding a *Lycopodium clavatum* spore tablet of batch #1031 (X = 20,848 per tablet, σ = ±1546, University of Lund) to each sample, they were treated with 20 mL of cold 10% hydrochloric acid (HCl) for the removal of calcium carbonate. After 20 min, the residue was rinsed with distilled water, and 20 mL of cold 40% hydrofluoric acid (HF) was added and left for 20 min to remove silicates. The HCl and HF steps were repeated 2–3 times. Afterwards, the cold HF was added to the residue, and after resting overnight and decantation, the cold HCl was added for 20 min. The final residues were washed with distilled water to neutralize the pH. To shorten settling time and avoid losing the residue, centrifugation was used at each step of decanting at 3000 r min−1 for 10 min. Then samples were passed through a 10-μm pore-sized mesh sieve and the residue was preserved in a 10-mL vessel with two to three drops of phenol added. Dinoflagellate cysts were counted with an Axio Imager A2 microscope (Carl Zeiss Microscopy GmbH) at 400× and 1,000× magnification. Dinoflagellate cyst identification

follows published morphological descriptions (Rochon et al., 1999; Head et al., 2001; Radi et al., 2001; Radi and de Vernal, 2004; Radi et al., 2013; Potvin et al., 2018). Most dinoflagellate cyst types were identified at the species level except for *Brigantedinium*, round brown cysts, which often did not allow clear observation of the archeopyle due to the orientation or folding of the cyst. These cysts were grouped as *Brigantedinium* spp without further identification. Another exception is the cysts produced by *Alexandrium*, which are also difficult to assign to species morphologically using microscopy. Therefore, these cysts with ellipsoidal and transparent wall surrounded by a mucous layer are counted as cysts of *Alexandrium* spp (Fig. 2a). We distinguished *Operculodinium centrocarpum* sensu Wall and Dale (1966) with long, fully developed processes and *O. centrocapum* characterized by short, poorly developed processes ("Arctic morphotype"), following Rochon et al. (1999), de Vernal et al. (2001) and Radi et al. (2001) – both morphotypes are assigned to *O. centrocarpum* sensu lato (s.l.) (Fig. 2d, e).

Where possible, at least 300 specimens of dinoflagellate cysts were counted per sample. Concentrations of each dinoflagellate cyst sum counted are expressed as concentrations of dinoflagellate cysts per weight of dry sediment. The concentration of palynomorphs was calculated as follows (Benninghoff, 1962):

$$c \text{ (dinoflagellate cysts g}-1 \text{ dry sediment)} = \frac{g_c \times L_t \times t}{L_c \times w}$$

where c is the concentration = number of dinoflagellate cysts per gram of dry sediment, g_c is the number of counted dinoflagellate cysts, Lt is the number of *Lycopodium* spores/tablet, t is the number of tablets added to the sample, Lc is the number of counted *Lycopodium* spores, and w is the weight of dried sediment (g).

[Insert Figure 1]

[Insert Table 1]

[Insert Figure 2]

2.2. Statistical treatments

Ordination techniques based on multivariate analyses were carried out to identify patterns in the distribution of species and assemblages and to attempt to relate them to environmental factors. We used the software PRIMER v7 (Clarke and Gorley, 2015) as it offers a large range of statistical functions to analyse abiotic and biotic datasets. For the dinoflagellate cyst assemblages, we performed a non-metric multidimensional scaling (nMDS) analysis on standardized and square-root transformed dinocyst raw data. All species were included in this analysis. For the examination of the distribution and importance of abiotic (environmental) parameters, a covariance based principal component analysis (PCA) was carried out, as recommended by Clarke and Gorley (2015). Environmental parameters were normalised as they can have a large range of measurement scales. We selected a number of surface environmental conditions that we know to influence dinoflagellate cyst distribution (e.g., de Vernal et al., 2020) (Table 2).

[Insert Table 2]

3. Results

3.1. Dinoflagellate cyst assemblages and abundance

Twenty-eight dinoflagellate cyst taxa were identified from the 32 study sites, excluding unidentifiable round brown spiny cyst (RBSC) type (Table 3). Dinoflagellate cysts were observed in all the sediment samples, and species richness at any single sample ranged between 2 (site 20) and 20 (site 1), with an average of 11 taxa per site. Total dinoflagellate cyst concentrations at each sampling site are shown in Table 1 and Fig. 3. The concentrations per sample ranged from 104 to 10179 cysts/g (1737 cysts/g on average). In general, higher concentrations are observed in the shallow shelf locations: sites 1–9 in the Chukchi Sea (981–10179 cysts/g, 3977 cysts/g on average) and sites 24–32 in the East Siberian Sea (522–4512 cysts/g, 1642 cysts/g). Samples from ice-covered/higher-latitude regions have lower concentrations (sites 10–23; 104–1029 cysts/g, 383 cysts/g on average).

[Insert Table 3]

[Insert Figure 3]

Overall, dinoflagellate cyst assemblages are dominated by cysts of *P. dalei*, *O. centrocarpum*, *O. centrocarpum*-arctic morphotype, *I. minutum*, *I. minutum* subsp. *barbatum* and *E. karaense*. Other taxa that have relatively high abundance include *S. elongatus*, *Brigantedinium* spp., *Islandinium*? *cezare* morphotype 1 (M1; Head et al. 2001) and *I. brevispinosum*. Composition of the cyst assemblages shows some significant spatial patterns within the shallow shelf sites, particularly distinguished by their trophic preferences (nutritional strategy): either "autotrophs" that are photosynthesizing primary producers, or "heterotrophs" feeding on light-dependent organisms such as diatoms (Jacobson and Anderson, 1986; Smayda and Reynolds, 2003). Samples from the Chukchi Sea shelf sites are characterized by an overwhelming dominance of autotrophic taxa cysts of *P. dalei* (max. 5505 cysts/g, 79%) and *O. centrocarpum* s.l. (max. 2687 cysts/g, 51%), as previously reported by Radi et al. (2001) and found in the 8 samples of the 1968 database (de Vernal et al., 2020). In contrast, the East Siberian Sea shelf samples are largely occupied by heterotrophs *I. minutum* (max. 1867 cysts/g, 58%), *I. minutum* subsp. *barbatum* (max. 957 cysts/g, 30%) and *E. karaense* (max. 523 cysts/g, 13%), although at some sites, the cyst of *P. dalei* is present in significant amounts.

I. minutum subsp. *barbatum* tends to be exclusively restricted to the shallow East Siberian Sea shelf (sites 24–31; 76–957 cysts/g, 7–30%), whereas only a few are found in the Chukchi Sea samples (except for site 2). Cysts of *Alexandrium* species also show a very restricted distribution, only being found at sites very close to the Bering Strait (sites 1–3; up to 325 cysts/g, 3.8%), while other samples turned out to be almost barren (Fig. 3).

3.2. Statistical analysis

The nMDS carried out on the dataset shows some significant patterns. The ordination of species (Fig. 4a) clearly highlights the grouping of species according to the trophic aspect; interestingly, the species *Trinovantedinium applanatum* appeared within the autotrophic cluster.

The covariance based PCA on environmental parameters (Fig. 4b) shows that the ordination of samples is mostly explained by summer productivity along the first axis (40.2%) and summer SST and sea ice along the second axis (23.6%). Other factors seem to have some influence of the samples' ordination, with a third PC dimension explaining 17.5% of the variation. The nMDS (Fig. 4c) shows a clear grouping of dinoflagellate cyst assemblages and

could be associated with dominating environmental factors (stress is 0.08), notably the assemblages from the East Siberian Sea (summer productivity and silicate).

[Insert Figure 4]

4. Discussion

In general, dinoflagellate cysts were well preserved in the investigated materials and their numbers are highly variable. Two distinctive features can be identified in the dinoflagellate cyst data and provide insight on the nature of dinoflagellate cyst assemblages and their distributional patterns. First, the dinoflagellate cyst data show high accumulations at locations of lower latitude, shallow-shelf environments. Second, there is a strong spatial disparity in the assemblage compositions and abundances at the cyst accumulation zone – geographically divided into two areas: sites 1–9 on the northern Chukchi Sea shelf (A) and sites 24–32 (B) on the East Siberian Sea shelf (Figs. 1 and 5).

