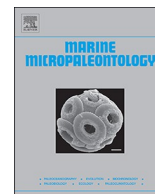




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Research paper

From bi-polar to regional distribution of modern dinoflagellate cysts, an overview of their biogeography

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ABSTRACT

This paper examines the distribution of 91 modern dinoflagellate cyst taxa from 3636 locations across the world's oceans. Patterns of distributions among the taxa included bi-polarity, cosmopolitan, northern versus southern hemispheres, and geographically restricted. Of the 91 taxa, three dominate these 3636 assemblages at the global scale, *Brigantedinium* species, *Operculodinium centrocarpum* sensu Wall and Dale 1966 and some species of *Spiniferites*. Whereas *Brigantedinium* is a true cosmopolitan taxon, with high abundances in each ocean, *Operculodinium centrocarpum* sensu Wall and Dale 1966 shows high abundances in polar to temperate regions in the Northern Hemisphere, and in tropical to sub-tropical waters in the Southern Hemisphere. *Spiniferites* species show highest occurrences in the Southern Hemisphere. This study also highlights three true bi-polar species, *Impagidinium pallidum*, *Islandinium minutum* and cyst of *Polarella glacialis*. Only a few taxa are strictly endemic, either being relics of ancient seas such as the Paratethys (*Spiniferites cruciformis*) or linked to specific environmental conditions. However, recent studies have shown recent worldwide dispersal of these endemic species possibly due to human activities. Overall, this compilation has highlighted the progress made since the early 1970s on our understanding of these important tracers of environmental conditions but also gaps in our knowledge of their distribution in pelagic regions of the Pacific and Indian Oceans as well as under Arctic sea ice.

1. Introduction

The taxonomy and distribution of modern dinoflagellate cysts (= dinocysts) have been increasingly studied over the last few decades because they demonstrate significant potential as tracers of past marine environmental conditions, in particular where other microfossils are rare or negatively affected by preservation (e.g., Aksu and Mudie, 1984; de Vernal and Marret, 2007). The pioneering work of Williams (1971) describing the modern distribution of cysts in recent North Atlantic sediments first triggered a keen interest in this group of microfossils, and subsequent studies such as those from Davey and Rogers (1975), Wall et al. (1977), Williams and Bujak (1977), Harland (1983), Turon

(1984), Edwards and Andrieu (1992) and Rochon et al. (1999) have highlighted the relationship between dinocyst species assemblages and surface water masses of the ocean. Mudie and Harland, (1996; text-Fig. 6) were the first to attempt a global-scale biogeographic synthesis for modern dinocyst-acritarch assemblages. Subsequently, a multitude of studies have helped to improve our knowledge on the biogeography of the dinocyst group from local (e.g., Radi et al., 2007; Limoges et al., 2010; Price et al., 2016) to global scale (Marret and Zonneveld, 2003; Zonneveld et al., 2013). The latest worldwide atlas published in 2013 illustrates the distribution of 71 taxa based on 2405 sites. Since 2013, additional studies (Table 1) investigating the modern distribution of dinoflagellate cysts regionally and worldwide have helped to refine

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Table 1
Location of datasets used for this compilation with type of data and references.

Location	Available data	References
Northern Hemisphere	Relative abundance	N = 1826 sites from de Vernal et al. (this VSI)
NW Atlantic estuaries	Concentrations (cyst/g)	Price et al. (2016, 2017a)
Black Sea	Relative abundance	Mudie et al. (2017)
Equatorial Atlantic Ocean	Relative abundance	Marret et al. (2008); Hardy et al. (2018)
Southern Ocean	Relative abundance	Marret et al. (2001); Crouch et al. (2010); Prebble et al. (2013); Esper and Zonneveld (2002) Verleye and Louwye (2010)
Izmir Bay, Mediterranean Sea	Concentrations (cyst/g)	Aydin et al., 2011, 2015b)
Aliağa and Nemrut Bay, Mediterranean Sea	Concentrations (cyst/g)	Aydin et al. (2015a)
Gemlik Gulf, Mediterranean Sea	Concentrations (cyst/cm ³)	Balkis et al. (2016)
Tierra del Fuego, Argentina	Presence/absence	Candel et al. (2012, 2013)
West coast India	Concentrations (cyst/g)	D'Silva et al. (2011)
East coast India	Presence/absence because data missing as numbers (plotted in graphs) (1)	D'Silva et al. (2013)
Gulf of Aqaba, Red Sea	Raw counts	Elshaway and Zonneveld (2016)
South China Sea	Raw counts	Gao et al. (2018)
Hudson Bay	Concentrations (cyst/g)	Heikkilä et al. (2014)
Indian Ocean	Raw counts	Hessler et al. (2013)
Yellow Sea	Concentrations (cyst/g)	Liu et al. (2012)
Bering Sea	Concentrations (cyst/cm ³)	Orlova and Morozova (2013)
South Korea	Raw counts	Pospelova and Kim (2010)
Yellow Sea and southern coast of Korea	Concentrations (cyst/g)	Shin et al. (2011, 2013)
Bay of Bengal	Concentrations (cyst/g)	Uddandam et al. (2017)
Gulf of Mexico	Concentrations (cyst/g)	Price et al. (2018)
Arctic	Raw Counts	Mudie (1992)
Antarctic (Weddell Sea)	Concentrations (cyst/g)	Pieńkowski et al. (2013)

ecological and biogeographical affinities of dinocyst taxa and confirmed biogeographical patterns, from endemism to bi-polarity. For example, a recent and regional atlas of the Black Sea corridor by Mudie et al. (2017) has filled some gaps in our knowledge of salinity tolerance for many modern taxa.

This paper provides a short overview of the global distribution of 91 modern dinoflagellate cyst taxa based on a literature review as well as an updated dinocyst database used for quantitative reconstructions, with a focus on bi-polar and endemic species.

2. Materials and methods

Global, regional and local cyst distributions were compiled mainly from the available literature (Table 1) reported since the publication of the worldwide Atlas of Zonneveld et al. (2013). These include dinocyst data from 21 Arctic Ocean sites not previously published in detail (Mudie, 1992), and now using up-to-date taxonomy. Where possible, cyst abundances and percentages were used except for some datasets reporting only the presence of taxa. All datasets were normalised (except for the ones with only presence available) and the relative abundance of each taxon was averaged within 2.5° band of latitude and longitude. The Tilia software of Grimm (1990) was used to create diagrams. Fig. 1 was made using the software Ocean Data View (<https://odv.awi.de/>). Three diagrams were produced to illustrate the cyst taxa distribution against longitude, one with sites located north of 65°N (780 sites), one with sites from the Pacific (857 sites), Atlantic (1048 sites) and Indian Oceans (540 sites) and excluding the Mediterranean, Marmara, Black, Caspian and Aral Seas, and finally, one illustrating only these five seas (411 sites).

Taxonomical identification following Williams et al. (2017) was carefully checked for each dataset to ensure consistency. For the purpose of this compilation, we did not consider the type of sample preparation for palynological analysis as the focus of this paper is to depict distribution patterns. We also did not include species of cysts of *Alexandrium* as preservation issues and possible confusion with cysts of *Scrippsiella trifida* (Head et al., 2006) could introduce a bias in observation. A list of the taxa that were included in this compilation can be found in Table 2. We have also listed the cyst taxa found in recent

sediments from studies published post 2013, but they were not included in the diagrams as they may have been previously ignored or grouped with other types such as round brown spiny cysts or peridinioids.

