

Dinoflagellate cysts in sediment traps from the Nordic Seas: Implications for their use as proxies in paleoceanography

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ABSTRACT

The Nordic seas are important for bottom water formation and heat transfer in global climate, and dinoflagellate cysts are a major microfossil group in cored sediments from high latitudes where mineralized fossils are absent due to dissolution. This first basin-wide study of dinoflagellate cysts in deep-sea sediment traps reassesses the basic assumptions of paleoceanographic proxies: that dinoflagellate cysts in bottom sediments represent primary environmental signals from overlying surface waters carried by cysts sinking without significant lateral transport. We studied 126 samples collected at 12–30 day intervals over one year from traps (approximately 400 m above bottom) at 9 stations. We recorded 27 cyst taxa quantitatively (cyst fluxes) and as assemblages calculated from the fluxes. Correspondence analysis was used to compare cyst assemblages from traps with those in recent bottom sediments used to create proxies. The generally high correlation shown between fluxes of cysts and lithogenic particles suggests common transport mechanisms for both. We show three different sources of cysts and environmental signals: primary, from oceanic surface waters; secondary, transported in from shallow adjoining waters and ocean currents; and tertiary, older cysts resuspended from shelves. We found poor correspondence between cysts in traps and those in bottom sediments mainly due to the dominance of *O. centrocarpum* in the sediments, but correspondence analysis identified the main current regimes in both. We propose that *O. centrocarpum* here and elsewhere in oceanic sediments reflects an opportunistic response to mixing of oceanic/shelf waters. Consideration of factors highlighted here should help to improve the use of proxies.

1. Introduction

The use of marine dinoflagellate cysts as paleoclimatic indicators for paleoceanography has increased in recent years, with the development of proxies for quantitative estimates of past climate and ocean parameters (Marret et al., 2020; Marret and de Vernal, 2024 and references therein). Environmental signals applied as proxies in Quaternary paleoclimate studies were first documented in the 1970s by comparing dinoflagellate cysts (here referred to as cysts for brevity) in recent bottom sediments with known environmental parameters in overlying waters (Williams, 1971; Davey and Rogers, 1975; Wall et al., 1977). Dale (1983, 1996) described recent cyst signals for climate (Sea Surface temperatures, SST), coastal/oceanic, salinity, and productivity, and their application to Quaternary studies. Zonneveld et al. (2013) collated global data from many of the cyst distribution studies since that contribute biogeographic information to an expanding database for cyst proxies. Here, we concentrate on the SST signals most used as climate

proxies in paleoceanography (de Vernal et al., 1994, 1997, 2004, 2010; Mudie and Harland, 1996; Rochon et al., 1999; Marret and Zonneveld, 2003; Pospelova et al., 2008; Radi et al., 2013; Marret and de Vernal, 2024), though our results suggest implications also for other environmental parameters.

The warmer or colder-water indicator cysts used in proxies were first identified from fjords and sheltered coastal bays. Their climatic signals are particularly robust since they reflect standard biogeographic (climatic) zones on both sides of the North Atlantic (Dale, 1983, 1986, 1996). However, the fact that cysts behave as fine silt particles subject to transport in the sedimentary regime (Dale, 1976; Wall et al., 1977) has important implications for paleoclimatic interpretations. The central question considered here is: do the cysts in sediment reflect environmental conditions (such as SST) in overlying waters, or were they transported out of their original environment, thereby potentially reflecting a different signal? This question is particularly critical for interpreting the deep-sea record of paleoceanography, where large

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expanses of deep water increase the potential for long distance transport of cysts produced in near surface waters.

The expanded database of cysts in recent coastal, neritic and oceanic sediments now allows comparisons with environmental conditions (e.g. SST) in overlying waters as well as with plankton records. Dale (1976) found good correspondence between cysts in sediments and plankton species in a Norwegian fjord. However, Dodge and Harland (1991) found that biogeographic ranges for some cysts in the deeper North and South Atlantic Oceans extended beyond that of their planktonic stages, suggesting broader ranges of SSTs for cysts. Biogeographic ranges of indicator species in the cyst atlas of Zonneveld et al. (2013) mostly support their status as climatic indicators, but some suggest higher or lower ranges comparable to observations by Dodge and Harland (1991). For example, the cold water indicators (sub-polar to polar) of particular interest here, such as *Spiniferites elongatus*, *Pentaparsodinium dalei* and *Impagidinium pallidum* (e.g. of Dale, 1976, 1996) are reported in the atlas to have SSTs ranging from $<0^{\circ}\text{C}$ to $>20^{\circ}\text{C}$. Marret et al. (2020) report occurrences of colder water indicators *Impadinium pallidum* and *Islandinium minutum* as far south as North Africa. Taken at face value, this might seem to challenge the basis for their application in paleoceanography. We postulate that the cold-water indicator species recorded in warmer environments, in these records and elsewhere, most likely represent cyst transport from colder to warmer environments in more open water sites. A better understanding of the role of cyst transport is crucial to the use of cysts as SST indicators in paleoceanography, and this is a primary focus of work presented here.

Earlier reports of oceanic cyst distribution can now be reassessed from today's perspective. For example, Harland (1983) classified cysts now identified as cold temperate indicators (e.g. *Bitectatodinium tepikiense* and *Spiniferites elongatus*) as also tropical, from a long, large “finger” of sediments into the western North Atlantic. This likely reflects the same long-distance transport shown by Needham et al. (1969) for the reworked Carboniferous palynomorphs transported from S.E. Canada to offshore Florida by the Western Boundary Current, as discussed in Dale (1996).

1.1. Background for the work presented here

Increasing efforts to better understand climate change have identified two important topics of particular interest for this work: the large oceanic systems that transport much of the heat from low to high latitudes, and the observed greater increased warming of the Arctic compared with other regions (Schmitt, 2018). A better understanding of the paleoceanography of the Nordic Seas is important for investigating both topics (Kaledina and Bashmachnikov, 2023; Smedsrud et al., 2022). Ocean sediments are one of the main archives of past climate, and micropaleontology is a powerful tool for investigating this. The pioneering role of micropaleontology in deciphering the paleoceanography of the North Atlantic is particularly important for addressing climate change in the Arctic.

The CLIMAP project established the use of microfossils in cored sediments as a routine method in paleoceanography (Imbrie and Kipp, 1971). Statistical transfer functions for the first time allowed estimates of paleo-SSTs from fossil assemblages of planktonic foraminifera in bottom sediments. CLIMAP provided a plausible scenario of climatic change in the North Atlantic Ocean during the last glacial cycle, but dissolution of calcareous foraminifera and other mineralized microfossils sometimes caused critical limitations to the method, particularly at higher latitudes. Palynological methods using acid-resistant (so-called organic-walled) dinoflagellate cysts provided a viable alternative (de Vernal et al., 1997; Guiot and de Vernal, 2007; Hohmann et al., 2023), that has developed into a standard method in palynology.

Research over the past five decades has produced a broad comprehensive database of organic-walled cysts in the surficial bottom sediments of the northern North Atlantic Ocean, the Nordic Seas and adjacent Arctic Ocean (Marret and de Vernal, 2024). Various statistical

methods have been applied to convert cyst data into estimated SSTs and other environmental parameters for interpreting climate change. The principle for applying cysts is the same as that previously developed for foraminifera: the fossils are presumed to reflect conditions (e.g. SSTs) in the overlying water (Boltovskoy and Correa, 2016). However, important questions arise in applying similar methods to these very different fossil groups. Planktonic foraminifera are known to live in overlying waters, whereas most dinoflagellates producing cysts are species recognized from coastal/neritic plankton; they have not generally been recorded from the oceanic plankton. This means that cysts are currently being used to provide critical paleo-SSTs for climate modelling, while adequate knowledge of where they are produced and how they are deposited in bottom sediments is still lacking.

There are no easy answers to the questions raised here. The logistical difficulties of sampling the vast deep oceans are clearly apparent. Nevertheless, a major international project was mounted in the early 1980s using large deep-sea sediment traps to investigate sedimentary processes in the deep ocean basins (Honjo et al., 1987a; Von Bodungen et al., 1995; U.S. JGOFS Project Office, n.d.). Subsamples from some of the traps deployed allowed us the unique opportunity to investigate which cysts are settling out and where in the deep ocean. The Nordic Seas and adjacent Western Barents Sea is a critical region for climate studies and is particularly suited to address questions of dinoflagellate cyst climate signals in paleoceanography not least because it has the most comprehensive data for cyst assemblages in recent deep-sea sediments and adjoining coasts on both sides of the basin (Heikkilä et al., 2016; Mäkelä et al., 2025; Matthiessen et al., 2005; Howe et al., 2010; Marret and de Vernal, 2024). A main objective of work presented here is to document the extent to which cyst assemblages deep in the oceanic waters correspond to the cyst assemblages in the underlying bottom sediments used in paleoceanography. Good correspondence would add confidence to the cyst proxies in paleoclimate models that presume this; poor correspondence would suggest the need for more complex paleoclimatic interpretations that address the role of cyst transport before sedimentation.

1.2. Cysts in deep-sea sediment traps

Work reported here is one of very few investigations so far documenting dinoflagellate contributions in deep sea traps (DST). The first study of cysts from DSTs was from the central oceanic gyres of the Atlantic and Pacific Oceans and the Panama Basin (Dale, 1986, 1992a, 1992b). Samples were not treated chemically since the objective was to assess the total dinoflagellate contribution. Diagnostic oceanic cyst types were identified settling out from the plankton. However, these were almost exclusively calcareous cysts that would be removed by palynological preparation methods. Non-mineralized cysts that possibly could contribute to palynological assemblages were absent from DST records in the central gyres of the North Atlantic (station S) and the Pacific Ocean (station P1) (Dale, 1992a). At two other stations, however, a steady supply of non-mineralized cysts was recovered from all depths, though these were restricted to undifferentiated spherical brown protoperidinioid forms (Dale, 1992a). These cysts were considered possibly to reflect the location of both of these stations (stations E and PB₁, from the northwest equatorial Atlantic and the Panama Basin, respectively), significantly nearer to continental land masses.

From the one station where cysts could be compared from both trap samples and bottom sediments (Station S, Sohm Abyssal Plain, North Atlantic Ocean), the assemblages proved to be totally different. The main conclusion was that “oceanic assemblages” of cysts from recent deep-sea sediments previously described by palynologists probably do not accurately reflect production in overlying surficial waters, but more likely represent long distance transport of cysts (Dale, 1992a, p.18). Subsequent comparisons between the more restricted ecological zonation of diagnostic cyst types in coastal/neritic sediments and their more widespread distribution in deep sea sediments of the North Atlantic have

suggested the coastal/neritic zones as the probable source of many cysts in deep sea sediments (Dale and Fjellså, 1994; Dale, 1996).

The present study of dinoflagellate cysts from 9 stations around the Nordic Sea Basin is the first comprehensive basin-wide analysis of the dinoflagellate flux from one region, herein referred to as the Nordic Sea Basin or Nordic Seas. In the present work, we have re-analyzed work published earlier and added results from five deployments at four additional stations: NB from the Norwegian Sea, IP from the Iceland Sea, WBS from the shelf edge between the Norwegian Sea and Barents Sea, and BS from the western Barents Sea (Figs. 1 and 2). We also compare our sediment trap data with the deep-sea sediment data most widely used for estimating paleoceanographic conditions in the region (de Vernal et al., 2020, and references therein) (Fig. 2) and discuss the paleoceanographic implications of our findings. The main objectives were to 1) investigate the primary dinoflagellate environmental signal settling out in the deep sea in this region, 2) characterize the extent to which transport may influence the distribution of the cysts, and 3) assess the overall potential for using cysts as paleoclimatic indicators in this high latitude deep sea region.

1.3. Hydrographic setting

The Nordic Seas include the Norwegian Sea, the westernmost Barents Sea, the Greenland Sea and the Iceland Sea, bounded by Greenland to the west, Iceland to the south, Norway to the east and Svalbard to the north (Figs. 1 and 2). They represent the largest oceanic passageway between the largely ice-free northeastern Atlantic Ocean and the partially ice-covered Arctic Ocean, and as such are a major area of heat exchange between the North Atlantic and Arctic regions. The Fram Strait, through which most Atlantic water entering the Arctic Ocean and most Arctic water exiting into the Nordic Seas passes, is the only opening to the Arctic at oceanic depths (sill depth: ca. 2600 m; Coachman and

Aagaard, 1974). The Nordic Seas are the primary area of North Atlantic Bottom Water formation, which plays a critical role in determining global circulation patterns affecting climate (Swift, 1986; Labeyrie et al., 1987; Broecker, 1991). Broecker (1994) postulated that warming temperatures might lead to extreme melting of arctic ice sheets, creating a freshwater pulse into the North Atlantic sufficient to prohibit deepwater formation, which could initiate a switch between glacial and interglacial modes of thermohaline circulation and trigger ice-age conditions (Broecker, 1991, 1994; Broecker and Denton, 1989). Models of global climate require an understanding of the present-day oceanography and paleoceanography of this critical region.

Bathymetry is an important factor controlling the dynamics of oceanic circulation in the region (Johannessen, 1986; Hopkins, 1991). The near surface hydrography is heavily influenced by major surface currents: the warmer, highly saline waters of the Norwegian Atlantic Current on the eastern side (approximate temperature range: 3–11 °C, salinity: 35.0 ‰), and by the colder, lower salinity waters of the East Greenland Current on the western side (approximate temperature range: < 1–4 °C; salinity: < 34.4 ‰) (Dietrich, 1969; Johannessen, 1991) (Figs. 1 and 2). Surface currents enter the region from the North Atlantic, proceed northward and lose some flow to the Barents Sea, before passing west of Spitsbergen into the Arctic Ocean. Polar waters enter from the northwest and proceed southward along the East Greenland shelf. Comparison of bathymetry and circulation shows that the eastern boundary of the East Greenland Current corresponds closely with the boundary of the continental slope of the Greenland Sea. Polar waters flow southward along the east coast of Greenland, transporting sea ice and ice floes from the Arctic Ocean and producing mixed-ice conditions in a large area along the eastern boundary of the East Greenland Current. Additionally, these two current systems are separated by cyclonic gyres in the Greenland and Norwegian Seas (Johannessen, 1986). Current velocities at surface are typically between 20 and 40 cm/s in the

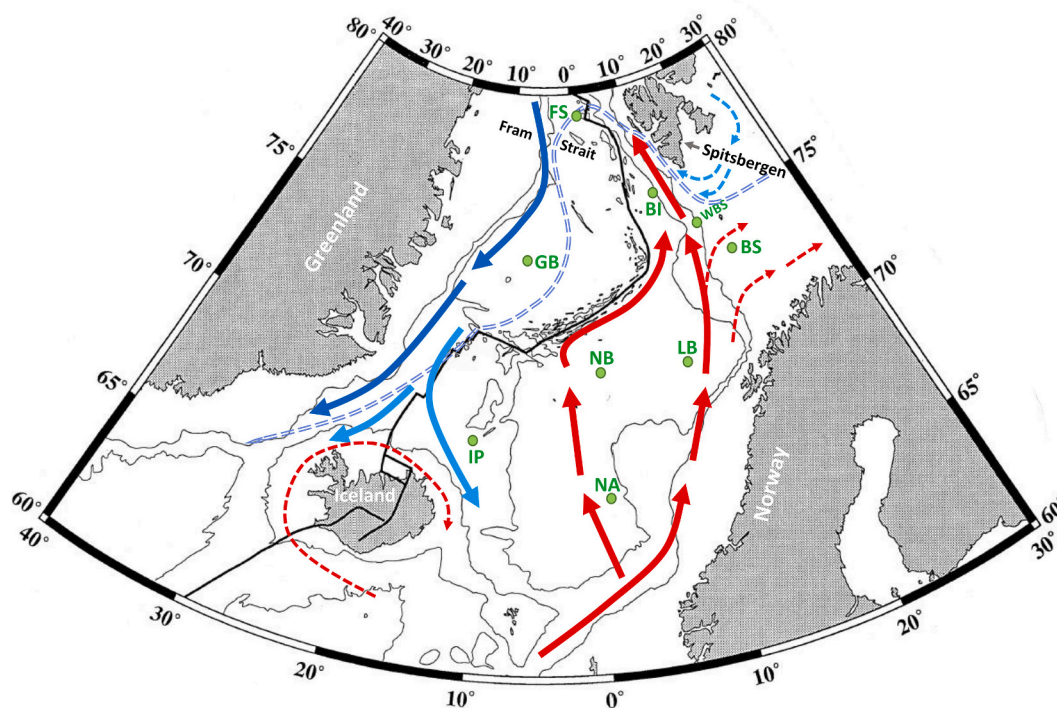


Fig. 1. Map showing locations of 9 sediment trap stations used in study (Green). NA = Aegir Ridge, LB = Lofoten Basin, NB = Norwegian Basin, WBS = Western Barents Sea, BS = Barents Sea, BI = Bear Island, FS = Fram Strait, GB = Greenland Basin, IP = Iceland Plateau. Solid thick red arrows indicate Norwegian Atlantic Current, dark blue arrows indicate East Greenland Current, lighter blue = E. Icelandic Current; Stippled red arrow around Iceland indicates warmer Irmingier Current. Solid thick black line = Mid-oceanic Ridge. Stippled double blue line = average ice edge (1983–1990 from Walsh et al., 2019). For details of warmer (red) and colder (blue) stippled currents in the Barents Sea see Loeng (1991). Schematic surface currents in Nordic Sea Basin after Johannessen (1986) and Morozov and Frey (2024). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

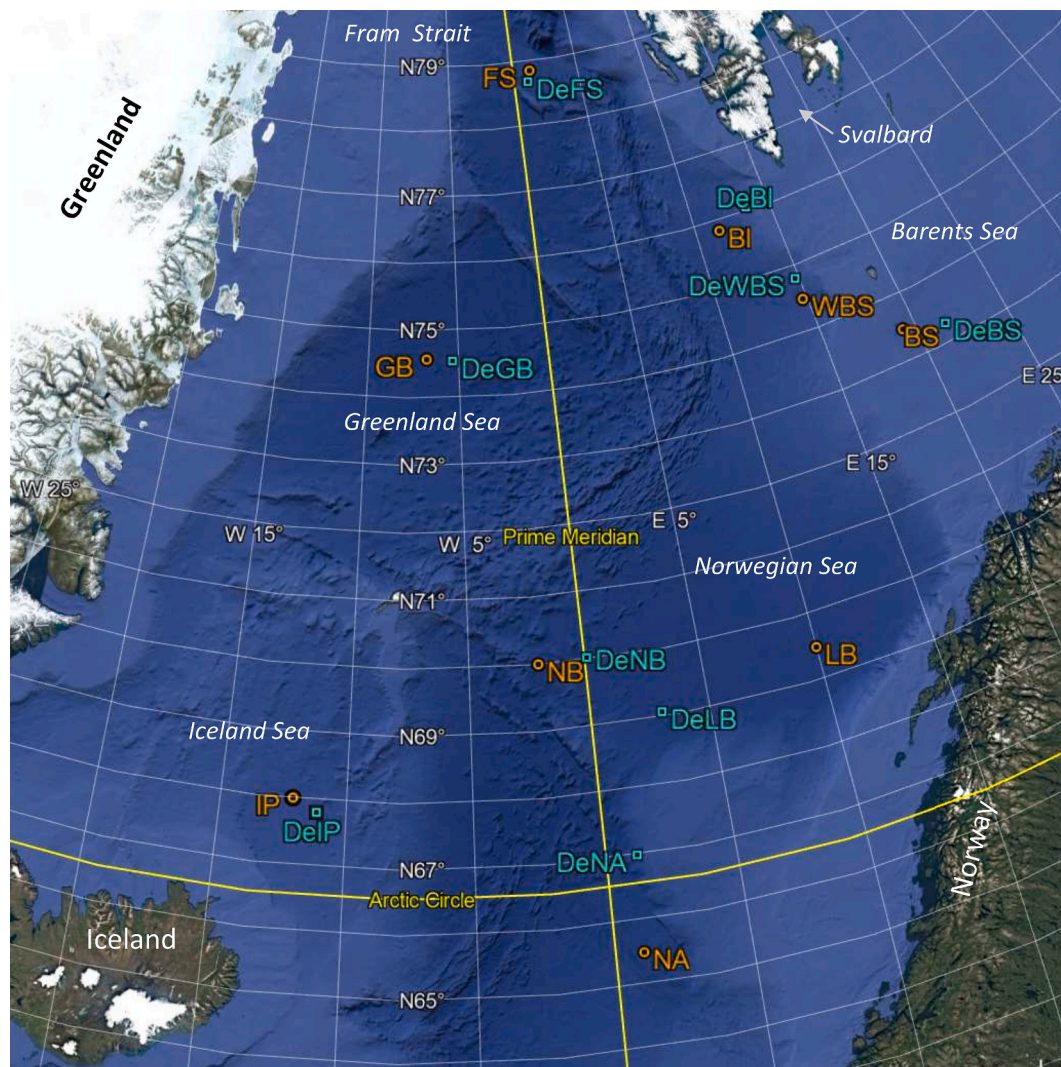


Fig. 2. Map showing sediment trap stations (orange) together with the nearest bottom sediment sample to the sediment trap stations from the de Vernal et al. (2020) $n = 1968$ database (teal). Detailed station information in Table 7. Map created using Google Earth Pro imagery (© Google, Maxar Technologies). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Norwegian Atlantic and Irminger Currents, and between 5 and 15 cm/s in the East Greenland Current (Brown et al., 2023; Morozov and Frey, 2024). Current speeds at the trap depths are generally very weak, typically less than 10 cm/s, but with tidal peaks in the Fram Strait and Barents Sea of 18–20 cm/s, respectively (Honjo et al., 1987b; Semper et al., 2019; Morozov and Frey, 2024).