4.1. Dinoflagellate cyst assemblages and their general trends

There are few published works focused on species-specific characteristics of organic-walled dinoflagellate cysts in the Chukchi Sea and East Siberian Sea shelf sediments (e.g., Natsuike et al., 2013, 2017; Potvin et al., 2018; Anderson et al., 2021). With the exception of Radi et al. (2001), we find no studies of spatial variability in species composition and assemblages of dinoflagellate cysts in the region. Therefore, comparisons of dinoflagellate cyst distribution patterns observed in the present study are geographically limited. Our study shows dinoflagellate cyst concentrations in the investigated area are generally high (104–10,179 cysts/g), and are in the same order of magnitude as those reported from other regions of the Arctic Ocean such as the northeastern Chukchi Sea (2000–25,000 cysts/cm^3; Radi et al., 2001), western Svalbard (88–33,234 cysts/g; Grøsfjeld et al., 2009) and West Greenland margin (> 10,000 cysts/g; Allan et al., 2020). It is known that species diversity of dinoflagellate cysts in sub-Arctic and Arctic environments generally constitutes ~ 20 species (e.g., de Vernal et al., 2001; Radi et al., 2001; Matthiessen et al., 2005; Grøsfjeld et al., 2009; Solignac et al., 2009; Allan et al., 2020; Marret et al., 2020), and this is well consistent with our study (6–20 cyst types per sample; Table 3). The dinoflagellate cyst assemblages in the present study include cosmopolitan taxa that are tolerant to a wide range of hydrographical

conditions (e.g., *O. centrocarpum*, *Brigantedinium* spp. and *Spiniferites* group). Typical cold polar water taxa – such as the Arctic morphotype of *Polykrikos* sp. (Potvin et al., 2018), *Islandinium*? *cezare* s.l. (i.e., *Islandinium*? *cezare* and *Islandinium minutum* subsp. *barbatum*; see Van Nieuwenhove et al., 2020), *Echinidinium karaense* and *Impagidinium pallidum* – were also the main components of the assemblages and generally well conform to those characterizing the Arctic type environment (e.g., Head et al., 2001; de Vernal et al., 2001; Radi et al., 2001; Potvin et al., 2018).

Notably, the dinoflagellate cyst concentrations show a clear latitudinal trend, characterized by high concentrations between 72°N and 75°N that gradually decrease towards the central Arctic Ocean (Fig. 3). Before interpreting such patterns and associated environmental factors in detail, it is important to discuss a possible effect of lateral transport. Because dinoflagellate cysts are generally about 15–100 µm in diameter behaving like silt particles in the water column, they can be transported over large distances by ocean currents or resuspended by bottom currents before their settling down to the sea floor (de Vernal., 2009; Dale, 1996; Mudie and Harland, 1996; Nooteboom et al., 2019, 2020). This implies that the dinoflagellate cysts accumulated at 72°N–75°N may have been formed elsewhere, not necessarily representing higher production of dinoflagellates above the sediment sampling site. Given that the depositional environment in the Chukchi Sea is strongly affected by the Pacific water inflows carrying fine particles via the Bering Strait throughflow (Barnes and Reimnitz, 1974; Viscosi-Shirley et al., 2003; Mathis et al., 2007; Kadko et al., 2008), long-range transportation of dinoflagellate cysts from the northern Bering Sea is possible. However, considering the circulation pattern of Pacific-origin water that is generally deflected eastwards after passing the Bering Strait and does not seem to extend far beyond the northern Chukchi shelf margin (Weingartner et al., 2005; Danielson et al., 2014, 2020), its influence delivering particle materials on the collection sites is unlikely significant. We also note that several studies on the dinoflagellate cyst assemblages in surface sediments from the Bering Sea region have reported a predomination of *O. centrocarpum* (e.g., Radi et al., 2001; Radi and de Vernal, 2004; Bonnet et al., 2012; Orlova and Morozova, 2013) – which disagrees with the present study that shows the highest abundance and percentage of cysts of *P. dalei* at the closest locations from the Strait (sites 1–3; Figs. 1 and 3). Such a clear disparity in the dinoflagellate cyst compositions between the Arctic- and Pacific sides of the Strait seems to infer that the dinoflagellate cyst assemblages in the study area were primarily

determined by *in-situ* ecological mechanisms, rather than long-range transport processes.

The dinoflagellate cyst accumulations that are almost exclusive to the shallow shelf locations (mostly < 130 m deep) may indicate a number of environmental factors that afford such large dinoflagellate production. Primarily, it can be explained by the ecological preference of dinoflagellates for neritic environments where a major part of marine phytoplankton communities originates from (Dale and Fjellså, 1994; Dale, 1996; Marret and Zonneveld, 2003). Another explanation would be that, in contrast to the higher latitude locations where heavy sea-ice cover blocks light and associated photosynthetic activities in the upper waters, seasonally ice-free conditions at these shelf sites would ensure more light availability for phytoplankton growth (de Vernal et al., 2001; Matthiessen et al., 2005). Further, a continuously reducing summer sea-ice extent in this region owing to an intensification of the warm Pacific water inflow in recent years may provide more open-water habitat for phytoplankton population therein (Woodgate et al., 2010, 2012; Woodgate, 2018). Another important factor to consider is a sufficient nutrient supply from the northern Bering Sea and/or adjacent large rivers such as Yukon and Anadyr rivers that appear to play a significant role in supporting higher primary productivity in the shallow Chukchi Shelf sites (Walsh and Dieterle, 1994; Grebmeier et al., 1995; Viscosi-Shirley et al., 2003; Naidu et al., 2003; Carmack et al., 2006).

4.2. Strong regional contrasts in the cross-shelf dinoflagellate cyst distributions

As previously described, surface sediments from the Chukchi-East Siberian seas show an important dinoflagellate cyst accumulation at the shallow-shelf locations subject to a longer open-water season with sufficient nutrient supplies, which may create favorable conditions for overall phytoplankton production. It is intriguing to note that there are site-specific patterns in the cyst assemblage compositions that divide the cyst accumulation zone into two spatial domains: the Chukchi shelf (A; sites 1–9) and the East Siberian shelf (B; sites 24–32) (Figs. 3, 4c and 5). Area A is characterized by a predominance of *P. dalei* cysts with the most intense accumulation at sites 1–4 (2622–5505 cysts/g, 46–67%) and, to a lesser extent, *O. centrocarpum* s.l. (307–2687 cysts/g, 12–51%). A particular note is for the exclusive occurrence of autotrophs including *Spiniferites* group, cysts of *Alexandrium*, *B. tepikiense* and *Impagidinium* species, which are virtually barren in area B. By contrast, area B is dominated by heterotrophic taxa, notably *I. minutum* (72–1867 cysts/g, 8–58%) and "round

brown spiny" cyst group including *I. minutum* subsp. *barbatum*, *E. karaense*, *I.*? *cezare* s.l. and *I. brevispinosum*. Our study questions whether the recognized heterogeneous patterns in the species compositions reflect different environmental forcing factors that separate the assemblages. Results from the nMDS analysis do highlight a relatively strong link between surface parameters and taxa distribution, particularly in relation to surface productivity and nutrients.

[Insert Figure 5]

In general, dinoflagellate cyst assemblages in Arctic environments are reported to be dominated by heterotrophic taxa such as *I. minutum* and *Brigantedinium* spp. (e.g., de Vernal et al., 1997; Rochon et al., 1999; Head et al., 2001; Radi et al., 2001; Grøsfjeld et al., 2009). Therefore, the co-predominance of *P. dalei* cysts and *O. centrocarpum*, which all relate to an autotrophic production, in the A region is noteworthy. A particular note is for the multifold-higher abundance of *P. dalei* cysts in area A, compared with all other specimens (Figs. 3 and 5a). The cyst of *P. dalei*, a cosmopolitan taxon tolerating large temperature and salinity ranges, is commonly observed in sub-Arctic sea sediments (e.g., de Vernal et al. 2001; Mudie and Rochon 2001; Marret et al., 2004; Grøsfjeld et al., 2009; Solignac et al., 2009). In particular, this taxon has a strong affinity for highly stratified and relatively productive waters at a distance from the multiyear sea-ice zone (Radi et al., 2001; Radi et al., 2007; Solignac et al., 2009; Milzer et al., 2013). We note that area A is located among the regions of the low-salinity surface layer where receives large inputs of freshwater from sea-ice melting and river outflow, fueled by increasing northward flow of the warm-Pacific water today (Carmack et al., 2006; Markus et al., 2009; Woodgate et al., 2012; Codispoti et al., 2013; Jung et al., 2021a). This is in accordance with the notion that the dominance of *P. dalei* cysts is resulted from an intense seasonal surface layer stratification led by the massive freshwater supplies, along with a lengthening of summer open-water season (e.g. Grøsfjeld et al., 2009; Heikkilä et al. 2014). It is also noteworthy to mention that *O. centrocarpum*, another cosmopolitan species with large environmental tolerances (Marret and Zonneveld, 2003; Zonneveld et al., 2013; Marret et al., 2020), co-dominates with *P. dalei* cysts at the southernmost Chukchi shelf samples (Figs. 3 and 5b). As this taxon is known to favor unstable water conditions associated with high turbidity, the neritic/oceanic transition and dynamic frontal systems

(Dale, 1996; Dale et al., 2002; Marret and Scourse, 2002), its high occurrence may indicate rather deteriorated water column stability, possibly induced by large temperature-salinity gradients and seasonally fluctuating stratification. This speculation gains further support from higher concentrations of the Arctic morphotype of *O. centrocarpum* in this area, because its morphological variation bearing poorly developed processes is resulted from phenotypic adaptation to rapidly changing salinity environments (e.g., de Vernal et al., 1989; Mertens et al., 2011). All of these seem to confirm a pivotal impact of the Pacific water inflow on the exclusive occupation of these opportunistic-nature taxa in area A; by not only rendering ample supplies of nutrient-rich water and increased light availability during open-water season (Walsh et al., 1989; Grebmeier et al., 1995; Naidu et al., 2003; Codispoti et al., 2005; Lee et al., 2012; Zhuang et al., 2016; Jin et al., 2017), but also creating extreme seasonality and associated environmental stress that are rather too harsh for most other species to thrive (Fig. 6).