3. Biogeographical patterns

A total of 3636 assemblages have been compiled for the global map (Fig. 1) that depicts the distribution of 91 dinocyst taxa. Fig. 2(a) and (b) presents the average relative abundance of each taxon according to a latitudinal gradient with a 2.5° resolution. Figs. 3, 4 and 5 show these data against a longitudinal gradient for the Arctic Ocean, Pacific–Atlantic–Indian Oceans, and Mediterranean–Aral Seas, respectively.

The latitudinal and longitudinal distributions have highlighted specific patterns, from cosmopolitan to bimodal or endemic, all of which are discussed in the following sections.

The number of species per site, which we refer here to as diversity, shows great variance across oceans and seas, with the highest being found in the Atlantic Ocean, around 50 to 30°N (up to 70 taxa when binned into latitudinal bands, or up to 35 in individual assemblages), and the lowest in the Caspian and Aral seas (on average 6 taxa) and above 65°N (on average 9 taxa). This pattern could be partly due to the number of sites studied in each ocean (1048 for the Atlantic, 857 for the Pacific and 540 for the Indian, and fewer in other regions) but also reflecting low temperature and short growing season in the semi-enclosed Arctic Ocean north of c. 80° N (> 100 sites) and low salinity combined with extreme seasonal temperature change in the land-locked Caspian and Aral seas (49 sites). Most significantly, this compilation shows that three taxa globally dominate dinocyst assemblages, notably *Brigantedinium* spp. which includes all identified species such as *Brigantedinium cariacense* and *Brigantedinium simplex*, and similar cysts not identified at species level. Except for some studies, such as Mudie et al. (2017), it was not possible to map the distribution of species of *Brigantedinium* as they tend to be grouped together due to difficulty in the identification. The other two main taxa are *Operculodinium centrocarpum* sensu Wall and Dale 1966 and species of *Spiniferites* except for *Spiniferites elongatus* (which includes the formerly distinct *S. frigidus* and *R. amphicavata*; see Van Nieuwenhove et al., 2018), *Spiniferites* sp. granular type and *S. cruciformis*. It should be noted that *Spiniferites* spp.

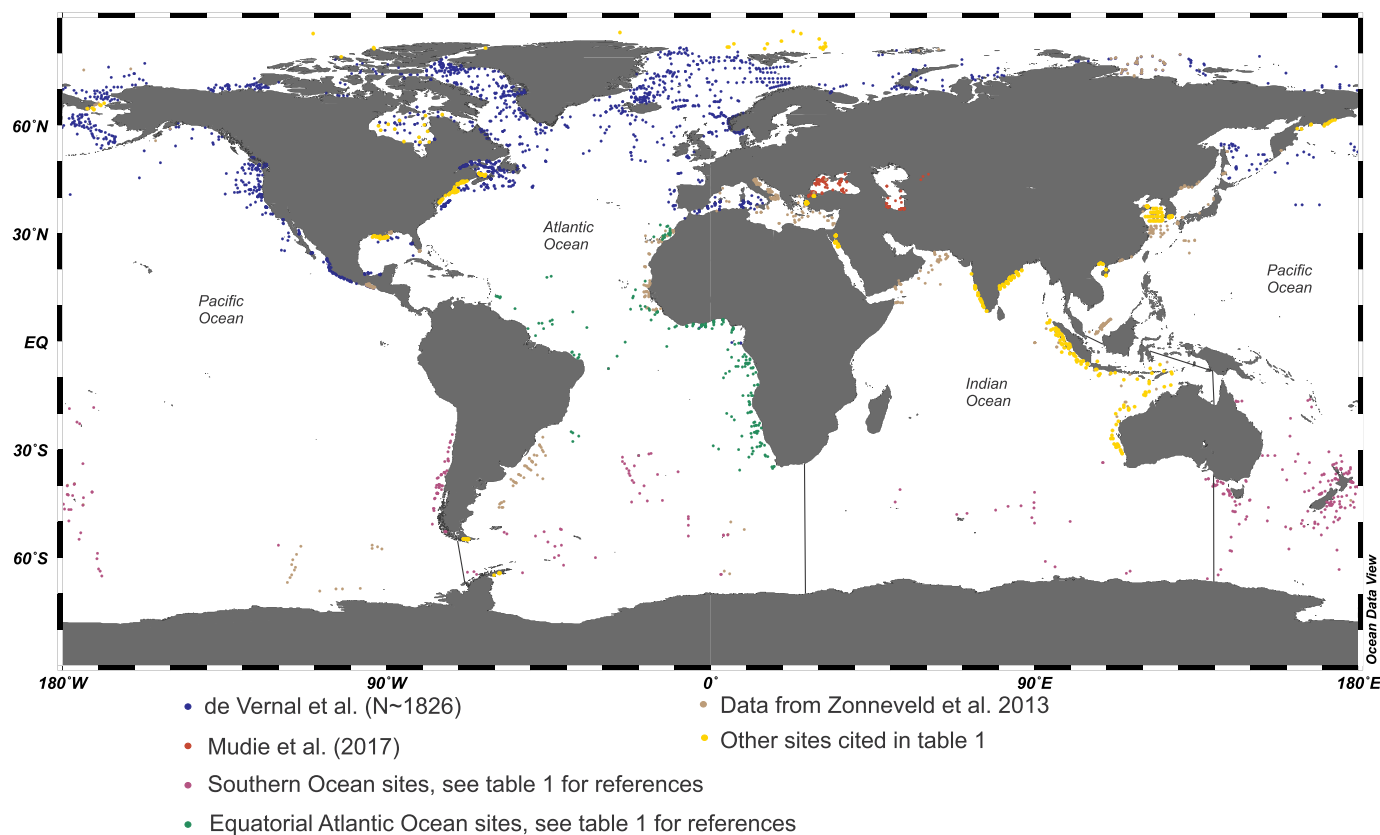


Fig. 1. Location of modern dinoflagellate cyst assemblages compiled from all available datasets.

include all *Spiniferites* species that were only identified at genus level. Overall, the 91 dinocyst taxa can be assigned to five biogeographic groups: cosmopolitan, northern latitude, southern latitude, bi-polar, and those of limited geographical range.

3.1. Cosmopolitan taxa

Overall, *Brigantedinium* species are present in all oceans, with maximal occurrence south of 45°S (Fig. 2a) but they are not the dominant taxa in the Mediterranean-Black Sea corridor (Fig. 5). Although the cysts are characterised as sensitive to degradation (e.g., Zonneveld et al., 2019), the heterotrophic *Brigantedinium* species appear to tolerate and thrive in a large range of environmental conditions, from brackish to high salinity conditions (e.g., Price et al., 2018), and from pack-ice margins where diatom food supplies are abundant in summer (e.g., Mudie and Harland, 1996; Harland and Pudsey, 1999) to tropical temperatures. The second most dominant species, found in both hemispheres is the autotrophic dinocyst *Operculodinium centrocarpum* sensu Wall and Dale 1966, although its relative abundance is higher in temperate to polar regions compared to subtropical and tropical areas. It also occurs in most oceans and seas except for the low salinity waters (ca. 5 to 17 psu) and the salinas of the inland Caspian and Aral seas, but has major occurrences in the Pacific and Atlantic Oceans. *Spiniferites* species, including all unidentified and recognised taxa, with *Spiniferites ramosus* being the most common and dominant, are also mostly present in all oceans and seas, although three of the species are geographically restricted to the Arctic (*Spiniferites elongatus*), the Mediterranean and Okhotsk Seas (*Spiniferites* sp. granular type) or low salinity epicontinental seas (*Spiniferites cruciformis*) (see sections below). Furthermore, a recent overview of *Spiniferites* taxa distribution in the Northern Hemisphere has suggested the existence of cryptic species, as illustrated by the cosmopolitan character and long biostratigraphic record of *Spiniferites ramosus* (de Vernal et al., 2018).