The Barents Sea is an extensive shallow sea, which only rarely exceeds a water depth of 300 m and includes one of the widest continental shelves in the world (Perry, 1986). The Barents Sea receives water input from both the Norwegian Coastal Current and the Norwegian Atlantic Current from the south. As the warmer waters progress northward, they cool by 0.25 °C per 100 km of distance travelled in this region (Cokelet et al., 2008). The Barents Sea acts as a heat sink for waters from the N. Atlantic and serves as a source of freshened surface water and some deep water back into the Norwegian Sea (Loeng, 1991). Summer SSTs in the Atlantic-influenced Barents Sea are lower than in the Norwegian Sea (< 6°C, as compared with 10–12 °C, respectively), at similar latitudes (Sakshaug, 2004).

The Iceland Plateau region is influenced by both the East Greenland Current flowing southward along the east coast of Greenland and the Irminger Current (approximate temperature range: 5–6 °C, salinity: > 35.0 ‰) which flows northward from the west coast of Iceland (Hopkins, 1991). The Irminger Current is a branch of the North Atlantic Current

that carries relatively warm Atlantic water northward.

and west of Iceland where it splits at the Greenland-Iceland Ridge. One branch of the Irminger Current swings west and south to form the cyclonic circulation of the Irminger Sea and the other branch (shown in Fig. 1), generally smaller, rounds the northwest peninsula of Iceland and flows eastward on the shelf as the North Iceland Irminger Current. The relative contributions from each of these two current systems may vary significantly from year to year (Malmberg, 1991). The Iceland Plateau is hydrographically isolated from the neighbouring Greenland and Norwegian Seas by prominent bathymetric features to its east and west (Stefánsson and Ólafsson, 1991a, 1991b).

The strongly contrasting hydrographic conditions within the relatively small Nordic Sea Basin provided an optimum framework for assessing the use of dinoflagellate cysts as water mass indicators in this area.

2. Methods

2.1. Samples

Between 1983 and 1990, a total of 126 time-series sediment trap samples were recovered from eleven deployments at nine stations in the Nordic Seas (Figs. 1 and 2, Table 1). Six of these were deployed as part of

Table 1

Station information for the 9 stations around the Nordic Seas Basin, including deployment information, trap depth, water depth and average annual surface water temperature. Surface water temperatures from World Ocean Atlas (2013) averaged for the year of trap collection. * indicates that trap malfunctioned, 2 cups remained closed. ** indicates that trap malfunctioned, WBS-S remained open for 357 days, and WBS-D functioned for the first three sampling intervals then the fourth remained open for 273 days. Locations shown in Figs. 1 and 2.

Station	Code	Latitude/ longitude	Trap depth (m)	Water depth (m)	Trap open - Trap closed (mo/day/yr)	# cups / duration (day:hrs)	Avg. Annual T (°C)
Aegir Ridge	(NA)	65° 31'N 00° 64' E	2630	3058	21/08/85- 16/06/86	13/ 23:00	7
Lofoten Basin	(LB)	69° 30'N 10° 00' E	2761	3161	15/08/83- 01/08/84	12/ 30:00	7
Norwegian Basin*	(NB)	70° 00'N 01° 58' W	2749	3296	25/08/85- 24/03/86	19/ 12:00	4
Western Barents Sea**	(WBS-S)	74° 29'N 15° 18' E	810	1608	18/05/89- 07/05/90	1/ 357:0	5
	(WBS-D)		1400	1608	18/05/89- 7/05/90	3/28:0 1/273:0	5
Barents Sea	(BS)	73° 29'N 19° 19' E	369	472	18/05/89- 07/05/90	13/ 28:00	5
Bear Island	(BI)	75° 51'N 11° 28' E	1650	2123	12/08/84- 10/08/85	12/ 30:40	5
Fram Strait	(FS)	78° 51'N 01° 22' E	2146	2527	20/08/84- 15/08/85	13/ 27:50	2
Greenland Basin	(GB)	74° 35'N 06° 43' W	2823	3445	04/08/85- 03/08/86	13/ 28:00	1
Iceland Plateau	(IP2)	68° 01'N 12° 40' W	1457	1884	19/10/87- 05/10/88	13/ 27:00	3
	(IP3)		1457	1884	22/10/88- 08/10/89	13/ 27:00	3

a joint United States/German program to study high latitude sedimentation (NA, NB, LB, BI, FS and GB); three as part of a joint United States/Norwegian study in the western Barents Sea (WBS-deep, WBS-shallow, and BS); and two as a joint United States/Icelandic sediment trap study on the Iceland Plateau (IP2 and IP3) (Figs. 1 and 2 and Table 1). Mark V sediment traps with an aperture of 1.17 m² were used at stations LB, BI, NB and GB; Mark VI sediment traps with an aperture of 0.51 m² were used at stations NA and FS; and Mark VII traps, also with an aperture of 0.51 m², were used at stations BS, WBS and IP. The design and construction of the Mark V and Mark VI traps are described by Honjo and Doherty (1988); the Mark VII trap differs from the Mark VI only in certain aspects of the electronics and stepping motor. Traps were suspended between 103 m (for the shallower Barents Sea) to an average of 436 m (for the Nordic Seas) above bottom in the water column (Table 1) by buoys while remaining anchored to the bottom, with an acoustic release mechanism to enable recovery. Nine of the traps were stationed at water depths of 1400 m or greater (NA, LB, WBS-deep, BI, NB, FS, GB, IP2 and IP3; Fig. 1), and two were positioned at shallower water depths: WBS-shallow at 810 m and BS at 369 m (Figs. 1 and 2). Samples were programmed to collect at a temporal resolution varying between 12 and 30 days, for roughly one year (Table 1).

Three of the sediment trap deployments malfunctioned due to battery failure in the colder waters (NB, WBS-deep and WBS-shallow), but these traps provided information that is included where appropriate. The first three samples in the western Barents Sea-Deep trap (WBSD) functioned, collecting at 28-day intervals between May 18th and August 10th, 1989, but rotation stopped after this and the fourth time-series sample, collected from August 10th, 1989, until May 7th, 1990, was open upon retrieval. Total sediment flux was only available for the three cups that functioned. Since an aliquot portion of the fourth sample was available, an average cyst flux for the total deployment was calculated from all four cups, shown in Fig. 4, but this would represent a minimum due to presumed outwash of the fourth sample during retrieval. The shallow trap at this station (WBSS) remained open from May 18th, 1989, until May 7th, 1990, so only percentage and presence/absence cyst data were obtained from this deployment.

Fig. 1 shows the locations of the nine sediment trap stations in relation to hydrography. Fig. 2 shows the locations of the sediment traps (hereafter referred to as “traps”) together with the oceanic bottom

sediments (hereafter referred to as “sediments”) from the $n = 1968$ database of de Vernal et al. (2020) labelled with the prefix “De”. Table 1 summarizes the station data for the 126 trap samples used in this study.

2.2. Sample preparation

2.2.1. Sediment trap samples

We received an aliquot of each sediment trap sample: 1/16 of those from IP2, 1/40 of those from IP3, WBS and WBS and 1/64 of the samples from the NA, LB, NB, BI, FS and GB deployments. After thoroughly shaking to homogenize the sample containing the <1 mm fraction, an aliquot portion of this was carefully measured, sonified to disperse particles, and wet sieved with a 25 µm mesh perforated metal sieve plate. In samples where sediments were heavily encased in a slimy matrix of organic matter (referred to as “marine snow”, after Alldredge and Silver, 1988), it was necessary to first disaggregate the sample by adding 37% Brij (Phipps and Playford, 1984) and allowing the sample to stand for at least one hour, before homogenizing and removing the aliquot portion. The size fraction 25 µm - 1 mm was then mounted in semi-permanent microscope slides using glycerine jelly, ringed with wax. The Dinoflagellate remains (mainly cysts) were examined in the light microscope and expressed both as fluxes (# cysts/m²/day) and as percentage composition of cyst assemblages. The <25 µm size fraction was checked to ensure that cysts were not lost by sieving.

2.2.2. Cyst counts

Achieving counts of at least 100 cysts from deep sea sediment trap samples proved considerably more time consuming than most other types of marine samples due to low cyst productivity, the varying abundance of viscous detritus, the seasonal nature of the samples and the relatively short sampling intervals. Total counts per station ranged from 116 to 3223 (Appendix A).

2.2.3. Deep sea sediment samples

The trap data was compared statistically with data from bottom sediment samples from the largest global deep sea cyst data set known to date used for paleoclimatic reconstructions, the $n = 1968$ data set published by de Vernal et al. (2020) (Fig. 2). Samples from the de Vernal et al. (2020) $n = 1968$ database were prepared according to

palynological methods described in de Vernal et al. (2010), summarized here as follows:

The “standardized” techniques basically follow the protocol established by de Vernal in the 1980s and presented in tutorials prepared for student training (de Vernal et al., 2010). The main steps of the sample preparation include wet sieving of the ~10–100 µm fraction of a measured volume or dry weight prior to mechanical and repeated chemical treatments with HCl and HF to dissolve carbonates and silicates. The preparations involve mostly HCl (10%) and HF (40–52%) treatments and centrifugation before decanting. The sieving mesh size was usually between 10 and 106 µm often aimed at counting all palynomorphs including acritarchs and pollen grains. However, some studies used mesh sizes of 15 µm and others used a mesh size of 63 µm as an upper limit to remove sand particles.

The bottom sediment database includes assemblages for which at least 60 specimens were counted per sample, with an average of 345 specimens per sample (Table S1, de Vernal et al., 2020). The sample data for the bottom sediments nearest to the trap samples is included in Appendix C.

2.3. Treatment of cyst data

2.3.1. Taxonomic notes

The cyst species encountered were all identified as those commonly reported in the literature for this region (e.g., de Vernal et al., 1994; Head et al., 2001; de Vernal et al., 2005; Matthiessen et al., 2005; Mäkelä et al., 2025). The species and taxa group names are shown together with the codes used in the analyses and cyst/motile correspondence in Table 2, and the main cyst types are illustrated in Plate 1. Following the recommendations by Dale (1983) and Head et al. (2024), a combination of motile stage-based and cyst-based taxonomy is used for the ease of comparison with previous literature:

“Round, brown cysts” - includes several types which are impossible to identify to species level in most specimens not showing the diagnostic archeopyle. Most spherical, brown cysts which could be identified were assigned to *Protoperidinium conicoides*; others included *Protoperidinium avellana*, *Protoperidinium denticulatum*, and *Brigantedinium majesculum* (Reid and Harland, 1977); and illustrated by (Dale, 1983, Fig. 19). These are referred to as “RBC” in the text, for “round, brown cyst”.

“Thoracosphaerids” - includes two forms, one of which is a spherical calcareous cyst approximately 30 µm in diameter, with an angular archeopyle, believed to be co-specific with *Thoracosphaera albatrosiana* Kamptner 1963. These cysts were previously referred to broadly as “Spherical calcareous cysts” in Dale and Dale (1992). The other form includes actual thoracosphaerids approximately 25 µm in diameter with a round pylome. These are believed to be morphologically identical to the *T. heimii* commonly found in warmer waters of the N. Atlantic (Dale, 1992b), but they can only be identified with certainty using SEM. These two forms are included separately in the cluster diagram in Fig. 9 but are referred to collectively as “thoracosphaerids” elsewhere.

Islandinium minutum refers to the cyst species originally called *Multispinula?minuta* by Harland and Reid in Harland et al. (1980) redescribed as *I. minutum* by Head et al. (2001).

Islandinium cezare refers to *Islandinium?cezare* by Head et al. (2001). For practical reasons, the question mark is often omitted, as here. Form 14 from Dale and Dale (1992) is synonymous with *I. cezare*.

?Echinodinium karaense (Head et al., 2001) is synonymous with Form 5 from (Dale and Dale, 1992).

Operculodinium centrocarpum sensu Wall and Dale, 1966. An Arctic type with shorter processes was not recognized, and any present are grouped into this taxon.

The cyst of *Polarella glacialis* was identified as an acritarch in our earlier work, but was described since by Montresor et al. (1999). However, because it is small (< 15 µm), many were probably washed through the 25 µm sieve during processing, so they were excluded from percentage calculations and its presence is noted only qualitatively. The

Table 2

Dinoflagellate cyst species and groupings observed in traps, corresponding codes used in the analyses and motile-stage equivalents. Species code consists in general of the first letter of the genus name followed by the first three letters of the species name.

Cyst name	Code	Motile-stage equivalent
<i>Bitecatodinium tepikiense</i>	Btep	<i>Gonyaulax digitale</i>
<i>Brigantedinium cariacense</i>	RBC	<i>Protoperidinium avelanna</i>
<i>Brigantedinium majesculum</i>	RBC	<i>Protoperidinium sinuosum</i>
<i>Brigantedinium simplex</i>	RBC	<i>Protoperidinium conicoides</i>
<i>Brigantedinium</i> sp.	RBC	<i>Protoperidinium denticulatum</i>
<i>Brigantedinium</i> spp.	RBC	unknown
Calcareous cysts	Calc	unknown
cyst of <i>Gymnodinium catenatum</i>	Gcat	<i>Gymnodinium catenatum</i>
<i>?Echinodinium karene</i>	Ekar	unknown
<i>Impagidinium pallidum</i>	Ipal	unknown
<i>Impagidinium sphaericum</i>	Isph	unknown
<i>Islandinium cezare</i>	Icez	unknown
<i>Islandinium minutum</i>	Imin	<i>Islandinium minutum</i>
<i>Lingulodinium machaerophorum</i>	Lmac	<i>Lingulodinium polyedra</i>
<i>Nematosphaeropsis labyrinthus</i>	Nlab	unknown
<i>Operculodinium centrocarpum</i> sensu Wall & Dale 1966	Ocen	<i>Protoceratium reticulatum</i>
cyst of <i>Pentaparsodinium dalei</i>	Pdal	<i>Pentaparsodinium dalei</i>
cyst of <i>Polykrikos schwartzii</i>	Psch	<i>Polykrikos schwartzii</i>
cyst of <i>Protoperidinium americanum</i>	Pame	<i>Protoperidinium americanum</i>
<i>Quinquecuspis concreta</i>	Qcon	<i>Protoperidinium leonis</i>
Round brown cyst (undifferentiated)	RBC	unknown
cf. <i>Scrippsiella trochoidea</i> sensu Dale 1992	Stor	<i>Scrippsiella trochoidea?</i>
<i>Selenopemphix quanta</i>	Squa	<i>Protoperidinium conicum</i>
<i>Spiniferites bulloideus</i> sensu Wall and Dale 1968	Sbul	<i>Gonyaulax scrippsae</i>
<i>Spiniferites elongatus</i>	Selo	<i>Gonyaulax ovum</i>
<i>Spiniferites mirabilis</i>	Smir	<i>Gonyaulax spinifera</i>
<i>Spiniferites ramosus</i>	Sram	<i>Gonyaulax spinifera</i>
cf. <i>Thoracosphaera albatrosiana</i>	Thal	unknown
<i>Thoracosphaera heimii</i>	Thhe	<i>Thoracosphaera heimii</i>
<i>Trinvariantinium applanatum</i>	Tapp	<i>Protoperidinium shanghaiense</i>
Undifferentiated <i>Spiniferites</i> spp	SPIN	unknown

presence of *Polarella glacialis* cysts is significant because it is shown to live in sea ice in both Arctic and Antarctic regions (Montresor et al., 1999, 2003; Lund-Hansen et al., 2024).

The reference to usage in the literature of cyst species (e.g. sensu Wall and Dale 1966) for *Operculodinium centrocarpum* is omitted in the text for the sake of brevity. This also applies for cf. *Scrippsiella trochoidea* sensu Dale 1992 and *Spiniferites bulloideus* sensu Wall and Dale 1968.

Similarly, “cyst of” is omitted in the text for cyst species.

The terms “heterotroph” and “autotroph” used here refer to the general feeding behavior reported in the literature, but emerging evidence shows that some dinoflagellates previously assigned to these categories are proving to be mixotrophic (Mitra et al., 2016). Because trophic mode in dinoflagellates is now understood to be plastic and context-dependent we therefore acknowledge that mixotrophy may also apply to species included here.

Cyst identification and image documentation in sediment trap samples proved more challenging than in many recent coastal samples. Actual cyst preservation was comparable, with no visible evidence of thinner or paler cyst walls, but morphological details of cysts were sometimes obscured by slimy aggregates of particles from marine snow.

2.3.2. Dinoflagellate thecae

Dinoflagellate thecae (predominantly species of the genus *Dinophysis*) were noted where seen, mainly in the two shallow traps, but because these do not fossilize they were not a focus of this work and are reported collectively as “thecae”. Data on cyst thecae is included in Appendix A.