[Insert Figure 6]

By contrast, the dinoflagellate cyst assemblage in area B is preferentially occupied by "round brown spiny cyst" taxa (collectively *I. minutum* subsp. *barbatum*, *E. karaense*, *I.*? *cezare* s.l. and *I. brevispinosum*) (Fig. 3). They generally characterize cold polar to subpolar waters of the high northern latitudes, particularly abundant to dominant in regions with an extensive seasonal sea-ice cover, and summer temperatures below 7°C (Rochon et al., 1999; de Vernal et al., 2001; Head et al., 2001). We find that the strong regionalism of this cyst group is well match with a spatial disparity in sea-ice conditions between the areas A and B (Fig. 1d). According to observational studies on the relative change of the sea-ice extent (e.g., Rigor and Wallace, 2004; Rodrigues, 2008), the East Siberian Sea shelf shows more extensive, thick sea-ice cover during the summer months when compared with the Chukchi Sea sector. This may explain the high abundance of *I. minutum* (~ 58%) in area B (Figs. 3 and 5d), as this taxon is known to have an affinity to cold (–2°C), longer sea-ice cover times (up to 12 months per year) (Harland and Pudsey, 1999; Head et al., 2001; Marret and Zonneveld, 2003; Grosfjeld et al., 2009). However, it should be noted that a number of recent studies report no statistical relationship between their occurrences and sea-ice conditions (e.g., Heikkilä et al., 2014, 2016; Allan et al., 2020; de Vernal et al., 2020) and thus, the controls on

their distribution require further investigation. Noteworthy is an exclusive occurrence of *I. minutum* subsp. *barbatum* at this area (Figs. 3 and 5e). Given its more robust geographical restriction than other round brown spiny cysts, we are tempted to suggest this cyst type as a more sensitive indicator of cold, sea-ice covered environments.

It should be noted, however, that cold polar conditions are not necessarily the sole explanation of their abundance in area B. As shown in Figs. 3 and 5, area B exhibits almost selective occupation of *I. minutum*, *I. minutum* subsp. *barbatum*, *E. karaense*, *I.*? *cezare* s.l. and *I. brevispinosm* that are all related to a heterotrophic behavior, compared with area A where their occurrences are overwhelmed by a strong domination of autotrophs (e.g., cysts of *P. dalei*, *O. centrocarpum* s.l. and *Spiniferites* species). This feature may reflect different trophic mode and nutritional environments in area B, which seem to play as a deterministic factor to foster heterotrophic dinoflagellate population therein. Heterotrophic dinoflagellates typically feed on other light-dependent organisms and therefore, their abundance and biomass strongly depend on production of diatoms and other prey groups such as bacteria, nanoflagellates, hapto- and prasinophytes or other dinoflagellate species (Matsuoka, 1999; Godhe and McQuoid, 2003; Kim et al., 2009; Jeong et al., 2010). Indeed, observation data – e.g., chlorophyll-a concentrations, phytoplankton photophysiological properties and microplankton communities – reported remarkably high marine productivity at area B (e.g., Yun et al., 2015a; Ko et al., 2020; Kim et al., 2021; Fig. 1d). In this respect, regardless of the favorable cold, polar conditions aforementioned above, the dominant prevalence of heterotrophic dinoflagellate cysts may strongly relate to such excessive marine primary production and ensuing prey availability. Effects of different nutritional structures and biochemical compositions of photosynthetic organisms on the grazing activity of heterotrophic dinoflagellates are possible (Lee et al., 2009; Yun et al., 2015b; Mills et al., 2018), but these ecophysiological processes are beyond the scope of this study and further in-depth investigations are needed to better understand trophic interactions in this marine ecosystem. Interestingly, our nMDS analysis on cyst taxa (Fig. 3a) highlighted an interesting feature, with the ordination of *T. applanatum* within the autotrophic species. A recent study on the chemical composition of the cyst wall indicates presence of sporopollenin, as well as the occurrence of nitrogen-containing functional groups (Gurdebeke et al., 2020). It is, therefore, possible that the trophic strategy of this species may favor nutrient-rich waters rather than productive waters. However, because there is only limited knowledge of nutrient

environments at the sites, our data cannot provide conclusive evidence and more research with *in-situ* observation data through monitoring schemes is needed to assess this question.

But what can drive such high primary productivity and ensuing opportunity for heterotrophic dinoflagellate population in area B? We tentatively link this feature to a very specific oceanographical phenomenon, the so-called "Atlantification"– i.e., growing intrusions of Atlantic water into the interior of the Arctic Basin as the Arctic becomes increasingly ice-free. It seems now evident that continuing sea-ice loss on the Atlantic side of the Arctic Ocean triggers a weakening of the ocean's cold layering system that blocks Atlantic inflows, and subsequently leads to a warmer, denser Atlantic water spreading toward the eastern Eurasian Basin (Polyakov et al., 2017, 2018, 2020; Bertosio et al., 2022). This notion gains further support from a recent work of Jung et al. (2021b). They observed an intrusion of Atlantic-origin water into the weakened halocline boundary between Pacific and Atlantic-origin waters at a site located in area B (Fig. 1; yellow star). That cold, saline water mass lifts the overlying nutrient-rich Pacific-origin waters up to the upper euphotic zone and consequently boosts anomalously high surface phytoplankton blooms in the area – where otherwise shows highly oligotrophic surface waters during summer (Carmack and Chapman, 2003; Tremblay et al., 2011; Williams and Carmack, 2015). Therefore, it appears conceivable that the heterotrophic dinoflagellate cyst accumulations in area B could be affected by a growing intrusion of the Atlantic-origin water spreading into the East Siberian Sea shelf waters during the time of the cyst production – being an ultimate driver of nutrient-rich, cold bottom water supplies to the surface layer and high level of biological productivity therein (Fig. 6). Considering relatively thicker, stronger summer sea-ice condition in the East Siberian Sea region, the phytoplankton bloom development in area B is likely to be led by photosynthetic ice algae rather than pelagic phytoplankton communities (Hill and Cota, 2005; Wassmann and Reigstad, 2011; Leu et al., 2015). We tentatively suggest that, in addition to the pivotal role of nutrient supply, sea-ice on light regime may act as a unique habitat for ice algae growth and ensuing dominance of heterotrophic dinoflagellates due to its ability to survive in the dark, harsh arctic environments with longer sea-ice cover times (Harland and Pudsey, 1999; Rochon et al., 1999).

If correct, our data may provide sedimentary evidence of the persistence of the aforementioned oceanographic phenomenon on a regional scale. Despite that information on sedimentation rates are lacking for the study area, there are reports of estimations made at the

Chukchi Shelf region – for instance, the southern/central Chukchi Sea (0.03 – 0.37 cm/yr; Cooper and Grebmeier, 2018), the central Chukchi Sea (0.04 – 0.91 cm/yr; Astakhov et al., 2019) and the northern Chukchi Sea (0.09 cm/yr; Kim et al., 2020a). Accordingly, it can be tentatively speculated that the sediment materials under study may represent about 1 – 30 years of sediment accumulation. We clearly stress that different depositional environments and taphonomic processes may have affected the dinoflagellate cyst concentration and hence, we cannot exclude the probability of aliasing errors in the interpretation of our data. In particular, magnitudes of terrigenous particulate matter input from nearby continents could have influenced accumulation rates of sediments at varying degrees, which in turn can dilute or enhance the sedimentary dinoflagellate cyst signals. Nevertheless, given that organic-walled dinoflagellate cysts are composed of refractory organic matter, a complex polymer similar to the sporopollenin (Dale, 1983; Versteegh and Blokker, 2004), the observed distribution patterns of dinoflagellate cysts don't seem to be severely biased by post-depositional degradation. In order to assess how accurately our data represent the originally deposited dinoflagellate cyst assemblages, further studies are needed to characterize various oceanographic and depositional environments (e.g., sedimentation rate, hydrodynamics and topography) in such a complex area.