Several other less abundant species are also found almost everywhere, such as *Nematosphaeropsis labyrinthus*, with maximum occurrences in the South Pacific; however, this species is rare in the Black Sea and absent in the Caspian and Aral seas. The cyst of *Pentapharsodinium dalei* which has been found at all latitudes, is relatively common in the Pacific and Atlantic Oceans, and very occasional in the Indian Ocean. Its maximum occurrence is found north of 65°N. It is worth noting that this taxon is also present in the low-salinity to brackish waters of the Black Sea-Caspian Sea corridor, which suggests also a large tolerance of environmental conditions. Within the less abundant species, *Impagidinium* taxa are also found almost everywhere seaward of estuarine environments, but with two species (*Impagidinium caspiense* and *Impagidinium variaseptum*) geographically restricted (see sections below). Finally, although *Lingulodinium machaerophorum* has a quasi-cosmopolitan distribution, it is most abundant in the Mediterranean-Black Sea-Caspian Corridor and widespread in the Atlantic Ocean. By contrast, it is sparse in the Pacific Ocean north of 40°N in waters with sea surface temperature above 15 °C (e.g., Pospelova et al., 2008) and absent south of latitude 45°S. This is quite surprising as relatively similar conditions in which this species thrives can be found in all oceans.

Overall, this compilation highlights that only few dinocyst taxa are found everywhere, which could imply their limited use as tracers of past global environmental conditions if used just individually. However, it is worth noting that their relative abundance is often related to specific oceanographic conditions as discussed in de Vernal and Rochon (2011), Zonneveld et al. (2013), Mudie et al. (2017) and de Vernal et al. (2018). The process morphology of *Operculodinium centrocarpum* sensu Wall and Dale 1966 and *Lingulodinium machaerophorum* is also very variable and correlates in some basins with temperature and/or salinity (e.g., Mertens et al., 2009, 2012b; Jansson et al., 2014; Gurdebeke et al., 2018). The case of *Operculodinium centrocarpum* sensu Wall and Dale 1966 is very interesting as the relationship between process length and salinity shows strong positive correlation in the

Table 2

List of dinoflagellate cyst species (with code name used for the metadata in supplementary material) with motile stage name included in this compilation and/or observed in surface sediments from studies listed in Table 1. T is for Trophic habit, with P including phototrophic and autotrophic species, H for heterotrophic species and M for mixotrophic. P+ includes species known to be phagotrophic.

T	Cyst name	Thecate equivalent
P/H	Cysts included in this compilation	
P	<i>Achomosphaera andalusiense</i> (Aand)	<i>Gonyaulax</i> sp.
P	<i>Ataxiodinium choane</i> (Atax)	<i>Gonyaulax spinifera</i>
P+	Cyst of <i>Biecheleria baltica</i> (Bbal)	<i>Biecheleria baltica</i>
P	<i>Bitectatodinium spongium</i> (Bspo)	Unknown
P	<i>Bitectatodinium tepikiense</i> (Btep)	<i>Gonyaulax digitale</i>
P	<i>Caspidium rugosum</i> (Crug)	Unknown
P	<i>Dalella chathamense</i> (Dcha)	Unknown
P+	Cyst of <i>Gymnodinium</i> spp. (Gymn)	<i>Gymnodinium</i> spp.
P	<i>Impagidinium aculeatum</i> (Iacu)	Unknown
P	<i>Impagidinium caspiense</i> (Icas)	<i>Gonyaulax baltica</i>
P	<i>Impagidinium japonicum</i> (Ijap)	Unknown
P	<i>Impagidinium pallidum</i> (Ipal)	Unknown
P	<i>Impagidinium paradoxum</i> (Ipat)	Unknown
P	<i>Impagidinium patulum</i> (Ipat)	Unknown
P	<i>Impagidinium plicatum</i> (Ipli)	Unknown
P	<i>Impagidinium sphaericum</i> (Isph)	Unknown
P	<i>Impagidinium striatum</i> (Istr)	Unknown
P	<i>Impagidinium variaseptum</i> (Ivar)	Unknown
P	<i>Impagidinium velorum</i> (Ivel)	Unknown
P	<i>Nematosphaeropsis labyrinthus</i> (Nlab)	Unknown
P	<i>Nematosphaeropsis rigida</i> (Nrig)	Unknown
P	<i>Operculodinium aguawense</i> (Oagu)	Unknown
P	<i>Operculodinium centrocarpum</i> sensu Wall and Dale 1966 (Ocen)	<i>Protoceratium reticulatum</i>
P	<i>Operculodinium giganteum</i> (Ogig)	Unknown
P	<i>Operculodinium israelianum</i> (Oisr)	Unknown
P	<i>Operculodinium janduchenei</i> (Ojan)	Unknown
P	<i>Operculodinium longispinigerum</i> (Olon)	Unknown
P	Cyst of <i>Pentapharsodinium dalei</i> (Pdai)	<i>Pentapharsodinium dalei</i>
P	Cyst of <i>Polarella glacialis</i> (Pgla)	<i>Polarella glacialis</i>
P	<i>Polysphaeridium zoharyi</i> (Pzoh)	<i>Pyrodinium bahamense</i>
P	<i>Pyxidiniopsis psilata</i> (Ppsi)	Unknown
P	<i>Pyxidiniopsis reticulata</i> (Pret)	Unknown
P+	Cyst of <i>Scrippsiella trifida</i> (Stri)	<i>Scrippsiella trifida</i>
P	<i>Spiniferites belerius</i> (Sbel)	<i>Gonyaulax scrippsae</i>
P	<i>Spiniferites bentorii</i> (Sben)	<i>Gonyaulax digitale</i>
P	<i>Spiniferites bulloideus</i> (Sbul)	<i>Gonyaulax</i> sp.
P	<i>Spiniferites cruciformis</i> (Scru)	<i>Gonyaulax scrippsae</i>
P	<i>Spiniferites delicatus</i> (Sdel)	<i>Gonyaulax</i> sp.
P	<i>Spiniferites elongatus</i> (including <i>Spiniferites frigidus</i> and <i>Rottnestia amphiavata</i>) (Selo)	<i>Gonyaulax elongata</i>
P	<i>Spiniferites lazus</i> (Slaz)	Unknown
P	<i>Spiniferites membranaceus</i> (Smem)	<i>Gonyaulax membranacea</i>
P	<i>Spiniferites mirabilis</i> (includes <i>S. hyperacanthus</i>) (Smir)	<i>Gonyaulax spinifera</i>
P	<i>Spiniferites pachydermus</i> (Spac)	<i>Gonyaulax ellegaardiae</i>
P	<i>Spiniferites ramosus</i> (Sram)	<i>Gonyaulax spinifera</i>
P	<i>Spiniferites</i> sp. granular type (Sgra)	Unknown
P	<i>Spiniferites</i> spp. (Sspp)	Unknown
P	<i>Tectatodinium pellitum</i> (Tpel)	<i>Gonyaulax spinifera</i>
P	<i>Tuberculodinium vancampoae</i> (Tvan)	<i>Pyrophacus steinii</i>
M	<i>Lingulodinium machaerophorum</i> (Lmac)	<i>Lingulodinium polyedra</i>
M	Cyst of <i>Polykrikos hartmannii</i> (Phar)	<i>Polykrikos hartmannii</i>
H	<i>Brigantedinium</i> spp. (Bspp)	<i>Protoperidinium</i> spp.
H	<i>Cryodinium meridianum</i> (Cmer)	Unknown
H	Cyst of <i>Polykrikos</i> sp. arctic morphotype (Parc)	<i>Polykrikos</i> sp.
H	<i>Dubridinium</i> spp. (Dubr)	<i>Preperidinium</i> sp.
H	<i>Echinidinium aculeatum</i> (Eacu)	Unknown
H	<i>Echinidinium bispiniformum</i> (Ebis)	Unknown
H	<i>Echinidinium delicatum</i> (Edel)	Unknown
H	<i>Echinidinium granulatatum</i> (Egra)	Unknown
H	<i>Echinidinium karaense</i> (Ekar)	Unknown
H	<i>Echinidinium</i> spp. (Espp)	Unknown
H	<i>Echinidinium transparentum</i> (Etra)	Unknown
H	<i>Echinidinium zonneveldiae</i> (Ezon)	Unknown
H	<i>Islandinium brevispinosum</i> (Ibre)	<i>Protoperidinium haizhouense</i>
H	<i>Islandinium cezare</i> (Imic)	Unknown
H	<i>Islandinium minutum</i> (Imin)	<i>Islandinium minutum</i>
H	<i>Lejeunecysta</i> spp. (Lspp)	<i>Protoperidinium</i> spp.
H	Cyst of <i>Oblea acanthocysta</i> (Oaca)	<i>Oblea acanthocysta</i>
H	<i>Peridinium ponticum</i> (Ppon)	Unknown
H	Peridinoids (Peri)	Unknown
H	Cyst of <i>Polykrikos kofoidii</i> (Pkof)	<i>Polykrikos kofoidii</i>