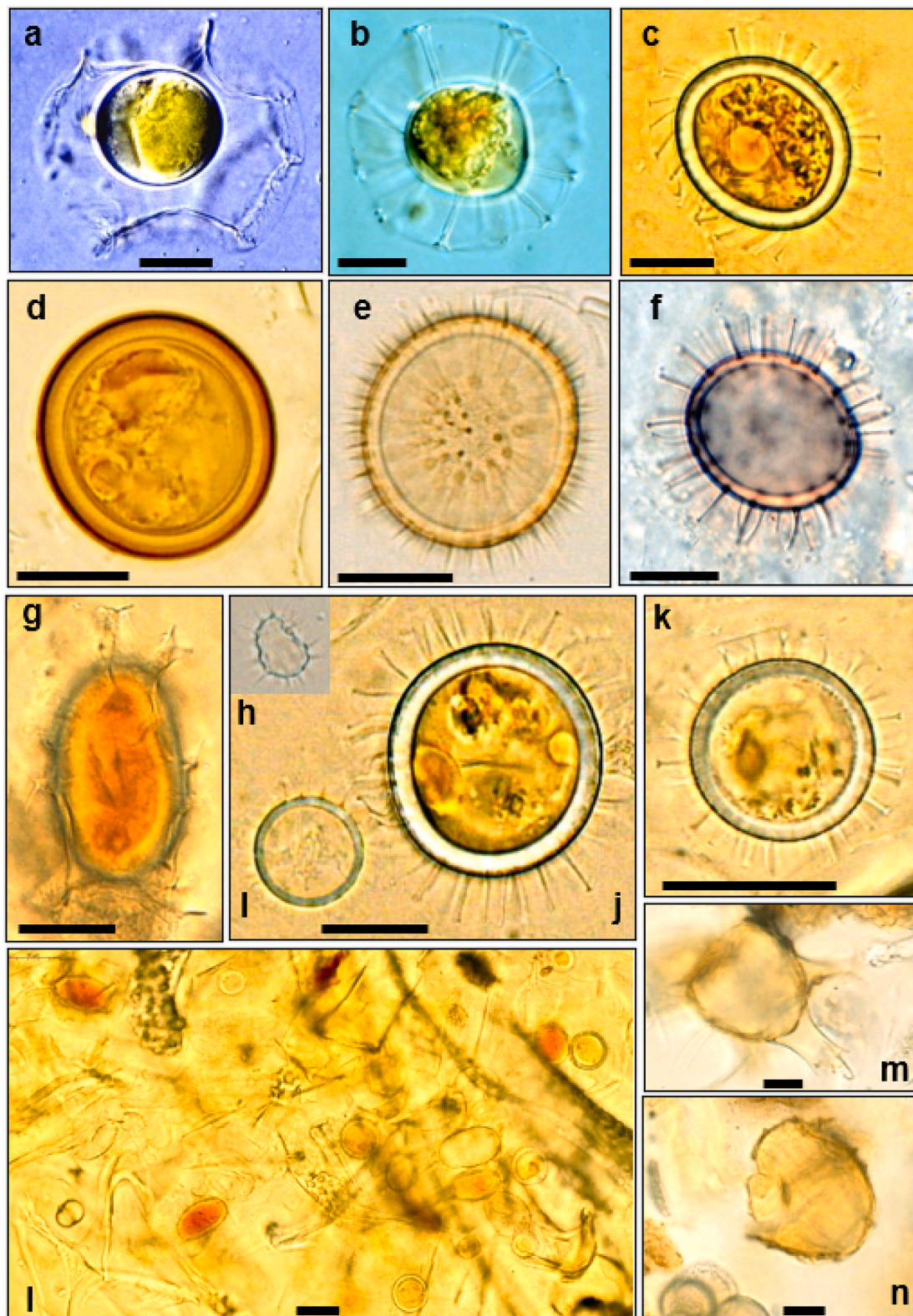


Plate 1. Key indicator species from the Nordic Seas (a-l). Scale bar = 20 μm for a-k. m and n, scale bar = 40 μm for l. a) *Impagidinium pallidum* with cell contents from the Fram Strait, b) *Nematosphaeropsis labyrinthus* with cell contents from the Norwegian Basin (NB), c) *Operculodinium centrocarpum* with cell contents from the Barents Sea (BS), d) *Protoperidinium coenicoides* with cell contents from the Barents Sea (BS). Sulcal depression discernible in a higher focus. e) *Islandinium minutum* from the Barents Sea, f) *Islandinium cezare* from the Bear Island station (BI), g) *Spiniferites elongatus* from Barents Sea (BS), h-j) *Polaris glacialis* from the Fram Strait (FS), *Pentapharsodinium dalei* and *O. centrocarpum* with cell contents, respectively, from the Iceland Plateau (IP) shown together for scale, k) *P. dalei* with cell contents from the Iceland Plateau (IP); note bifurcate processes. l) overview showing cyst production in Barents Sea (BS) sample 5, with high proportions of *S. elongatus*, *O. centrocarpum* and *P. dalei* with cell contents (see Fig. 12). m) and n) Miocene cysts of *Hystriocholpoma rigaudiae* and *Cribroperidinium* sp., respectively, from the resuspension event in Lofoten Basin sample 12 (July 2nd – August 1st, 1984), discussed in section 3.4.3. For accessory cyst types see Plate 1 in Dale and Dale (1992).

2.3.3. Standardization of cyst data for comparison between samples

It was necessary to use different aliquot portions from different cups of the trap samples depending on the nature and total amounts recovered per time interval, therefore results were first converted into fluxes (# cysts/m²/day) to standardize the data. Percentages of the flux of each species as a proportion of the total assemblage were calculated to investigate the assemblage changes around the Nordic Seas Basin.

Since the oceanic bottom samples had of necessity been palynologically prepared, the calcareous cysts (thoracosphaerids and cf. *Scippsella trochoidea*) were removed from the sediment trap data and percentages recalculated to compare the trap samples with the palynological record.

Standardization of cyst data by conversion to fluxes was calculated for all stations except for WBS according to the following formula:

$$\text{Cyst flux} = (\text{total cysts} \times \text{aliquot fraction of sample}) \times (\text{days in sampling interval})^{-1} \times (\text{area of trap opening})^{-1}$$

Cyst fluxes for the WBSD trap are based on 3 cups that remained open for 28 days and 1 cup that remained open for the remaining 273 days of the deployment. Flux data for the latter cup is included in Appendix A only. Cyst fluxes were not calculated for the WBS trap that remained open, but percentages abundances were calculated on the basis of the total count.

See Appendix A for total counts, time-series flux values, aliquot portions used, and species percentages based on fluxes and Appendix B for percentage and flux data of main species only.

Total sediment fluxes and lithogenic content were obtained for stations NA, LB, NB, BI, FS, GB from Honjo et al. (1987a) and for station BS from Honjo and Manganini pers. comm. (1992). Total fluxes for IP2 and IP3 were obtained from Jon Olafsson pers. comm. (2024) and Olafsson et al. (2000). The lithogenic flux is that portion of the total sediment flux that is left after the carbonate, biogenic silica and organic carbon components are removed, and generally consists of land-derived particles ranging from 1 to 51 µm in size (Ohnemus and Lam, 2015). To explore possible mechanisms of transport, correlations between cyst flux and total and lithogenic flux were calculated using the Pearson's correlation coefficient (r).

Diversity was measured according to the species richness concept, where diversity equals the total number of species/ taxonomic groups documented (Peet, 1974). We use the term "species richness" for comparison with other work, while acknowledging that "round brown cysts" and "unidentified *Spiniferites* species" are groupings of taxa indistinguishable at species level.

2.3.4. Statistical treatments

The cluster diagram shown in Fig. 9 was created using the MVSP-PLUS ("Multivariate Statistical Package") program, written by Dr. Warren L. Kovach, University College of Wales, Aberystwyth, to schematically illustrate the main assemblage data (Kovach, 1990). The unweighted pair group, hierarchical agglomerative method was used, with the percent similarity coefficient as a similarity measure. A "Cluster" was defined as a group of stations with a similarity of 0.5 or greater.

The Pearson Product Moment correlation coefficient was used to construct the correlation matrix.

The strength of associations between stations, species and environmental variables was explored using Correspondence analysis (CA) and canonical correspondence analysis (CCA). These were performed using Canoco for Windows version 4.5 and presented graphically using CanoDraw (ter Braak and Šmilauer, 2002). Data were not transformed, and Hill's scaling was used. Results of the CA and CCA are shown graphically in Figs. 15–16 and 18–19, and numerical results are provided in Appendices D–G.

The schematic summary of assemblages shown in the cluster diagram in Fig. 9 included also the calcareous component and presence of rare forms that were occasionally seen during sample preparation but are not included in Appendix A.

3. Results and discussion of cyst analyses

Dinoflagellate cysts were recovered at all 11 deployments and all 9 stations around the Nordic Sea Basin. A total of 27 cyst taxa were documented. Dinoflagellate thecae were seen only occasionally in most of the deeper traps but were common in the shallower trap in the Barents Sea (BS) and on the Iceland Plateau (IP2 and IP3). Results are discussed first as cysts related to: cyst and sediment flux (section 3.1); cyst assemblages in the traps (section 3.2); cyst supply to the deep sea (section 3.3); and cyst transport (section 3.4). Results and discussion of comparisons between assemblages in trap and bottom sediments is included in section 4, and implications for paleoceanography are discussed in section 5.

3.1. Cyst and sediment fluxes

The sediment collected in the DSTs is from two distinct origins: marine biological production and lithogenic material transported from land. Cyst fluxes were compared to total sediment flux, and to lithogenic fluxes since the <1 mm fraction studied here is considered the most likely to include cysts transported in the water.

3.1.1. Total cyst and sediment fluxes

Total cyst and sediment fluxes are shown in Figs. 3 and 4. Cyst data is shown in Appendix A. Sediment data is from Honjo et al. (1987a), Honjo and Manganini pers. comm. (1992), Jon Olafsson pers. comm. (2024), and Olafsson et al. (2000). Although the cysts account for only a miniscule fraction of the sediment, an understanding of the relationship between cyst fluxes and the different components of the sediment fluxes may shed light on the processes of cyst deposition in bottom sediments. Total cyst fluxes were markedly higher for the two shallowest stations for which fluxes could be measured, BS in the Barents Sea (369 m) and IP3 on the Iceland Plateau (1457 m) (3385 and 1920 cysts/m²/day, respectively). Within the main Nordic Sea Basin, total fluxes were significantly higher for stations influenced by the warmer, Norwegian Atlantic Current (NA, LB and BI) than for those influenced by the colder, East Greenland Current (FS and GB) (averaged fluxes for the two current regimes: 349 and 125 cysts/m²/day, respectively) (Fig. 3). The WBS trap located at the shelf edge between the Norwegian and Barents seas malfunctioned and collected only 3 intervals of reliable flux; nonetheless, total cyst flux from these three alone averaged over the entire year of deployment was greater than for the average from any other deep sea station (exceeded only by the shallower BS trap). Average sediment

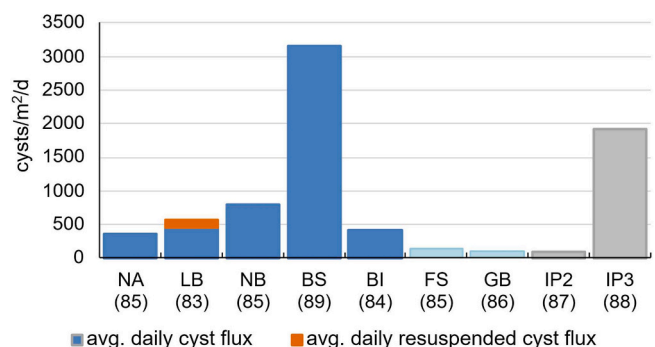


Fig. 3. Average daily cyst flux from nine deployments around Nordic Sea Basin, WBS omitted. Darker blue = warmer Norwegian Atlantic Current influence, lighter blue = colder East Greenland Current influence, grey = Iceland Plateau. Red = resuspended Pre-Quaternary cysts (explained in section 3.4 on cyst transport), documented primarily in one cup but standardized to the entire year for comparison. Date of trap deployment indicated under station, all collected into the next calendar year. For exact dates see Table 1. Data in Appendices A and B. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

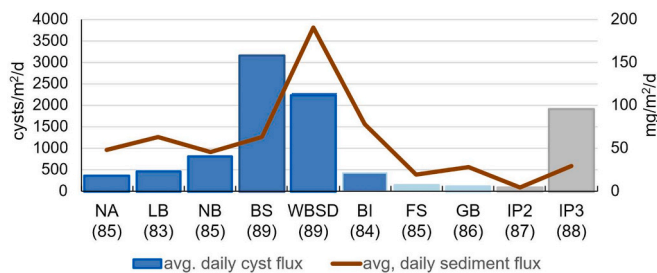


Fig. 4. Average daily cyst (blue) and sediment (red) flux around Nordic Sea Basin, with WBSD on the shelf edge included. Note that data from WBSD is minimal, based on only 3 cups due to trap malfunction, averaged for the whole deployment. Year of deployment indicated under station, all collected into the next calendar year. For exact length of deployment see Table 1. Flux data in Appendices A and B. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fluxes from these three alone were more than double the average for any other station, including the Barents Sea (Fig. 4).

3.1.2. Seasonal sediment and cyst fluxes

The seasonal fluxes are shown in Figs. 5 to 8 in a counterclockwise direction around the basin. Table 3 shows the correlation coefficients (r) between cyst and total sediment flux, and cyst and lithogenic flux.

The timing of fluxes generally follows biological production followed by a winter pause, probably due to both cysts and sediment being transported by marine snow from biological production (discussed in section 3.4). At most stations, the correlations between cysts and the lithogenic flux were consistently higher than for cysts and the total sediment flux, as expected since cysts are transported in the lithogenic size fraction. Correlations between cysts and the lithogenic showed the following:

1. The correlations between total cyst and lithogenic fluxes were correspondingly high at all stations where lithogenic flux was available, except for NB. Correlations were over 0.6 for all other stations but for FS (see pt. 2 below) and IP3.
2. A notable peak in sediment flux occurred during the March 30 to April 27, 1985, interval at the Fram Strait station (FS). This sample was shown by Honjo et al. (1987a) to consist almost entirely of sand-sized rock fragments, about 60% of which were larger than 1 mm. A transmissometer set horizontally 50 m above the seafloor recorded a sudden change in transmissivity during this interval that was interpreted by Honjo (1990) to be the flow of ice-rafted material to the seafloor. If this interval representing ice melt is omitted from the calculation, the correlation coefficient (r) for sediment and cyst flux, and lithogenic and cyst flux, increases to 0.93 and 0.90, respectively.
3. The somewhat lower correlation at NB probably reflects its greater distance from coastal influence (see Table 3 and map in Fig. 2), supporting the suggestion of some cyst transport from the basin margins.
4. Lithogenic data was not available for the Iceland Plateau, but IP2 and IP3 showed very different total sediment and cyst fluxes. IP3 (1988–1989) showed relatively high sediment fluxes compared with the record of Olafsson et al. (2000) spanning 1987–1998 (only 1998 was higher). This variation is attributed here to the high interannual variability in the currents influencing this station (Fig. 1) (Stefánsson and Olafsson, 1991a, 1991b). According to Olafsson et al. (2000), the interannual hydrographic variability is much greater north of Iceland in the Iceland Sea than south of Iceland, and it results mainly from the input of different proportions of Atlantic Water via the Irminger Current and Polar or Arctic water. This is reflected also in its distinctive cyst assemblage (discussed in section 3.2.1).

3.2. Cyst assemblages

Cyst counts are included in Appendix A and cyst fluxes are shown in Appendices A and B. Assemblage groupings are shown in the Cluster diagram in Fig. 9, and main cyst types are illustrated in Plate 1 (accessory cyst types also in Plate 1 of Dale and Dale, 1992). Cyst assemblages varied systematically around the basin, with progressively higher proportions of colder water indicators *Impagidinium pallidum*, *Islandinium minutum* and *Islandinium cezare* in a counterclockwise direction (indicated in blue in Figs. 10 and 11).

3.2.1. Assemblage composition

The cluster analysis shown in Fig. 9 distinguished 4 main station clusters of assemblages. Cluster 1 consists of the four most southeasterly stations: Aegir Ridge (NA), Lofoten Basin (LB), the Norwegian Basin (NB) and the western Barents Sea (WBS), all located within the Norwegian Atlantic Current regime (Fig. 1). Two subclusters are defined, one with the three southeasterly stations (NA, LB and NB) distinguished by dominance of undifferentiated, round brown proto-peridinioid cysts, and the other, station WBS located on the shelf edge, distinguished by dominance of *Operculodinium centrocarpum* (discussed in section 4.5) followed by round, brown cysts. Calcareous cysts only featured prominently in Cluster 1 (Fig. 9), reflecting long distance transport by currents (discussed in section 3.4).

Cluster 2 consists of the Barents Sea (BS) and Bear Island (BI) stations. BS was in the Bear Island Trough in the western Barents Sea and BI was located off the shelf edge near the western opening to the Barents Sea (Fig. 1). Cluster 2 is distinguished by the high abundance of *I. minutum* (38% and 10% at BS and BI, respectively), and *P. dalei* (13% and 26%, respectively), and the markedly lower but still considerable abundance of undifferentiated, round brown cysts (16% and 19%, respectively) and *O. centrocarpum* (13% and 15%, respectively). BI and BS differ, however, in their respective abundances of *I. pallidum* and *Nematosphaeropsis labyrinthus*, which were common at Bear Island (10% and 12%, respectively) but only negligible in the shallower Barents Sea (< 1% each); and *Spiniferites elongatus* and *Protoperidinium americanum*, which were abundant in the Barents Sea (7% and 6%, respectively) but only negligible at Bear Island (1% each). Clusters 1 and 2 share several other accessory cyst types in common at low levels of abundance, including *Selenopemphix quanta*, *Bitectatodinium tepikiense* and *Trivantedinium applanatum*.

Increased proportions of the oceanic *I. pallidum* and outer neritic *N. labyrinthus* reflect more oceanic influence at the deeper BI than at the shallower BS.

The clustering of BS and BI probably reflects transported cysts from the Barents Sea contributing to the assemblage at BI (discussed in section 3.4).

Cluster 3 consists of the Greenland Basin (GB) and Fram Strait (FS) stations, influenced by East Greenland Current (Fig. 1). These two stations exhibit a high degree of similarity and are distinguished from the others by their dominance of *I. pallidum* (31% and 51%, respectively), and high abundance of round brown cysts (30% and 37%, respectively, at FS and GB). *I. minutum* is also abundant at these stations (21% and 5%, respectively). No other cyst type makes up more than 5% at either station. In addition, a characteristic small cyst type now ascribed to the species *Polarella glacialis* (Montresor et al., 1999) was seen in high concentrations only at stations FS and GB. Since this cyst is smaller than the mesh size of the sieve used for sample preparation it is assumed that many were lost during sample preparation, and it is therefore not included in the percentage calculations. The large amounts nevertheless recorded here are significant.

P. glacialis, a widely used ice cover indicator species (e.g. de Vernal et al., 2004; Lund-Hansen et al., 2024; Mäkelä et al., 2025) reflects ice cover here. The possible relevance of high proportions of *I. minutum* is discussed in section 3.3.1.

Dominance of *I. pallidum* reflects cold oceanic conditions.

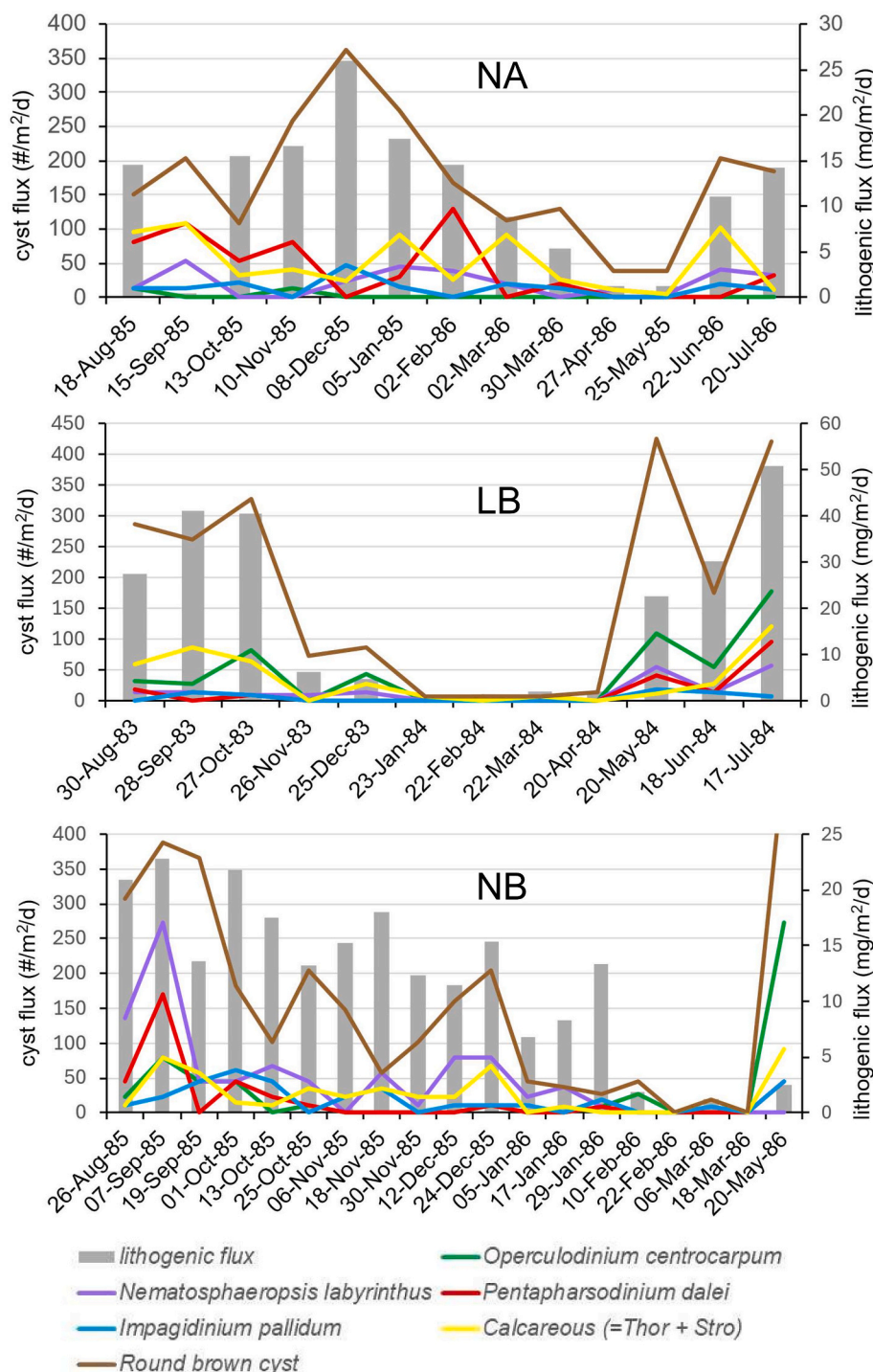


Fig. 5. Species distributions over time for species amounting to over 5% of the assemblage at stations in Group 1 of the station cluster diagram in Fig. 9, including the stations in the Norwegian Sea, (Y-axis 1), shown together with total lithogenic flux (grey bars, Y-axis 2). Mid-dates of sampling intervals (23, 30 and 12 days for NA, LB and NB, respectively.) along X-axis. NB malfunctioned after March 1986. Numerical data in Appendices A and B.

Cluster 4 consists of only one station (IP), which is located on the Iceland Plateau, under the influence of the southerly-flowing East Greenland Current and the northeasterly-flowing Irminger Current (Fig. 1). There were two deployments at this station in different years and assemblage differences between these are attributed to interannual variations in hydrography (discussed in section 1.3). An average of both cyst assemblages is used in the cluster analysis (called IPA). This station is characterized by an exceptionally strong dominance of *P. dalei* (88%), discussed in section 3.3.3. *O. centrocarpum* comprised 8% of the cyst assemblage, but no other cyst type exceeded 1%.

The distribution of the main cyst types and indicator species varied systematically around the basin, with progressively higher proportions of colder water indicators in a counterclockwise direction (Fig. 10).

3.3. Species richness

Table 4 shows the total number of species documented, or “species richness” (Peet, 1974), and how this varies progressively around the basin.

Species richness was distinctly higher for the stations influenced

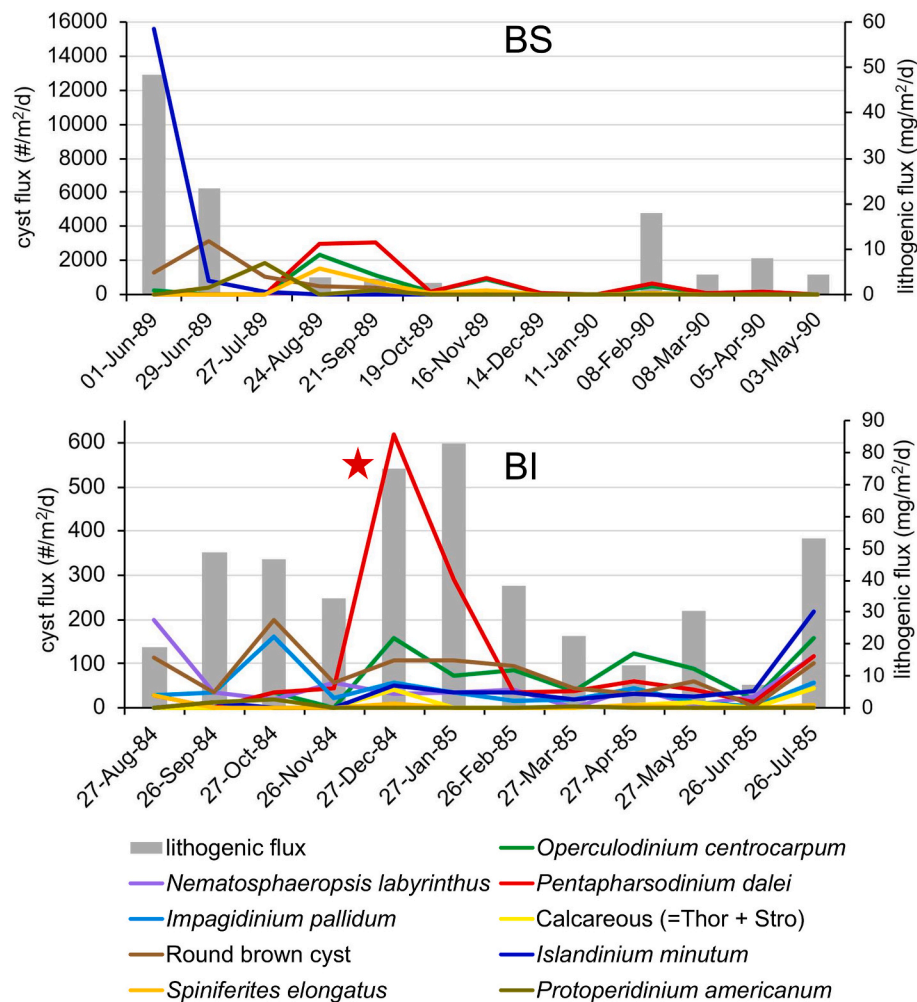


Fig. 6. Species distributions over time for cyst types amounting to over 5% of the assemblage at stations in Group 2 of the station cluster diagram shown in Fig. 9, near or in the Barents Sea, shown together with lithogenic flux (grey bars). Red star indicates “winter outburst sedimentation”, discussed in section 3.4.2. Numerical data in Appendices A and B. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

primarily by the Norwegian Atlantic Current (NA: 17; NB: 17; LB: 17; WBS: 18; and BI: 17) than for those influenced primarily by the East Greenland Current (FS: 11 and GB: 6). The species richness documented at the Barents Sea station, receiving influence from the Norwegian Atlantic Current, also was comparatively high (17), whereas only relatively few cyst types were documented at the Iceland Plateau (7 at IP2 and 10 at IP3) (Table 4).

The concept species richness is not straight-forward, however, in a system where cyst input can be traced to several different sources, including possible transport by oceanic currents, coastal input, and primary production (discussed section 3.3). Nonetheless, the systematic changes in assemblage diversity are presumed to broadly reflect the general biological principle that species richness decreases from warmer to colder climatic zones. The assemblages with lower species richness characterizing the colder, East Greenland Current-influenced stations are comprised mainly of colder water species *I. pallidum* and *I. minutum*, whereas the assemblages with higher species richness in the Norwegian Atlantic Current influence (Table 4) are comprised mainly of cyst types previously documented from temperate to sub-polar coastal/neritic regions around the basin.

The relatively low diversity at the Iceland Plateau is presumed to reflect relatively colder water inputs by the East Greenland Current from the north and the warmer Irminger Current from the south, and its relative hydrographic isolation due to the surrounding bathymetry.

Species richness is also interpreted to reflect mechanisms of cyst

transport from adjacent shallower regions, summarized in section 3.4.

3.4. Cyst supply to the deep sea Nordic Sea Basin

Two distinct sources of cyst supply for deep sea sediments were identified: 1) oceanic species *I. pallidum* and oceanic/neritic *N. labyrinthus* (and possibly *I. minutum*?) living and producing cysts in the open ocean; and 2) well known coastal/neritic species producing cysts in adjoining coastal/neritic sources for transport to the deep sea.

Understanding where the cysts are produced is an important requirement for understanding how to interpret environmental signals from cysts in ocean floor sediments. It is particularly important to identify cysts produced in the open ocean overlying the deep-sea bottom sediments given that these would carry the primary environmental signals of paleoceanographic climate. Here we use cysts with full cell contents as indicators of recently produced cysts. The basic relationship of cell contents to cyst production is reasonably well recognized for coastal species through the work of many incubation experiments carried out in the past sixty years linking cysts to motile stages. This required selecting likely viable cysts from assemblages based on visual assessment of cell contents (Wall and Dale, 1968; Dale, 1983). The ages of cysts with full contents in the upper layer of bottom sediments in coastal samples is generally assumed to be limited to a few years, often including cysts waiting to complete an annual cycle within one year after production. These cysts may thus be regarded as “recently

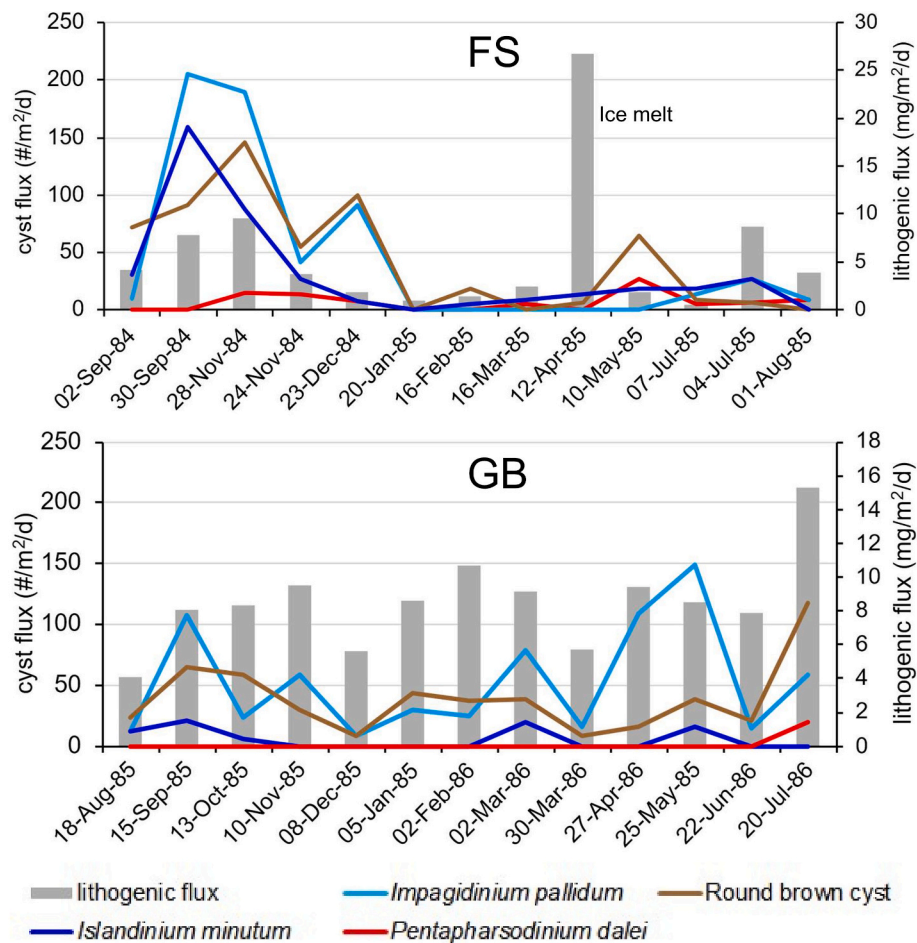


Fig. 7. Species distributions over time for cyst types amounting to over 5% of the assemblage at stations in Group 3 of the station cluster diagram shown in Fig. 9, in the Greenland Sea, shown together with lithogenic flux (grey bars). Numerical data in Appendices A and B.

produced” compared to potentially older empty cysts, though some species are believed to retain viable cell contents in bottom sediments from shallower coastal waters for at least one hundred years (Lundholm et al., 2011). There is no established precedent for using cell contents as indicators of recent production in cysts recovered from the deep sea. Nevertheless, some of the cysts produced in surface waters of the deep ocean would be expected to reach the traps with intact cell contents, given the relatively short travel time from surface to bottom (on the order of weeks to months) for some faecal pellets and aggregates of marine snow carrying cysts. Any such evidence of “recent” cyst production is particularly valuable within the large-scale framework for the present study, vast expanses of deep water overlying bottom sediments that may vary between tens to thousands of years old. The results here justified this approach; unquestionably recently produced cysts in the seasonal sequence observed at the Barents Sea station (section 3.3.2) allowed comparison with cysts recovered from the deep sea. The distribution of cysts with contents showed supporting evidence for cyst production in deep sea surface waters and suggestions of cyst transport to the deep sea from coastal/neritic sites.

3.4.1. Cyst production

The distribution of cysts with cell contents around the basin is shown in Fig. 11 and data in Appendix A. By far the highest proportions of cysts containing cell contents (63%) were seen at the shallowest trap, in the Barents Sea (BS, 369 m in 472 m water depth), and the next highest were at the IP station (32% and 55% at IP2 and IP3, respectively).

3.4.2. Seasonal cyst production at the Barents Sea (BS)

The proportions of cysts with or without cell contents is shown in Fig. 12 (species data in Table 5). Six of the cyst types contained significant proportions of cell contents and the highest occurrence of total cysts for those species during the year coincided with the highest proportion having cell contents. However, it should be noted that cell contents were not always possible to recognize in round brown cysts due mainly to the more darkly pigmented cell wall; a higher proportion of the cysts at the Barents Sea station therefore possibly contained cell contents than was recorded.

Three phases are recognized between May 1989 and May 1990:

Phase I (May–July): *I. minutum*, round brown cysts, and *P. americanum* show peaks of cyst contents in succession and only empty cysts after. This reflects heterotroph predation on other spring-bloom species (e.g. diatoms) followed by seasonal encystment in bottom sediments. The accompanying high sediment flux presumably includes remains of peak organic production from the spring bloom.

Phase II (August–December): *S. elongatus*, *P. dalei*, and *O. centrocarpum* show very high proportions of cyst contents, with none seen in phase I, and very few in phase III. This reflects the characteristic autotrophic / mixotrophic production during summer into autumn in the plankton with accompanying cyst production.

Phase III (December–April): Almost only empty cysts seen, reflecting the absence of cyst-producing motile dinoflagellates during winter after successful encystment.

The species found in the BS trap are common in local recent assemblages within the Barents Sea (Matthiessen et al., 2005; Grøsfjeld et al., 2009; Solignac et al., 2009; Howe et al., 2010; Telesiński et al.,

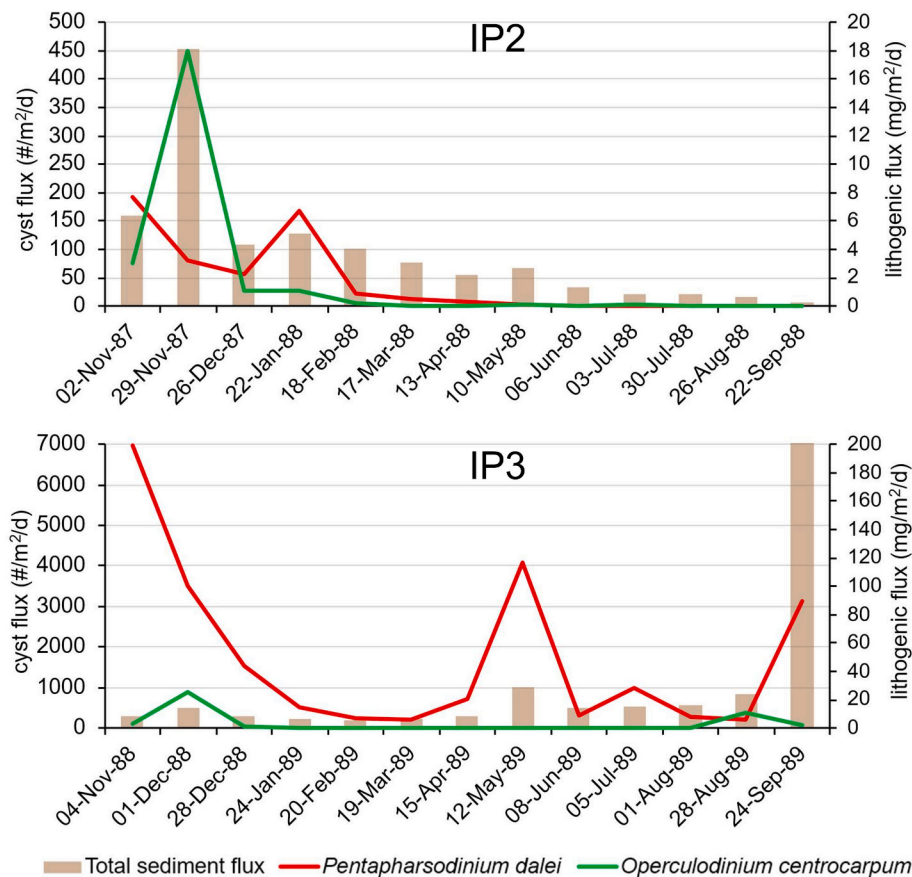


Fig. 8. Species distributions over time for cyst types amounting to over 5% of the assemblage at stations in Group 4 of the station cluster diagram shown in Fig. 9, on the Iceland Plateau, shown together with total sediment flux (brown bars). Lithogenic flux was not available for this station. IP2 collected during 1987–88 and IP3 from 1989 to 90. Numerical data in Appendices A and B. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Pearson's correlation coefficients (r) between total cyst flux and sediment flux, and between total cyst flux and the lithogenic component of the total flux. No lithogenic fluxes were available for the IP station. Asterisk (*) indicates stations with correlations of 0.6 or higher. ** indicates that correlations for Fram Strait increase to >0.9 when sampling interval recording ice-melt is removed (discussed in section 3.1.2).

Station and code	Correlation cyst vs. tot. sediment flux (r)	Correlation cyst vs. lithogenic flux (r)
Aegir Ridge (NA) *	0.63	0.76
Lofoten Basin (LB)*	0.80	0.91
Norwegian Basin (NB)	0.47	0.31
Bear Island (BI)*	0.57	0.70
Barents Sea (BS)*	0.85	0.84
Fram Strait (FS)**	0.52	0.09
Greenland Basin (GB)*	0.62	0.63
Iceland Plateau 2 (IP2)*	0.95	–
Iceland Plateau 3 (IP3)	0.22	–

2023). The precision of successional occurrences of species shows a clear seasonal arctic SST-related cyst signal similar to that seen elsewhere in shallower waters on both sides of the basin: in a Greenland fjord and Hudson Bay on the western side (Heikkilä et al., 2016; Mäkelä et al., 2025), on Svalbard (Howe et al., 2010) and in the Eastern Barents Sea (Agafonova et al., 2023) on the eastern side of the basin.

Occasional cysts with contents in winter are presumed to be resuspended.

The Barents Sea trap was deployed in waters affected by inflow from the Norwegian Atlantic Current. Therefore, cyst transport to the deep

sea from there may be negligible. However, this seasonal record suggests the Barents Sea as a source of cysts most likely transported to the deep sea from further north in the Bear Island Trough by the “winter outburst sedimentation” recorded in the BI trap (section 3.4.2).

3.4.3. Cyst production at Iceland Plateau (IP2 and IP3)

Both cyst fluxes and proportions of cysts with cell contents varied considerably between the years sampled at IP, with 95% of the total combined cyst flux coming down during IP3 (1998–1999) and 5% during IP2 (1997–1998). The main species fluxes are therefore plotted as time series data for IP3 only (Fig. 13, Table 6).

At IP2 (1987–1988), 26% of the *P. dalei* cysts contained cell contents whereas only 4% of the *O. centrocarpum* cysts did. The majority of *P. dalei* with contents came down between October 1987 and February 1988, when the fluxes of this species were highest. The majority of *O. centrocarpum* with cell contents came down during one sampling interval, from November to December 1987, also when the total flux for this species was highest (Table 6).

At IP3 (1988–1989), proportions with cell contents were significantly higher than for the IP2 deployment (1987–1988). 54% of *P. dalei* cysts and 1% of *O. centrocarpum* had cell contents.

The succession of cysts containing cell contents could be divided roughly into two phases (Fig. 13). From Oct. 22, 1988 - May 28, 1989, between 57% and 90% of the cysts contained cell contents (almost exclusively *P. dalei*), and from May 28 to Oct. 8, 1989, 0 to 31% contained cell contents. *P. dalei* shows particularly large cyst fluxes in autumn both here and in the Barents Sea. This is consistent with the authors' own database showing abundance of *P. dalei* in 6 samples of

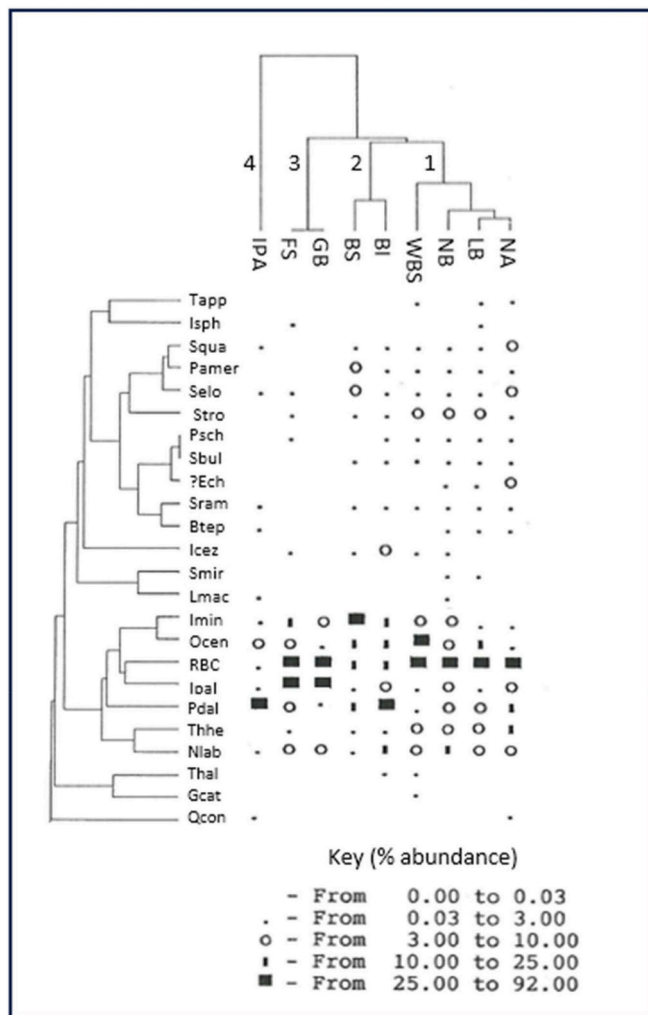


Fig. 9. Cluster diagrams for stations and species plotted with a schematic illustration of main cyst assemblage groupings at 9 stations around the Nordic Sea Basin. Clusters are based on the percentage abundances calculated from the total cyst fluxes at each station. IP2 and IP3 deployments are combined here as “IPA”.

recent sediments from the W. Iceland coast (average 35%), and in assemblages from recent sediments from the region (Marret et al., 2004).

The high proportions of *P. dalei* with contents at IP3 suggests year-round transport from local autumn blooms by winnowing from the shelf, particularly during winter storms, discussed in section 3.4.

3.4.4. Cyst production in the open ocean

The proportion of cysts with cell contents in the deeper traps (> 1900 m) was much lower than at BS or IP, discussed in sections 3.3.2 and 3.3.3. However, high proportions of cell contents for *I. pallidum* in the deeper traps, especially FS (20%) and GB (15%), confirm this species as a cold oceanic indicator living and producing cysts in these cold oceanic waters. Significant amounts also of *I. minutum* with contents at these stations suggests the interesting possibility that this species, well-documented from coastal/neritic samples elsewhere, may also live and produce cysts in the open ocean; and if so, could this also apply to other species? Oceanic waters differ fundamentally from coastal waters (the neritic-oceanic boundary discussed in Wall et al., 1977) and most dinoflagellate species live in one or the other realm (Taylor, 1987). Braarud (1935) reported one exception, *Prorocentrum balticum*, which was found both in the shallower Baltic Sea as well as the open North Atlantic Ocean. Heterotrophic species such as *I. minutum* would benefit

greatly from occupying the seasonal offshore ice break-up to feed on diatoms and other groups in the spring bloom. However, it seems unlikely that this could be achieved by motiles transported far out to stations FS and GB from nearshore waters in the limited time available to both reach the open ocean and encyst. Braarud (1935) reported one such species, *Protopteridinium conicoides*, living and forming cysts in the very cold water between patches of sea ice off Eastern Greenland. Sakshaug (2004) also raised the possibility for heterotrophs to utilize the large pool of dissolved organic carbon (DOC) available during winter, and for the possibility of some diatoms to reduce their physiological requirements in “resting mode” without changing cell morphology. The possibility that heterotrophic dinoflagellates follow a similar strategy to diatoms seasonally encysting in the ice or otherwise “resting” should be further explored.

I. pallidum and *N. labyrinthus*, accounting for 27% of the total cyst flux in the deep sea traps, thus produce the only unequivocal primary oceanic signal in our data. The heterotrophs noted above, species of *Islandinium* and round brown cysts, may well contribute to this, but since some of the same species are also transported in secondarily from shallower localities their presence in deep sea sediments does not comprise an unequivocal primary signal for paleoceanography.

3.5. Cyst transport in the Nordic Seas

Cyst transport away from their source of production prior to incorporation into bottom sediments is a major factor potentially affecting the accuracy of cyst proxies in paleoceanography, as explained in section 1. Results here generally confirm our earlier conclusions that assemblages in bottom sediments result from a mixture of cysts from different sources (Dale and Dale, 1992). We show three different forms of cyst transport: a) from nearby production in the overlying waters of the open ocean; b) from shorter- or longer-distance transport from coastal/neritic production; and c) from resuspension of older cysts from nearby shelves. These are referred to here as primary, secondary and tertiary transport, respectively, since they carry primary, secondary, and tertiary environmental signals (discussed in section 6).

3.5.1. Primary transport of oceanic cysts

In the deep sea, cell contents in cysts of the recognized oceanic-neritic indicators, cold water *Impagidinium pallidum* and *Nematosphaeropsis labyrinthus*, strongly suggests primary production followed by “rapid transport” several thousand metres from overlying waters. This primary transport from production in overlying waters is most likely mainly via sinking aggregates of marine snow and faecal pellets which enhance their descent, as described by Alldredge and Silver (1988). Marine snow is a diffuse agglomerate of decaying phytodetritus and sticky mucus that gathers other particles as it sinks. Faecal pellets are covered by a robust smooth outer wall that facilitates rapid sinking without notable agglomerates of attached particles. Without these sinking mechanisms, individual cysts would take years to complete the journey simply following Stokes Law, and in the hydrodynamic Nordic Seas would likely travel hundreds to thousands of kilometres laterally, according to general estimates by Nooteboom et al. (2019). The traps used here contained seasonally large amounts of “snow” and pellets co-occurring with sediment and cyst fluxes, supporting cyst entrapment in aggregates of marine snow as a major transport mechanism.

However, particularly marine snow is presumed to collect particles from different depths during its descent and thus also contributes to the eventual final stage of settling to bottom sediments of cysts transported also by both secondary and tertiary transport.

3.5.2. Secondary transport of recent cysts from coastal/neritic sources

The overall pattern of species distribution (Fig. 10) suggests long distance secondary cyst transport driven by strong currents. On the eastern side of the basin, cyst distribution is interpreted as following the waters influenced by the relatively warm North Atlantic Current as it

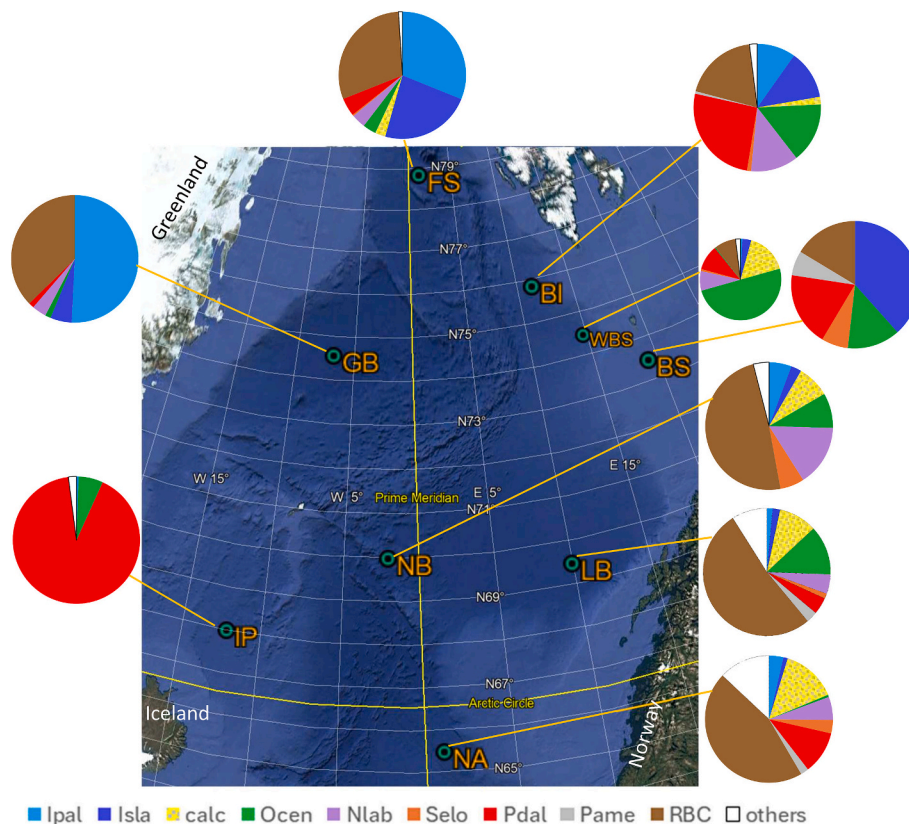


Fig. 10. Cyst assemblages for species over 5% of the total assemblage at any station, shown schematically around Nordic Sea Basin in relation to ocean bathymetry. Percentages based on total fluxes except for WBS, shown smaller to indicate percentages based on total counts due to trap malfunction (explained in [section 2.1](#)). *Islandinium minutum* and *I. cezare* were combined as “Isla” (darker blue), since both are colder water indicators of the same genus with *I. cezare* present only in small numbers. Blue colour indicates colder water indicator. Data in Appendix A. Map created using Google Earth Pro imagery (© Google, Maxar Technologies). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

gradually cools northwards. The proportion of calcareous cysts, characteristic of warm water in open oceans to the south, gradually diminishes in a counterclockwise direction from NA to FS, succeeded by cold temperate cysts and increasing proportions of cold temperate/sub-polar species of *Islandinium*. The changing proportions of calcareous cysts is interpreted as transport from their centres of production, with the signal weakening proportionally to increasing distance from their origin in the warmer water open oceans to the south. The occasional inclusion of cysts of the warmer-water coastal/neritic species *Gymnodinium catenatum* (WBS) and *Spiniferites mirabilis* (LB and NB) and oceanic species *Impagidinium sphaericum* (LB and FS) here north of their centres of production also supports this interpretation.

In addition, some colder temperate forms were wafted from the Barents Sea by secondary transport into the deeper Norwegian sea via winter outburst sedimentation caused by the sinking of denser waters as they cooled in winter (Fig. 6) (e.g. [Honjo et al., 1988](#); [Blindheim, 1989](#); [Dale and Dale, 1992](#); [Skagseth et al., 2006](#)).

The seasonal sequence of coastal/neritic cysts with cell contents at the Barents Sea station together with the same species with cell contents at the deeper Bear Island station further out in the system strongly suggests the shallower Barents Sea as a major source of cyst transport. The “winter outburst” of [Honjo et al. \(1988\)](#) identified this as a particular transport mechanism for shelf sediments at these high latitudes. Living coastal/neritic cysts transported into the deep sea presumably play no further role in the life cycle. Even if they could excyst at depth the motile stage would have to survive the oceanic waters, a different water mass characterized by different phytoplankton species ([Wall et al., 1977](#)). We see no evidence in the trap samples of cyst morphology adaptation to hydrodynamic behavior that would suggest modification

of assemblages due to transport.

Recent research has most likely identified a further mechanism transporting recent coastal/neritic cysts from the Lofoten shelf. [Damerell et al. \(2025\)](#) refer to anticyclonic (counterclockwise) eddies, up to 20 km across, shed from various parts of the eastern flank of the Norwegian Atlantic Current and merging into an intense and apparently permanent anticyclone known as the Lofoten Vortex. This vortex, central in the Lofoten Basin, drives the upper 1000–1500 m around in about a 50 km diameter at up to 0.5 m/s, a high speed for such large movement of oceanic waters. [Damerell et al. \(2025\)](#) cite a velocity of 0.8 m/s for the contributing eddies, suggesting these could displace water from the Lofoten shelf as far as 69 km/day into the Norwegian Sea. The presence of cysts with cell contents at the Lofoten Basin station (LB) suggests a local source. Although these authors do not address particle transport, the enormous energy revealed clearly has the potential to distribute cysts widely within the oceanic system.

[Johnston et al. \(2025\)](#) suggest that the eddy-driven vorticity flux is of greater importance in the Lofoten Basin, accounting for approximately half of the circulation here, whereas wind is much more important elsewhere in the circulation of the Norwegian Sea.

3.5.3. Tertiary transport of older resuspended recent and Quaternary cysts

An example of resuspension of older cysts was recorded at the Lofoten Basin station during the June–July 1984, sampling intervals. A cyst flux of 1003 cysts/m²/day, the highest total for the deployment, was deposited between July 2nd and August 1st, 1984, and this was accompanied by a flux of recycled Miocene cysts of 2686/m²/day (Figs. 3 and 5, Appendix A), or 99% of the total recycled pre-Quaternary cyst flux seen at this station (examples [Plate 1](#), n and m). The remaining

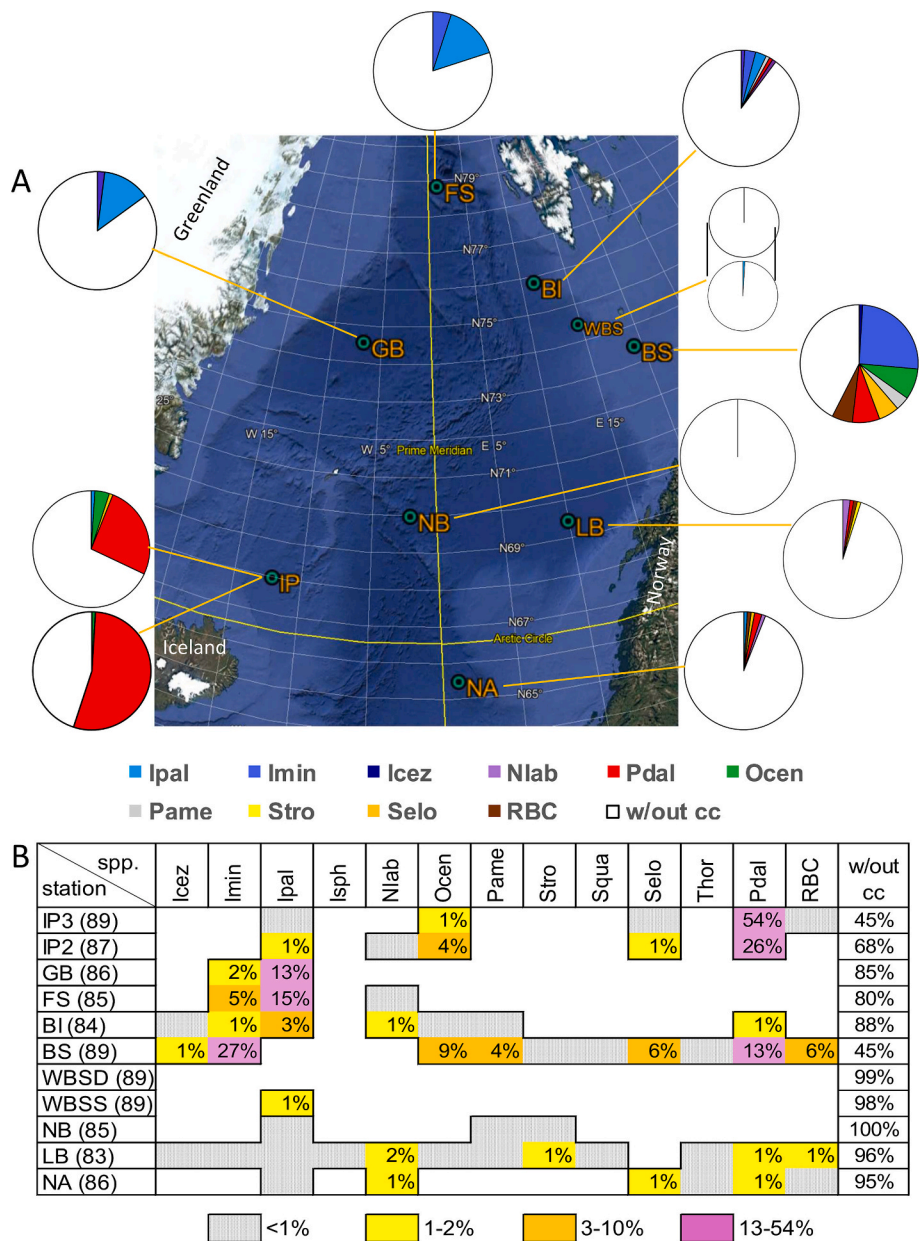


Fig. 11. A) Pies indicating proportions of species at each station with cell contents, shown schematically around Nordic Sea Basin in relation to ocean bathymetry. Colder water indicators in blue. See Table 2 for species codes. Percentages with cell contents based on cyst fluxes except for WBS, where percentages were based on total counts due to trap malfunction (explained in section 2.1). Shallow and deep traps at WBS station shown smaller also reflecting trap malfunction. Data in Appendix A. Map created using Google Earth Pro imagery (© Google, Maxar Technologies). B) Main cyst types containing cell contents. Lower rows include stations in the Norwegian Atlantic Current flowing northward from the North Atlantic, and upper rows include stations influenced by the Greenland Current flowing south from the polar seas. Numbers after station codes indicate year of deployment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1% occurred during the previous sampling interval, between June 3rd and July 2nd, 1984. The resuspended assemblage, which included the only pre-Quaternary cysts in the entire investigation, included a suite of at least 14 cyst species dated as Lower Miocene age (S. Manum per. Comm. 1993). Since Lower Miocene sediments are known to occur on the Lofoten shelf (Mokhtari et al., 1987; Manum et al., 1989), this points to resuspension of nearby shelf edge/slope sediments as a probable result of turbidity flow. This event probably began during the latter part of the June 3–July 2, 1984, interval, when the first reworked cysts were documented, with most of the resuspended matter reaching the sediment trap depth during the July 2–August 1, 1984, interval. This may possibly have been triggered by one or more of the seven earth tremors measuring between 5.0 and 5.8 on the Richters Scale that occurred in the

region between on May 3rd and July 30th, 1984 (U.S. Geological Survey, 2023), although sediment slumping is probably a regularly occurring sedimentary process from the Lofoten shelf. The shelf adjacent to the LB trap is narrow and steep (Ghaffari et al., 2018), a bathymetric setting that would be expected to be susceptible to sedimentary slumping.

Since the highest flux of recent cysts of the entire deployment occurred during the same sampling interval as the reworked cyst pulse and because many of the cyst types documented at the station are known coastal forms (Appendix A), it is considered likely that the turbidity flow also carried with it a higher than normal number of “recent” cysts (i.e. cysts identical to recent cysts but which theoretically could be of Quaternary origin).

Table 4
Species/ taxonomic group richness listed in counter-clockwise direction around Nordic Sea Basin.

Station	species richness
Aegir Ridge (NA)	17
Lofoten Basin (LB)	17
Norwegian Basin (NB)	17
Western Barents Sea Deep (WBD)	18
Bear Island (BI)	17
Barents Sea (BS)	17
Fram Strait (FS)	11
Greenland Basin (GB)	6
Iceland Plateau 2 (IP2)	7
Iceland Plateau 3 (IP3)	10
Average Norwegian Sea stations:	17
Average Greenland Sea stations:	8

Thus, the Lofoten shelf is considered a likely source of cyst (and sediment) input at the Lofoten Basin station.

This is analogous to the winnowing and along-slope transport seen for other microfossils discussed in Wall et al. (1977), and it is probably a widespread process contributing to cyst transport elsewhere in the basin and other oceans.

3.5.4. Cyst transport after settling to bottom sediments

Work from other regions (Matthiessen et al., 2005; García-Moreiras et al., 2024) suggests that cysts may be transported by nepheloid layers after first settling to bottom sediments. The nepheloid layer of particular interest here is the layer of up to several hundred meters of bottom water with sufficient turbulence to resuspend and transport particles from bottom sediments in the deep sea. Indeed, the sediment traps used in our study were purposely deployed above this layer to avoid such resuspension. Though not directly sampled in our work, the nepheloid layer has potential for cyst transport laterally within the Nordic Seas.

4. Results and discussion of comparison between cyst assemblages in traps and bottom sediments

We compared our trap data with cyst assemblages from the recent bottom sediment database of de Vernal et al. (2020) used to develop proxies, to consider implications for paleoceanography. Good correspondence between the two would add support for cysts as proxies inferred to reflect overlying waters; poor correspondence would add complexity to their application. To compare data from the nine traps with bottom sediment samples in the database it was necessary to first select only the 176 samples from the Nordic Sea region.

4.1. Selection of comparable samples

The 176 sediment samples encompassing the trap region spanned from 62.65°N to 79.76°N and 27.51°W to 22.00° E. From these, the five nearest to the traps were considered.

Several factors were evaluated when selecting the nearest of these to represent the bottom sediments underlying a given trap locality. These included nearest global coordinates, best match to depth (e.g. to assess broader consideration of bathymetry) and similar placement with respect to known current influence (Fig. 1). The five nearest sediment localities to a given trap revealed large variations in key species within a radius of less than 2 degrees latitude and 4 degrees longitude (Appendix C). For example, the nearest to the trap at FS was 31 km away and had a depth difference of 10 m (AI375-FS). The farthest away from among the nearest five was 124 km and the greatest depth difference 483 m. The abundances of *Impagidinium pallidum*, a key indicator species for the FS site, ranged from 0.6% to 16.9% (Fig. 14A).

At IP, the distance to the nearest sediment sample was 69 km, with a

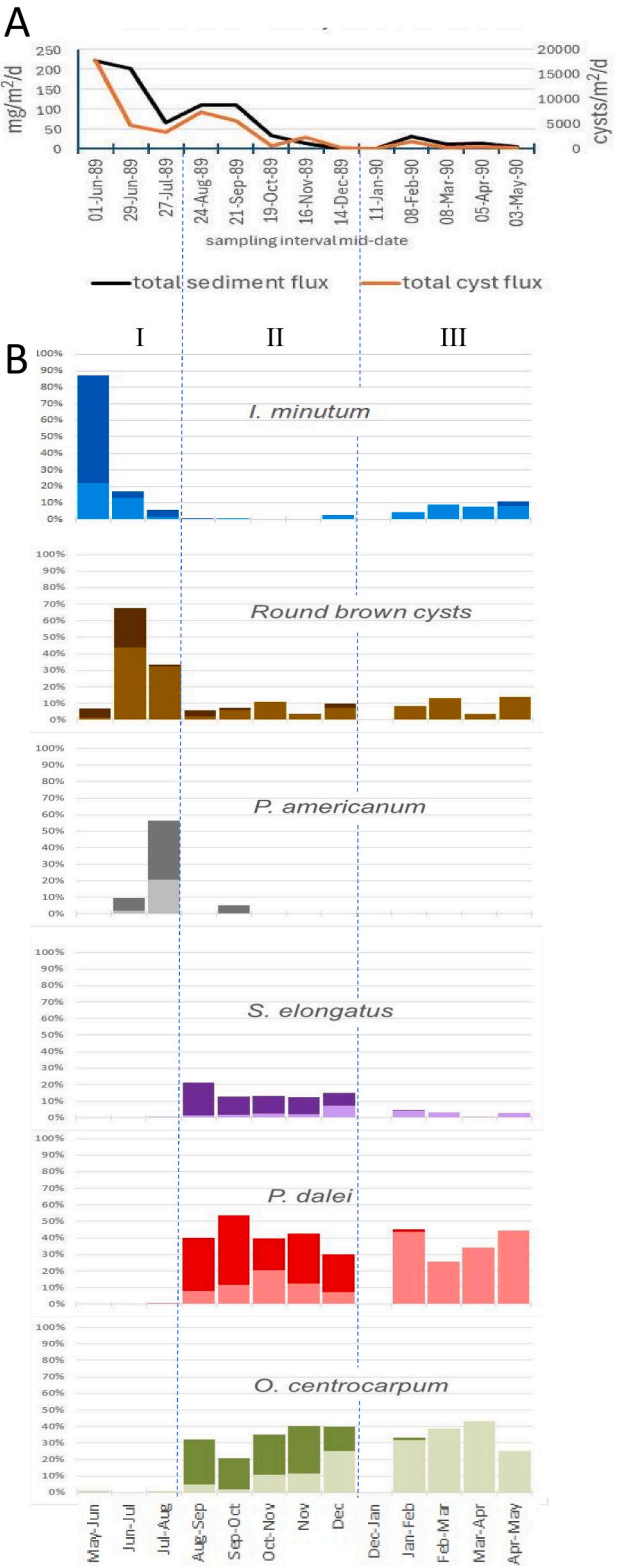


Fig. 12. Sediment and cyst fluxes at Barents Sea station. (A) Totals. (B) showing time-series assemblage changes in percent for main species at Barents Sea station. Darker shading indicates cysts containing cell contents, lighter indicates empty cysts. Mid-dates for sampling intervals under total sediment and cyst flux graph, months only under species graphs. Seasonal sedimentation of cysts is divided into three categories denoted I, II and III, explained in text. Sediment flux data is shown in Appendix B and cyst flux and cell contents data in Table 5.

Table 5
Time-series assemblage data for Barents Sea station, showing total cysts seen and percentage data for species amounting to over 5% of the assemblage. Shading indicates component with cell contents. Categories amounting to less than 1% of the total observed at the station were omitted here but are shown in Appendix A. Data for main cyst types having cell contents shown graphically in Fig. 12.

Sample ID	Opening date	Closing date	Middle date	% <i>Islandinium cezare</i> (w/cc)	% <i>Islandinium cezare</i>	% <i>Islandinium minutum</i> (w/cc)	% <i>Islandinium minutum</i>	% <i>Nematosphaeropsis labyrinthus</i>	% <i>Operculodinium centrocarpum</i> (w/cc)	% <i>Operculodinium centrocarpum</i>	% cyst of <i>Pentapharsodinium dalei</i> (w/cc)	% cyst of <i>Pentapharsodinium dalei</i>	% cyst of <i>Protoperidinium americanum</i> (w/cc)	% cyst of <i>Protoperidinium americanum</i>	% <i>Selenopemphix quanta</i> (w/cc)	% <i>Selenopemphix quanta</i>	% <i>Scrippsiella trochoidea</i>	% Round brown cyst (w/cc)	% Round brown cyst	% <i>Spiniferites elongatus</i> (w/cc)	% <i>Spiniferites elongatus</i>	% other <i>Spiniferites</i> spp.	total cysts counted
BS1-1	18-May-89	15-Jun-89	01-Jun-89	2%	0%	65%	22%	0%	0%	1%	0%	0%	0%	0%	0%	1%	0%	6%	1%	0%	0%	0%	212
BS1-2	15-Jun-89	13-Jul-89	29-Jun-89	2%	1%	4%	13%	0%	0%	0%	0%	0%	8%	2%	1%	2%	0%	24%	44%	0%	0%	0%	167
BS1-3	13-Jul-89	10-Aug-89	27-Jul-89	1%	1%	4%	2%	0%	0%	1%	0%	1%	36%	21%	0%	0%	0%	1%	32%	0%	1%	0%	117
BS1-4	10-Aug-89	07-Sep-89	24-Aug-89	0%	0%	0%	0%	0%	27%	5%	32%	8%	0%	0%	0%	0%	0%	4%	2%	20%	1%	0%	663
BS1-5	07-Sep-89	05-Oct-89	21-Sep-89	0%	0%	0%	1%	0%	19%	2%	42%	12%	5%	0%	0%	0%	0%	1%	6%	11%	2%	0%	504
BS1-6	05-Oct-89	02-Nov-89	19-Oct-89	0%	0%	0%	0%	0%	24%	11%	19%	20%	0%	0%	0%	0%	0%	0%	11%	11%	2%	0%	83
BS1-7	02-Nov-89	30-Nov-89	16-Nov-89	0%	0%	0%	0%	0%	29%	11%	30%	12%	0%	0%	0%	0%	0%	0%	3%	10%	2%	0%	412
BS1-8	30-Nov-89	28-Dec-89	14-Dec-89	0%	0%	0%	3%	3%	15%	25%	23%	8%	0%	0%	0%	0%	0%	3%	8%	8%	8%	0%	40
BS1-9	28-Dec-89	25-Jan-90	11-Jan-90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BS1-10	25-Jan-90	22-Feb-90	08-Feb-90	0%	1%	0%	4%	1%	2%	32%	2%	44%	0%	0%	0%	0%	0%	0%	8%	0%	4%	0%	252
BS1-11	22-Feb-90	22-Mar-90	08-Mar-90	0%	0%	0%	9%	4%	0%	39%	0%	26%	0%	0%	0%	1%	2%	0%	13%	0%	3%	1%	90
BS1-12	22-Mar-90	19-Apr-90	05-Apr-90	0%	2%	0%	8%	5%	0%	43%	0%	34%	0%	0%	0%	0%	0%	0%	3%	0%	1%	0%	144
BS1-13	19-Apr-90	17-May-90	03-May-90	0%	0%	3%	8%	3%	0%	25%	0%	44%	0%	0%	0%	0%	0%	0%	14%	0%	3%	0%	36
BS total percentages based on avg. daily flux				1%	P	27%	11%	P	9%	4%	13%	6%	4%	2%	P	1%	P	6%	10%	6%	1%	P	2720

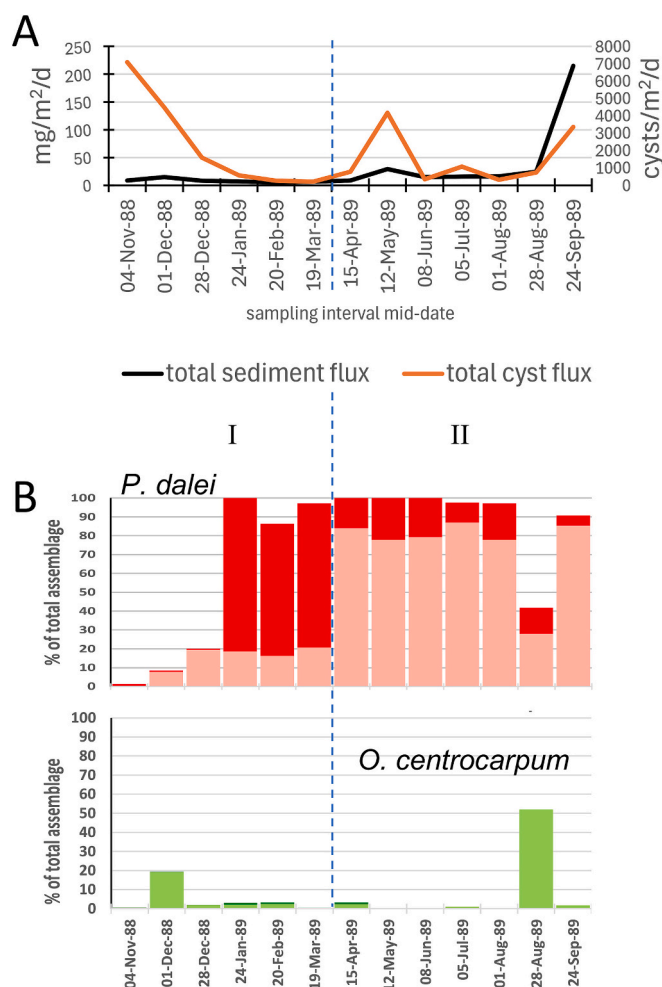


Fig. 13. Total sediment and cyst flux (A) and time-series assemblage changes in percent for main species (B) at Iceland Plateau (IP3). Darker shading indicates % of total cysts seen that contained cell contents, lighter indicates empty cysts. Mid-dates for sampling intervals under total sediment and cyst flux graph, months only under species graphs. Seasonal sedimentation of cysts is divided into two categories denoted I and II, explained in text. Sediment flux data is shown in Appendix B and cyst percentages with cell contents in Table 6.

depth difference of 222 m. The farthest away of the five nearest was 190 km and the depth differences ranged from 3 m to 600 m. The abundances of *Pentapharsodinium dalei*, a key indicator species for the site, ranged from 1.1% to 62.7% (Fig. 14B).

Given this large variability in proximity to the trap, water depth, local sedimentary regime and percentage abundance of key species within the five nearest samples, only the one with nearest geographic proximity was selected for the statistical analyses. Despite the large variability, a comparison of the selected sample with the mean percentage for each species from the five nearest bottom sediment samples reveals that the assemblage proportions for the selected sample was generally within one standard deviation of the mean for all five (Appendix C). The total percentages of the palynological equivalent cysts from traps and sediments are shown in Table 7, together with environmental data for sea surface temperatures (SST) and ice cover. Cyst types amounting to more than 5% in the combined database were included in the CA and CCA analyses used for the comparisons.

4.2. Correspondence analysis results

An explanation of why CA and CCA were chosen for extracting ecological data from our data set is explained in Dale and Dale (2002).

CA, in which the species data is unconstrained, is considered the most effective method for exploring the relationship between cyst assemblages and possible causal ecological gradients, whereas CCA, in which the data are constrained to reflect measured environmental variables, is most useful for testing the strength of relationship between the assemblages and the given variable(s). Here, we used CCA to test the strength of relationship between the assemblages and the ecological variable most widely used in paleoenvironmental reconstructions: sea surface temperature (SST).

4.2.1. CA of combined sediment trap and bottom sediment data

Combining different sample types introduces inherent complexity. The sediment trap samples cover a time span of roughly one year, and mostly different years, whereas the cysts in bottom sediments cover many tens possibly up to thousands of years, depending on sedimentation rates. The first two axes of the combined CA (Fig. 15) had high eigenvalues (0.5 and 0.4, respectively), indicating a strong relationship between species and station distributions. The main variance on Axis 1 was between end members *Operculodinium centrocarpum* from bottom sediments, vs. *I. pallidum* from sediment trap stations GB and FS. On Axis 2, the main variance was attributable to *P. dalei* from the Iceland Plateau from both datasets (IPA and DeIP), which plotted several standard deviations away from the other stations. The three groupings are distinguished in Fig. 15, consisting mainly of either sediment trap samples (positive on Axis 1), oceanic bottom sediments (negative on Axis 1) or the Iceland Plateau station (positive on Axis 2). Numerical results are shown in Appendix D. Clearly, the main variation in the combined CA is more attributable to sample type than environment. The different sample types therefore were run individually and the stations plotting several standard deviations from the main groupings (IP for both and WBS for the trap samples) were excluded from the subsequent correspondence analyses in order to improve the resolution and better assess the remaining variation (Figs. 16–18). Despite sample DeGB plotting more than 1.5 standard deviations away from the main grouping for bottom sediments (grouping in lower left of Fig. 15), the eigenvalue for Axis 1 declined from 0.3 to <0.1 when more than one sample was removed so only IP was omitted in the subsequent analysis of bottom sediments (Fig. 18).

4.2.2. CA of sediment trap samples only

Fig. 16 shows the CA biplot of the trap samples only and species responsible for the main variation, with IP and WBS removed to better express the remaining variation, as discussed in section 4.2.1 (data in Appendix E). The eigenvalues for Axes 1 and 2 were 0.3 and 0.2, respectively. The main variation on Axis 1 is attributable to dominance by *I. pallidum* at FS and GB stations (positive), and the RBC-, *O. centrocarpum*- or *P. dalei*-dominated stations (negative). The main variation on Axis 2 reflects the high abundance of *Islandinium minutum* and *Islandinium cezare* in the Barents Sea (BS) and at the E. Greenland-Current influenced stations (FS and GB) plotting positive, whereas RBC-dominated assemblages of the stations in the southernmost Norwegian Atlantic Current (NA, LB and NB) plot negative. The four groupings shown in Fig. 16, together with the two groupings plotting several standard deviations from the main grouping shown in Fig. 15 (IP and WBS), are shown for comparison with the equivalent results for the bottom sediments in Fig. 17A.

The groupings clearly differentiate the different current influences affecting the Nordic Seas: the Norwegian Atlantic Current in the Norwegian Sea (NA, LB and NB), the mix of Norwegian Atlantic Current and Polar waters in the Barents Sea (BS), the shelf edge influence between the Norwegian and Barents Seas (WBS), polar waters from the Barents Sea combining with Norwegian Atlantic Current-influence (BI), the E. Greenland Current (FS and GB), and the combined influence of the E. Greenland Current and the Irminger Current in the Iceland Sea (IP); see Fig. 17A.

Table 6

Time-series assemblage data for Iceland Plateau 3 deployment (IP3), showing total cysts seen and percentage data for species amounting to over 5% of the assemblage. Shading indicates component with cell contents. Categories amounting to less than 1% of the total observed at the station were omitted here but are shown in Appendix A. Data for main cyst types having cell contents shown graphically in Fig. 13.

Sample ID	Opening date	Closing date	Middle date	% <i>Impagidiniumpallidum</i> (w/cc)	% <i>Impagidiniumpallidum</i>	% <i>Operculodiniumcentrocarpum</i> (w/cc)	% <i>Operculodiniumcentrocarpum</i>	% cyst of <i>Pentapharsodiniumdalei</i> (w/cc)	% cyst of <i>Pentapharsodiniumdalei</i>	total cysts counted
IP3-1	Oct-22-88	Nov-18-88	04-Nov-88	0%	0%	1%	0%	97%	0%	1223
IP3-2	Nov-18-88	Dec-15-88	01-Dec-88	0%	0%	1%	19%	70%	8%	772
IP3-3	Dec-15-88	Jan-11-89	28-Dec-88	0%	1%	0%	2%	77%	19%	273
IP3-4	Jan-11-89	Feb-07-89	24-Jan-89	0%	1%	1%	2%	74%	19%	97
IP3-5	Feb-07-89	Mar-06-89	20-Feb-89	0%	0%	0%	2%	81%	16%	43
IP3-6	Mar-06-89	Apr-02-89	19-Mar-89	0%	0%	0%	0%	76%	21%	34
IP3-7	Apr-02-89	Apr-29-89	15-Apr-89	0%	1%	0%	2%	11%	84%	132
IP3-8	Apr-29-89	May-28-89	12-May-89	0%	2%	0%	0%	19%	78%	360
IP3-9	May-28-89	Jun-22-89	08-Jun-89	0%	3%	0%	0%	14%	79%	29
IP3-10	Jun-22-89	Jul-19-89	05-Jul-89	1%	1%	0%	1%	5%	87%	92
IP3-11	Jul-19-89	Aug-15-89	01-Aug-89	0%	0%	0%	0%	15%	78%	27
IP3-12	Aug-15-89	Sep-11-89	28-Aug-89	0%	0%	0%	52%	0%	28%	25
IP3-13	Sep-11-89	Oct-08-89	24-Sep-89	2%	0%	1%	2%	8%	85%	116
IP3percentages based on average daily flux				P	1%	1%	6%	54%	37%	3223

4.2.3. CA of bottom sediment samples

The result of the CA for the bottom sediment samples from de Vernal et al. (2020) is shown in Fig. 18 and the numerical data in Appendix F. The eigenvalues for Axes 1 and 2 with IP omitted to more clearly express the remaining variation (Fig. 15) were 0.3 and 0.1, respectively. The main variation on Axis 1 is between the Greenland Basin (DeGB) and the remaining localities, whereas the main variation on Axis 2 is between the Barents Sea sample (DeBS) and the remaining localities. The CA analyses distinguished 4 groupings, the distribution of which is shown on the map in Fig. 17B. The clusters from the bottom sediments correspond to the main current regimes, but with less detail than the sediment trap data (see Fig. 17B). Bottom sediment stations DeNA, DeNB, DeLB, DeWBS, DeBI and DeFS all seem to be associated with the Norwegian Atlantic Current; BS with the mix of Norwegian Atlantic Current and Polar waters presumed for the Barents Sea Barents Sea; DeGB is associated with the E. Greenland Current and DeIP with the combined influence of the E. Greenland Current and the Irminger Current around Iceland (Figs. 15, 17B and 18).

The strong dominance by *O. centrocarpum* in the bottom sediment samples overshadows the influence of main known cold-water indicators such as *I. pallidum*, *I. minutum* and *I. cezare* as compared with the sediment trap samples.

4.3. Canonical correspondence analysis

To assess the extent to which the main species variance relates to sea surface temperature, a CCA was run for trap and bottom sediments. The assemblage data for the traps were constrained to reflect average annual water temperature for the year of deployment; and an average of the

years 1955 to 2012 was used for the bottom sediments (de Vernal et al., 2020). SST data for both traps and bottom sediments are from the World Ocean Atlas 2013 (Locarnini et al., 2013) (Table 7). The CCA results for the trap and bottom sediment samples are shown in Appendix G and illustrated in Fig. 19.

For the CCA of the sediment trap samples, with species abundance constrained to SST, the eigenvalue for the canonical Axis 1 was 0.2 and the species-environment correlation was 0.9.

For the CCA of ocean bottom sediments from de Vernal et al. (2020) the eigenvalue for the canonical Axis 1 was 0.1 and the species-environment correlation was 0.6.

The results of the SamE scores (Sample scores based on Environmental variables) are plotted for trap samples in Fig. 19A and for bottom sediments in 19B. The triplots show the samples dispersed as linear combinations of the SST data used to constrain the ordination. Numerical results of the CCA for Axes 1 and 2 are shown in Appendix G.

The main cyst types are shown in blue, and the samples are plotted as pies to illustrate the notable differences between cyst assemblages in traps and sediments. Note the large difference in the influence of *O. centrocarpum* (green) between sediment and trap samples.

Testing the strength of relationship between SST and species distributions in the CCA showed a clearly stronger species-environment correlation on Axis 1 for trap samples than for bottom sediments (0.9 vs. 0.6, respectively) (Appendix G). The remaining unconstrained variance shown on the higher axes is considered irrelevant for testing SST, since the remaining species variance is better reflected by the unconstrained CA analyses in Figs. 15–17. The spread of species along Axis 1 (constrained to SST) is essentially the same in both CCAs, which supports the temperature signals used for the bottom sediments despite the notable

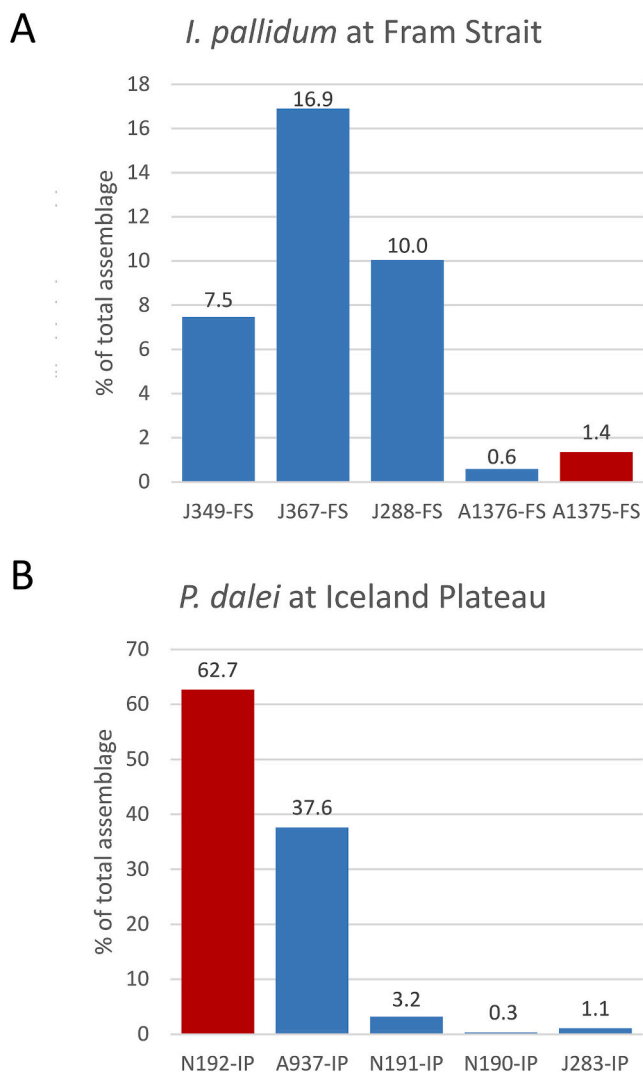


Fig. 14. Bar graphs showing **A)** percentages of *I. pallidum* in the five bottom sediment samples from the de Vernal et al. (2020) $N = 1968$ data set nearest the Fram Strait station (FS), and **B)** *P. dalei* in the five bottom sediment samples nearest the Iceland Plateau station (IP). The sample selected from among these for the statistical comparisons is shown in red. Note variation in percentages. Data in Appendix C. Station data and codes from de Vernal et al. (2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dominance by *O. centrocarpum*.

4.4. Summary of correspondence analyses (CA and CCA)

The statistical comparison of the trap and sediment data reveals that a) differences in the time interval represented by the type of sample, roughly one vs. possibly up to several thousand years, overshadows regional environmental differences; b) the main colder cyst species are identified by the CA and CCA as *I. pallidum*, *I. minutum* and *I. cezare* in both data sets, with *I. pallidum* and *I. minutum* particularly abundant in the more open oceanic samples; c) regional influences from the main current systems in the region are reflected in the assemblage differences in both the traps and bottom sediment samples; and d) the trap samples more closely reflect the environmental influences known for the region today than do the nearest underlying bottom sediments, as would be expected given the narrow vs. broad time intervals they represent.

The results support the use of cysts as water mass indicators, but the extent of poor correspondence between trap and sediment samples does

not support the assumption that cysts in bottom sediments represent primary signals from overlying waters.

4.5. Questions arising from comparison between cysts in traps and cysts in bottom sediments

Comparisons between trap and bottom sediment samples raised questions relevant for the use of cyst proxies in paleoceanography. Some questions may result from the very different sampling intervals (discussed in 4.2.1). Nevertheless, evidence unlikely to result from sampling differences alone raises questions about the robustness of the SST proxies, discussed in the following points:

1. Fig. 19 clearly shows the high degree of dominance of one species, *Operculodinium centrocarpum*, in all but one sediment sample, whereas only the trap sample at the Barents Sea shelf edge (WBS) showed dominance by *O. centrocarpum*. Where do these relatively large amounts of *O. centrocarpum* throughout the deep-sea sediments originate from, and what consequence does this dominance have for the robustness of the cysts signal? The questions concerning *O. centrocarpum* are particularly relevant for paleoceanography since this species features prominently in cored deep sea Quaternary records in the North Atlantic, Nordic Seas and other oceans (Mudie and Harland, 1996, and references therein; Marret et al., 2020; Marret and de Vernal, 2024). *O. centrocarpum* is a common cosmopolitan species (Wall et al., 1977), opportunistically thriving in difficult and changing environments. It is also a prolific cyst producer such that it may be overrepresented in the sedimentary record, as in a Norwegian fjord (Dale, 1976) or in the North Atlantic (Dodge and Harland, 1991). Of interest here is its notable “spikes” of proportional increase in assemblages marking environmental change in Quaternary records and especially its association with the mixing of neritic and oceanic waters near the shelf break in Wall et al. (1977), and the nearshore-offshore cyst signal of Dale (1996). The WBS trap was the only trap ideally situated to collect cysts from a possible “spike” of *O. centrocarpum* near the shelf edge. It also accounted for a large proportion of this species seen in the trap study, suggesting the possibility that its increase is associated with the mixing of neritic and oceanic waters near the shelf edge as a major source for the deep-sea cysts. However, this alone does not explain the overwhelming dominance of *O. centrocarpum* in the deep-sea sediments associated with the Atlantic Norwegian Current, which was not seen in the traps (difference shown in Fig. 19A and B).

1. Several factors reducing other cysts may contribute to the elevated proportion of *O. centrocarpum* in bottom sediments compared to the traps: a) “round brown cysts” dominate assemblages in trap samples NA, LB and NB, and these are susceptible to oxidation in the environment and during some palynological preparations (Zonneveld et al., 2001); and b) *P. dalei*, one of the three most common cysts in traps, was often previously misidentified as *O. centrocarpum*. We propose that dominance of *O. centrocarpum* in deep sea sediments here and potentially in other oceans is in (large?) part the combined result of elevated input from neritic-oceanic mixing “spikes” often seen in the nearshore-offshore cyst signal and in the shelf edge trap, possibly combined with the above-mentioned moderating factors affecting species proportions. The contribution of *O. centrocarpum* may have been much greater in response to past periods of pronounced environmental changes, reflected in the paleoceanographic record.
2. The large differences between assemblages in the five nearest sediment samples initially selected for comparison with the traps (Fig. 14) raised further questions. Why is the ocean bottom sediment database made up of a patchwork of significantly different cyst assemblages rather than a uniform pattern of change reflecting the main current system? Theoretically, this could be caused by different ages of adjoining samples reflecting different environmental signals, differences in bottom water turbulence, or differences in

Table 7

Total assemblage and environmental data for sediment trap stations with calcareous cysts removed and percentages recalculated, together with nearest sea floor samples from the [de Vernal et al. \(2020\)](#) $n = 1968$ database (code in CA indicates correspondence between sediment trap and bottom sediment stations by inserting prefix “De” before trap station code). Blanks = zero percentage values. SST for sediment trap stations from World Ocean Atlas ([Locarnini et al., 2013](#)) averaged for the year of trap collection. SST for the bottom sediments, and ice cover for both datasets, from [de Vernal et al. \(2020\)](#), except for BI and WBS which were known to have no ice cover during the year of deployment. 0 value here indicates no ice cover.

Code in source database	cyst spp:	<i>Impagidinium pallidum</i>	<i>Islandinium cezare</i>	<i>Islandinium minutum</i>	<i>Nematosphaeropsis labyrinthus</i>	<i>Operculodinium centrocarpum</i>	<i>Pentaparsodinium dalei</i>	<i>Selenopemphix quanta</i>	Round brown cyst	<i>Spiniferites elongatus</i>	non- <i>S. elongatus</i> <i>Spiniferites</i> spp.	total cysts counted	Latitude (°)	Longitude (°)	Water depth (m)	Summer sea surface temperature (°C)	average sea ice concentration (%)
		code in CA	lpal	lcez	lmin	Nlab	Ocen	Pdal	Squa	RBC	Selo						
NA	NA	4		1	7	0.5	15	0.2	52	5	2	380	65° 31'N	00° 64' E	3058	7	0
N212-NA	DeNA				12	76	7			1	1	> 60	66° 61'N	01° 13' E	3046	10.9	0
LB	LB	2		2	6	15	5		59	1	1	631	69° 30'N	10° 00' E	3161	7	0
J300-LB	DeLB	1		1	13	78	1	0.3	4	1	1	> 60	69° 05'N	03° 00'E	3240	9.9	0
NB	NB	6		3	18	10	7		54	0.1	1	449	70° 00'N	01° 58' W	3296	4	0
J322-NB	DeNB	1			13	71	3	0.5	9	1	1	> 60	70° 01'N	00° 08' E	3177	9.3	0
WBSD	WBS	1	1	3	9	58	12	1	10	2	1	282	74° 29'N	15° 18' E	1608	5	0
Z1410-WBSD	DeWBS	1			6	81	2		1	2	5	> 60	74° 81'N	14° 78' E	1506	6.9	0.02
BS	BS		2	41		14	13	1	23	7	1	2457	73° 29'N	19° 19' E	472	4	0
Z1405-BS	DeBS	0.5		2	5	62	23	0.1	1	5	0.4	> 60	73° 17'N	20° 95' E	469	7.5	0
BI	BI	10	3	9	12	15	27		20	1	1	563	75° 51'N	11° 28' E	2123	5	0
Z11411-BI	DeBI	1		2	7	78	6		1	3	3	> 60	75° 64'N	12° 92' E	1502	6.4	0.32
FS	FS	32	2	22	4	3	5		31	0.3		139	78° 51'N	01° 22' E	2527	2	3.94
A1375-FS	DeFS	1		9	7	74	1		4	2	0.4	> 60	78° 41'N	01° 06' E	1172	2.8	3.94
GB	GB	51		5	4	1	1		37			116	74° 35'N	06° 43' W	3445	1	2.2
J361-GB	DeGB	23	1	9	26	28	1		12	0.4	0.4	> 60	74° 33'N	05° 18' W	3477	3.9	2.2
IPA	IPA	1				8	90			1		3686	68° 01'N	12° 40' W	1884	3	0.12
N192-IP	DeIP	3			5	25	63	0.1	2	2	1	> 60	67° 05'N	11° 66' W	1663	6.3	0.12

bioturbation. Irrespective of the causes, this introduces further unanswered questions concerning the cyst signal and its potential precision as proxies.

3. *Impagidinium pallidum* and *Nematosphaeropsis labyrinthus* represent the only unequivocal primary oceanic signals in our data, but they account for less quantitatively than other species in assemblages. This reflects the much lower levels of available nutrients for these autotrophs in the open ocean than is available in the coastal/neritic zones providing cysts via secondary signals. Heterotrophs may produce correspondingly more cysts, since the diatoms they feed on are more prolific than autotrophic dinoflagellates.

5. Implications for paleoceanography

Quaternary indicator species have living representatives mainly from coastal to neritic environments, and their climatic signals were determined by linking measured SSTs to biogeographic distribution

from known cyst sources. The equivalent linkage is more problematic for the deep sea where neither source of cyst production nor transport can be reliably determined. Yet, paleoceanographic proxies rely on the unverified assumption that cysts in bottom sediments reflect environmental conditions in near-surface waters above. This study sheds light on two questions pertinent for the accuracy and reliability of the proxies: 1) are the cysts in deep sea sediments formed in surface waters above? and 2) do they transport a primary signal (e.g. SST) to the bottom sediments directly below? Deep sea sediment traps so far provide the only available evidence for the deep sea, though subject to limitations discussed here.

5.1. Contrasts between sediment trap evidence and the assumptions of deep-sea cyst proxies

Our work cannot directly trace the source and transport of individual cysts to the bottom sediment, but the data show evidence of cyst sources

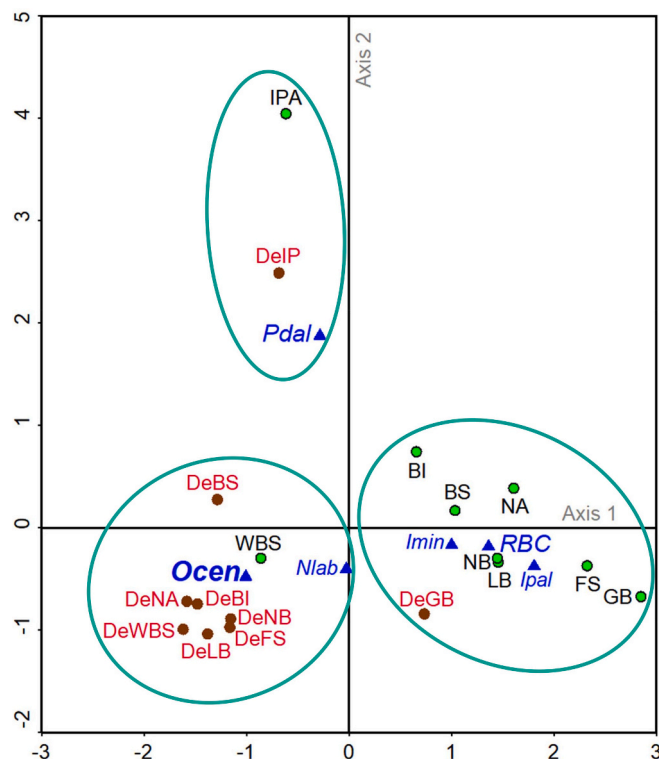


Fig. 15. Biplot of CA analysis, showing sediment trap samples (green symbols), bottom sediment samples (red text with brown symbols) and species responsible for main variation (blue italic). Size of species label corresponds to its relative weight in the analysis. *Ocen* bold to indicate more than double the weight of any other taxon in the analysis. Green rings denote separation between trap and bottom sediment samples on Axis 1, and all other stations and IP on Axis 2. Station groupings identified by the CA in Figs. 15–16 are shown in relation to main water currents in Fig. 17A. Station codes in Table 7. Numerical results in Appendix D. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

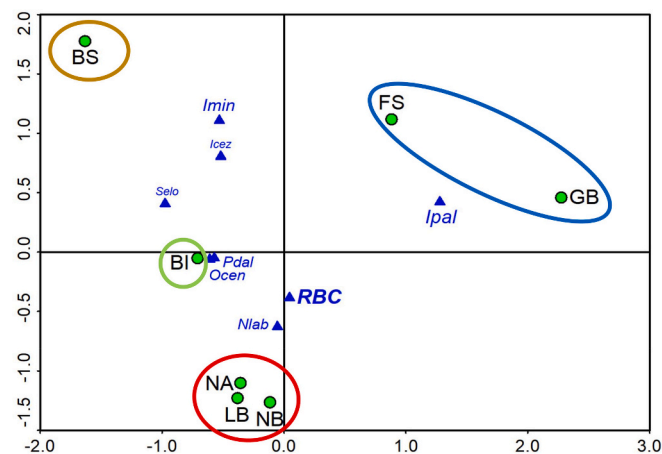


Fig. 16. Biplot of CA analysis, showing sediment trap samples (green dots) and species responsible for main variation (blue italic). Size of species label corresponds to its weight in the analysis. Stations IP and WBS were excluded to increase the resolution of remaining sample structure (see Fig. 15). Assemblage groupings identified by CA in Figs. 15–16 are shown in relation to main water currents in Fig. 17A. Station codes in Table 7. Numerical results in Appendix E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(section 3.3), and cyst distributions at approximately 400–500 m above bottom around the Nordic Sea basin suggesting likely methods of cyst transport (section 3.4). If the cysts provide a primary SST signal a closer comparison would be expected between cyst fluxes in the traps and bottom sediments than is shown here. The most recent review of cyst proxies as indicators of climate change by Marret and de Vernal (2024), subsequently referred to as “the review”, offers a basis for comparison to present agreements and contrasts with our sediment trap work (Dale and Dale, 1992 and here).

We provide supportive evidence for the general point in the review (p. 6) that cysts are useful paleoceanographic tracers in marine environments of continental margins, as there is reasonable agreement between the cyst fluxes and cysts in sediments as tracers of the main water masses (Fig. 17). We also confirm *Impagidinium pallidum* as a cold-water oceanic species providing a primary environmental signal from near-surface waters in the deep sea (Figs. 11, 16). However, the contrasts shown here raise questions about the potential precision of quantitative estimates and may help to explain the sometimes large error margins shown in paleo-SST estimates produced using proxies.

Our work provides alternative evidence for the general assumptions in the review (p. 7) concerning cyst sources, that cysts are largely transported from upper water masses through settling and transported by marine snow and faecal pellets “with limited impact of distal transport”, and “... limited impact of oxidation”. Our evidence shows two sources of cysts transporting secondary signals from shallow adjoining locations as well as long distance transport by major currents. Our data also show tertiary signals transported by resuspension of older cysts, including Pre-Quaternary. In addition, we show dominating amounts of round brown cyst fluxes along the eastern margin not represented in bottom sediments (Fig. 15), for which oxidation could explain the difference (e.g. Zonneveld et al., 2001).

We consider the assumption in the review that most cyst transport is transported directly from “the upper water masses” (implying cyst origins in near-surface waters) to be too simplistic. It is important to note that particularly marine snow has likely gathered cysts potentially from anywhere in the water column above before landing in traps, not just the surface. Marine snow is an important contribution to the food web where it is constantly broken down and added to as it sinks, potentially releasing cysts to possibilities of lateral transport (well illustrated by Von Bodungen et al. (1995), Fig. 12; Alldredge and Silver, 1988). This, together with the lateral transport demonstrated here, suggests that the assemblages in the traps do not unequivocally represent a primary signal directly from surface waters as presumed by proxies.

5.2. Inherent inconsistencies in the ecological basis for proxies

A main factor affecting the precision of the proxies here and elsewhere is the inherent inconsistencies in the ecological basis for cyst proxies.

Living plankton reflects the interplay between different species and groups and their ecological adaptations to the environmental parameters affecting them. This complex web of biological and physical factors causes challenges to efforts to create proxies for any one parameter such as SST. For example, complexities from feeding strategies affects the SST signal in coastal dinoflagellates which must tolerate broad ranges of temperature and salinity due to short-term variations characteristic of coastal environment. Rather than SST, the availability of diatoms and other prey is a main factor determining the distribution of heterotrophic dinoflagellates in the Nordic Seas; and other factors not as important for dinoflagellates, such as turbulence and availability of dissolved nutrients and silica, determine the distribution of diatoms. The only certain temperature information from the dinoflagellate cysts therefore is that SSTs are within the broad range shown by their biogeographic distributions. Proportions of “warmer” and “colder” species allow for broad environmental interpretations when using proxies created from such recent data, showing warming and cooling trends in paleoceanography,

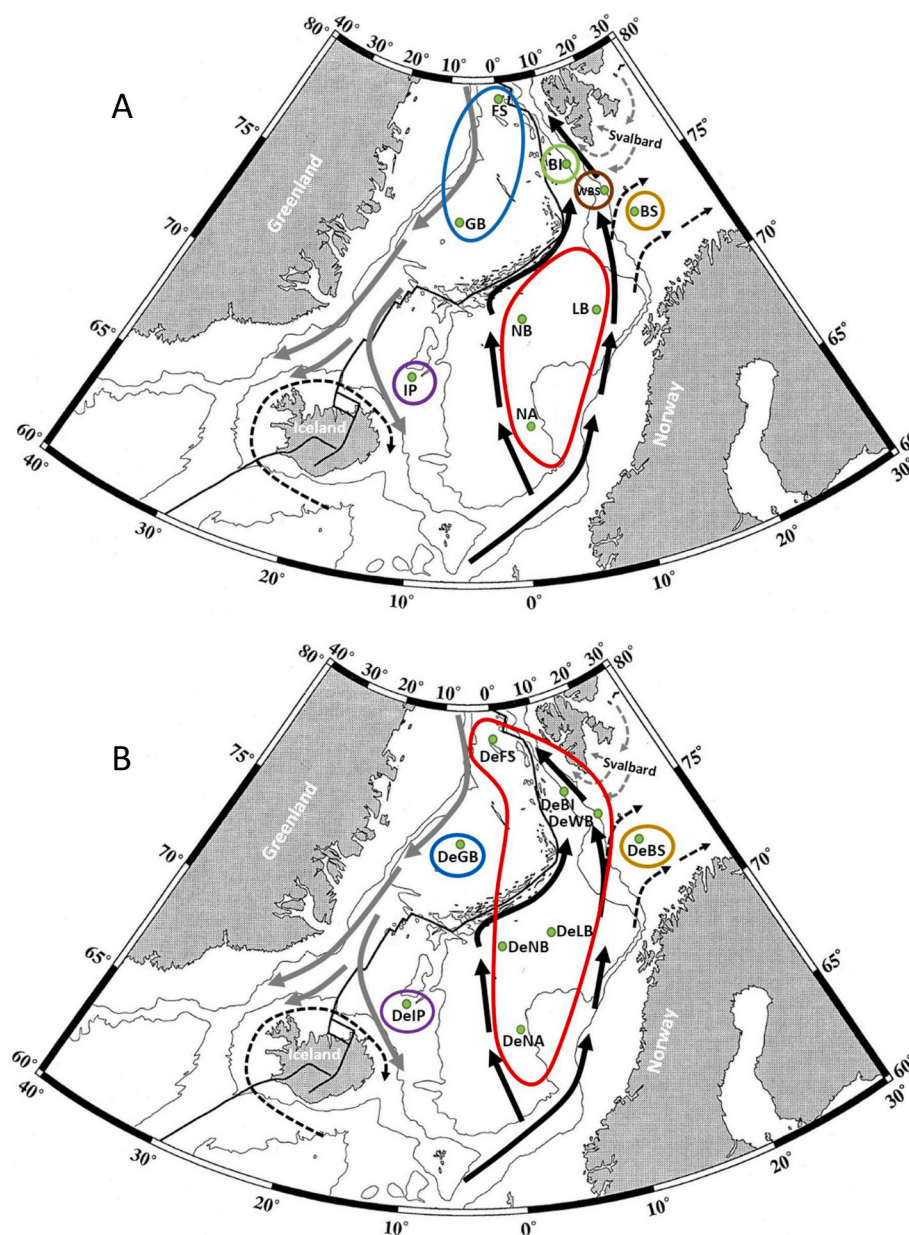


Fig. 17. Map showing CA groupings for A) trap samples, 4 groups shown in Fig. 16 plus 2 groups IP and WBS shown in Fig. 15; and B) bottom sediment samples, 3 groups shown in Fig. 18 plus 1 group IP shown in Fig. 15. Station codes in Table 7. Darker arrows show warmer current influence, lighter show colder. Bold line indicates mid-oceanic ridge. Schematic surface currents after Johannessen (1986); Loeng (1991); and Morozov and Frey (2024).

but detailed SST limits for the few indicator species are poorly understood, limiting the precision of SST proxies.

The precision of proxies in protected coastal situations may be increased if seasonal signals are distinguished in a primary signal, as shown here in the Barents Sea, indicating which species are living there and when cysts are formed. However, the precision of proxies in the Nordic Seas must be adversely affected by the existence of primary, secondary, and tertiary signals of unknown proportions in the bottom sediments. Applying these proxies in paleoceanography requires interpreting environmental changes that could at the same time have different effects on the variables forming the basis for the proxy signal. For example, large scale global temperature changes would potentially change current strengths or even direction due to the dynamics of bottom water formation (BWF), since BWF is increased by cooling temperatures. Might this simultaneously increase the northward transport of warmer water indicators from further south?

Sea level changes in paleoceanography could further reduce

precision of proxies, potentially affecting sources of secondary signals from long distance transport and/or tertiary signals from resuspension/re-sedimentation of older cysts from the continental margins.

How precisely would it be possible to interpret such contrasting sources for cyst proxies with such variable signals as seen here in a modern setting?

5.3. Implications for the use of cyst proxies as climate indicators

The Transfer function methods for developing cyst proxies have been challenged ecologically (Dale, 1996; Dale and Dale, 2002), statistically (Telford, 2006; Telford and Birks, 2009), and by cyst transport modeling (Nooteboom et al., 2019, 2020). In response, “the best analogue method” is increasingly used as an alternative, seeking a best fit for past assemblages in paleoceanography from a global database of modern cyst distributions (Duran, 2013; Hohmann et al., 2023; Marret and de Vernal, 2024). Ecologically, best analogue methods also assume that the cysts in

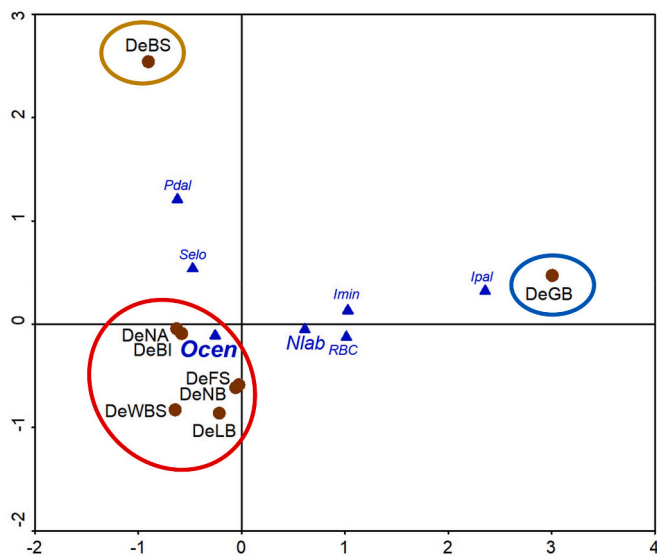


Fig. 18. CA biplot of bottom sediment samples from the de Vernal et al. (2020) data base nearest to the sediment trap stations (brown dots), and main species (blue italics), with size of species label proportional to its weight in the analysis. Note that Ocen is bold to reflect its weight more than five times greater than that of any other taxon. CA groups shown on map in Fig. 17B. Station codes in Table 7. Numerical results in Appendix F. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bottom sediments of an analogue represent primary signals from overlying surface waters. Our results show the need to also assess influences from secondary and tertiary signals in formulating proxies in the Nordic Seas Basin, and “best analogues” from other oceanic basins are expected to be similarly affected to varying degrees. The mixture of primary, secondary and tertiary ecological signals here are practically impossible to quantify in the bottom sediments and would be impossible to identify in fossils. The transfer function methods establish a reasonable signal for SSTs today in the Nordic Seas most likely because most secondary signals are injected from the same general climatic zone, though average SSTs for the Norwegian Sea are twice as warm as those for the Barents Sea (Sakshaug, 2004), and even reworked Quaternary cysts are less likely to include a “warmer signal” from so far north.

The dominance of *O. centrocarpum* means that relatively small changes in the other species play a disproportionately important role in the proxy signal, and uncertainty about the source of these inherently extends this uncertainty to interpreting changes in past assemblages. Our work shows that many of these other species are most likely transported in from the Barents Sea, and many of these in the traps to the south (NA, LB, NB) may well be transported by hydro-sedimentary mechanisms carrying secondary and tertiary signals from the shelf. The extent to which such secondary transport supplied cysts to paleoceanographic sediments will not be easier to assess than in recent sediments. This is further complicated by the fact that primary oceanic species *Impagidinium pallidum* and *Nematosphaeropsis labyrinthus* reflect low nutrient outer neritic to deep sea surface waters, producing low cyst fluxes compared with higher fluxes transported in from coastal species in nutrient rich coastal waters (23% oceanic species in our deep sea trap data). Thus, the secondary cyst signals may dominate assemblages in bottom sediments as shown here, though the possibility of some coastal species also living in icy oceanic waters remains open.

6. Summary and conclusions

Organic-walled dinoflagellate cysts are particularly important in paleoceanography providing environmental proxies from relatively high

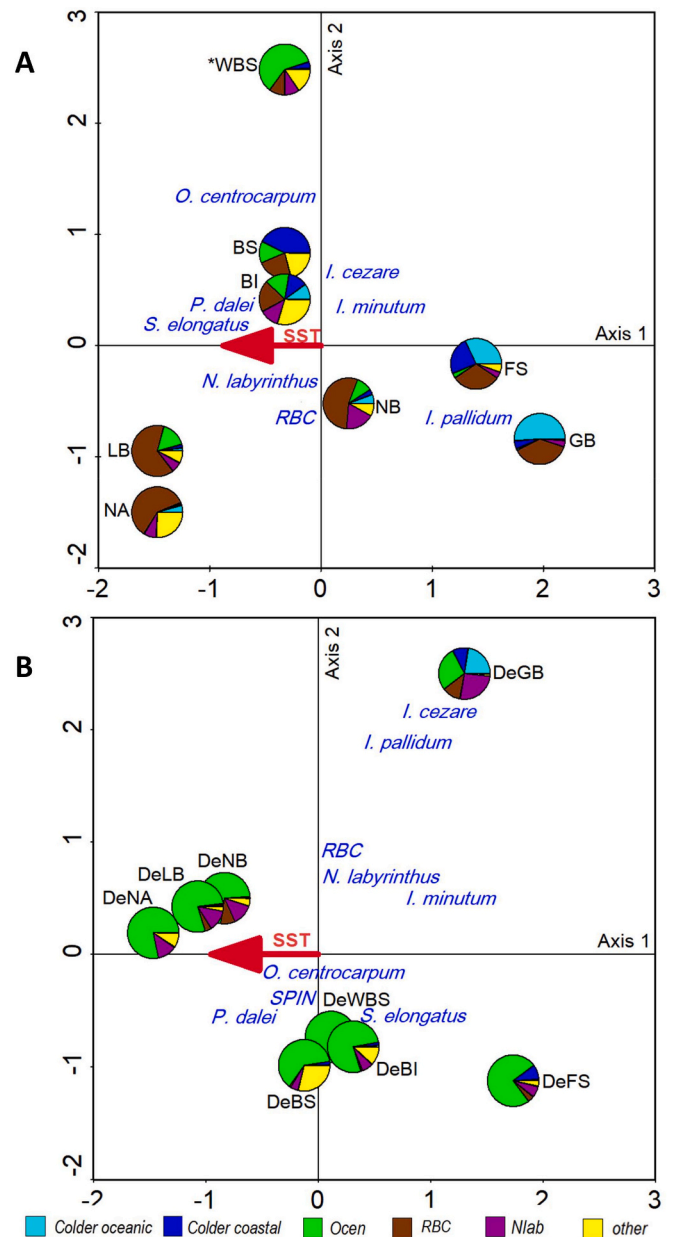


Fig. 19. CCA triplot of the sediment and sediment trap samples, constraining species data to sea surface temperature. Station IP omitted (see section 4.2.1). A) sediment trap data, and B) bottom sediments from de Vernal et al. (2020). Species responsible for the variation included in blue, centered over coordinates. Samples shown as pies centered on coordinates. * indicates trap malfunction, described in section 2.3.3. See key for species groupings: colder water indicators in blue, lighter = colder oceanic species *I. pallidum*, darker blue = species of the genus *Islandinium*; Green = *O. centrocarpum*, dominant in the bottom sediment samples and WBS; Brown = Round Brown cysts; Purple = outer neritic/oceanic species *N. labyrinthus*; Yellow = others (*P. dalei*, *S. quanta* and other *Spiniferites* species). Numerical results in Appendix G. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

numbers of species in deep sea cores where other mineralized groups such as foraminifera, radiolaria and coccoliths may be absent due to dissolution. A better understanding of factors controlling their distribution in recent marine sediments would improve the accuracy of proxies, particularly in oceanic environments. This first basin-wide study used deep sea sediment traps to investigate such factors in the Nordic Seas by comparing cysts potentially sedimenting out from the

deep sea in different hydrographic regimes with assemblages in bottom sediments underlying the same sites. The proxies in cored bottom sediments used in paleoceanography rely on the unverified assumption that cysts originate in open ocean surface waters and sink without significant lateral transport to transfer primary environmental signals to the bottom sediments. This study provides evidence to help assess the viability of these assumptions: good correspondence between cysts in trap samples and those in bottom sediments would support the use of the proxies in paleoceanography; poor correspondence would suggest the need for more complex paleoenvironmental interpretations that address the role of cyst transport before sedimentation. The following conclusions helped to offer a comprehensive perspective on the processes contributing to the cyst fossil record in this region:

1. Cyst and total fluxes were significantly higher for stations influenced by the warmer Norwegian Atlantic Current (NA, LB, BS and BI) than for those influenced by the colder East Greenland Current (FS and GB). In addition, cyst and total fluxes were markedly higher for the two shallowest stations for which fluxes could be measured: BS in the Barents Sea (369 m) and IP3 on the Iceland Plateau (1457 m).
2. Cyst fluxes showed a high correlation with lithogenic flux at all stations except the Norwegian Basin station located in the central gyre and for the IP2 deployment at the Iceland Plateau. This generally high correlation supports the likelihood of similar transport mechanisms conveying both sediment and cysts to the sea floor.
3. We recorded primary, secondary and tertiary cyst signals reaching the traps. We show two primary signals denoted by cysts with cell contents, one for the shallower Barents Sea (trap at 369 m) and one primary signal for the deeper Nordic Sea Basin. The Barents Sea (BS) was the only trap in which cell contents appeared in a clear seasonal sequence, first heterotrophs (*Islandinium minutum*, *I. cezare*, round brown cysts including *Protoperdinium conicoides*, and *P. americanum*), followed by autotrophs (*Spiniferites elongatus*, *Pentaparsodinium dalei* and *Operculodinium centrocarpum*).
4. The primary oceanic cyst signal in the present-day Nordic Seas is composed of the autotrophic species *Impagidinium pallidum* and *Nematosphaeropsis labyrinthus*. These oceanic species produce relatively low cyst fluxes, and their proportional representation in bottom sediment assemblages may be “diluted” by coastal/neritic species transported from other environments.

I. pallidum cysts with cell contents had highest abundance in the colder waters of the Greenland Sea, confirming this as a truly oceanic cold-water species. *N. labyrinthus* with cell contents contributes more to the primary oceanic signal closer to the basin margins in the Norwegian Sea.

The occurrence of significant numbers of *Islandinium minutum* with cell contents in the northerly traps of the Nordic Seas Basin suggests that this species may live year-round in these ice prone oceanic waters with an equivalent over-wintering strategy to the diatoms on which it feeds. Further evidence is needed from the living open ocean plankton to clarify the extent to which the presence of this and other species with cell contents reflects cyst production or transport.

5. We show two sources of cysts carrying transported signals from different environments: 1) secondary signals from cysts transported in from adjoining shallower waters or from the main oceanic gyres to the south; and 2) tertiary signals from Pre-Quaternary cysts and older Quaternary cysts resuspended from the Lofoten shelf.
6. We identify possible mechanisms of lateral cyst transport to the mixture of different signals reaching bottom sediments: the “winter outburst sedimentation” from the Barents Sea, the Lofoten Vortex eddy system transporting cysts from the Lofoten shelf, and sediment slumping that caused resuspension of Miocene cysts and potentially Quaternary cysts from the Lofoten shelf edge.

More distant lateral transport from the central oceanic gyres of the North Atlantic was reflected by calcareous thoracosphaerids in decreasing amounts in a counter-clockwise direction around the NS Basin, and by the sparse presence of warmer water indicators *Spiniferites mirabilis* (LB and NB), *Impadidinium sphaericum* (LB and FS) and *Gymnodinium catenatum* (WBS).

P. dalei comprised an almost monospecific assemblage on the Iceland Plateau and is believed to be transported from the northwest coast of Iceland via the Irminger Current and winnowing of shelf sediments by winter storms.

7. Species richness was higher for stations influenced by the Norwegian Atlantic Current (average 17) than for the stations influenced by the East Greenland Current (average 8). This most likely reflects the warmer water inputs to the eastern Nordic Sea Basin and colder arctic input on the western side, but it probably also reflects a higher secondary and tertiary input into the Norwegian Sea relative to the Greenland Sea Basin.
8. Correspondence analysis revealed associations between the cyst assemblages and current regime and enabled quantitative comparison between assemblages in the traps and bottom sediments. Trap samples corresponded more closely with hydrographic parameters known from today than did the bottom sediments, but bottom sediments also grouped according to known current regime.
9. Canonical correspondence analysis of the relationship between assemblages in the traps and bottom sediments, and measured variable SST, showed a significantly stronger species-environment relationship for the trap samples ($r = 0.9$) than for the bottom sediments ($r = 0.6$). Comparisons between the assemblages in the sediment traps and bottom sediments in the region reveal major discrepancies, particularly the extreme dominance by one species in bottom sediments: *O. centrocarpum*. These discrepancies may to some extent be related to sampling methods and analytical techniques, but we find no similarly strong dominance by *O. centrocarpum* in the deep sea in this region.
10. We interpret the dominance by *O. centrocarpum* cysts seen off the shelf in the Western Barents Sea (WBS) trap as an example of the opportunistic increase of this cosmopolitan species at the mixing of shelf and oceanic waters. We believe this feature to be reflected in the oceanic signal seen in this region and elsewhere, and we propose that this contributes significantly to its frequent abundance in Quaternary deep sea sediments globally. We also suggest the strong possibility that some cysts of the morphologically similar *P. dalei* may previously have been misidentified as *O. centrocarpum* in some of the larger databases that include many-decade old analyses as an additional factor contributing to the marked predominance of this species in bottom sediments. *O. centrocarpum* is also a more prolific cyst producer that is often “over-represented” in bottom sediments.
11. The documentation of primary, secondary and tertiary signals in deep sea sediments of the Nordic Sea Basin poses complications for proxies assuming only primary signals.

This work supports the use of non-quantitative cyst proxies used as climatic indicators in Quaternary coastal/neritic sequences where the cysts are more representative of primary signals from overlying waters.

Studies using transfer function methods such as the Modern Analogue Technique for deep sea sediments should show consideration of possible secondary and tertiary signals and cyst transport by stating their choice of cyst assemblages for comparison (e.g. are these also deep sea analogues?) and the assumptions made.

12. Results here suggest possibilities for future work. The cysts with cell contents of coastal/neritic species found in deep waters far

offshore are of particular interest. Are there viable populations of such species living in surface waters there? The few available plankton records have not provided answers; they are heavily biased towards the overwhelming dominance by diatoms, and the equivalent motile stages for some cysts remain unknown. Renewed efforts are needed to investigate open ocean dinoflagellates. Barcoding could now be applied to identify cyst producing species in the open ocean plankton, and sediment traps deployed just below the euphotic zone could collect any freshly formed cysts. Deployments including several sediment traps from near surface to just above bottom would help fill the existing gaps following our work.

13. Consideration of where cysts come from and how they are transported may improve cyst proxies, but until the primary, secondary and tertiary transport mechanisms affecting the deep sea record are better understood the precision of SSTs and other paleoclimate indicators will remain open to challenge.

CRedit authorship contribution statement

Amy L. Dale: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Barrie Dale:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marmicro.2026.102554>.

Data availability

Data will be made available on request.

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