4.3. Further implications

Our results show a strong regional contrast in patterns of the dinoflagellate cyst distributions across the Chukchi–East Siberian Sea shelves. This is the region where currently experiences drastic changes in hydrographic environments due to increasing advections of southern waters on the Pacific and Atlantic sides of the Arctic Ocean, along with greater areas of open water (e.g., Woodgate et al., 2010, 2012, 2018; Polyakov et al., 2017, 2018, 2020). Tentatively, we speculate that the distinct geographic contrasts observed in our dinoflagellate cyst data can be a result of species-specific responses to such prominent regional oceanographic characteristics, probably affected by the growing intrusions of the Atlantic- and Pacific-origin water on both sides of the Arctic Ocean. This notion is in line with recent observations of widespread structural changes in species distribution and biological community of Arctic marine environments, triggered by a poleward expansion of warm currents from lower latitudes (e.g., Fossheim et al., 2015; Frainer et al., 2017; Lewis et al., 2020).

From a climatic point of view, our data may also have implications for a potential impact of the current Arctic warming trend on phytoplankton community changes through biological-physical coupling processes. Recent climate model studies highlight a certain role of marine phytoplankton biomass in modifying physical properties of the ocean and thereby affecting the global climate system (e.g., Manizza et al., 2005; Anderson et al., 2009; Lengaigne et al., 2009; Jochum et al., 2010; Patara et al., 2012). This biogeophysical feedback appears to significantly influence the Arctic climate – i.e., higher phytoplankton biomass increases phytoplankton pigments in the ocean that are related to more light absorption and ocean surface warming, which in turn lead to higher phytoplankton growth (Park et al., 2015; Lim et al., 2019a,b). Current climate models forecast greater areas of open water in the Arctic Ocean following an increase in water temperature and loss of sea-ice in the coming decades (e.g., Wang and Overland, 2009; Stroeve et al., 2012b; Stocker et al., 2013; Casas-Prat and Wang, 2020; Wang, 2021). Therefore, it seems evident that, if the regional contrasts identified in our dinoflagellate cyst data indeed are the result of a poleward expansion of southern waters into the warming Arctic Ocean, the sharp biogeographic divide is expected to only intensify into the future. This raises important questions regarding a potential impact of such on-going structural changes of the marine phytoplankton community on the Arctic climate, particularly in light of its phenological significance. It should be noted that there is uncertainty associated with different depositional environments and taphonomic processes – obviously, this is an important factor limiting our interpretation of the dinoflagellate cyst distribution at specific sites and their linkages to the prevailing conditions at those sites. What becomes apparent is that sediment cores will be one of the most important sources of information about long-term changes in the aforementioned biological and oceanographical coupling processes in the context of recent climate warming, for which our study can be based.

4.4. *Alexandrium* cyst accumulations

Although limited in numbers, our data show preferential accumulations of *Alexandrium* cysts at the southeastern location (sites 1–4; Figs. 3 and 5). Given that these cysts mostly occur in coastal sediments of temperate regions with mesotrophic and eutrophic settings (e.g., Anderson et al., 2005a,b; Zonneveld et al., 2013; Kim et al., 2018), the *Alexandrium* cysts found in the sites under study are likely to have exogenous origin rather than *in-situ*

production under site-specific favorable habitat conditions. It is interesting to consider these findings in the light of a recent study by Anderson et al. (2021) that reported massive *Alexandrium* cyst deposits in the Alaskan Arctic sediments; hypothetically being formed via a long-range transportation from the north Pacific region by the Bering Strait throughflow, or *in-situ* germination from the cyst bed originally existed in the region. This indicates a high probability of its delivery to the aforementioned location (sites 1–4, this study) from the Alaskan Arctic cyst deposits, potentially facilitated by local hydrodynamics and wind-induced currents causing cyst dispersal in the sedimentary regime. It should be noted that the distribution and concentrations of *Alexandrium* cysts in the present study can be underestimated, because they are difficult to detect at light microscopy. Thus, regardless of the transporting mechanisms, our data infer that the *Alexandrium* cysts may distribute over a considerable stretch of this shelf region that extend well beyond the Alaskan Arctic area. However, this remains speculative until further data on the presence and magnitude of their distribution becomes available. Other questions also remain whether the continual sedimentary accumulations of cysts of *Alexandrium*, the dinoflagellate genus that produce paralytic shellfish poisoning toxins, have a potential risk to the Arctic's marine ecosystems; given the increasing probability for rapid cyst germination and ensuing *Alexandrium* bloom initiation in response to habitat amelioration led by further Arctic warming (Anderson et al., 2021). However, our data cannot provide conclusive evaluations and more investigations are needed to assess these issues.

5. Conclusions

This study provides the first detailed description of recent dinoflagellate cyst assemblages from 32 surface sediment samples distributed in the Chukchi and East Siberian Sea shelves, the Pacific sector of the Arctic Ocean. In this region, increasing Pacific water inflows through the Bering Strait play as a major factor determining its hydrographic characteristics and a wide range of variations in oceanic temperature, salinity and seasonal sea-ice cover. Our data document an intense dinoflagellate cyst accumulation at the shallow-shelf sites, owing to a longer open-water season and sufficient nutrient supplies that provide favorable habitat conditions for overall dinoflagellate population growth therein. The most prominent feature is a strong geographic pattern of the dinoflagellate cyst species composition and distribution, which separate the cyst accumulation zone into two spatial

domains: the Chukchi Sea shelf and the East Siberian Sea shelf. The Chukchi Sea shelf sediments exhibit an exclusive occupation of cosmopolitan, opportunistic-nature taxa (*P. dalei* cysts and *O. centrocarpum*), induced by warm-Pacific water inflows that may have caused not only extreme seasonality and unstable water conditions but also sufficient nutrient supplies and higher light availability. By contrast, the East Siberian Sea shelf sites with more extensive sea-ice cover and lower temperatures is primarily occupied by "round brown spiny cyst" taxa (e.g., *I. minutum* subsp. *barbatum*, *E. karaense*, *I.*? *cezare* s.l. and *I. brevispinosum*) that have a strong affinity for cold, polar conditions. We speculate that such strong occupation of heterotrophic dinoflagellate population is primarily linked to Atlantic-origin water intrusions into the East Siberian Sea shelf, by way of uplifting nutrient-rich, cold bottom water to oligotrophic surface layer for the growth of primary producers. The robust regionalism reflected in our dinoflagellate cyst data signifies a growing impact of southern waters flooding on the Arctic Ocean, which seems to exert a determinant role on restructuring hydrographic conditions and associated phytoplankton communities therein. In light of emerging climate amelioration for Arctic phytoplankton habitats, the unique assemblage structure of dinoflagellate cyst distributions in the present study may infer substantial shifts in the Arctic phytoplankton phenology and associated biogeophysical feedback, possibly prompting further climate impacts in the future. Further, cyst accumulations of toxin-producing dinoflagellate *Alexandrium* at the Chukchi Sea shelf may signal the urgency for in-depth investigations on their distributions and dispersal dynamics in the Arctic Ocean, as well as their potential for rapid germination and ensuing bloom initiation under the current warming trends. Our study highlights considerable potential of dinoflagellate cysts as a valuable proxy for changes in hydrographic conditions and plankton communities in the Arctic marine ecosystem. For longer-term perspectives, especially whether the postulated dinoflagellate cyst signals are indeed a response to climate-driven environmental perturbations, a promising approach is to reconstruct dinoflagellate cyst proxy time-series from sediment cores, along with a robust chronological framework at time-scales relevant for climate studies. Such information will be essential to provide insights into how Arctic marine ecosystems with greater areas of open water will potentially react to a future climate change.