(continued on next page)

Table 2 (continued)

T	Cyst name	Thecate equivalent
P/H	Cysts included in this compilation	
H	Cyst of <i>Polykrikos schwartzii</i> (Psch)	<i>Polykrikos schwartzii</i>
H	Cyst of <i>Protoperidinium americanum</i> (Pame)	<i>Protoperidinium americanum</i>
H	Cyst of <i>Protoperidinium minutum</i> (Pmin)	<i>Protoperidinium minutum</i>
H	Cyst of <i>Protoperidinium monospinum</i> (Pmon)	<i>Protoperidinium monospinum</i>
H	Cyst of <i>Protoperidinium nudum</i> (Pnud)	<i>Protoperidinium nudum</i>
H	Cyst of <i>Protoperidinium stellatum</i> (Pstel)	<i>Protoperidinium stellatum</i>
H	<i>Quinquecuspis concreta</i> (Qcon)	<i>Protoperidinium leonis</i>
H	<i>Selenopemphix Antarctica</i> (Sant)	Unknown
H	<i>Selenopemphix nephroides</i> (Snep)	<i>Protoperidinium subinerme</i>
H	<i>Selenopemphix quanta</i> (Squa)	<i>Protoperidinium conicum</i>
H	<i>Stelladinium bifurcatum</i> (Sbif)	Unknown
H	<i>Stelladinium reidii</i> (Srei)	Unknown
H	<i>Stelladinium robustum</i> (Srob)	Unknown
H	<i>Trinovantedinium applanatum</i> (Tapp)	<i>Protoperidinium shanghaiense</i>
H	<i>Trinovantedinium pallidifuvum</i> (Tpal)	<i>Protoperidinium louisianensis</i>
H	<i>Trinovantedinium variabile</i> (Tvar)	Unknown
H	<i>Votadinium calvum</i> (Vcal)	<i>Protoperidinium oblongum</i>
H	<i>Votadinium spinosum</i> (Vspi)	<i>Protoperidinium claudicans</i>
H	<i>Xandarodinium xanthum</i> (Xxan)	<i>Protoperidinium divaricatum</i>
?	<i>Melitasphaeridium choanophorum</i> (Mcho)	Unknown
	Cysts not included in this compilation but identified in recent sediments from literature listed in Table 1	
P	Cyst of <i>Alexandrium</i> species	<i>Alexandrium</i> species
H	Cyst of <i>Archaeperidinium minutum</i>	<i>Archaeperidinium minutum</i>
P	Cyst of <i>Barrufeta resplendens</i>	<i>Barrufeta resplendens</i>
H	<i>Brigantedinium asymmetricum</i>	Unknown
H	<i>Brigantedinium irregulare</i>	Unknown
H	<i>Brigantedinium majusculum</i>	Unknown
M	Cyst of <i>Cochlodinium</i> spp.	<i>Cochlodinium</i> spp.
?	Cyst of <i>Enciculifera carinata</i>	<i>Enciculifera carinata</i>
M	Cyst of <i>Fragilidium</i> sp.	<i>Fragilidium</i> sp.
?	Cyst of <i>Gyrodinium</i> cf. <i>instruatum</i>	<i>Gyrodinium</i> cf. <i>instruatum</i>
?	Cyst of <i>Gyrodinium impudicum</i>	<i>Gyrodinium impudicum</i>
?	Cyst of <i>Heterocapsa triquetra</i>	<i>Heterocapsa triquetra</i>
H	Cyst of <i>Kolkwitzia acuta</i>	<i>Kolkwitzia acuta</i>
?	Cyst of <i>Lebouraia minuta</i>	<i>Lebouraia minuta</i>
	<i>Lingulodinium hemicystum</i>	Unknown
P	Cyst of <i>Peridinium</i> cf. <i>willei</i>	<i>Peridinium</i> cf. <i>willei</i>
?	Cyst of <i>Peridinium minutum</i> sensu Wall and Dale 1968	<i>Peridinium minutum</i> sensu Wall and Dale 1968
H	Cyst of <i>Protoperidinium oblongum</i>	<i>Protoperidinium oblongum</i>
H	Cyst of <i>Protoperidinium paraoblongum</i>	<i>Protoperidinium paraoblongum</i>
H	<i>Xandarodinium variabile</i>	Unknown

Baltic Sea and the opposite in the North Pacific (Mertens et al., 2009). This phenomenon can now be explained by cryptic speciation in *Protoperidinium reticulatum* (a name of the motile stage for *Operculodinium centrocarpum* sensu Wall and Dale 1966) that was proposed by Mertens et al. (2012a) and supported by molecular evidence recently reported by Wang et al. (2019). Similarly, in low salinity seas, high variability of process development in *Spiniferites cruciformis* and the cyst of *Gonyaulax baltica* may be weakly correlated with surface salinity (Ellegaard et al., 2002; Mudie et al., 2002).

3.2. Northern latitude taxa

This compilation generally confirms previous studies on the distribution of taxa restricted to the Northern Hemisphere although it also has raised some questions with regards to the true occurrence of some species. Fig. 2 shows that overall there is a greater diversity of dinocyst taxa in the Northern Hemisphere compared to the Southern Hemisphere, despite the relatively smaller area encompassed by the northern oceans. However, there is a greater number of samples in the Northern Hemisphere (3019) compared to the Southern Hemisphere (617). In both hemispheres, there is a strong decrease in dinocyst diversity poleward of about 50° latitude, this decline being steepest in the Southern Hemisphere where it corresponds to the outer margin of the

drift ice zone (see Mudie, 1992; text-Fig. 5).

Within these northern latitude taxa, only few species occur in relative high abundances north of 40°N, such as *Echinidinium karaense*, cyst of *Polykrikos* sp. arctic morphology (previously assigned to *Polykrikos quadratus* and now excluded from the order Gymnodinales (Potvin et al., 2018)), which are observed in most oceans. *Islandinium cesare*, *Echinidinium zonneveldiae*, *Trinovantedinium variabile*, *Spiniferites elongatus*, *Achomospaera andalouisiense*, *Nematosphaeropsis rigida*, *Spiniferites* sp. granular type, Cyst type A (possibly cyst of *Protoperidinium fukuyoi* (Mertens et al., 2013)), and cyst of *Scripsiella trifida* can also be characterised as strictly Northern Hemisphere taxa, with no occurrence south of 15°N.

Other taxa apparently confined to the Northern Hemisphere may have been previously mis-identified as species with similar morphology or have recently been described and were possibly overlooked in earlier studies. One of such taxa is the cyst of *Protoperidinium nudum* which has only been identified in northern latitude assemblages. It is possible that the cyst of *P. nudum* occurs more widely but may have been mis-identified or grouped with *Selenopemphix quanta* as they share a very similar morphology. A similar situation may pertain for the cyst of *Polykrikos hartmannii*, which has a morphology resembling *Echinidinium granulatum* (Zonneveld and Pospelova, 2015). Observations of the thecate stage of *P. hartmannii* have been reported for all oceans (e.g., Aktan and

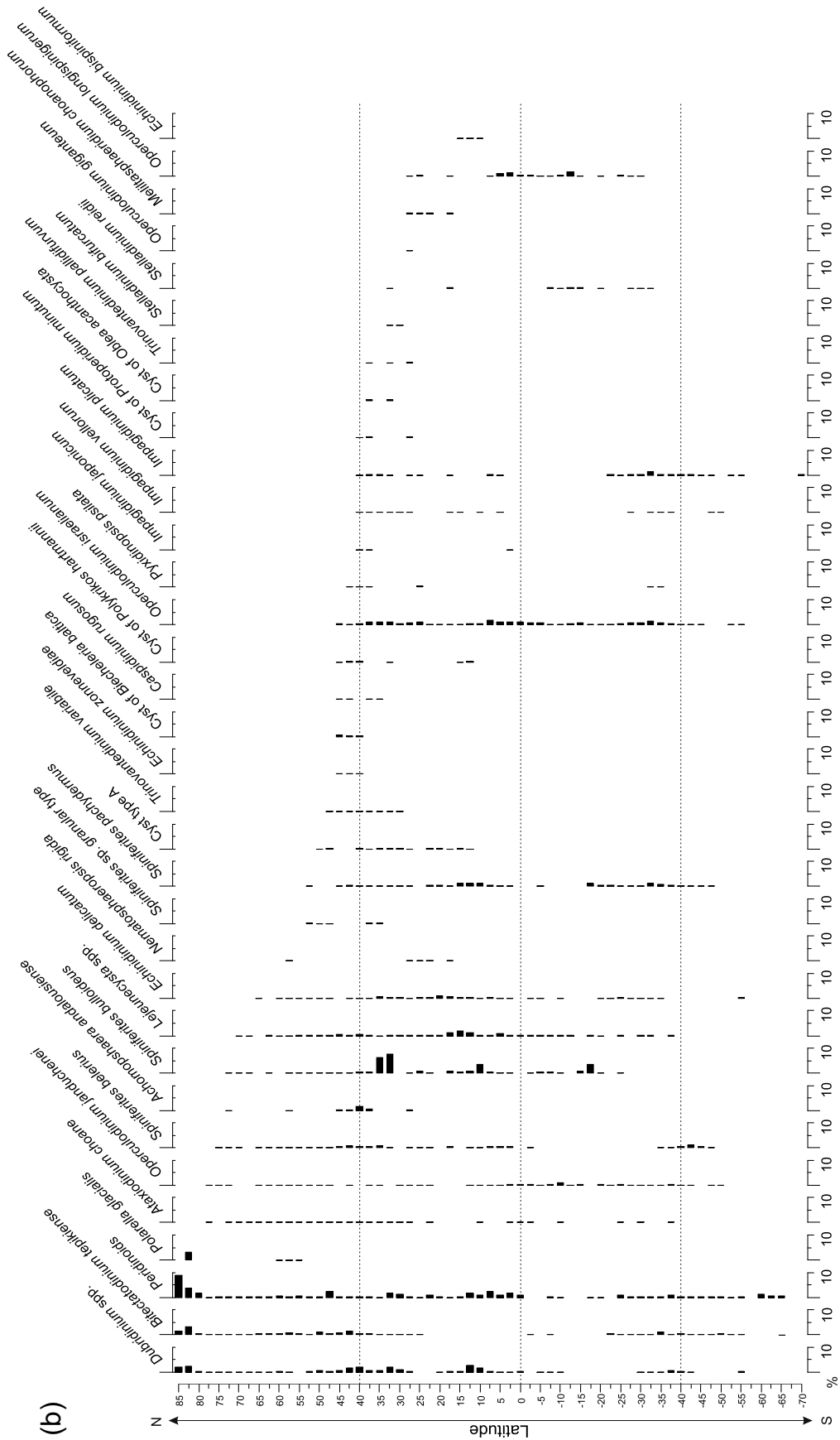


Fig. 2. (continued)

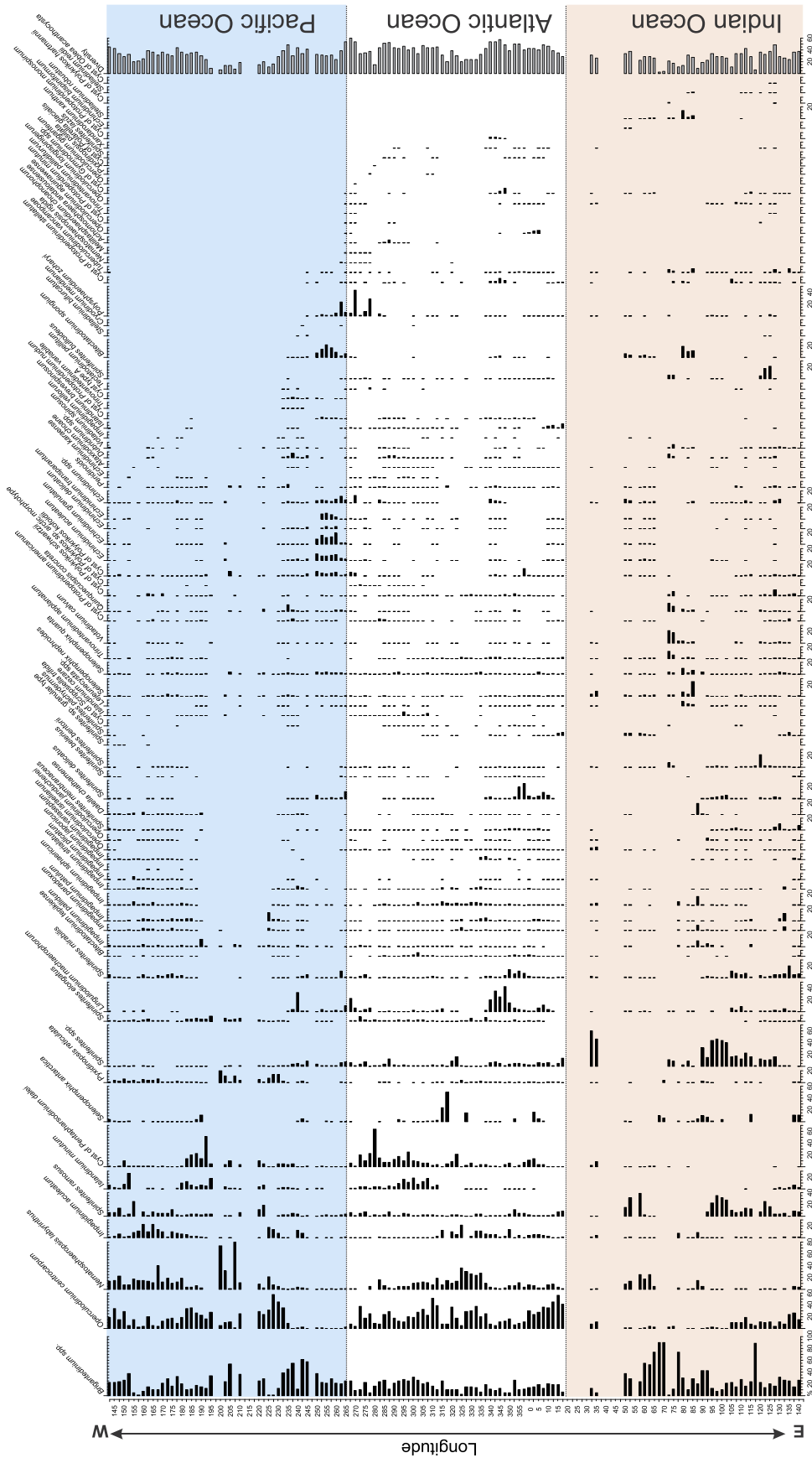


Fig. 4. Longitudinal distribution of dinocyst taxa found below 65°N. Relative abundance for each taxon was averaged in a 2.5° longitudinal band. Number of taxa (diversity) is plotted against a 2.5° longitudinal band. Colour bands highlight the Pacific Ocean (blue), Atlantic Ocean (green) and Indian Ocean (orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

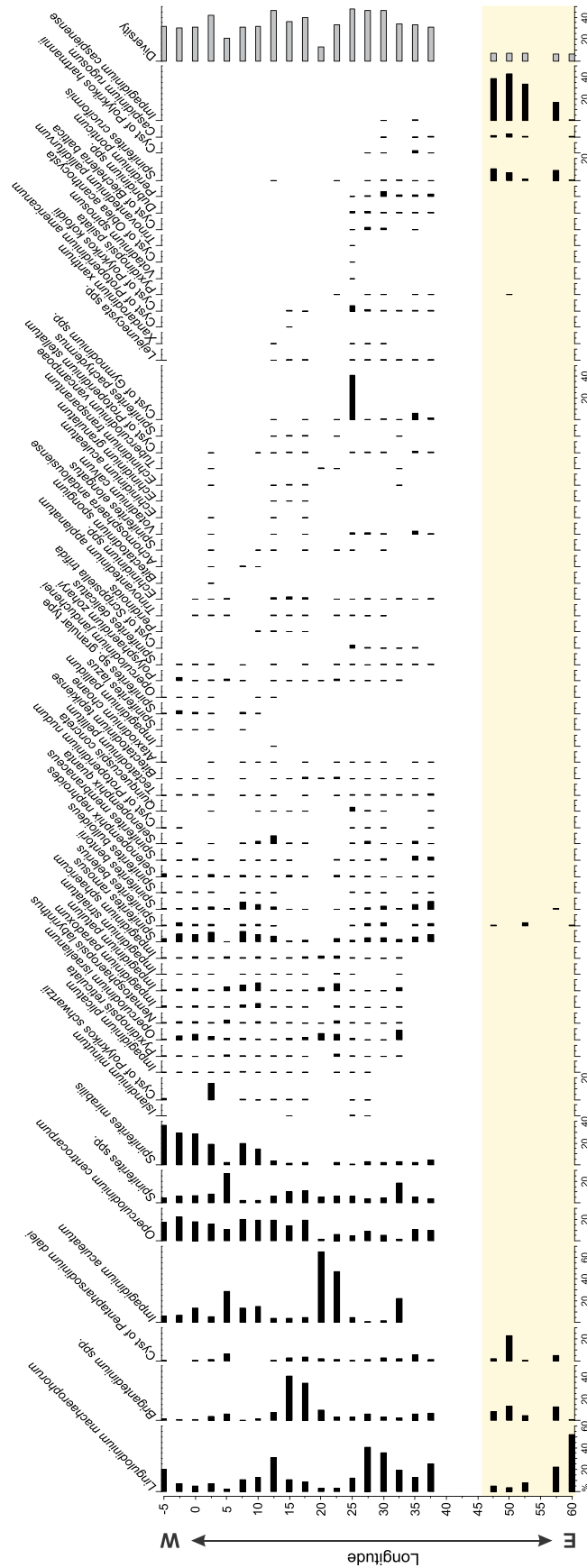


Fig. 5. Longitudinal distribution of dinocyst taxa found from the Marmara Sea to the Aral Sea. Relative abundance for each taxon was averaged in a 2.5° longitudinal band. Number of taxa (diversity) is plotted against a 2.5° longitudinal band. Colour band highlights the Caspian and Aral seas.

Keskin, 2017), notably along the eastern coast of the US and in the Gulf of Alaska. The only matching distribution between the thecate stage and its cyst can be found in the Black Sea. *Trinovantedinium pallidifulum*, which has been recently described in Mertens et al. (2017a), has probably been identified as *Trinovantedinium applanatum* in previous studies. *Stelladinium bifurcatum* (see Head et al., this issue) and *Echinidinium bispiniformum* are also likely to have been mis-identified.

The cyst of *Biecheleria baltica* has been mapped in the Black Sea (Mudie et al., 2017) but also occurs in the Baltic Sea, possibly for at least the last 100 years (Kremp et al., 2018); it is therefore likely that these small transparent cysts have been ignored in previous studies. Alternatively, this species is a recent immigrant transported in the ballast of ships that travel canals and rivers linking the low salinity waters from Baltic to Black seas. Other studies have also reported the presence of *Biecheleria* cysts, but due to their small size (< 15 µm) some are likely to be lost during processing (e.g., Price and Pospelova, 2011) and therefore not included in total cyst counts (e.g., Bringué et al., 2013; Heikkilä et al., 2014; Price et al., 2017a; Gurdebeke et al., 2018). Finally, *Oblea acanthocysta*, revisited by Mertens et al. (2015), bears some resemblance with *Echinidinium* species and may have been included in this group in routine counts. However, it may also be geographically restricted off Japan, although it has recently been identified in the Izmir Bay (Aydin et al., 2011, 2015b, Aydin et al., 2015a) and British Columbian fjords (Gurdebeke et al., 2018).

3.3. Southern latitude taxa

Compared with the Northern Hemisphere there are very few dinocysts which have ranges that are restricted to the Southern Hemisphere. On average, diversity is also lower. Only two species are restricted south of 35°S, *Selenopemphix antarctica* and *Cryodinium meridianum*. One other species, *Impagidinium variaseptum*, has an extended distribution just slightly above the equator. *Dalella chathamense* was initially described in the Southern Ocean (McMinn and Sun, 1994) but has now been found in low occurrences up to 42°N (Pospelova et al., 2008; Bonnet et al., 2012), mostly in the Pacific Ocean.

It is also worth noting that among cosmopolitan taxa, some species seem to have their highest abundance in the South Pacific Ocean, such as *N. labyrinthus* and *Impagidinium aculeatum*. *Spiniferites ramosus* shows highest occurrences in the eastern region of the Indian Ocean.

3.4. Bi-polar taxa

Of the 91 taxa compiled here, only two, *Impagidinium pallidum* and *Islandinium minutum*, are present in polar-subpolar regions of both poles. *Islandinium minutum* does not occur south of 15°N and north of 40°S and *I. pallidum* does not occur south of 25°N and north of 30°S. However, it is worth noting that *Polarella glacialis* is another true bi-polar species, as it has been first described in Antarctica (Montresor et al., 1999) but was previously identified in Arctic sediments (Mudie, 1992). Subsequently, a phylogenetic study has confirmed that this species does occur in both polar regions (Montresor et al., 2003). Our data show that in the Arctic Ocean, *Polarella glacialis* is mostly found north of 80° N and is associated with multiyear sea ice duration over the Nansen Basin, as also reported for Independence Fjord, NE Greenland by Limoges et al. (2018). However, *P. glacialis* does not occur under permanent pack ice on the Canadian Polar Margin which, together with the NW Greenland Polar Margin, is the coldest sector of the Arctic Ocean (August SST is less than -1.5°C; <https://nsidc.org/>). It has also been observed in the sub-arctic waters of Hudson Bay (Heikkilä et al., 2014) as well as in plankton net samples from the Labrador Sea (July 2018), Baffin Bay in 2008 and 2014 (Rochon, unpublished data), and in faecal pellets of *Calanus* from Hargrave et al. (2002) North Water Polynya sediment traps (Mudie, unpublished SEM data), and in Holocene sediment cores from the same region (Limoges et al., 2018, unpublished data). *Polarella glacialis*, which produces small and fragile

cysts, might have been missed due to sieving mesh and/or preservation issue (see Heikkilä et al., 2014; Limoges et al., 2018; de Vernal et al., this issue). It has, indeed, rarely been found in palaeosequences, although it has been detected in late Holocene Antarctic sediments through genomic studies (Boere et al., 2009) as well as in a very high sedimentation context where organic matter was very well preserved (Hartman et al., 2018).

3.4.1. *Impagidinium pallidum*

There is one reported occurrence of this species in the Mediterranean Sea, south of Sicily (Zonneveld et al., 2013), but it is not present in the Marmara or Black Sea. Maximum occurrence of *Impagidinium pallidum* is found in the Northern Hemisphere, in particular in the Greenland Sea, with other large occurrences in the Norwegian and Barents Seas. In the Southern Hemisphere, it occurs in both coastal and oceanic locations. In the fossil record, it has been described in assemblages from the Mid Eocene in the Labrador Sea (Head et al., 1989), the Late Eocene from the Northern Pacific (Bujak, 1984) and the Pliocene of Alpha Ridge, central Arctic Ocean (Aksu and Mudie, 1984). In the Southern Hemisphere, *I. pallidum* is recorded for the Early Oligocene offshore Wilkes Land, Antarctica (Bijl et al., 2018). De Schepper et al. (2011) discuss the possibility that this species could have crossed the equator during periods of severe global cooling but it has not been recorded from equatorial Cenozoic sediments. The morphology of the dinocyst is the same in both hemispheres but the cyst-thecate relationship has yet to be described, although its phylogeny shows some closeness to *Impagidinium caspiense*/*Gonyaulax baltica* and *Spiniferites belerius* (Mertens et al., 2017b).

3.4.2. *Islandinium minutum*

Its distribution in modern sediments is mainly located in the Northern Hemisphere with only a couple of occurrences in the Southern Hemisphere. These are the north-west Weddell Sea (Pieńkowski et al., 2013) where it is found in relatively high abundances (~90% of some assemblages), and east of New Zealand but in very low relative abundances (< 5%). Aksu and Mudie (1984) reported it (as *Multispinula minuta*) in Pleistocene sediments of the Arctic Ocean Alpha Ridge and Bijl et al. (2018) mention *Islandinium* sp. in early Miocene sediments from Wilkes Land, Antarctica. Williams et al. (2017) incorrectly gave a Holocene age for *Islandinium minutum*.

The existence of bi-polar species, either in the dinoflagellates or other phytoplanktonic groups such as Radiolarians (e.g., Boltovskoy and Correa, 2016) is rather challenging to explain. An early study by Mudie et al. (1990) used records from ocean drilling cores to trace the migration of *I. pallidum* from the Pacific to Atlantic Oceans via the Panama gateway before c. 5 Ma and during successive opening of Arctic gateways. However, a mechanism of transport from the sub-Arctic to Antarctic regions between the Eocene and Oligocene remains enigmatic.

3.5. Dinocysts with limited and small geographical ranges

There are very few endemic dinocyst taxa, defined as those belonging to only one geographic region. *Stelladinium robustum* is currently limited to the Indian Ocean. *Peridinium ponticum* was thought to be restricted to the Black Sea until a recent study has observed this species on the Iberian margin (García-Moreiras et al., 2018). Two other species that are strongly associated with the Black Sea region are *Spiniferites cruciformis* and *Pyxididopsis psilata*. In surface sediments, *S. cruciformis* is occasionally present in many areas of the Ponto-Caspian region but also rarely occurs off southern Italy in the Mediterranean Sea. It also has been reported, apparently with living cytoplasm, in modern freshwater lakes near the Marmara Sea (e.g., Leroy and Albay, 2010). This species is abundant in the lacustrine phases of the Pleistocene-early Holocene interval of the Black Sea and was a member of the Late Miocene Paratethyan basins in Europe, implying that the

Mediterranean populations are relict. *P. psilata* was previously thought to be endemic to the Black Sea where it is common and widespread. However, it has been reported in southern Florida and in the east-coast of South America (Zonneveld et al., 2013; unconfirmed identification) and at one site on the west coast of Northern America (Zonneveld et al., 2013). There are no fossil records for occurrences of *P. psilata* outside of the Black Sea Corridor and it is likely that the trans-Atlantic and Pacific populations are recently introduced, transported from the Marmara-Black Sea region by ships (see Mudie et al., 2017). Two other species were found in the Caspian Sea (Marret et al., 2004), *Impagidinium caspiense* and *Caspidium rugosum*, and were also thought to be endemic to this sea. However, a recent phylogenetic study by Mertens et al. (2017b) has related *I. caspiense* to *Gonyaulax baltica*, a species currently occurring in the Baltic Sea. A possible Arctic origin of *I. caspiense* at the end of the Pliocene has been recently discussed in Richards et al. (2018). *Caspidium rugosum* is also thought to be a Paratethys relict, occurring in the European Pannonian Basin during the late Miocene. It is worth noting that the cyst of *Oblea acanthocysta* was initially observed solely off Japan (Omura Bay, Kawami et al., 2006) but has recently been identified in estuarine waters of British Columbia, Canada (Gurdebeke et al., 2018) and the Izmir Bay, Turkey (Aydin et al., 2011, 2015b; Aydin et al., 2015a). This example raises the question of the occurrence of this species in the eastern Mediterranean Sea, which could be the consequence of long-distance transport due to human activities or the result of being overlooked or lumped as a spiny brown cyst in other palynological studies.

Finally, observation of previously thought extinct taxa suggests that these taxa are probably extant in modern time as endemic and/or relic species. This is notably the case of *Melitasphaeridium choanophorum* which occurs in recent sediments of the Gulf of Mexico (Limoges et al., 2013; Price et al., 2017b) and the South China Sea (Li et al., 2017), as well as *Dapsilidinium pastielsii* found in surface sediments from the Indo-Pacific warm pool region (Mertens et al., 2014).

4. Discussion

The new biogeographic data we have presented, using 3636 assemblages in modern sediments of the global oceans and major inland seas, represent the enormous progress made since the first efforts of Williams, 1971 (with 44 taxa at 35 North Atlantic-Equatorial sites) and of Mudie and Harland, 1996 (65 taxa, 215 sites world-wide). These earlier studies also noted the very widespread distributions of most dinocyst species. However, Williams (1971) singled out four primary palaeoceanographic marker species: *Operculodinium centrocarpum* sensu Wall and Dale 1966 (for coastal North America and northern Atlantic), *Impagidinium aculeatum* (NW Africa), *Spiniferites mirabilis* (coastal eastern North Atlantic) and *Nematosphaeropsis* cf. *N. labyrinthus* (N. Atlantic Drift). Williams and Bujak (1977) then used data from 25 North Atlantic well sites and two deep-sea drilling cores to select *O. centrocarpum*, *L. machaerophorum*, *Polysphaeridium zoharyi* and *Homotryblium floripes* as important biogeographical and palaeoenvironmental indicators for North Atlantic water masses. These studies and the work of Wall et al. (1977) have subsequently strongly influenced the palaeoenvironmental interpretations assigned to pre-Quaternary dinocyst assemblages. Our new data show that caution is required in assigning palaeoenvironmental characteristics to assemblages based on single indicator taxa, such as *Polysphaeridium zoharyi* or *Tuberculodinium vancampoeae*. The same caution now applies to the use of the ecofacies and biogeographical provinces delimited by Williams (1971) and Mudie (1992) using multivariate factor analysis to link assemblages with sea-surface temperature and salinity, and to relate geographic provinces with ocean circulation and sea-ice margins (Mudie and Harland, 1996). The analytical methods tend to heavily weight the ecological characteristics of a dominant species.

Our new biogeographic data once again raise the question of whether cyst-producing dinoflagellate species live in/under sea ice within

the Arctic Ocean (i.e., the ocean area north of Europe, Russia, Alaska and Canada), in contrast to the Antarctic where in-ice dinoflagellate cyst production has been documented (see Zheng et al., 2012; Stoecker et al., 1998). This question was first asked in 1980, at which time only *Protoperidinium* species were reported for plankton records from Canadian or West Greenland waters at 80°N (the highest latitude with plankton records at that time; Mudie, 1992). Subsequently Okolodkov (1999) extended this database to 82°N in the eastern Arctic Ocean and showed the absence of *Protoceratium reticulatum* north of ca. 70°N, and only *Protoperidinium* spp. further north. Our new data show that within the Arctic region (Fig. 3), there is a notable decrease in dinocyst species diversity eastwards of 0 to 25°E and westwards of 325°E. This pattern appears to reflect the influence of relatively warm inflowing surface Atlantic water mass through the Fram Strait in the east, and warm Pacific water (Alaskan Coastal Current) through the Bering Strait in the west. The cyst diversity distribution pattern is also consistent with earlier biogeographical studies of theca-stage dinoflagellates (Okolodkov and Dodge, 1996; Okolodkov, 1999). These surveys correlated maximum species diversity with the Dunbar Line that encloses the Northern Hemisphere region with surface water of mixed Arctic and sub-Arctic or Boreal origin. Dinoflagellate studies from Antarctic sea ice clearly demonstrate the capacity of *P. glacialis* to bloom within the ice (Zheng et al., 2012; Stoecker et al., 1998), which suggests that sea ice is not a limiting factor for this species.

The question of possible long-distance dinocyst transport to sediments beneath the pack-ice further north requires more research and is of particular importance because the inflow of warm, saline water of Atlantic origin increases with climate warming (Polyakov et al., 2012). However, the presence of *P. reticulatum* and *Gonyaulax* cf. *spinifera* as well as numerous cysts of *O. centrocarpum* and *S. ramosus* with cell content in plankton net samples in a polynya around 76°N-73°W suggests in-situ populations in waters south of the Arctic Ocean and therefore questions this long distance transport for these species (Rochon, unpublished data). It is possible that recent ice-thinning and/or increased shipping traffic within the Arctic Ocean will see the northern expansion of dinocyst diversity. There is a need for more data from moored, year-round Arctic sediment traps to avoid loss of small cysts in plankton nets and to cover seasons other than the summer ice-minimum interval when ships have access. A sediment trap sampling bi-monthly intervals that was moored under permanent pack-ice on the Canadian Polar margin in the Arctic Ocean north of Axel Heiberg in 1989–90 failed to capture any cysts (Hargrave et al., 1994), although a through-ice vertical plankton sample in August 1986 recovered *Peridiniella catenata*, *Protoperidinium depressum*, *P. pallidum* and *P. ovata*. Cysts of *P. catenata* were not recovered in the Polar Margin shelf sediments although they are common in deeper water sediments of the sub-arctic Baltic Sea (Spilling et al., 2006). Two sub-arctic sediment traps moored in eastern and western Hudson's Bay (Canada) (Heikkilä et al., 2016) documented cyst assemblages at bi-weekly to bi-monthly intervals from October 2005 to September 2006. These sub-arctic sites experience 5–7 months of consolidated sea ice. Over 20 cyst taxa were recorded in the traps, including cysts of *P. glacialis*, *E. karaense* and *I. minutum*. Cyst production was negligible under ice during the Arctic winter, but ranged from 2700 to 394,800 cysts m⁻² day⁻¹ during spring and summer.

Despite a plethora of phytoplankton studies in the Antarctic region, very few focus only on dinoflagellates and even fewer on dinoflagellate cysts. The first studies at the beginning of the 20th century were focused on phytoplankton in general (Karsten, 1905; Mangin, 1915), with only few dinoflagellate species being described. It is with the work of Enrique Balech in 1974 that the richness in dinoflagellate species was discovered, with many new species being later described (e.g., Balech, 1975). In 1995, McMinn commented on the absence of dinoflagellate cysts in recent sediments around Antarctica but later on, several new and endemic species were discovered, such as *Selenopemphix antarctica* (Marret and de Vernal, 1997) and *Cryodinium meridianum* (Esper and

Zonneveld, 2002). A recent study on dinoflagellate cysts near the Antarctic continent (Hartman et al., 2019) formally describes a new dinoflagellate cyst genus and species, *Nucicla umbiliphora*. It is therefore likely that there are still potentially new discoveries to be made in the southern polar regions.

5. Conclusions

This paper gives a brief overview of an updated worldwide distribution of 91 taxa of dinoflagellate cysts, highlighting the following observations:

- Of the 91 taxa that were studied here, their global distribution shows that only three modern taxa (*Brigantedinium* species, *Operculodinium centrocarpum* sensu Wall and Dale 1966 and some species of *Spiniferites*) dominate cyst assemblages worldwide. Caution is needed in using these taxa as key-indicators and we recommend that palaeoecological interpretation of their fossil occurrence is made in conjunction with the full cyst assemblage.
- Only a few species are truly restricted geographically, such as *Stelladinium robustum* in the Indian Ocean and *Peridinium ponticum* in the Black Sea-Caspian Sea corridor (other taxa from this region are relicts of the former pan-Eurasian Paratethyan Sea, e.g., *Impagidinium caspiense*, *Spiniferites cruciformis*), although recent studies have highlighted recent dispersal possibly linked to human activities.
- Only three true bi-polar species were identified — *Islandinium minutum*, *Impagidinium pallidum* and cyst of *Polarella glacialis* — but recent studies raise questions about cryptic species and morphological identification issues. Although there is no ambiguity with regard to the routine identification of *I. pallidum*, the recent finding of new *Islandinium* and morphologically similar species suggests higher diversity in this group, which would urge us to proceed with further culture experiments and phylogeny especially for Antarctic specimens, for which we have little information.
- The global distribution confirms the relatively rich diversity in environments where other palaeoceanographic tracers are rare or monospecific, in particular in polar environments or enclosed seas.
- This global overview highlights the need for more information from oceanic sites, in particular pelagic regions of the Pacific and Indian Oceans.
- Further information on cyst production beneath Arctic sea ice, seasonal and perennial, would help to better understand the life history of these important primary producers.

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Appendix A. Supplementary data

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