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Figure captions

Figure 1. Map of the study area illustrating locations of sampling sites and main oceanographic features. a) Surface sediment samples used in our study are indicated by their

numbers (black dots; details in Table 1). Arrows indicate major ocean current patterns (red=Pacific-origin and blue=Atlantic-origin): the upper right map visualizes the two dominant ocean current systems in the Arctic Ocean (after Hunt et al., 2013; Polyakov et al., 2020). Dashed white line represents sea-ice extent during August in 2017, obtained from the National Snow and Ice Data Center (drawn following Kim et al., 2020b). The yellow star marks location of the study site of Jung et al. (2021) mentioned in the text. b, c) The mean summer sea-surface temperature and salinity distributions obtained from sites nearby the sediment sampling location during the ARAON cruises in 2015–2017 (from the KOPRI data server; https://kpdc.kopri.re.kr/search/80785502-2cb4-4146-a799-b7c76d65f47c). d) The GlobColour-merged chlorophyll-a concentration (mg/m^3) derived from satellite observation during the summers of 2015–2017. e) The mean satellite-observed sea-ice concentrations during the summers of 2015–2017 retrieved from NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration. Geographic locations are divided into two major regions: the Chukchi Sea (sites 1-9; area A) and the East Siberian Sea (sites 24-32; area B).

Figure 2. Photomicrographs of selected dinoflagellate cysts collected in surface sediments from the Chukchi–East Siberian Seas (Scale bar = 20 μm). a) *Alexandrium* species. b) Cyst of *Pentapharsodinium dalei*. c) *Trinovantedinium applanatum*. d) *Operculodinium centrocarpum*. e) *Operculodinium centrocarpum*–Arctic morphotype, with incompletely developed and sparsely distributed processes (red box). f) *Islandinium brevispinosum*. g) *Islandinium minutum*. h) *Echinidinium karaense*. i) *Islandinium*? *cezare* with smooth process, stems of uniform thickness and tips minutely expanded distally with recurved margins (red box). j) *Islandinium minutum* subsp. *barbatum* with process stems that are tapered and bear unusual barbs on (red box).

Figure 3. Total cyst concentrations (cysts/g; curve) and relative abundances of selected cyst taxa (contributing >1%; bar) in surface sediment samples (autotrophic taxa=green and heterotrophic taxa=blue). Spatial domains of areas A (sites 1-9) and B (sites 24-32) are denoted on the top of the diagram (shaded in grey).

Figure 4. a) non-metric multidimensional scaling (nMDS) plot of the 28 cyst taxa. Green dot represents autotrophic species and brown inverted triangle, heterotrophic ones. b) Covariance

based principal component analysis on normalised abiotic parameters. Blue dots are samples from the Chukchi Sea (A), red inverted triangles are samples from the East Siberian Sea (B), and green squares are the other samples (OS). c) nMDS plot of the 32 dinoflagellate cyst assemblages with multiple regression vectors for environmental parameters (stress of 0.08, indicative of a good fit).

Figure 5. Distributions of key dinoflagellate cyst taxa and groups, expressed as percentages and concentrations (cysts/g). a) *Pentapharsodinium dalei*. b) *Operculodinium centrocarpum*. c) Autotrophs. d) *Islandinium minutum*. e) *I. minutum* subsp. *barbatum*. f) Heterotrophs. g) *Alexandrium* cysts.

Figure 6. Conceptual overview of mechanisms causing regional contrasts in dinoflagellate cyst distributions between the Chukchi Sea (area A) and the East Siberian Sea (area B) under the current Arctic warming trend. Area A (left panel) exemplifies the increasing northward Pacific water flow (red arrow) affecting dinoflagellate production in the Chukchi Sea environment. The warm, nutrient-rich Pacific water inflow not only supplies enough nutrients for dinoflagellate population growth, but also increases freshwater input by melting sea-ice and delivering riverine waters (gray shaded circles) that generate more open water habitat with strong seasonal stratification (gray dotted line) favored by autotrophic and opportunistic dinoflagellate taxa (green stars). The black dashed arrow indicates a possible transport of PSP-causative *Alexandrium* cysts from the Alaskan Arctic cyst deposits by local hydrodynamics and wind-induced currents. Area B (right panel) illustrates an intensification of the Atlantic-origin water intrusion (blue arrow) to the East Siberian Sea. The increased saline, dense Atlantic-origin water mass lifts the overlying nutrient-rich Pacific-origin waters up to the oligotrophic surface water, which boosts high production of photosynthesizing primary producers (purple dots) and ensuing heterotrophic, polar water dinoflagellate taxa (blue stars).

Table 1. Sediment sampling site number, geographical coordinates, water depth and total dinoflagellate cyst concentrations of analyzed samples.

Site No.	Cruise	Gear	Latitude	Longitude	Water depth (m)	Total dinoflagellate cyst concentrations (cysts/g)
1	ARA08	Box corer	72.36°N	168.67°W	59	10179
2	ARA08	Box corer	73.58°N	168.28°W	125	5762
3	ARA09	Box corer	73.74°N	166.42°W	126	8512
4	ARA02	Multi corer	74.3°N	167.65°W	244	4583
5	ARA07	Box corer	74.80°N	167.81°W	223	981
6	ARA02	Multi corer	75.11°N	166.34°W	442	2531
7	ARA09	Box corer	75.69°N	166.64°W	290	1124
8	ARA09	Box corer	75.24°N	171.97°W	495	1097
9	ARA07	Box corer	75.15°N	176.03°W	350	1019
10	ARA07	Box corer	75.79°N	176.99°W	1278	518
11	ARA07	Box corer	76.00°N	170.5°W	1319	327
12	ARA01	Multi corer	75.17°N	160.00°W	1962	853
13	ARA01	Multi corer	75.43°N	156.01°W	3084	593
14	ARA01	Multi corer	75.94°N	156.02°W	1207	159
15	ARA01	Multi corer	75.89°N	163.01°W	2064	1029
16	ARA02	Multi corer	76.29°N	167.16°W	395	485
17	ARA07	Box corer	77.43°N	164.12°W	325	145
18	ARA07	Box corer	77.86°N	175.88°W	1613	104
19	ARA02	Multi corer	78.00°N	175.66°W	1595	142
20	ARA02	Multi corer	78.00°N	179.33°W	1567	200
21	ARA02	Multi corer	78.00°N	174.00°E	1332	152
22	ARA02	Multi corer	76.40°N	176.03°W	1920	178
23	ARA02	Multi corer	76.40°N	179.33°W	1002	114
24	ARA08	Box corer	75.16°N	179.99°W	591	1583
25	ARA08	Box corer	75.77°N	177.16°E	582	522
26	ARA09	Box corer	75.60°N	176.50°E	340	1334
27	ARA09	Box corer	75.99°N	173.58°E	265	954
28	ARA08	Box corer	75.00°N	173.60°E	107	1932
29	ARA09	Box corer	74.64°N	174.92°E	70	4512
30	ARA07	Box corer	74.74°N	170.46°E	59	1098
31	ARA08	Box corer	74.00°N	170.00°E	46	1770
32	ARA07	Box corer	73.82°N	169.19°E	43	1075

Table 2. Selected sea-surface environmental variables and sources.

Abiotic parameters	Code used for multivariate analysis	Sources
% Sea ice: Annual average for the period 1955-2012	SICE	http://nsidc.org/data/G10010
Dissolved oxygen (ml/l)	DOxy	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Nitrates (µmol/l)	Nitr	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Phosphates (µmol/l)	Phos	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Silicates (µmol/l)	Sili	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Salinity Summer Winter	SSUM SWIN	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Temperature (°C) Summer Winter	TSUM TWIN	World Ocean Atlas 2013 V2 https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Productivity (mgC/m²/day) July August September	PJul PAug PSep	Standard VGPM Monthly files from MODIS R2018 Data http://orca.science.oregonstate.edu/2160.by.4320.monthly.xyz.vgpm.m.chl.m.sst.php

Table 3. List of dinoflagellate cyst taxa identified in the investigated sediments, trophic type and relative abundance of cyst species (%).

Taxa name	Motile affinity	Code	Trophic mode	Percentage range (%)
Cyst of *Alexandrium* species	*Alexandrium* species	Alex	A	0–3.8
Cyst of *Pentapharsodinium dalei*	*Pentapharsodinium dalei*	Pdal	A	1.1–78.6
Operculodinium centrocarpum sensu Wall and Dale 1966	*Protoceratium reticulatum*	Ocen	A	0.7–72.4
Operculodinium centrocarpum–Arctic morphotype	Unknown	OceA	A	0–13.3
Bitectatodinium tepikiense	*Gonyaulax digitale*	Btep	A	0–5.9
Spiniferites bentorii	*Gonyaulax digitale*	Sben	A	0–0.7
Spiniferites elongatus	*Gonyaulax elongata*	Selo	A	0–7.5
Spiniferites mirabilis	*Gonyaulax spinifera*	Smir	A	0–0.4
Spiniferites membranaceus	*Gonyaulax membranacea*	Sme m	A	0–1.3
Spiniferites spp.	Unknown	Sspp	A	0–2.1
Nematosphaeropsis labyrinthus	Unknown	Nlab	A	0–0.5
Impagidinium sphaericum	Unknown	Isph	A	0–0.9
Impagidinium pallidum	Unknown	Ipal	A	0–3.5
Impagidinium spp.	Unknown	Ispp	A	0–1.4
Brigantedinium spp.	*Protoperidinium* spp.	Bspp	H	0–23.2
Echinidinium karaense	Unknown	Ekar	H	0–45.6
Islandinium brevispinosum	*Protoperidinium haizhouense*	Ibre	H	0–12.9
Islandinium? *cezare*	Unknown	Icez	H	0–3.3
Islandinium? *cezare* sensu lato – Morphotype 1 (Head et al., 2001)	Unknown	Icez M1	H	0–12.9
Islandinium minutum	*Islandinium minutum*	Imin	H	0–58.4
Islandinium minutum subsp. *barbatum*	Unknown	Ibar	H	0–30.3
Cyst of *Polykrikos* sp.–Arctic morphotype	Unknown	Parc	H	0–2.8
Cyst of *Polykrikos kofoidii*	*Polykrikos kofoidii*	Pkof	H	0–0.3
Cyst of *Polykrikos schwartzii*	*Polykrikos schwartzii*	Psch	H	0–2.4
Cyst of *Protoperidinium americanum*	*Protoperidinium americanum*	Pame	H	0–0.8
Selenopemphix quanta	*Protoperidinium conicum*	Squa	H	0–0.8
Selenopemphix nephroides	*Protoperidinium subinerme*	Snep	H	0–0.7
Trinovantedinium applanatum	*Protoperidinium shanghaiense*	Tapp	H	0–1.4

Figure 1

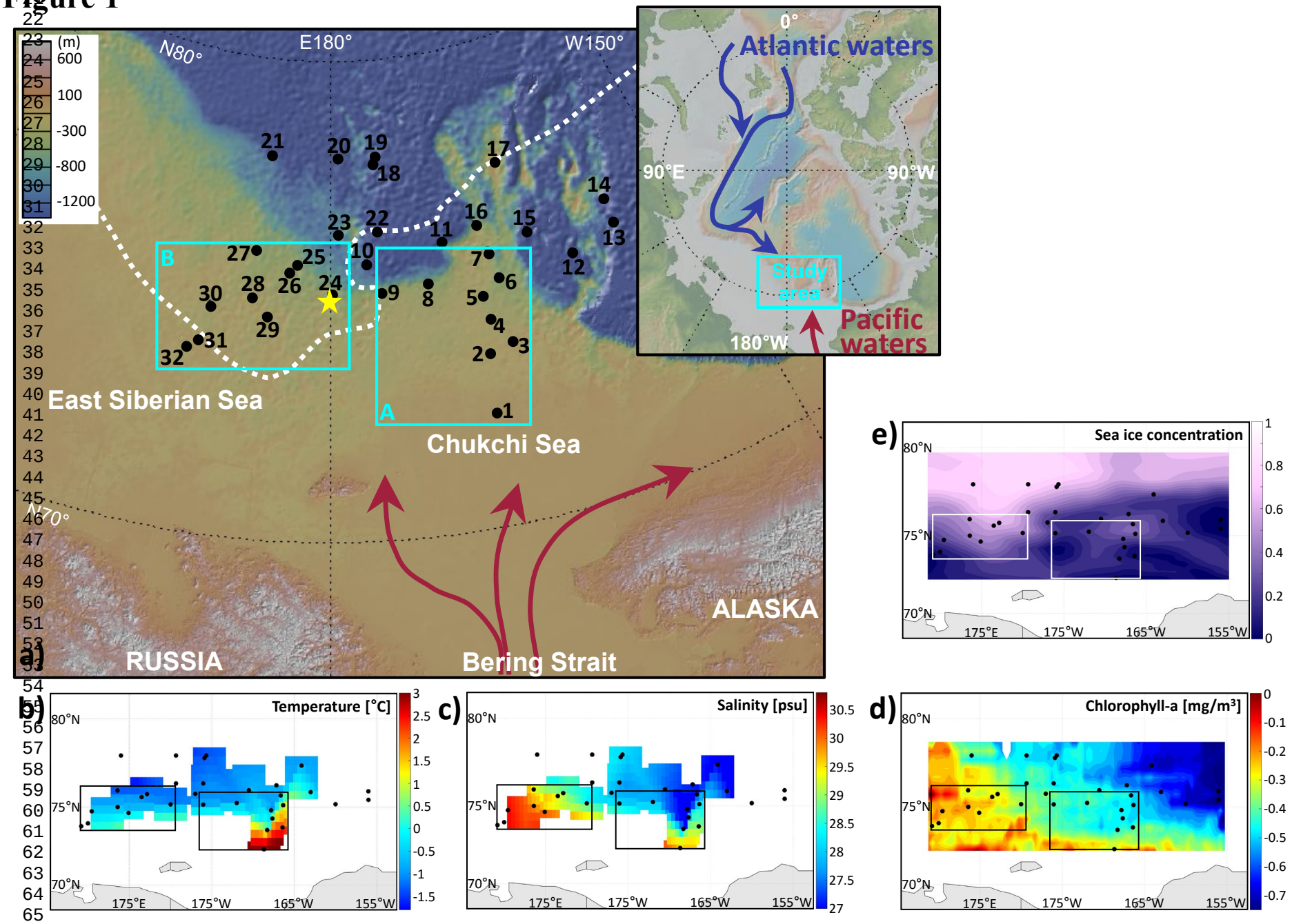


Figure 2

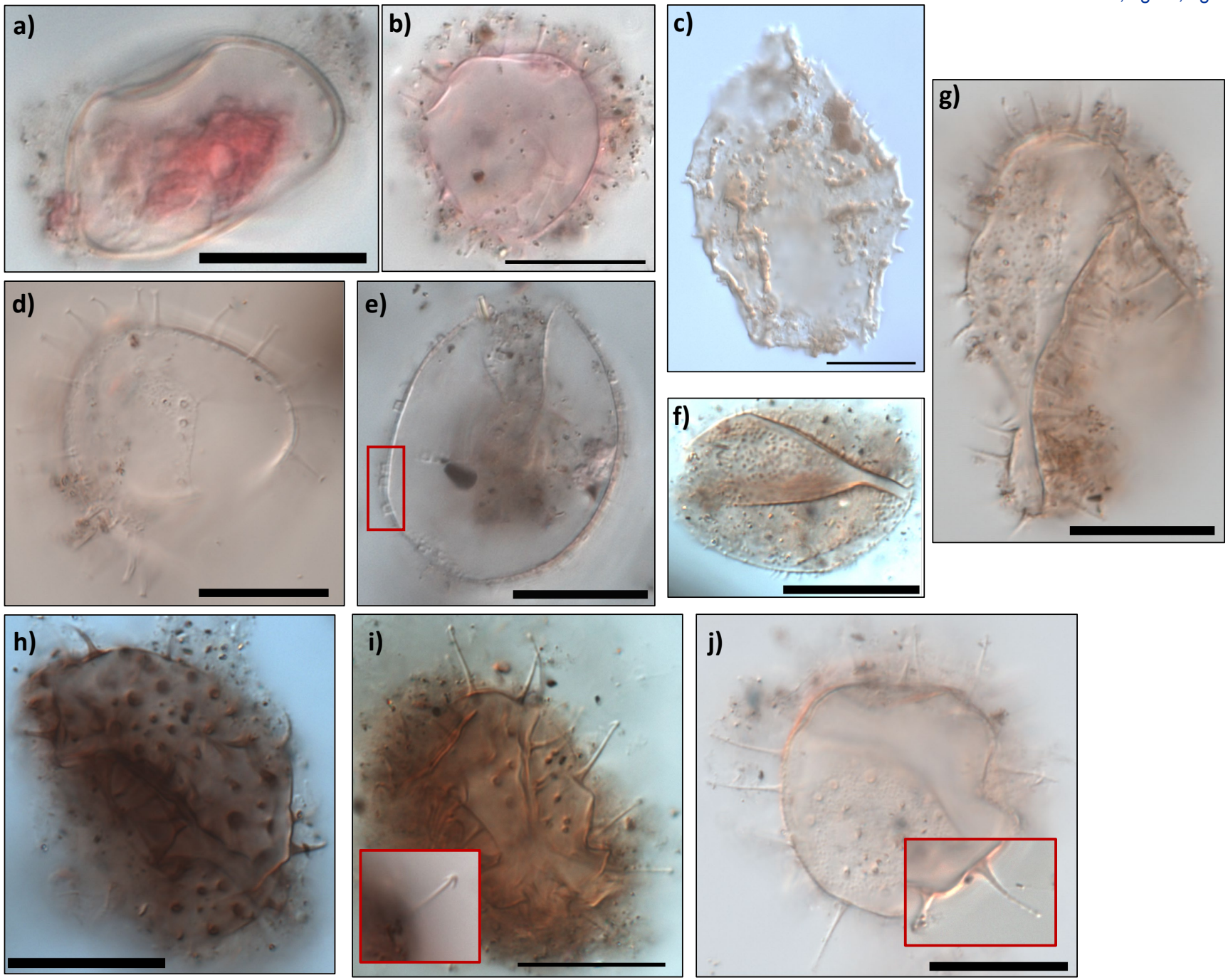


Figure 3

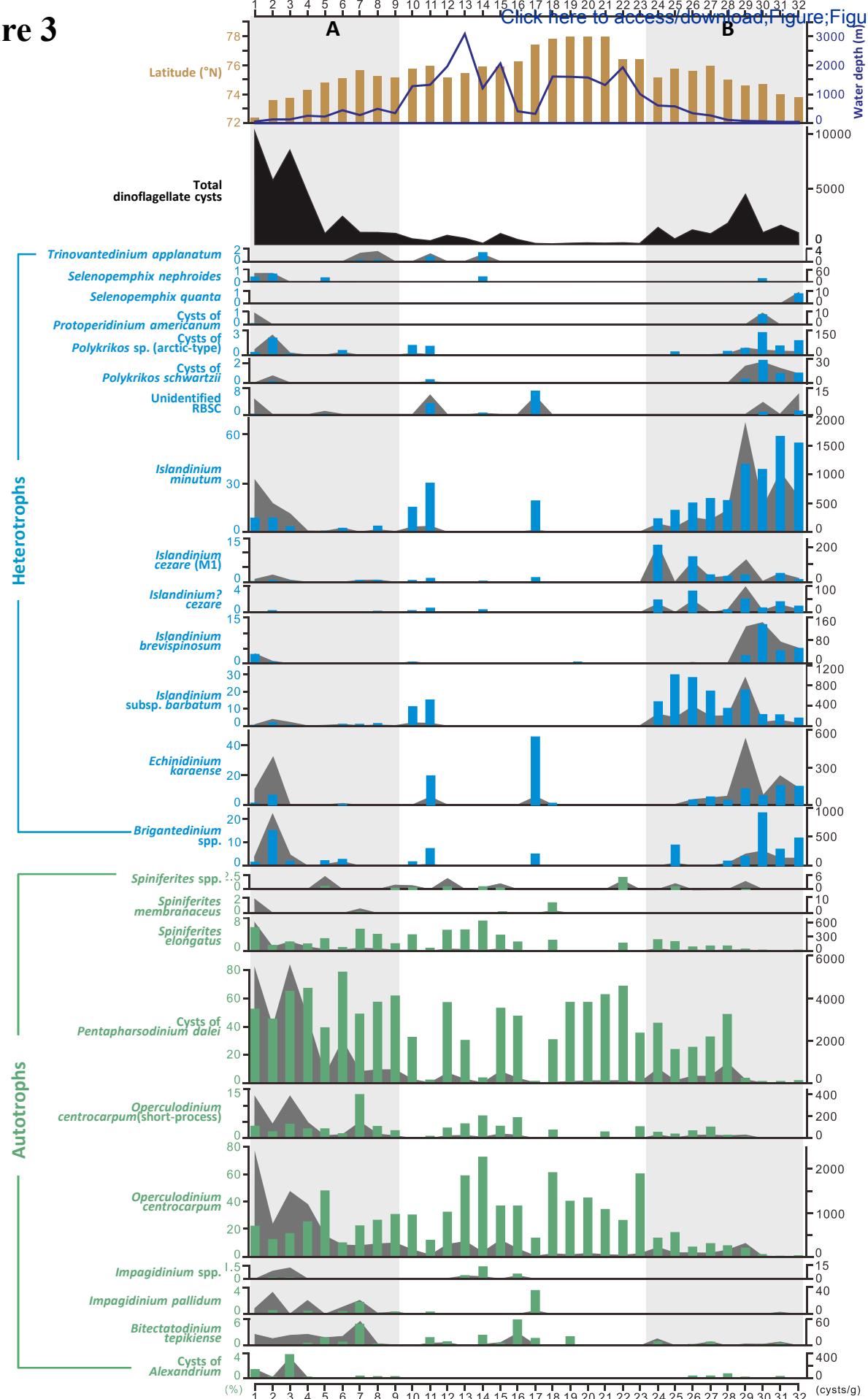
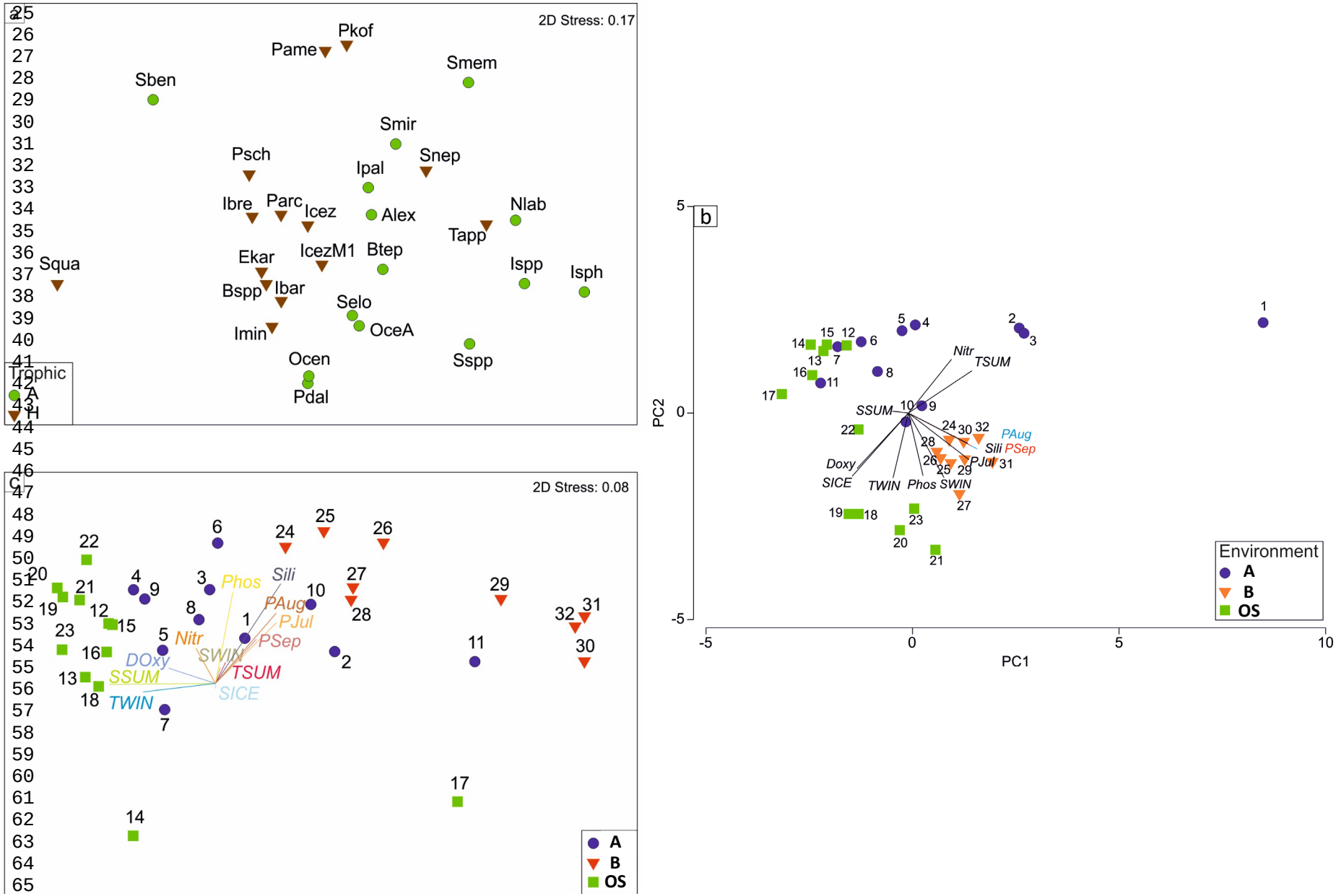


Figure 4



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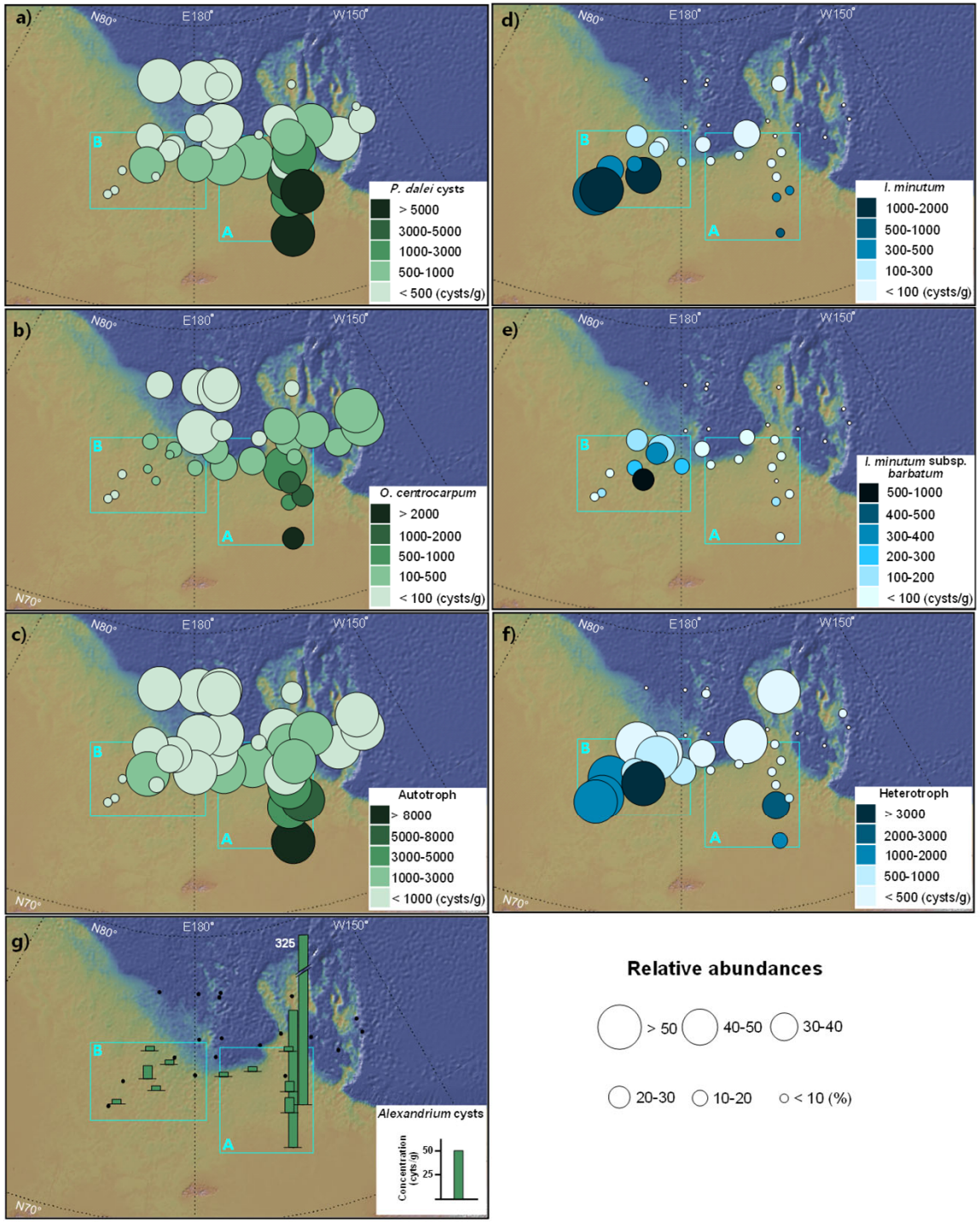
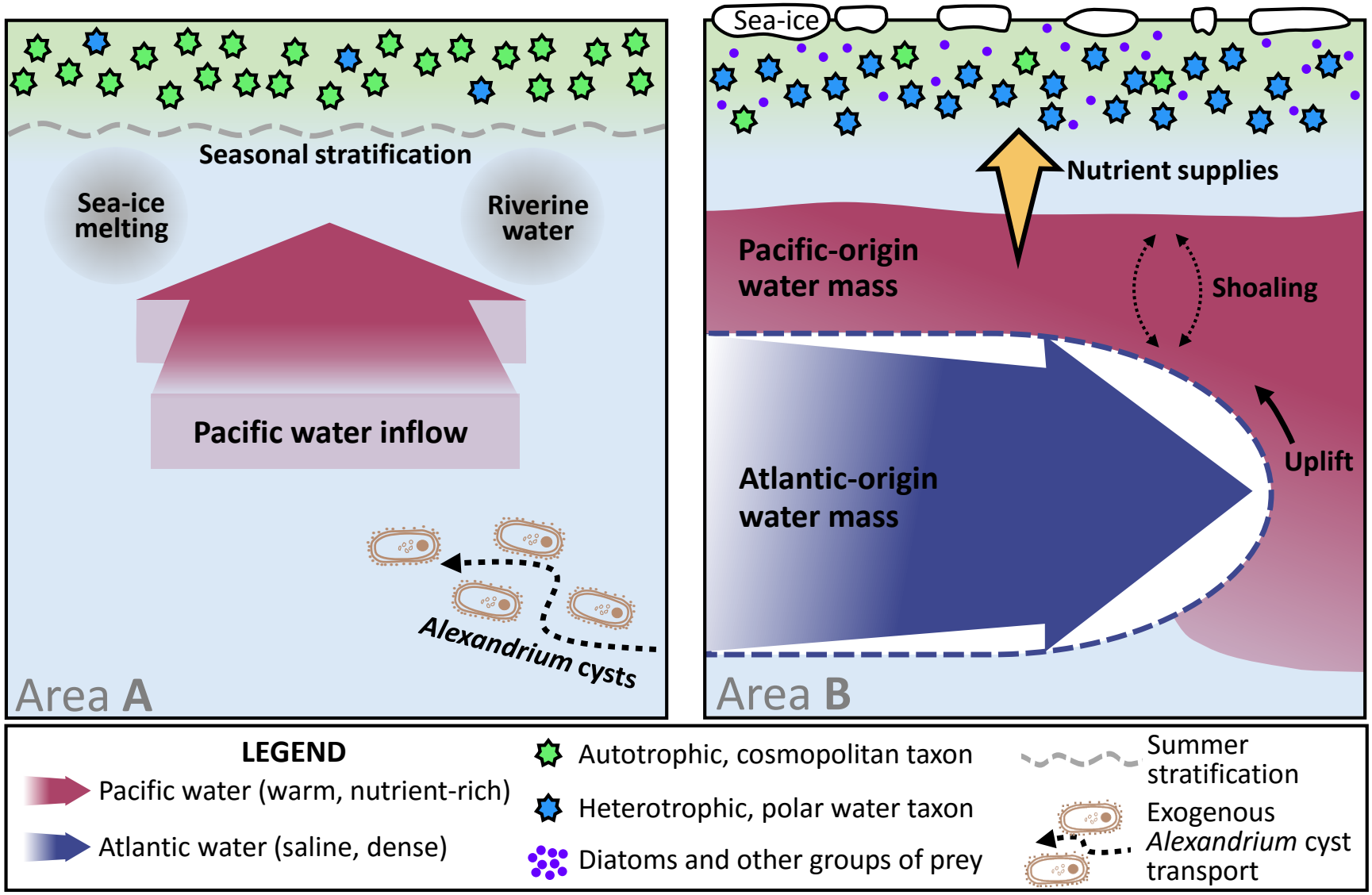

a)
N80°
E180°
W150°
B
A
P. dalei cysts
> 5000
3000-5000
1000-3000
500-1000
< 500 (cysts/g)
b)
O. centrocarpum
> 2000
1000-2000
500-1000
100-500
< 100 (cysts/g)
N70°
c)
Autotroph
> 8000
5000-8000
3000-5000
1000-3000
< 1000 (cysts/g)
d)
I. minutum
1000-2000
500-1000
300-500
100-300
< 100 (cysts/g)
e)
I. minutum subsp. barbatum
500-1000
400-500
300-400
200-300
100-200
< 100 (cysts/g)
f)
Heterotroph
> 3000
2000-3000
1000-2000
500-1000
< 500 (cysts/g)
g)
325
Alexandrium cysts
Concentration (cysts/g)
50
25
Relative abundances
> 50
40-50
30-40
20-30
10-20
< 10 (%)

Figure 6



Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: