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Research paper

Progress, challenges and future directions in marine organic-walled dinoflagellate cyst research: New insights from an international workshop☆

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ABSTRACT

Cysts are resistant life-cycle stages that play a key role in the survival and dispersal of some dinoflagellate species. Given their preservation and fossilisation potential, the organic-walled dinoflagellate cysts have been widely used as bioindicators of past and present environmental conditions. Living cysts are studied extensively due to their roles in bloom initiation, termination, and species adaptation. The use of cysts in various fields such

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as taxonomy, biogeography, evolution, (palaeo)ecology, and (palaeo)oceanography has expanded significantly in recent years. In this paper, we review recent developments, identify research needs, and outline future directions in marine organic-walled dinoflagellate cyst research based on round-table discussions held during the International Workshop on Dinoflagellate Cysts, which took place from 18 to 21 June 2024 in Vigo (Spain).

Key priorities in taxonomy, evolution, and biogeography include the need to continue establishing connections between the cyst and motile forms along with their associated sequences, particularly for Harmful Algal Bloom (HAB) species, and updating reference databases for metabarcoding studies. Emerging molecular techniques, such as metabarcoding, provide complementary information on cyst diversity, distribution, and geographic connectivity, thereby aiding in the monitoring and reconstruction of HAB dynamics. Given the impacts of climate change on biogeographical ranges, cysts could serve as valuable indicators for tracking HAB shifts. Combining multi-omics with morphological methods could offer deeper insights into character evolution and support the construction of the dinoflagellate tree of life. Advances in the biogeochemical analysis of dinoflagellate cyst walls, particularly through the detailed study of dinosporin, are also promising for evolutionary research, as demonstrated by recent methodological advances in Fourier Transform Infrared (FTIR) and Raman spectroscopy. In palaeoceanography and palaeoecology, improving quantitative cyst-based reconstructions requires expanding the database of living cyst assemblages and their relationships with environmental variables, especially in underrepresented regions, notably in the Southern Hemisphere. Despite progress towards standardisation, there remains no universally adopted standardised methods for extracting and concentrating cysts from sediments or for quantifying cysts—essential steps for inter-site comparisons. Additionally, sediment trap studies and field observations of associated plankton are needed to complement surface sediment research and enhance our understanding of species ecology. The emerging field of palaeogenomics is promising as it complements cyst-based research. Finally, the integration of biological and geological studies to address key scientific questions is emphasised. For example, investigating the discrepancy between the accepted geological emergence of dinoflagellates and earlier suggestions from geochemistry, molecular analysis, and re-examination of acritarchs could help resolve the early phylogeny of the group.

1. Introduction

Dinoflagellates (Alveolata, Dinophyceae) are a large group of protists characterised by an enormous genome and a unique nucleus, the dinokaryon. These organisms exhibit a remarkable diversity of habitats, life cycles and trophic modes (e.g., Lin, 2011). Among the 2400 extant dinoflagellate species currently recognised, 82 % are marine-brackish, whilst 18 % are freshwater; 91 % of free-living forms are planktic, and 9 % are benthic, colonising a wide range of substrates (e.g., epiphytic, epilithic and sand-dwelling) (Gómez, 2012a, 2012b). Regarding their trophic mode, there is growing evidence that most dinoflagellates are capable of capturing and ingesting live prey (phagotrophs) (Mitra et al., 2016). Dinoflagellates are now classified into three groups: i) constitutive mixotrophs (species with inherited chloroplasts, previously considered as strict autotrophs), ii) non-constitutive mixotrophs (species requiring stolen chloroplast—kleptoplastids—from their live prey or from an ecto/endosymbiont to survive), and iii) heterotrophs (Hansen and Tillmann, 2020). All the extant cyst-forming dinoflagellates currently known are either constitutive mixotrophs or heterotrophs. The former can photosynthesise (but requires vitamins and other trace substances for growth) and switch between autotrophic and heterotrophic modes of nutrition to overcome nutrient limitations and fuel its growth (Schnepf and Elbrächter, 1992). However, in most organic-walled cyst (palynological) studies, an outdated dichotomy of "autotrophs" versus "heterotrophs" is still used to classify cyst-forming dinoflagellates, which does not allow for consideration of mixotrophy in interpretating ecological signals. The term "autotrophs" is inaccurate to denominate dinoflagellate taxa (and their corresponding cysts) with photosynthetic capacity. Instead, the term "mixotrophs" should be used.

As part of their haplontic life cycle, some dinoflagellates can produce thin-walled —usually haploid— cysts (pellicle cysts) and thick-walled —usually diploid— cysts (resting cysts) (Figure 1AB), although a few haploid resting cysts have been described (see Bravo and Figueroa, 2014 for a review; Li et al., 2024). Pellicle cysts are also referred to as temporary or ecdysal cysts; however, following the recommendations by Bravo et al. (2010a) the term "pellicle cysts" will be used here. Pellicle cysts are typically non-dormant but may remain quiescent for hours to weeks and in laboratory cultures, they appear to form in response to short-term stress conditions (e.g., Dale, 1977a; Anderson and Wall, 1978; Anderson and Keafer, 1987; Blackburn et al., 1989; Ellegaard et al., 1998; Kremp and Anderson, 2000; Matsuoka and Fukuyo, 2000; Figueroa et al., 2008; Bravo and Figueroa, 2014). In contrast, resting cysts have an endogenously controlled mandatory dormancy period that can range from a few days to several months, depending on the species (Anderson, 1980; Blanco, 1990; Bravo and Anderson, 1994; Amorim et al., 2002; Figueroa and Bravo, 2005; Figueroa et al., 2008). The metabolic activity in resting cysts is very low, whereas pellicle cysts remain more metabolically active. Notably, resting cysts of some mixotrophic species often show chlorophyll fluorescence immediately before germination (Binder and Anderson, 1990; Anderson et al., 2014).

Approximately 13–16 % of known living dinoflagellate species produce resting cysts (Wall and Dale, 1968; Head, 1996), while around 20 % of species in coastal assemblages may be cyst-forming (Dale, 1976). In most cases, resting cysts are produced through sexual reproduction (Dale, 1977a; Anderson et al., 1984; Bravo and Figueroa, 2014; Figueroa et al., 2018), involving the production of gametes that fuse to form swimming zygotes (planozygotes) (Fig. 1C), which under the right environmental conditions subsequently encyst into non-motile, diploid resting cysts or hypnozygotes (Fig. 1B) (e.g., Dale, 1977a, 1983; Anderson and Wall, 1978; Bravo and Figueroa, 2014; Brosnahan et al., 2017).[1] The resting cyst wall is synthesised de novo and the resting cyst is morphologically distinct from its motile counterpart. Resting cysts are a key strategy in the species' dynamics and ecology. Although the formation of cysts does not necessarily have to be linked to blooms, in bloom-forming species they are typically formed during bloom termination and deposited in sediments, enabling species to survive unfavourable seasons (e.g., Dale, 1976; Montresor et al., 1998; Smayda, 2002; Smayda and Trainer, 2010; Brosnahan et al., 2017). Subsequent blooms are inoculated via cyst germination (excystment), a process that produces single diploid cells (planomeiocytes) (Fig. 1D) which then undergo meiosis to generate new haploid plankton populations (von Stosch, 1973).

[1] Some dinoflagellate species have additional pathways in their complex life cycle, enabling short-term adaptive responses. These include planozygote division leading to new vegetative cells, bypassing encystment. This transition is common in holoplanktic dinoflagellates, such as *Dinophysis* species (Escalera and Reguera, 2008), which for many years were considered to lack sexual processes.

Resting cysts and their walls can be preserved in the sediments, while remains of pellicle cysts and motile stages (haploid cells) are rarely preserved, if at all. A notable exception to motile stage preservation may be the silicious remains of the fossil genus *Peridinites* preserved in Eocene sediments (Harding and Lewis, 1994) or thecate stages of *Succiniperidinium inopinatum* preserved in amber (Masure et al., 2013). The resistance of resting cysts arises from their wall composition, which is most commonly organic, occasionally calcareous, and very rarely silicious (e.g., Elbrächter et al., 2008; Bogus et al., 2014; Chapman et al., 1982). The existence of two life stages with markedly distinct morphology, which were initially studied by different scientific fields, led to separate biological and palaeontological classification systems. According to the International Code of Nomenclature for algae, fungi and plants (ICN, Turland et al., 2018), separate names are allowed for the fossil and living dinoflagellates —effectively cyst and motile stage (Head et al., 2024).

This paper focuses on non-mineralised marine organic-walled resting cysts, as they are well-preserved in the geological record and extensively studied by both biologists and geologists. Biologists primarily use cysts to investigate life cycle transitions and plankton population dynamics (e.g., Anderson et al., 1983; Bravo and Anderson, 1994; Amorim et al., 2004; Brosnahan et al., 2020; Anderson et al., 2021). Cyst records are also crucial for biogeographical studies (e.g., Wall et al., 1977; Dale, 1983; Dodge, 1994; Amorim and Dale, 2006; Ribeiro et al., 2012; Marret et al., 2020). Geologists employ cysts for biostratigraphical applications (e.g., Louwye et al., 2004; Fensome et al., 2008), as well as palaeoecological reconstructions (e.g., Dale, 1996; de Vernal and Marret, 2007; Pospelova et al., 2015; Marret and de Vernal, 2024). Their taxonomically distinctive morphology and generally excellent preservation in sediments make them valuable proxies for studying past environmental conditions (e.g., Dale and Fjellså, 1994; Thorsen and Dale, 1997; Zonneveld and Brummer, 2000; Pross and Brinkhuis, 2005; de Vernal et al., 2013a; Ellegaard et al., 2017). Sedimentary cyst records have been used to reconstruct bloom histories of cyst-forming dinoflagellates and their relationship with climate variability and environmental changes (e.g., Dale, 2001a; Matsuoka et al., 2003; Amorim and Dale, 2006; Ellegaard et al., 2013). They can provide records of long-term changes in past marine productivity that can be used to improve the predictive capacity of ecosystem change models (Hochfeld et al., 2025). Fossil cyst records are used by geologists and palaeobiologists to study the evolution of these protists, whose origins date back to at least the Triassic (e.g., Fensome et al., 1996; Riding et al., 2022), and possibly much earlier (Dale, 2023).

The increasing global population and economic growth, resource extraction, human-induced climate variability, and pollution, among other anthropogenic factors, intensify pressure on marine ecosystems, resulting in significant losses of marine biodiversity and alterations to ecosystem services (e.g., Jackson, 2008; Buonocore et al., 2021). We need to increase efforts to achieve a better understanding of marine biodiversity and ecosystem functioning, to develop more effective management and conservation strategies, as well as monitoring and forecasting tools (e.g., Wells et al., 2015, 2020). In many coastal regions,

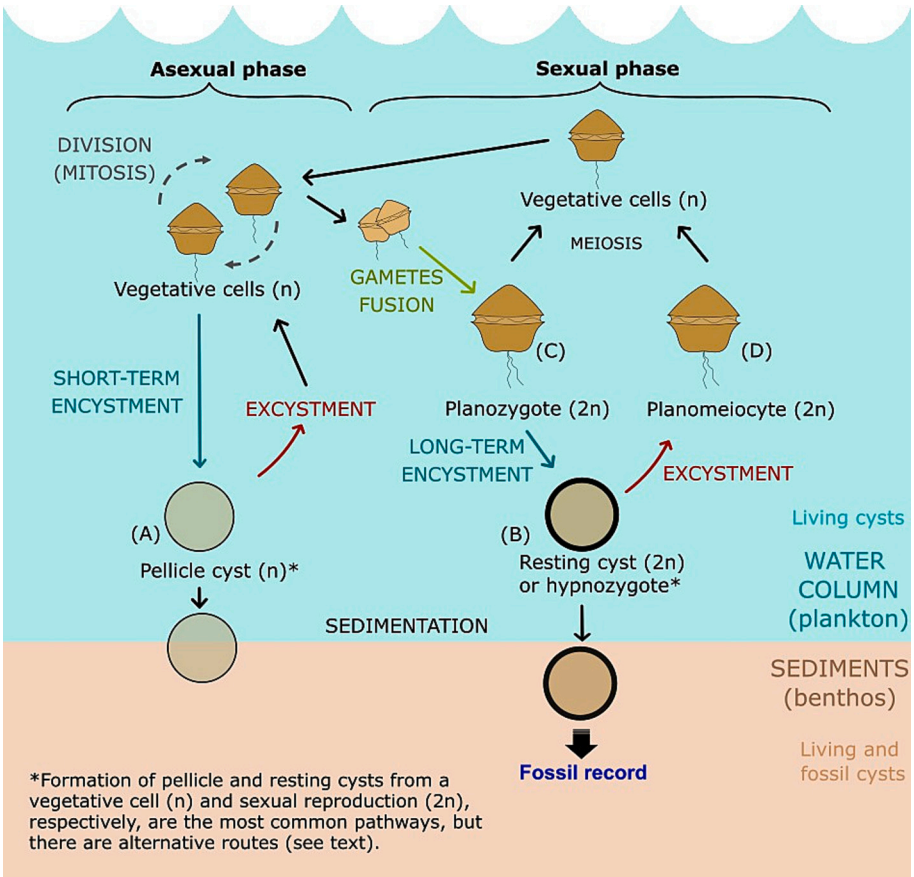

Fig. 1. Haplontic life cycle in dinoflagellates. Thin-walled, usually haploid, cysts (pellicle cysts) (A) and thick-walled, usually diploid, cysts (resting cysts) (B) produced by some dinoflagellates. Resting cysts are mostly produced through sexual reproduction (hypnozygotes), involving the fusion of gametes and formation of motile zygotes (planozygotes) as a transitional phase (C). Cyst germination (excystment) generates new haploid vegetative cells, passing through a diploid transition phase called planomeiocyte (D) that undergoes meiosis. 2n = diploid, n = haploid. Adapted from Bravo and Figueroa, 2014 (© Bravo and Figueroa, 2014, Towards an Ecological Understanding of Dinoflagellate Cyst Functions, doi: https://doi.org/10.3390/microorganisms2010011, published in *Microorganisms*, MDPI Open Access Journals, under a CC BY 3.0 license).

HABs are intensifying, disrupting ecosystem equilibrium and threatening public health, fisheries, shellfish production and other economic activities (e.g., Griffith and Gobler, 2020; Wells et al., 2020; Anderson et al., 2021; Hallegraeff et al., 2021; Zingone et al., 2021; Rodríguez et al., 2023). A significant proportion of HABs are caused by dinoflagellates, including toxin-producing species (e.g., Lundholm et al., 2009; Lassus et al., 2016). Studying cyst distribution in marine sediments enable the identification of seed beds of harmful dinoflagellates and the determination of factors triggering new blooms, contributing to risk assessments and attempted HAB forecasting (e.g., Pospelova and Kim, 2010; Anderson et al., 2014, 2021; Davidson et al., 2016; Pan et al., 2024). The study of dinoflagellates and their cysts also addresses questions related to climate change, invasive species, and cumulative human impacts on marine biodiversity and phytoplankton community structure and functioning (e.g., Pospelova et al., 2005; Amorim and Dale, 2006; Dale et al., 2006; Ribeiro et al., 2012, 2016; de Vernal et al., 2013a; Van de Waal et al., 2013; Bringué et al., 2014; Wells et al., 2015; Berdalet et al., 2017; Dhifallah et al., 2022).

Scientific workshops foster discussion and coordination of strategies to tackle these challenges through international and interdisciplinary collaboration. This paper stems from round table discussions at the International Workshop on Dinoflagellate cysts, held from 18 to 21 June 2024 in Vigo, Spain. Its objectives were to summarise the current state of the art and outline future directions in dinoflagellate cyst research. The applications of dinoflagellate cysts in diverse marine science fields and emerging techniques to address scientific questions are detailed.

2. How to identify dinoflagellate cysts and how many are left to describe?

2.1. Cyst identification methods

The identification of cysts can be achieved through morphological and molecular analyses. The morphology of resting cysts is traditionally analysed using light microscopy, inverted microscopes or compound microscopes with differential interference contrast (DIC). Key morphological characters for identification include: general outline, cyst diameter, archeopyle shape, the wall surface pattern, and presence and morphology of processes (e.g., Zonneveld and Pospelova, 2015). Typically, magnifications of 400× and 1000× are used, as high-resolution light microscopy is essential for species-level identification in many cases. For example, detailed observation of process morphology is critical to identify round brown process-bearing cysts (e.g., Radi et al., 2013; Gurdebeke et al., 2020a). Similarly, gonyaulacoid cysts require high-resolution observation of wall texture, where scanning electron microscopy and transmission electron microscopy can also be valuable tools (e.g., Head, 1994; Price and Pospelova, 2014) (Fig. 2).

However, species-level identification is not always possible based on morphology. Some species exhibit minimal morphological features, such as the cyst of *Protoperidinium thulesense* (Matsuoka et al., 2006) and *Alexandrium catenella* (Dale, 1977a; Anderson and Wall, 1978). In such cases, germination experiments are necessary to link the cyst to its corresponding motile stage. This can only be done in modern (living) cysts; not fossilised ones. Nowadays, modern molecular techniques, such as Polymerase Chain Reaction (PCR), Sanger sequencing or Next

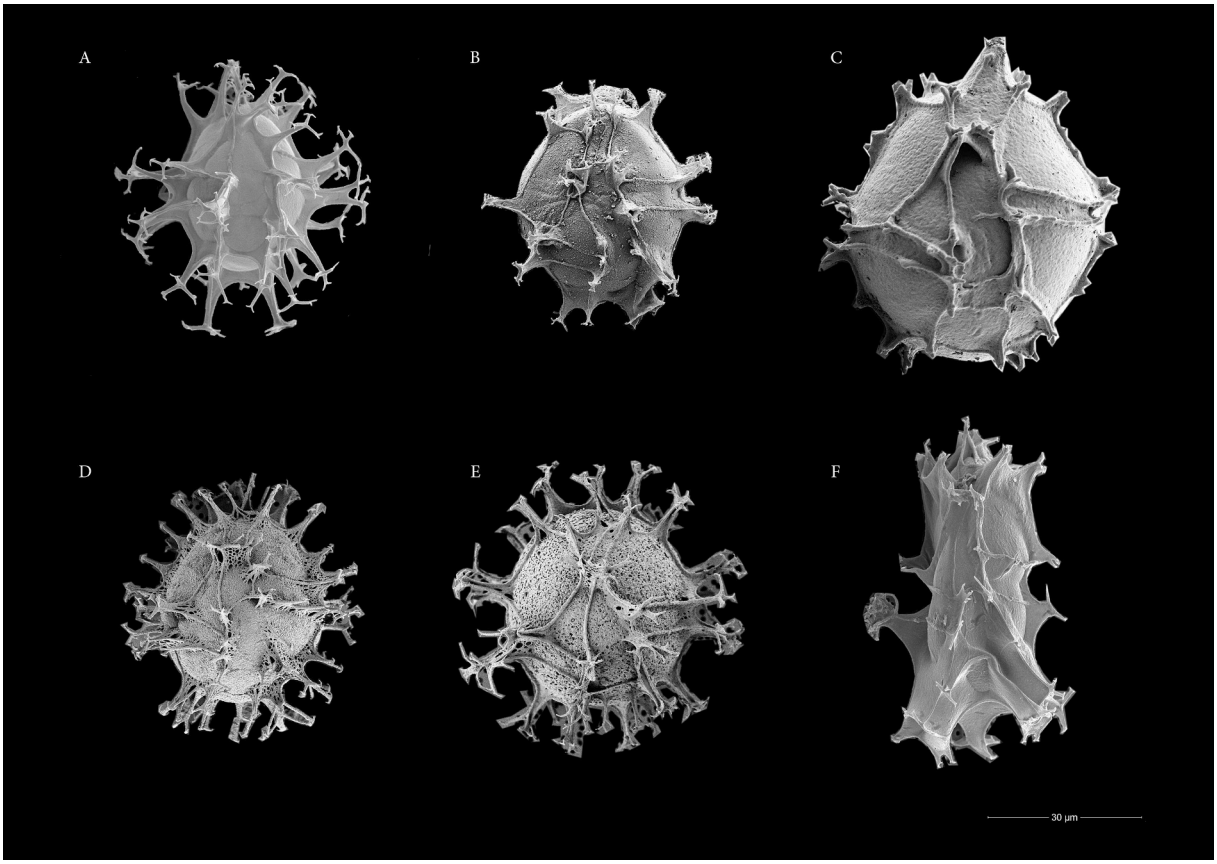

Fig. 2. Illustration of the diversity within the genus *Spiniferites* in modern sediments: *Spiniferites ramosus* from Vilaine Bay (Bretagne, France) (A); *Spiniferites belerius* from Locquénolé (Bretagne, France), note trumpet-shaped antapical process (B); *Spiniferites bentorii* from South China Sea (SHG-CJ-2018), note apical boss (C); *Spiniferites hainanensis* from Kastela Bay (Croatia), note presence of intergonal processes (D); E. *Spiniferites pachydermus* from Izmir Bay (Turkey), note specific ornamentation (E); *Spiniferites elongatus* from offshore Spitzbergen (F). All specimens to scale. All images by Kenneth N. Mertens.

Generation Sequencing, provide complementary information to identify species from hatched motile stages (e.g., Stern et al., 2010; Liu et al., 2015) (Fig. 3). While sequencing single cysts is feasible, hatching the cysts and performing Sanger sequencing on the germinated motile stages is preferred, as it ensures identification of the corresponding motile stage (e.g., Matsuoka et al., 2006; Ribeiro et al., 2010; Gu et al., 2022). Typically, sequences of the Large Subunit (LSU), Small Subunit (SSU) and Internal Transcribed Spacer (ITS) ribosomal RNA genes are obtained and compared against reference databases for accurate identification.

2.2. How many cysts are left to describe?

Among the ~2400 dinoflagellate species identified in marine ecosystems (Gómez, 2012b), a census from 1996 suggested that 260 species are known to produce organic-walled resting cysts (Head, 1996). Since then, at least another hundred species have been identified as cyst-producers, suggesting that ~15 % of all dinoflagellates produce cysts (Penaud et al., 2018). Living cysts are primarily associated with planktic species belonging to the taxa Gonyaulacales, Peridiniales, Suessiales, Thoracosphaerales and Gymnodiniales. To date, resting cysts have not been described among the Dinophysales, although this group may exhibit sexual reproduction involving planozygote meiosis and division that bypasses the hypnozygote stage (Reguera and González-Gil, 2001; Koike et al., 2006; Escalera and Reguera, 2008). The existence of cysts in Dinophysales has been suggested, but this interpretation should be approached cautiously (Reguera et al., 2012, 2024). Some cyst forms previously attributed to Dinophysales (Bardouil et al., 1991; Moita and Sampayo, 1993; Reguera et al., 1995) were later identified as either sporangia of *Parvilucifera*-like parasites within *Dinophysis acuminata* (Norén et al., 1999) or pellicle cysts of mixophagotrophic dinoflagellates mimicking the shape of ingested *Dinophysis* prey (*D. caudata/tripos, D. acuta* ingested by *Fragillidium* spp.) (Reguera et al., 2012, 2024). Cysts are also known for some benthic species from the genera *Prorocentrum* (Prorocentrales; Mertens et al., 2017a), *Vulcanodinium* and *Bysmatrum* (Peridiniales; Satta et al., 2013; Limoges et al., 2015), as well as *Ostreopsis*, *Fukuyoa* and *Gambierdiscus* (Gonyalaucales; Accoroni et al., 2014; Fraga et al., 2016; Leung et al., 2018).

While it is impossible to estimate how many cysts have yet to be identified, new ones continue to be discovered, suggesting that a significant number likely remain uncharacterised. Conversely, the motile stages of many known cysts have not yet been described. For example, cysts of the oceanic taxa *Impagidinium* and *Nematosphaeropsis* have been recognised for a long time, but their corresponding motile stages remain poorly known, even after sequencing some *Impagidinium* species (Mertens et al., 2017b). In addition, cysts have been discovered from species previously thought to be extinct, such as *Dapsilidinium pastielsii* (Mertens et al., 2014). Given that cysts are known only for a minority of living dinoflagellates, it is plausible that many dinoflagellates do not produce resting cysts, but this remains to be resolved.

In summary, our understanding of the relationships between cysts and motile dinoflagellates remains incomplete. There is a pressing need to establish more cyst-motile stage connections with associated molecular sequences and update reference databases for metabarcoding studies (see below).

3. Where do cysts typically accumulate and how can they be quantified?

3.1. Cyst distribution in sediments

Dinoflagellate cyst concentration in sediments varies significantly depending on the sediment type and environmental conditions. Fine-

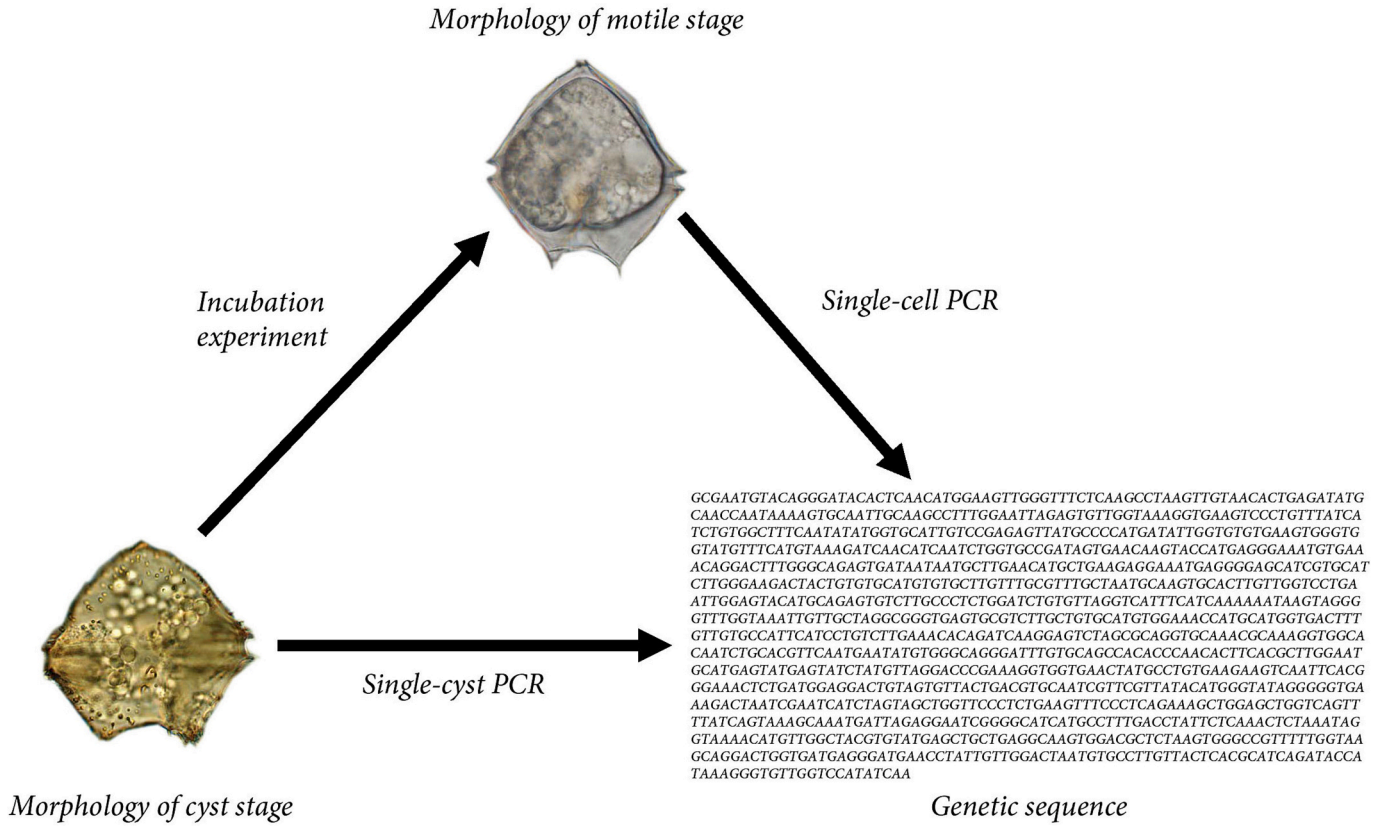

Fig. 3. Methodological approach linking the motile-defined *Protoperidinium louisianense* to the cyst-defined *Trinovantedinium pallidifulvum* through an incubation experiment and/or genetic sequences obtained through single-cell/cyst PCR. All images by Kenneth N. Mertens.

grained sediments, such as silty to clayey mud, tend to have higher cyst concentrations (e.g., Dale, 1976; Lewis, 1988; Butman et al., 2014; Triki et al., 2014; García-Moreiras et al., 2021; Rachman et al., 2022), particularly in regions of high primary productivity along coastal margins, where nutrients from terrestrial inputs and upwelling fuel phytoplankton growth (e.g., Radi et al., 2007; Pospelova et al., 2008; Zonneveld et al., 2013). Due to their silt-like behaviour in sedimentary regimes (Dale, 1976), cysts accumulate in deposition zones with other small and low-density materials. Conversely, high-energy environments with coarser, sandy substrates typically exhibit lower cyst abundance due to earlier deposition from an active water transport source or the subsequent removal of finer particles by winnowing (e.g., Marret and Scourse, 2002; Anderson et al., 2003; Pospelova et al., 2004).

Anoxic and oxygen-poor conditions may favour organic matter (and therefore cyst) accumulation and preservation (e.g., Zonneveld et al., 1997; Lundholm et al., 2011; Koutsodendris et al., 2015; van Helmond et al., 2015; Zwiep et al., 2018; Persson and Smith, 2022). High cyst concentrations are often observed in areas with high sedimentation rates, such as fjords and semi-isolated coastal basins, particularly near river mouths (e.g., Thorsen and Dale, 1997; Grøsfjeld and Harland, 2001; Sangiorgi and Donders, 2004; Orlova et al., 2004; Pospelova et al., 2005, 2006, 2008; Bringué et al., 2014, 2016; Lambert et al., 2022; García-Moreiras et al., 2023a; Yedema et al., 2023). These high accumulation rates are often linked with high primary productivity from river-borne nutrients in overlying waters.

Additionally, the inhibition of cyst germination under anoxia conditions may contribute to a high abundance of living cysts, as many cysts require oxygen for germination (Anderson et al., 1987; Kremp et al., 2018). Consequently, the absence of sufficient oxygen reduces losses due to germination in sediments. Even in well oxygenated waters, surface sediments often show reduced oxygen levels with burial depth, which may increase concentrations of subsurface living cysts unable to excyst. By contrast, sediment disturbances, such as burrowing and reworking by benthic organisms and human activities (for instance, bottom trawling, underwater construction and fishing activities), can increase sediment oxygenation (e.g., Michaud et al., 2010) potentially leading to germination, but also to the degradation of organic matter—and, consequently, empty cysts—(e.g., Zonneveld et al., 1997, 2010).

3.2. Methods to extract and concentrate cysts from sediments

For quantitative studies, accurate estimation of cyst abundance in sediment samples is essential. Cyst studies in surface (contemporary) sediments may have the objective of comparing cyst distribution patterns with hydrographic and other environmental parameters to extract ecological signals from cyst assemblages (e.g., Dale et al., 2002; Pospelova et al., 2004, 2008; Sangiorgi et al., 2005; de Vernal et al., 2020; García-Moreiras et al., 2021, 2023a; Lambert et al., 2022; Dzhembekova et al., 2024). Others may aim at linking sediment cyst assemblages with the distribution of their motile phases (vegetative stages) in the overlying waters to study cyst production, dispersal and accumulation patterns, and the factors influencing them (e.g., Godhe and McQuoid, 2003; Anderson et al., 2014; García-Moreiras et al., 2023b; Salgado et al., 2023).

To identify and count living cysts, it is necessary to determine their horizontal and vertical distributions, expressing cyst abundance relative to sediment weight or volume (Anderson et al., 1982, 2014; Dale et al., 1999). Horizontal cyst maps delineate the population's spatial distributions and identify potential seedbeds (Tyler et al., 1982; White and Lewis, 1982; Mardones et al., 2016; Anderson et al., 2014, 2021; García-Moreiras et al., 2021). Aerial contour maps smooth out small-scale irregularities, providing a clear representation of cyst distribution in surface sediments (Fig. 4A). To construct these maps, a depth interval must be selected over which the cyst abundance is to be tabulated. Since marine sediments are typically anoxic below the top few centimetres, counting cysts in the oxygenated surface layer could be an option.

However, a peak of living cysts is generally observed near the sediment surface, just below the oxygenated surface layer. This is the top layer of sediment where oxygen from the overlying water column can diffuse into the pore water and be available for biological processes. Oxygen is primarily consumed by microorganisms in the upper sediment layers, leading to a decline in oxygen concentration with depth (e.g., Cai and Sayles, 1996; Glud, 2008). The oxygenated surface layer is also called the mixed surface layer (MSL) because it is constantly being mixed by biological and physical processes, such as bioturbation, water transport, sediment resuspension, etc. (Song et al., 2022). The MSL thickness—and thereby the depth at which the living cyst peak occurs—is variable between sites and over time: it can extend from a few

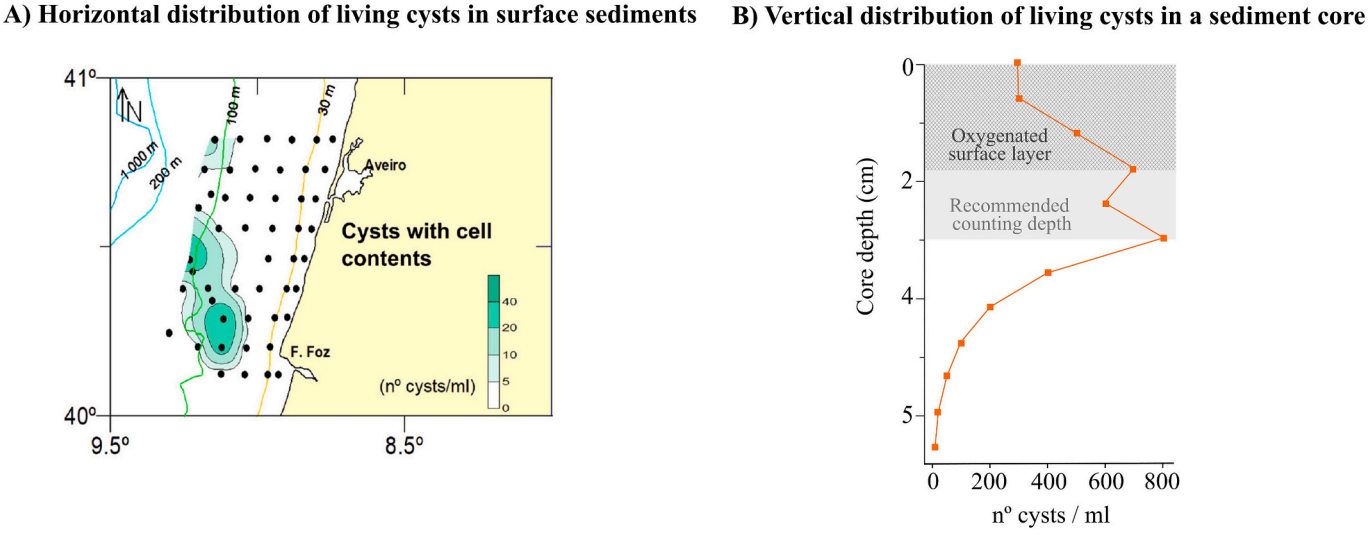

Fig. 4. Examples of hypothetical horizontal (A) and vertical (B) cyst profiles in sediments. The horizontal distribution of cysts in surface sediments (contour curves, A) is based on cyst mapping performed by García-Moreiras et al. (2021) on the Portuguese coast, NW Iberia (© 2021 García-Moreiras et al., doi: https://doi.org/10.3389/fmars.2021.699483, published in *Frontiers in Marine Science* under a https://creativecommons.org/licenses/by/4.0/deed.en CC BY 4.0 license). The vertical distribution (sediment core, B) illustrates a peak of cysts in the subsurface layer (near the oxygenated surface layer), as it is commonly observed in some sediment cores (e.g., Anderson et al., 1982; Keafer et al., 1992). The grey shading within 0–3 cm indicates the recommended depth for counting (living) cysts in surface sediments, and the darker grey the presence of a hypothetical oxygenated surface (mixed) layer.

millimetres to centimetres into the sediment, depending on the sediment composition, the rate of sediment deposition and resuspension, biological activity, germination and species-specific mortality rates (Keafer et al., 1992; Song et al., 2022) (Fig. 4B shows a hypothetical cyst distribution profile for illustrative purposes).

Counting cysts only within the MSL may exclude the majority of living cysts present at a site and would not account for the resuspension of deeper cysts by storms, trawling or bioturbation. Therefore, the ideal depth for counting living cysts should extend below the MSL. However, determining the thickness of this layer, as well as other factors affecting vertical distribution is usually challenging. As a compromise, many studies quantify cysts in the top 2–3 cm of sediment (e.g., Anderson et al., 1982, 2021; Matsuoka and Fukuyo, 2000) (Fig. 4B).

Depths of 1 to 3 cm have commonly be used for mapping recently deposited cysts (e.g., White and Lewis, 1982; Amorim and Dale, 1998; Rochon et al., 1999; Matsuoka and Fukuyo, 2000; Cho et al., 2003; Pospelova et al., 2005; Radi et al., 2007; D'Silva et al., 2010; Anderson et al., 2014, 2021; Mardones et al., 2016; Faye et al., 2018; García-Moreiras et al., 2021; García-Moreiras et al., 2023a; Coussin et al., 2022; Lambert et al., 2022; Kim et al., 2023). Despite surface samples integrate the accumulation of sediments (and cysts) deposited over variable time frames, ranging from several years to centuries depending on the local sedimentation conditions (Dale, 1976; Dale, 2001b), the cysts in the upper few centimetres of sediment generally reflect recent cyst production and environmental conditions prevailing in recent times, as supported by the previously cited studies. Moreover, it is often difficult, if not impossible, to assign a precise age to this surface layer, as the top centimetres of seafloor sediment are typically subject to mixing due to bioturbation, resuspension and other processes. Consequently, some intrusion of older cysts is almost always present. Nevertheless, in studies aimed at detecting and mapping viable cysts near the surface—such as those focused on HABs (see section 10)— the exact age of the cysts is not a critical factor, since these surface cysts can potentially be resuspended into the water column and initiate new blooms.

Vertical profiles of cysts within the top few centimetres of a core help estimate the number of cysts near the oxygenated surface layer, where germination is possible, and the total number of living cysts in a sample (Fig. 4B). The analysis of deeper cores enable to explore the long-term history of cyst deposition, such as in studies of species dispersal (Keafer et al., 1992; McMinn et al., 1997) or environmental changes (Dale et al., 1999). In this case, it is necessary to determine the sedimentation rate at the study site, date the sedimentary sequence and calculate cyst accumulation rates (cysts·cm^{-2}·yr^{-1}). The sedimentation and sediment mixing rates in recent environments (the last ~200 years) can be estimated from the vertical profile of ^{210}Pb isotopes (Keafer et al., 1992; Kemp et al., 2012).

Sample preparation methods are adapted according to the study objectives. Biologists often need to distinguish between living (containing cell contents) and germinated, empty cysts. Therefore, they use preparation methods that enable cyst quantification without disrupting the sediment matrix while preserving the viability of living cysts. In studies aiming to assess the distribution of viable cyst beds with the potential to germinate and initiate new blooms—particularly relevant in the context of HABs—it is essential to determine the presence or absence of protoplasm (i.e., to distinguish between living and empty cysts). For species that produce resting cysts with very short mandatory dormancy periods (e.g., *Gymnodinium catenatum*), pellicle and sexual cyst formation and germination may occur continuously during the late phases of a bloom. As a result, a large proportion of the empty cysts found in the upper sediment layer may originate from the germination of recently formed sexual cysts throughout the maintenance and decline phases of the bloom (Figueroa et al., 2008).

The basic process of sample preparation involves sonication to disaggregate sediment particles, followed by sieving to isolate the appropriate size fraction containing the cysts—although sonication is not recommended when studying the physiology of cyst germination (e.g., the mandatory dormancy period) as it could stimulate germination—. However, using this method alone has the drawback of making microscope-based detection of cysts difficult and enumeration very time-consuming due to the high concentration of other particles (sediment and detritus). For non-quantitative studies, a simple improvement involves shaking the sieved fraction in filtered seawater within a pointed centrifuge tube and allowing it to settle. This produces a thin top layer of finer material enriched in cysts, which can be easily pipetted off for cyst isolation. Additionally, density gradient methods are frequently employed to concentrate and separate cysts from sediment particles for the isolation and enumeration of living cysts (Anderson et al., 2003). Among these, the "Bolch method"—which uses a solution of sodium polytungstate (SPT) with a density of 1.0–1.3 g·cm^{-3} to separate intact cysts from heavier, mostly inorganic particles—is one of the most widely used (Bolch, 1997). Because SPT is non-toxic, cysts isolated using this method remain viable and can be germinated for physiological and other studies. Both living and empty cysts can also be isolated from sediments using SPT at a higher density, close to 2.016 g·cm^{-3} (e.g., Amorim et al., 2002; Marret and Scourse, 2002). Alternatively, colloidal silica can be used to create a density gradient for separation (Schwinghamer et al., 1991).

The primulin staining technique was developed by Yamaguchi et al. (1995) and is generally used to facilitate the identification and enumeration of cysts of *Alexandrium* spp. (e.g., Yamaguchi et al., 2002; Anderson et al., 2005, 2014; Erdner et al., 2010; Dai et al., 2020). Primuline fluorescence highlights cyst walls, allowing detection even in complex sediment matrices at low magnification and often with greater sensitivity than transmitted light microscopy. However, this staining method is not useful for observing morphological details that require greater resolution, such as the spines of some cysts (Matsuoka and Fukuyo, 2000). Furthermore, the walls of the brown cysts formed by some protoperidinioid and gymnodinioid taxa do not stain with primulin (Matsuoka, 1989; Anderson et al., 2003).

When quantifying living dinoflagellate cysts in sediments, researchers must choose between two metrics: cysts per sediment volume—e.g., cysts·cm^{-3}—("wet approach"), and cysts per dry weight —e.g., cysts·g^{-1}—("dry approach"). While the dry approach is standard in geological studies, the wet approach may be more suitable for biological research. For example, when mapping cyst distribution to estimate the number of germinated cells inoculating the overlying water column or the number of cysts produced at the end of a bloom, estimates of cysts·m^{-2} of sediment are needed. This metric must be calculated using the wet volume of sediment. However, variations in the sediment water content and lithology have the potential to introduce errors in the wet approach; the wet volume method is not recommended for cores unless corrected for water content since water content routinely varies with sediment depth. Studies conducted in the Gulf of Maine and northern Alaska (Anderson et al., 2014; Anderson, pers. com.) have shown a strong correlation between the wet and dry methods for the top 1–3 cm of sediment. This suggests that the wet approach can provide reliable data for biological studies in specific contexts (examples in Anderson et al., 2005, 2014; McGillicuddy Jr et al., 2008; Gracia et al., 2013; Lopez et al., 2016; Mardones et al., 2016). It should be noted, however, that cyst assemblages from an oxygenated surface sediment may change significantly from the time of sampling due to disturbance, for example, by bioturbation. Researchers are encouraged to select metrics based on their study goals and, where appropriate use both methods for comprehensive results. Standardising approaches will improve data consistency and facilitate comparisons across studies.

Palaeontologists interested in getting reference data and developing models from living cyst ecology for palaeoecological interpretations employ modified palynological treatments adapted from palaeopalynology. These treatments involve HCl and HF acids to remove the calcareous and siliciclastic fractions of the sediment (e.g., Mertens et al., 2009). These methods have the advantage of cleaning and concentrating dinoflagellate cysts, and overall significantly speed up cyst identification

and census analysis. Absolute cyst concentrations can be determined using volumetric methods (aliquots of known volume; Dale and Fjellså, 1994) or by adding a known quantity of *Lycopodium clavatum* spores as a spike (e.g., Mertens et al., 2009, 2012a; Price et al., 2016). Furthermore, gentle palynological extraction—i.e., using room-temperature acids, limited time in HF (≤2–3 days), oven drying the samples at a temperature of ≤40 °C, etc.—enable the recovery of cysts with and without protoplasm (e.g., Price and Pospelova, 2011).

However, palynological methods have limitations. They most likely kill living cysts, rendering them unsuitable for germination or sequencing studies. Additionally, the procedures are selective; they dissolve calcareous (e.g., cysts of *Scrippsiella*) and siliceous walls (e.g., cysts of freshwater species of the genus *Ceratium*) and can destroy cysts of certain species. For instance, cysts of *Alexandrium* are often underrepresented after palynological treatment.

One consideration is the degree of preservation of *Alexandrium* cysts in sediments; little is known about how long they can remain intact there. Due to their different cyst wall composition, Ando et al. (2024) suggested that these cysts might be more susceptible to degradation than other transparent cysts. Nevertheless, a recent study by Obrezkova et al. (2023) found that *Alexandrium* cysts were well-preserved in most surface samples from the Chukchi Sea, sometimes dominating cyst assemblages (up to 56.6 %; ~3900 cysts·cm^{-3} or ~ 4300 cysts·g^{-1} of dry sediment). *Alexandrium* cysts may have been overlooked in other studies due to their small size, transparent nature, and lack of ornamentation. In such cases, confirmation of the presence of the species through genetic analysis is useful —e.g., via PCR analyses—(Erdner et al., 2010; Bastianini et al., 2016). Another factor that may explain their scarcity or absence in many sediment samples is the mesh size used for sieving. For instance, *Alexandrium* cysts, which can be relatively small (~20 μm in width for *A. tamarense/catenella*; e.g., Bravo et al., 2006), may pass through larger pore meshes and be lost, especially if folded. Many palynological studies use mesh sizes of 20–25 μm to expedite sample processing and cyst concentration, reducing count time (e.g., Ellegaard et al., 1994; Dale et al., 1999; Zonneveld et al., 2001a; Bockelmann et al., 2007; Holzwarth et al., 2010; García-Moreiras et al., 2024). In contrast, in middle- to high-latitude palaeoecological studies, a 10-μm mesh size is standard (e.g. de Vernal et al., 2001, 2013b, 2020). Reliable methods for recovering empty *Alexandrium* cyst records from HAB sites have yet to be developed.

Different extraction methods used for quantitative and qualitative studies of dinoflagellate cysts can significantly affect the results. During the workshop, it became evident that, despite numerous efforts to standardise methodologies, including the use of the *Lycopodium* method (Mertens et al., 2009, 2012a; Price et al., 2016), no single uniform method currently exists for cyst extraction and quantification from sediment. This variability arises partly from site-specific sediment properties, which require technique adjustments. Sieving size is often dictated by the study's objectives. We highlight the need for further methodological studies to investigate how variations in extraction methods affect cyst assemblages and to standardise palynological extraction protocols for better comparability between research groups, particularly for studies focusing on living cysts of HAB species (see below). However, we also acknowledge that minor protocol differences may stem from differences in sediment types (e.g., silica content). Collection and preparation methods should align with study objectives: biological methods for living cysts and palynological methods for fossils and comparisons. Both approaches are valuable for environmental research, where acid-resistant cysts provide insights into ecological changes associated with climate and pollution impacts (Dale, 2000).

It is worth noting two factors common to both methods that may cause different results, and therefore are worth testing in efforts to standardise methods. The first concerns the various types of sieve material used: the often-used flexible woven thin threads of metal or nylon netting, and the more expensive rigid metal plate sieves with precise holes. Differences may be expected between these meshes under water pressure while sieving. In all cases, the size and nature of other particles, which often far outweigh the cysts, will help determine the "effective" sieve size by the extent to which they clog the pores. The degree of sonication will, in turn, affect the "clogging" effect. Nonetheless, the most critical point to make at this stage is that studies referenced in this paper, using different sieves, have confirmed useful signals for tracking the effects of environmental change in dated cores. This includes systematic increases and decreases in small indicator species such as cysts of *Pentapharsodinium dalei* in studies using 25-μm mesh sieves (Dale, 1996).

4. How can we reveal the composition of organic dinoflagellate cyst walls?

4.1. Dinoflagellate cyst wall structure

The basic structure of a dinoflagellate cyst wall consists of a simple wall (named as autophragm by Evitt, 1985) that includes the pedium and, often, another more external layer developed from it, the luxuria. The later usually form ornamentations or projections in the form of columellae (tectum), granules, cones, ridges, processes, etc. (Head, 1994; Williams et al., 2000). The pedium and luxuria are composed of dinosporin, a fossilizable and acid-resistant compound, which is thought to be the main—if not the only—component of fossilised cysts (Fensome et al., 1993). Beneath this dinosporin wall there may be other layers composed of other non-fossilizable labile materials that may be only present in modern cysts (Kennaway and Lewis, 2004).

Most of the compositional analysis methods discussed in the following subsections assess the overall (i.e., bulk) chemical makeup of all the dinoflagellate cyst wall layers, unless stated otherwise. However, these methods are often paired with preceding purification steps (also described below) that remove labile materials inside or adhering to cyst wall layers. Such purification of dinosporin fractions makes the walls of modern cysts chemically more comparable to those of fossil counterparts.

4.2. Dinosporin composition and extraction methods

The chemical nature of dinosporin in resting cyst walls can be examined using analytical methods that provide qualitative and quantitative molecular, atomic, or isotopic information. One of the main methodological challenges is obtaining robust data from small volumes of purified dinosporin fractions. Extracting these purified fractions is labour-intensive and often involves handpicking individual cysts from processed residues. Highly concentrated residues from dinoflagellate blooms are particularly valuable, as they enable more convenient upscaling of sample volumes, at least up to several hundred specimens (Versteegh et al., 2007). Alternatively, large quantities—on the order of milligrams—purified dinosporin fractions can be obtained through laboratory culturing for subsequent analysis (Kokinos et al., 1998; Versteegh et al., 2012). To purify dinosporin fractions, a combination of chemical (e.g., concentrated HCl and HF acids), enzymatic (e.g., cellulase), and physical (e.g., heavy liquid density separation, ultrasonication and filtering) methods can be employed. If chemically unaltered dinosporin fractions are desired, aggressive techniques such as oxidation, acetolysis, and KOH hydrolysis should be avoided (e.g., Wang et al., 2023; Meyvisch et al., 2023).

The field of dinosporin analysis has steadily developed over the past 30 years, following the biopolymer's initial distinction from sporopollenin, the inert compound found in the walls of pollen and spores (Fensome et al., 1993). Currently, our understanding of the molecular nature of dinosporin is largely derived from fragmentation techniques such as pyrolysis gas chromatography–mass spectrometry (Py-GC/MS), which requires several hundred specimens for one analysis, and non-destructive Fourier transform infrared (FTIR) spectroscopy (e.g., Kokinos et al., 1998; Versteegh et al., 2012; Bogus et al., 2014; Gurdebeke

et al., 2020b; Meyvisch et al., 2023; and references therein). FTIR spectroscopy has been widely applied as it enables the collection of macromolecular compositional information from single dinoflagellate cyst specimens when combined with a microscope (micro-FTIR). A contact-based attenuated total reflection (ATR) micro-FTIR method has yielded robust and reproducible data (Meyvisch et al., 2022).

The idea for multiple dinosporin types was proposed based on observed differential preservation of gonyaulacoid and peridinioid cysts (Versteegh and Blokker, 2004; and references therein). This hypothesis was supported by ATR and micro-FTIR data, which revealed five distinct cyst wall compounds potentially related to ecological niches (Meyvisch et al., 2023; Mertens et al., 2024). The most common and well-studied dinosporin type is a transparent variety typical of gonyaulacoid cyst walls, believed to be a cellulose-like macromolecule. Other types of dinosporin are characterised by pigments (possibly eumelanin), proteins, and aromatic or aliphatic moieties. Further research is necessary to establish the connections between these compound classes and their corresponding ecological niches. FTIR spectroscopy enables chemotaxonomical applications (e.g., Bogus et al., 2012; Gurdebeke et al., 2018a, 2020b) and facilitates assessments of compound-specific molecular preservation related to depositional environments (e.g., Versteegh et al., 2020), and molecular alterations during fossilisation (Meyvisch, pers. com.).

4.3. Advances in dinosporin analyses

Despite decades of research, the detailed molecular structure of dinosporin remains elusive. To uncover its structure, a broad range of methodological approaches is needed, employing complementary analytical methods similar to those used for studying other resistant biopolymers, such as sporopollenin (Li et al., 2018a). The most promising method for providing in situ structural molecular information on dinosporin is solid-state nuclear magnetic resonance (ssNMR) spectroscopy, particularly when combined with heteronuclear cross-polarisation magic angle-spinning (2D CP-MAS). However, the primary challenge lies in acquiring milligram quantities of purified dinosporin, ideally ^{13}C and ^{15}N labelled, necessary for such analysis. Realistically, these quantities can only be obtained through laboratory culturing of mixotrophic cyst producers. Another promising method is time-of-flight secondary ion mass spectrometry (ToF-SIMS), which enables nanometre-scale (laterally) molecular fragmentation and subsequent analysis through ionization of the target. The probing depth range of ToF-SIMS can be increased from a few nanometres (in static mode) to several micrometres (in dynamic mode) (Thiel and Sjövall, 2014), allowing separate analyses of different dinoflagellate cyst wall layers. The high spatial resolution of ToF-SIMS essentially overcomes the sample size constraints that challenge classical fragmentation methods, such as Py-GC/MS. However, a recently developed laser-assisted micropyrolysis GC/MS setup appears promising for single-specimen bulk analyses, though does not yet enable depth profiling (Mendonça Filho et al., 2024).

A more convenient single-specimen technique is micro-Raman spectroscopy which provides macromolecular information by revealing the identity and abundance of functional groups associated with polar bonds. This method complements FTIR spectroscopy, which is more sensitive to non-polar bonds. Successful application of micro-Raman spectroscopy requires overcoming two main challenges: reducing spectral interference from autofluorescence and preventing laser-induced photodamage to the sample. Recently, Ando et al. (2024) published the first micro-Raman spectra of dinosporin, achieving this by employing a near-infrared 785 nm laser to reduce the autofluorescence and a 63× water immersion objective, to dissipate heat from the specimens. Moreover, micro-Raman operates at sub-micron spatial resolution, enabling compositional mapping of individual specimens. This capability is paralleled by optical photothermal infrared (O-PTIR) spectroscopy, which has been used to demonstrate compositional homogeneity in dinoflagellate cyst walls at the probed scales (Meyvisch et al., 2023). To investigate macromolecular compositional heterogeneity at even higher spatial resolutions (~10 nm), techniques such as atomic force microscopy-infrared spectroscopy (AFM-IR) and tip-enhanced Raman spectroscopy (TERS) are promising (dos Santos et al., 2023).

In summary, while much work remains to elucidate the composition of dinosporin, several decades of research have laid a solid foundation. It is now established that dinosporin is a biopolymer with variable compositions, distinct from other resistant compounds, such as sporopollenin and algaenan, found in green algae. Recent advancements in robust and accessible methodologies for FTIR (Meyvisch et al., 2022) and Raman spectroscopy (Ando et al., 2024) provide momentum for expanding spectral databases. These advancements will facilitate the exploration of dinosporin's compositional variability, biological and geological implications, and origins.

Significant progress can be expected with the incorporation of state-of-the-art analytical techniques and innovations from rapidly advancing fields such as biomedical and materials sciences. Special focus should also be given to the characterisation of other resistant, insoluble biopolymers. As analytical and culturing methodologies continue to improve, overcoming the current limitations related to dinosporin sample volumes will become increasingly feasible. A detailed understanding of the molecular structure of dinosporin would mark a significant step forward, offering fundamental insights into its biosynthetic pathways, biological functions, and preservability in the fossil record. Furthermore, if the equivalent wall material of ancient acritarchs could be analysed for comparison with modern cyst dinosporin, it could help resolve longstanding questions about potentially shared affinities (see below).

5. How useful are dinoflagellate cysts in phylogeny and evolution?

Cyst morphology, particularly paratabulation features (cyst wall pattern equivalent to motile stage tabulation), has been instrumental in establishing evolutionary relationships among taxa (e.g., Fensome et al., 1993; Mertens et al., 2020a). Cyst morphology is significant at all taxonomic levels, with paratabulation being especially critical at the family rank and above. In the genus *Spiniferites*, which presents a high morphological variability, the presence of an apical boss, as well as the shape of the processes and their type of insertion (gonal or intergonal), are key characteristics for the differentiation of the species (Fig. 2). The shape of the archeopyle is another taxonomic character that also helps classify cysts and establish phylogenetic relationships between them (e.g., Mertens et al., 2020b). For most genera, morphological identification of cysts is meaningful at the species and genus levels. However, in some genera such as *Alexandrium,* morphological identification of cysts is rarely feasible at the species level. Fukuyo (1985) was the first to demonstrate that the cysts of *Alexandrium catenella* and *Alexandrium tamarense* are morphologically indistinguishable. Nonetheless, cysts of some other *Alexandrium* species can still be differentiated based on their morphology, such as *Alexandrium pseudogonyaulax*, which exhibits a paratabulation (Montresor et al., 1993).

Modern techniques, including molecular phylogenetic and multi-omic approaches, contribute to accurate species identification. Omic analyses offer powerful tools to explore the genomic, transcriptomic, proteomic, and metabolomic responses of organisms to external stressors. Integrating these datasets enables validation or refinement of inferences drawn from individual omic levels, offering a comprehensive understanding of biological processes. For example, this approach revealed the roles of alternative splicing and polycistronic expression in generating different isoforms of secondary metabolite biosynthesis (Beedessee et al., 2020). Multi-omics have also elucidated molecular responses to heat stress in bloom-forming species such as *Prorocentrum cordatum* and *P. shikokuense* (Dougan et al., 2023).

Genetic and transcriptomic studies could also lead to a better understanding of the genes that control not only the physiology but also the morphology of cysts. To date, the tools necessary to functionally examine these gene systems are not yet available. The morphological traits of dinoflagellates are likely to be genetically complex, and the genes that determine them could have pleiotropic effects. However, the increased availability of new genetic sequences could facilitate such research in the future.

Additionally, coupling multi-omics with ecophysiological studies and stable isotope tracing can uncover mechanisms underlying dissolved organic nitrogen or phosphorus utilisation (e.g., Smith and Erdner, 2011). These techniques also help reveal the impact of stressors—such as ocean warming, acidification, and eutrophication—on harmful algal bloom (HAB) species, aiding in their prediction, management, and prevention (Wang et al., 2021; Zhang et al., 2022). Combined with morphological methods, these approaches provide deeper insights into character evolution and contribute to reconstructing the tree of life (e.g., Janouškovec et al., 2017; Bolch, 2022). However, resolving deeper nodes in phylogenetic trees remains challenging, and further sequencing efforts are necessary to improve tree rooting. A promising method for generating high-throughput sequence data from uncultured dinoflagellates is single-cell transcriptomics (Cooney et al., 2024), which has been used for swimming cells but could be potentially applied to other life stages, including cysts.

Re-examining the acritarch record has also been emphasised in discussions during the workshop as a way to obtain a more comprehensive understanding of dinoflagellate diversity and evolution. Molecular and biochemical evidence suggests that dinoflagellates originated ~650 Ma ago (Medlin and Fensome, 2013). However, the known (undisputed) fossil record of dinoflagellate cysts does not extend beyond the Triassic period (250 Ma; Fensome et al., 1999; Riding et al., 2022). Acritarchs are organic microfossils with unknown affinity (e.g., Evitt, 1963; Wall, 1965; Dale, 1977b, 2021; Sarjeant, 1978); some of them have turned out to be fossil organic-walled dinoflagellate cysts. The interpretation of the fossil cyst record is challenging because some microfossils cannot be confirmed as dinoflagellate cysts by morphological analyses. Notably, in some dinoflagellate cysts the dinoflagellate tabulation and cyst archeopyle —typical characteristics of dinoflagellates— are not reflected in their morphology (e.g., in cysts of *Alexandrium* spp. and *Karenia mikimotoi*) (Dale, 1977a; Anderson and Wall, 1978; Matsuoka et al., 2006; Liu et al., 2020a; Hu et al., 2022; Li et al., 2024). In these cases, it is possible to obtain evidence that these cysts are formed by dinoflagellates (and that help in their taxonomy and evolutionary studies) through the germination of the cysts and the morphological and genetical analyses of the motile stages; however, germination is not possible in fossilised cysts, and hence other techniques must be explored to study the fossil cyst record.

The sporadic occurrence of triaromatic sterol precursors of dinosterolsin acritarch assemblages from the Proterozoic to Devonian (Moldowan and Talyzina, 1998; Moldowan et al., 2000) suggests that dinoflagellates may have emerged earlier than indicated by the dinoflagellate cyst fossil record. This implies that some acritarchs may represent ancestral forms of modern dinoflagellate cysts. Nonetheless, the potential affinities between Proterozoic acritarchs and contemporary dinoflagellates remain a topic of debate (Servais et al., 2004; Martin and Servais, 2020; Dale, 2023). Reassessing the morphological features of the oldest acritarchs and comparing them to an updated list of known living cysts could provide valuable insights. Particular attention should be given not only to classical features such as archeopyle morphology and tabulation but also to previously overlooked characteristics (Dale, 2023).

In tandem with morphological analysis, advancements in infrared spectroscopy techniques, such as FTIR spectroscopy, have been employed to establish evolutionary relationships and address gaps in dinoflagellate phylogenetic reconstructions (e.g., Bogus et al., 2014; Gurdebeke et al., 2020b).

6. How can the biogeography and ecology of cyst-forming dinoflagellates be studied from cysts?

Dale (1996) demonstrated that dinoflagellate cysts exhibit distinct biogeographical ranges consistent with standard oceanographic biogeographic zones, enabling studies on biogeography and the identification of alien and invasive species (e.g., McMinn et al., 1997; Amorim and Dale, 2006; Ribeiro et al., 2012). The use of dinoflagellate cysts as sedimentary proxies for past environmental conditions relies on the assumption that cyst assemblages reflect the overlying plankton community and prevailing environmental conditions at the time of their formation (e.g., Ellegaard et al., 2017). This approach leverages the known ecology of cysts to reconstruct historical environments from sedimentary cyst records.

Several methods can be employed to study spatial and temporal distributions of dinoflagellate cysts and infer their ecology:

6.1. *Surface sediment studies*

Studying dinoflagellate cyst distribution in surface sediments along environmental gradients provides crucial insights into the relationships between individual taxa and environmental parameters, which is essential for interpretating downcore records. Certain cyst taxa assemblages have been associated with parameters such as sea-surface temperature, salinity and primary productivity, as well as sea-ice cover and pollution, enabling their use as proxies for these parameters in the geological records (e.g., Dale and Fjellså, 1994; Sætre et al., 1997; Thorsen and Dale, 1997; Rochon et al., 1999; de Vernal et al., 1994, 2001, 2013b, 2013c, 2020; Matsuoka, 1999; Dale, 2001a, 2009; Mudie et al., 2002; Pospelova et al., 2002, 2006; Radi et al., 2007; Kim et al., 2009, 2012; Holzwarth et al., 2010; Limoges et al., 2018; Sala-Pérez et al., 2020; García-Moreiras et al., 2021, 2023a; Likumahua et al., 2021; Fatourou et al., 2023; Yedema et al., 2023).

The development of standardised databases linking modern cysts with environmental variables has been instrumental in enabling quantitative palaeoenvironmental reconstructions (e.g., de Vernal et al., 1993, 2001, 2005, 2020; Rochon et al., 1999; van Nieuwenhove et al., 2020). The latest update for the Northern Hemisphere (de Vernal et al., 2020; van Nieuwenhove et al., 2020) includes 1968 sites and 71 taxa. This database can be further expanded through regional additions that adhere to standardised preparation techniques and taxonomy (e.g., Sala-Pérez et al., 2020; García-Moreiras et al., 2021, 2023a; Likumahua et al., 2021; Mudie et al., 2021; Ramírez-Valencia et al., 2021; Coussin et al., 2022; Lambert et al., 2022; Wang et al., 2022; Kim et al., 2023; Li et al., 2020, 2023; Obrezkova et al., 2023; Salgado et al., 2023; Telesiński et al., 2023; Aydin et al., 2024). At the workshop, it was encouraging to see scientists actively gathering new data on cyst distributions in underrepresented modern environments (surface sediments), such as ongoing studies by Winifred and Iratçabal (and collaborators) in the northern Bering Sea and on the French Atlantic coast, respectively. However, many environments remain poorly represented or entirely unrepresented, including deep oceanic environments in warm-temperate latitudes and large areas of the Southern Hemisphere (e.g., Zonneveld et al., 2013; Li et al., 2020; Marret et al., 2020; Thöle et al., 2023; de Vernal and Rochon, 2025).

6.2. *Sediment trap studies*

Sediment trap data complement surface sediment studies by enhancing our understanding of the factors controlling dinoflagellate cyst distribution in marine sediments, phenology of cyst production, and calibration of environmental signals from cyst assemblages. Sediment traps, which are moored or suspended in the water column, collect settling particulate matter, including dinoflagellate cysts (e.g., Honjo et al., 2008). Early uses of traps for cyst analyses were from the major ocean gyres and the Nordic Seas (Dale, 1992; Dale and Dale, 1992).

However, sediment-trap studies providing time series of organic-walled dinoflagellate cyst fluxes and assemblages in estuarine, coastal, and offshore settings are limited (Fig. 5). Among these studies, only a few provide information on the multi-seasonal and occasionally annual or interannual variability of cyst production and sinking fluxes, and even fewer include environmental parameters (e.g., Fuji and Matsuoka, 2006; Pospelova et al., 2010, 2018; Price and Pospelova, 2011; Bringué et al., 2013, 2018, 2019; Pilskaln et al., 2014a; Li et al., 2018b; Shin et al., 2018; Roza et al., 2024a; Table 1, Fig. 5). These data support palaeoceanographic and palaeoenvironmental reconstructions based on dinoflagellate cyst records, and help understand the species ecology—as is the case for the only sediment trap inter-site comparison conducted so far for the genus *Spiniferites* (Pospelova et al., 2018). Sediment trap studies also help elucidate cyst species succession and bloom dynamics, including for HAB-forming species (e.g., Pilskaln et al., 2014a). Challenges associated with sediment trap studies include high deployment and operational costs, mooring difficulties, and trap clogging, particularly for technologically advanced traps. Consequently, these studies require significant funding and time investment, making them more demanding than those from surface sediment and core studies.

One area that remains understudied is the abundance and dynamics of dinoflagellate cysts in the benthic or near-bottom nepheloid layer (BNL), where high concentrations of suspended particles occur. Studies of suspended *Alexandrium catenella* cysts by Kirn et al. (2005) and Pilskaln et al. (2014b) highlight the challenges of measuring and interpreting cyst abundance in the dynamic BNL, which can extend dozens of metres above the seafloor. The existence of widespread BNLs containing substantial numbers of viable cysts indicate a potential source of germinating cysts in certain regions, such as on the Portuguese coast (Atlantic Iberian margin; García-Moreiras et al., 2023b) and the Gulf of Maine (Pilskaln et al., 2014b).

Likewise, few studies have investigated the mechanisms of cyst resuspension caused by storms and tides. A comprehensive study by Butman et al. (2014) explored how resuspension by waves and currents could alter the distribution of overwintering *A. catenella* cysts observed in the previous autumn or contribute cysts to the water column during spring when cysts are viable. Observations and modelling results suggest that sediment layers, including cysts, can be resuspended by waves and currents, with the frequency of resuspension varying interannually. The resuspended cysts in the BNL, are probably deposited and resuspended episodically in shallower waters (e.g., Aretxabaleta et al., 2014), eventually reaching deeper deposition sites with lower energetic conditions which would favour fine sedimentation and the formation of cyst beds on the seafloor. BNLs merit further study because cysts in this layer are not constrained by anoxia, unlike those in sediment. Additionally, they can receive light which, even at very low levels, accelerates germination rates (Anderson et al., 1987; Binder and Anderson, 1986). More intense phenomena, such as tsunamis, could cause massive cyst resuspension events (Kamiyama et al., 2014). In Ofunato Bay, Northeast Japan, historical studies of sedimentary cores have revealed several redeposition events of *Alexandrium* cysts, which have been attributed to the occurrence of tsunamis (Matsuoka et al., 2018).

6.3. Comparison of the cyst and vegetative cell records

Comparing the distribution of cysts in sediments and the water column with the distribution of their vegetative counterpart (planktic motile stage) in overlying waters can provide valuable insights into local ecological signals. However, as highlighted during the workshop, comparative studies involving water, sediment trap and surface sediment data remain extremely rare. In such comparisons, the diversity of palynologically extracted cysts from sediment trap material may exceed the number of dinoflagellate cyst-producing taxa recorded in extensive local phytoplankton datasets (Dale, 1976; Persson et al., 2000; Orlova et al., 2004; Pospelova et al., 2010; Salgado et al., 2023). This discrepancy may stem from the traditionally low-level taxonomic identification

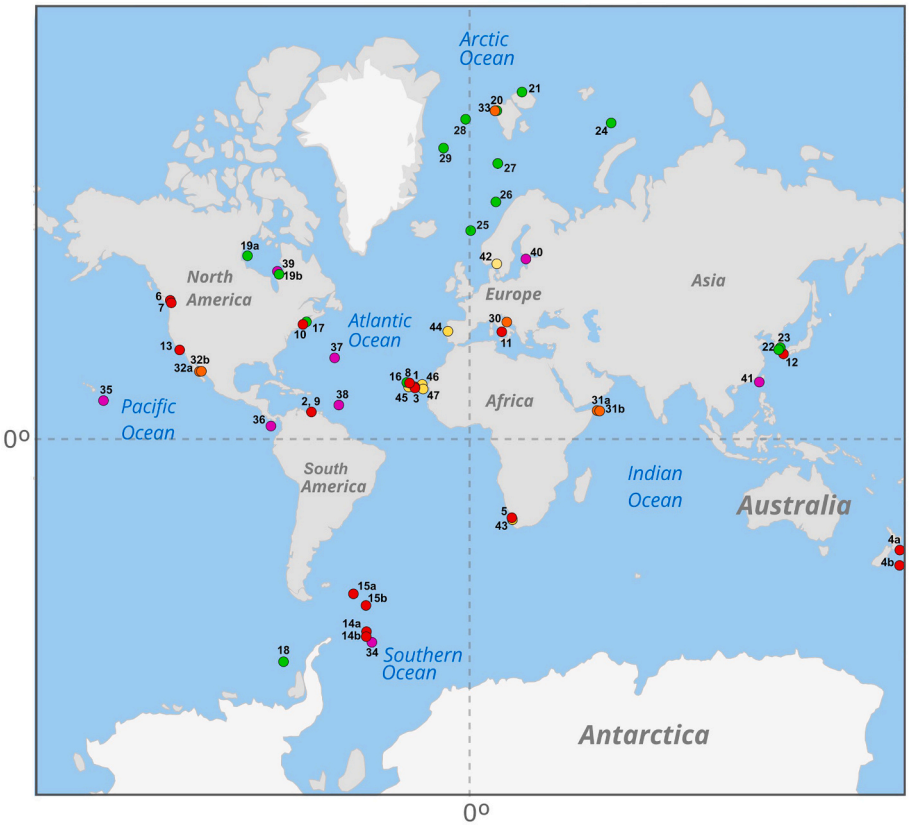

Fig. 5. Map showing locations of sediment traps that include studies of dinoflagellate cyst assemblages. For colour references, see Table 1.

of gonyaulacaceans and protoperidiniaceans in phytoplankton records and spherical brown cysts in sediments.

It is also essential to consider that some species may be more easily detectable in sediments, as they spend most of their life cycle in the sediment as cysts (e.g., Dale, 1983; Zonneveld et al., 2001a). Additionally, rare species may be better represented in sediments and sediment traps, where cysts are more concentrated compared to cells in plankton. Surface sediment samples represent the accumulation of cysts produced in a more or less wide area, at all depths and over a longer time interval—spanning years or even decades, depending on the local sedimentation rate and environmental conditions, e.g., anoxia (e.g., Dale, 1976). Conversely, plankton samples provide only instantaneous space and time snapshots of total annual diversity (Dale and Murphy, 2014).

7. Application of dinoflagellate cysts in palaeoclimatology and palaeoceanography: prospects and applications

Dinoflagellate cysts have been widely used to quantitatively or semi-quantitatively reconstruct sea-surface parameters, including temperature, salinity, sea-ice cover, seasonality, productivity, and human-induced eutrophication (e.g., Edwards et al., 1991; de Vernal et al., 1993, 2000, 2001, 2005, 2013b, 2013c; Dale and Dale, 2002; Pospelova et al., 2002, 2005, 2008, 2015; Sangiorgi et al., 2002, 2003; Sangiorgi and Donders, 2004; Leroy et al., 2013; Datema et al., 2017; Falardeau et al., 2018; Eynaud et al., 2012; Radi and de Vernal, 2008; Hardy et al., 2018; Correa et al., 2021; Fatourou et al., 2023). Reconstructions rely on empirical relationships between cyst assemblages (composition and abundance of taxa) and modern environmental variables, which can then be applied to sedimentary records to infer palaeoenvironmental conditions, often using transfer functions and analogue techniques (e.g., de Vernal et al., 2001, 2013c).

The application of these methods is not without limitations, regardless of the chosen technique (e.g., Guiot and de Vernal, 2007). A primary challenge is ensuring consistency between reference modern data derived from direct observations and sediment samples. Calibration techniques or transfer functions, which use equations to link assemblages with ocean parameters, can yield varying results depending on the assumptions made (linear, modal, non-linear) and the extent of the reference dataset. Analogue techniques, which require extensive reference databases, may suffer from a lack of suitable analogues or analogues with broad ecological affinities. Furthermore, environmental factors driving compositional changes in dinoflagellate cyst assemblages are often region-dependent, adding another layer of complexity (Telford and Birks, 2009; Zonneveld and Siccha, 2016; Hohmann et al., 2020). Validation tests on modern datasets are necessary for assessing the reliability of these techniques (e.g., Guiot and de Vernal, 2007). While analogue techniques often perform best, they have been criticised for potentially overestimating their accuracy due to spatial autocorrelation (e.g., Telford, 2006; Telford and Birks, 2009; Guiot and de Vernal, 2011). Robust regional calibrations can produce reliable reconstructions using transfer functions, provided that all conditions represented by past assemblages are included in the calibration dataset (e.g., Pospelova et al., 2008; Heikkilä et al., 2014; Hohmann et al., 2020).

Given the utility of dinoflagellate cysts for the reconstruction of environmental conditions in marginal marine settings where other micropalaeontological tracers are absent or ambiguous, further efforts to document cyst distributions in these regions are vital. In future studies, the following points should be considered:

- Coastal and estuarine areas where pronounced environmental gradients occur are particularly valuable for understanding relationships between cyst records and environmental factors.
- New cyst records should follow standardised extraction methodologies and nomenclature to ensure comparability across regions and facilitate down-core record interpretation.
- Differentiating nearshore and offshore distributions is crucial to account for cyst transport processes.

Dinoflagellate cysts also hold promise for developing new proxies. For instance, process length variations have been explored as environmental proxies (Mertens et al., 2009, 2011; Gurdebeke et al., 2018b). Early studies identified cyst morphologies associated with low-salinity environments in the Black Sea (Wall et al., 1973). The results from such approaches are promising and warrant further investigation (Mertens et al., 2012b; Hoyle et al., 2019). Additionally, dinoflagellate cysts can help reconstruct some integrative components of the ocean environment. For example, the abundance of *Nematosphaeropsis labyrinthus* has been proposed as a tracer of the mixed layer depth (Wu et al., 2024). This species is widely distributed across oceanic environments, making its ecological signal complex to interpret; however, its potential as an indicator of water mixing depth could prove invaluable for palaeoceanographic studies.

Statistical modelling of ecological signals from modern cysts (Dale et al., 2005) has proven useful for palaeoenvironmental interpretations in biostratigraphy for hydrocarbon exploration—data in company reports, offering similar possibilities for non-industrial applications (Dale and Dale, 2002).

8. How can novel molecular techniques be used in dinoflagellate cyst (palaeo)ecology?

The study of past and present distributions of dinoflagellate cysts has

Table 1
Sediment trap records with dinoflagellate cyst assemblages studied to date. They are arranged by the time period they cover, and the labels and colors refer to those shown on the map (Fig. 5). Most studies sampled at more or less regular intervals during the period indicated, ranging from 3 days to 2 months (some showing several gaps), but a few (marked with *) are integrated samples, thus, they do not show temporal variability in cyst production. This is only a summary with a few features of the sediment trap studies, for more details, we refer to the original publications. (Roza et al. (2024a)); (Bringué et al. (2019)); (Romero et al. (2020)); (Prebble et al. (2013)); (Pitcher and Joyce (2009)); (Pospelova et al. (2010)); (Price and Pospelova (2011)); (Zonneveld et al. (2010)); (Bringué et al. (2018)); (Pilskaln et al. (2014a)); (Montresor et al. (1998)); (Fujii and Matsuoka (2006)); (Bringué et al. (2013)); (Harland and Pudsey (1999)); (Harland and Pudsey (1999)); (Susek et al. (2005)); (Pilskaln et al. (2014a)); (Harland and Pudsey (1999)); (Heikkilä et al. (2016)); (Howe et al. (2010)); (Howe et al. (2010)); (Shin et al. (2012)); (Shin et al. (2018)); (Agafonova et al. (2022)); (Dale and Dale (1992)); (Dale and Dale (1992)); (Dale and Dale (1992)); (Dale and Dale (1992)); (Dale and Dale (1992)); (Bastianini et al. (2016)); (Zonneveld and Brummer (2000)); (Morquecho and Lechuga-Deveze (2004)); (Howe et al. (2010)); (Harland and Pudsey (1999)); (Dale (1992)); (Dale (1992)); (Dale (1992)); (Dale (1992)); (Luostarinen et al. (2023)); (Heiskanen (1993)); (Li et al. (2018b)); (Godhe et al. (2001)); (Joyce and Pitcher (2004)); (García-Moreiras et al (2023b)); (Zonneveld et al. (2018)); (Zonneveld et al. (2021)); (Zonneveld et al. (2022)).

Duration	Reference	Environment	Time record	Region	Label (map)
Multiannual	Roza et al., 2024a	Offshore	~18 yrs	off Cape Blanc (NW Africa)	1
	Bringue et al., 2019	Coastal	12.5 yrs	Cariaco Basin (S Caribbean Sea)	2
	Romero et al., 2020	Offshore	~4.7 yrs	off Cape Blanc (NW Africa)	3
	Prebble et al., 2013	Offshore	~4.1* yrs	E of New Zealand (S Pacific) [2 sites]	4ab
	Pitcher and Joyce, 2009	Coastal	3.5 yrs	Lambert's Bay (Namaqua shelf, S Africa)	5
	Pospelova et al., 2010	Estuarine	~2.8 yrs	Strait of Georgia (BC, Canada, Pacific)	6
	Price and Pospelova, 2011	Estuarine	~2.2 yrs	Saanich Inlet (BC, Canada, Pacific)	7
	Zonneveld et al., 2010	Offshore	~2.7 yrs	off Cape Blanc (NW Africa)	8
	Bringue et al., 2018	Coastal	2.5 yrs	Cariaco Basin (S Caribbean Sea)	9
	Pilskan et al., 2014a	Coastal	~2.2 yrs	Gulf of Maine (NE America)	10
	Montresor et al., 1998	Coastal	2.1 yrs	Gulf of Naples (Mediterranean Sea)	11
	Fujii and Matsuoka, 2006	Estuarine	2 yrs	Omura Bay (Japan)	12
	Bringue et al., 2013	Coastal	~2 yrs	Santa Barbara Basin (S California)	13
	Harland and Pudsey, 1999	Offshore	~2 yrs*	Jane Basin (Antarctica) [2 sites]	14ab
	Harland and Pudsey, 1999	Offshore	~2 yrs*	Scotia Sea (Antarctica) [2 sites]	15ab
Annual	Susek et al., 2005	Offshore	~1.5 yr	off Cape Blanc (NW Africa)	16
	Pilskan et al., 2014a	Coastal	1-1.5 yr	Gulf of Maine (NE America) [3 sites]	17
	Harland and Pudsey, 1999	Offshore	~1 yr*	Bellingshausen Sea (Antarctica)	18
	Heikkilä et al., 2016	Estuarine	~1 yr	Hudson Bay (Canada, Artic) [2 sites]	19ab
	Howe et al., 2010	Estuarine	~1 yr	Inner Kongsfjorden (Svalbard, Artic fjords)	20
	Howe et al., 2010	Estuarine	~1 yr	Rijpfjorden (Svalbard, Artic fjords)	21
	Shin et al., 2012	Estuarine	~1 yr	Gamak Bay (Korea)	22
	Shin et al., 2018	Estuarine	~1 yr	Jinhae-Masan Bay (Korea)	23
	Agafonova et al., 2022	Offshore	1 yr	Eastern Barents Sea (Arctic)	24
	Dale and Dale, 1992	Offshore	~1 yr	Aegir Ridge (Nordic Seas)	25
	Dale and Dale, 1992	Offshore	~1 yr	Lofoten Basin (Nordic Seas)	26
	Dale and Dale, 1992	Offshore	~1 yr	Bear Island (Nordic Seas)	27
	Dale and Dale, 1992	Offshore	~1 yr	Fram Strait (Nordic Seas)	28
	Dale and Dale, 1992	Offshore	~1 yr	Greenland Basin (Nordic Seas)	29
0.5-1 yr	Bastianini et al., 2016	Estuarine	8 months *	Gulf of Venice (NW Adriatic Sea)	30
	Zonneveld and Brummer, 2000	Offshore	~7 months	Somali Basin (NW Arabian Sea) [2 sites]	31ab
	Morquecho and Lechuga-Deveze, 2004	Coastal	5 months (spring-summer) in 2 different years	Bahía Concepcion (Mexico, Pacific) [2 sites]	32ab
	Howe et al., 2010	Estuarine	2 months in spring + 2 months in summer	Outer Kongsfjorden (Spitsbergen, Artic fjords)	33
>1 month <0.5 yrs	Harland and Pudsey, 1999	Offshore	~4 months*	Weddell Sea (Antarctica)	34
	Dale, 1992	Offshore	~3 months*	E Hawaii (N Central Pacific)	35
	Dale, 1992	Offshore	~4 months*	Panama Basin (Tropical Pacific)	36
	Dale, 1992	Offshore	~3 months*	Sargasso Sea (Atlantic)	37
	Dale, 1992	Offshore	~4 months*	Demerara Abyssal Plain (Tropical Atlantic)	38
	Luostarinen et al., 2023	Estuarine	~3 months	Hudson Bay (Canada, Artic)	39
	Heiskanen, 1993	Estuarine	~3 months (in different seasons)	Gulf of Finland (N Baltic Sea)	40
	Li et al., 2018	Coastal	1 month in spring and 1 in summer	W Taiwan (S China sea)	41
< 1 month	Godhe et al., 2001	Estuarine	21 days	Gullmar Fjord (Sweden)	42
	Joyce and Pitcher, 2004	Estuarine	20 days	Lambert's Bay (Namaqua shelf, S Africa)	43
	García-Moreiras et al., 2023b	Coastal	12 days*	Portuguese shelf (E Atlantic)	44
	Zonneveld et al., 2018	Offshore	3 days	off Cape Blanc (NW Africa) [3 drifting traps at different water depths]	45
	Zonneveld et al., 2021	Offshore	7 days	off Cape Blanc (NW Africa) [several drifting traps at different water depths]	46
	Zonneveld et al., 2022	Offshore	5 days	off Cape Blanc (NW Africa) [2 drifting traps]	47

traditionally relied on morphological analyses of cyst assemblages using microscopy. Moreover, molecular techniques, such as single-cell (and single-cyst) PCR and next-generation sequencing have been instrumental in identifying cyst stages of living dinoflagellate species (e.g., Park and Park, 2010; Jung et al., 2018; Liu et al., 2020b) (Fig. 3). However, in recent years, novel molecular techniques, such as metabarcoding, have emerged as valuable tools (e.g., Shokralla et al., 2014). These molecular approaches have proven effective for detecting invasive species (e.g., Holman et al., 2019), particularly in ballast waters (Rey et al., 2019). They also hold promise for studying biogeographical changes driven by climate change (e.g., Beaugrand et al., 2009) and for monitoring invasions via sedimentary ancient DNA (*sed*aDNA) (e.g., Armbrecht et al., 2021).

Metabarcoding complements morphological analyses in biodiversity

and biogeographic studies by enabling the detection of taxa that are difficult to identify based on cyst morphology, including cryptic species (e.g., Wang et al., 2019, 2025). Ancient DNA metabarcoding enables the comparison of molecular assemblages with morphological cyst assemblages and their diversities, offering a more rapid approach to palaeoclimate reconstructions (e.g., Siano et al., 2021). A quantitative comparison between both methods is feasible when metabarcoding data are corrected for gene copy numbers (e.g., Martin et al., 2022). However, methodological advancements are required to ensure DNA is extracted directly from cysts (e.g., Gao et al., 2017). Developing robust reference databases, such as the Protist Ribosomal Reference database (PR^2; Guillou et al., 2012), remains critical, particularly with a focus on single-cell sequences of heterotrophic species. While short-read sequencing has been the dominant approach in metabarcoding, long-read sequencing is gaining importance for improved resolution.

Comparisons of the species diversity derived from cyst morphology and metabarcoding (e.g., Wang et al., 2022, 2025; Liu et al., 2023) reveal that the two methods identify overlapping yet distinct taxa, making them complementary. Discrepancies arise because certain cyst taxa are difficult to identify morphologically at the species level (e.g., *Alexandrium*), and many morphologically identified cyst species lack associated molecular sequences. Additionally, primer choice significantly affects the number of Amplicon Sequence Variants (ASVs). For instance, the V4 and V9 regions of the SSU often yield lower resolution (Mertens et al., 2023).

Different cyst extraction methods, such as palynological or heavy-liquid techniques (Bolch, 1997), and volumetric methods can alter cyst wall morphology, complicating morphological-molecular comparisons. Only cysts containing cell contents, and thus intracellular DNA, should be counted for such comparisons. Furthermore, DNA and cyst assemblages exhibit differential preservation, adding complexity to diversity analyses. To ensure that metabarcoding data accurately reflects cyst assemblages, DNA should ideally be intracellular, extracted directly from inside the cysts. However, the presence of extracellular DNA can contaminate metabarcoding results, though this issue can be mitigated by removing extracellular DNA before extraction (Bairoliya et al., 2022). Finally, DNA records generally do not extend very far back in time (geological scales), which limits their application, although eDNA has been extracted from approximately 2 Ma year old Late Pliocene sediments (Kjær et al., 2022). More comparative studies of morphological and molecular cyst assemblages are needed to identify the limitations of both methods. Applying both approaches together is crucial for developing comprehensive cyst distribution maps, particularly for HAB species, to resolve potential discrepancies. While metabarcoding has primarily been applied to plankton samples and sediments, it has also been used with sediment trap samples to identify dinoflagellate species (Lin et al., 2022a). However, sediment trap samples are usually fixed (typically with formalin), and it is uncertain how this process might affect the preservation of cyst DNA.

Finally, molecular techniques can aid in the development of palaeoenvironmental proxies. For example, the ITS1 nuclear ribosomal DNA of *Polarella glacialis* has been used to reconstruct the occurrence of sea ice (Harðardóttir et al., 2024). Similarly, metabarcoding data have shown potential for reconstructing past sea-ice conditions (De Schepper et al., 2019; Zimmermann et al., 2024).

9. Influence of transport and preservation on sedimentary dinoflagellate cyst assemblages: current knowledge and future directions

Oceanographic and sedimentary processes (e.g., advection by currents, vertical mixing, reworking, bioturbation, and biochemical degradation) can alter the local signal left by dinoflagellate communities in sediments. These processes influence the source-to-sink trajectory of cysts, redistributing those already accumulated in sediments through lateral transport (e.g., Aretxabaleta et al., 2014; Nooteboom et al., 2019; Zonneveld et al., 2018, 2022). Moreover, some of these processes can enhance organic matter oxidation and cyst degradation, which is species-specific, resulting in selective preservation (e.g., Aller, 1994; Zonneveld and Brummer, 2000; Zonneveld et al., 2009, 2021, 2022). These factors collectively modify the original sedimentary signal. Understanding these processes in areas where palaeoceanographic or palaeoclimatic reconstructions are intended enables better interpretation of sedimentary archives. Similarly, understanding cyst resuspension and lateral transport processes (e.g., Butman et al., 2014; Aretxabaleta et al., 2014) is crucial for studies on the bloom dynamics of modern dinoflagellates. One relevant question is how to identify the origins of sedimented cysts. This section explores how lateral transport and selective preservation influence sedimentary dinoflagellate cyst archives and proposes sampling strategies to investigate these effects on palaeoenvironmental and ecological signals.

9.1. Lateral transport

Studies investigating the impact of lateral transport on dinoflagellate cysts are scarce. Investigations have demonstrated that, in the studied regions, lateral transport affects the distribution of cysts in the water column: in estuarine environments in the Gulf of Maine, NE North America (Aretxabaleta et al., 2014; Pilskaln et al., 2014a, 2014b), in the Baltic Sea (Sildever et al., 2017), on the shelf of the Iberian Peninsula, Portugal (García-Moreiras et al., 2023b), on the slope of the Somali Basin, NW Arabian Sea (Zonneveld and Brummer, 2000), and the slope off Cape Blanc, NW Africa (Zonneveld et al., 2018, 2022; García-Moreiras et al., 2024). Sedimentary records in these regions are, to a certain extent, influenced by allochthonous cysts produced in areas variously distant from the sampling point. However, these studies demonstrated that the extent, magnitude and direction of cyst transport can vary greatly between regions, and within the same region, spatially and temporally, depending on the distance from the coast, water depth, and hydrographic changes over time.

In coastal environments with complex hydrodynamics, the deposition site of newly formed cysts may vary somewhat from the location of the vegetative, motile stages. In other locations, there is a tight association between the distributions of blooming vegetative stages and deposited cysts. One example of the latter is when cyst formation and deposition occur at convergence fronts, where a combination of dinoflagellate swimming behaviour and hydrographic structure leads to dense blooms at the frontal interface and cyst deposition in that area (e.g., García-Moreiras et al., 2021; García-Moreiras et al., 2023b). In some estuaries where salinity fronts form and oscillate with tides and storm runoff, a well-defined cyst accumulation zone can develop (e.g., Tyler et al., 1982; Anderson et al., 2005).

Despite the variability in bloom location and extent in some areas, cyst beds can be remarkably persistent through time, reflecting the general consistency of coastal currents, water quality conditions, sedimentary dynamics, and bottom topography (e.g., Pospelova et al., 2004, 2005; Krepakevich and Pospelova, 2010; Anderson et al., 2014; Gurdebeke et al., 2018a; Price et al., 2016). For example, a nine-year time series of *Alexandrium catenella* cyst maps in the Gulf of Maine showed remarkable geographic consistency from year to year, with cyst hotspots persisting at the same locations, despite interannual variations in cyst abundances (Solow et al., 2014). This enabled the generation of a mean cyst map highlighting persistent areas of high and low abundance that can be linked to hydrographic and topographic features. The mean cyst distribution map is currently being used to generate an annual cyst map for *A. catenella* based on a subset of new sediment samples. The mean deviation at those sites is estimated, and differences are extrapolated to other unsampled stations to derive a regional distribution, significantly reducing the cost of annual cyst surveys.

Studies of dinoflagellate cysts in surface sediments from nearby New England estuarine waters have demonstrated for the first time that dinoflagellate cysts reflect the variability of water quality parameters at

small spatial scales (approximately 200 m) (Pospelova et al., 2004, 2005). This research highlighted that cyst assemblages reflect the differences in complex hydrological characteristics between coastal lagoons, which exhibit substantial spatial variability in water quality parameters, and also within each lagoon or bay. Thus, the cyst assemblages provide valuable insights into the environmental conditions even in highly heterogeneous estuarine or coastal environments where lateral cyst transport is limited or absent.

In some regions, back-track particle modelling combined with spatio-temporal observations suggested that lateral advection of cysts can significantly vary in intensity and direction depending on the distance from the coast and over a few days, along with hydrodynamic changes driven by upwelling events (García-Moreiras et al., 2023b). On the other hand, a modelling study by Aretxabaleta et al. (2014) demonstrated that resuspension of *A. catenella* cysts in the Gulf of Maine is limited, with most sediment redepositing near its source, and only a small fraction travelling long distances. Despite erosion events, the impact on overall cyst concentration is minimal, as the majority of cysts remain buried deeper in the sediment.

Particle transport in oceanic environments is controlled by complex interactions between hydrodynamics and other environmental factors, such as bathymetry and particle aggregation (e.g., Wang and Andutta, 2013; Aretxabaleta et al., 2014; Nooteboom et al., 2019). Flocculation and the formation of aggregates can increase the sinking velocity of particles, reducing lateral advection (e.g., Iversen and Ploug, 2010; Wang and Andutta, 2013). Consequently, untangling the respective contributions of local production, lateral advection, and vertical mixing to the cyst assemblages preserved in sediments remains challenging.

During the workshop, diverse sampling strategies were discussed that may provide insight into the role of lateral transport on cyst distribution and accumulation patterns on the seabed. Cyst assemblages can be analysed from sediment traps placed at different depths and positions along a transect, together with surface sediment sampling (Fig. 6A). Some studies using this type of methodology have shown interesting insights into the effects of surface and deep transport, resuspension and degradation on cyst distribution in the water column (Dale, 1992; Dale and Dale, 1992; Zonneveld and Brummer, 2000; Pilskaln et al., 2014b; Zonneveld et al., 2021). Ideally, the sediment traps are placed along ocean currents to investigate the influence of currents on cyst advection. However, sediment trap deployment, particularly in oceanic (deep) environments, requires a high investment of human and financial resources to organise cruises and collect samples regularly. Early studies from the open ocean were only possible by participation in large, expensive global programs aimed at much broader scientific objectives (Dale and Dale, 1992) and future studies will most likely have to follow suit, due to funding restrictions.

Alternatively, sampling water at different depths and distances from the coast, following an inshore-offshore transect, using in-situ pumps or other water sampling devices (for instance, oceanographic bottles and rosette samplers as in Tyler et al., 1982), also enables studying the influence of lateral transport on the vertical and horizontal distribution of cysts. Such studies can provide useful data to investigate deep and surface cyst transport and sediment resuspension processes, particularly if they are compared with cyst records in the underlying surface sediments (e.g., Zonneveld et al., 2010, 2018, 2022; García-Moreiras et al., 2023b, 2024). When cyst assemblages are similar at different water depths in the same station, it can be inferred that vertical transport dominates over lateral transport (pink samples in Fig. 6B). In contrast, if lateral transport prevails, similar cyst assemblages at the same depth in different stations are likely (blue samples in Fig. 6B). Moreover, if local resuspension of sediments is significant, with vertical advection from sink to source, similar cyst assemblages will be found between surface sediments and overlying water samples (yellow samples, Fig. 6B). Some similarities between cyst assemblages in sediment and water could occur when vertical transport is reversed, especially when cyst export flux is prominent. For example, when a cyst-forming species proliferates and encysts massively in water, large abundances of its cysts could be seen in both types of samples, sediment and water (e.g., round brown process-bearing cysts in García-Moreiras et al., 2023b). However, the species composition between the samples should differ because the surface sediment sample contains cysts accumulated over a long time (years to decades, depending on the sediment accumulation rate), unlike the water samples. In any case, analysing cyst assemblages at various depths in the water column should help identify the dominant type of vertical transport, source-to-sink or sink-to-source.

A limitation of the water sampling method is that profile cyst distributions are obtained as snapshots at a given moment. Therefore, to study the variation of cysts over time, several surveys must be conducted regularly, with significant increases in the resources invested. This method also makes it challenging to track large-scale oceanographic events that may be infrequent and whose impact on cyst transport, and therefore on the local sediment signature, may be significant. Ocean modelling and particle tracking techniques, in combination with in situ observations, help trace dinoflagellate cyst dispersal and assess how oceanographic processes, such as upwelling, affect their transport and accumulation in the sediments. In all cases, it is recommended to guide sampling site selection by using seafloor multibeam bathymetry and sub-bottom profile data, which provide insights into the depositional environment, thereby helping to avoid scoured or eroded seafloor and disturbed sediments.

9.2. Selective preservation

As mentioned earlier, organic matter (and hence most dinoflagellate cysts) can be degraded by microbial or chemical action in the water column and sediments, especially in the presence of oxygen (e.g., Zonneveld et al., 1997; Wakeham and Canuel, 2006; Gray et al., 2017; Persson and Smith, 2022). The degradation of cysts accumulated in sediments is species-specific: some cyst taxa such as most mixotrophic gonyaulacoids are resistant to degradation and could be overrepresented in the sedimentary records, while abundances of heterotrophic peridinioids that are more sensitive to degradation, decrease (Zonneveld et al., 1997, 2001b, 2008, 2010, 2019; Sangiorgi et al., 2002; Versteegh and Zonneveld, 2022; van Helmond et al., 2015; Gray et al., 2017; Zwiep et al., 2018). These differences in preservation are caused by the varying chemical compositions of the cyst walls (Kokinos et al., 1998; Versteegh and Zonneveld, 2022; Ando et al., 2024).

Understanding the factors controlling the preservation of cysts is essential for a reliable interpretation of their fossil record. Comparing sediment trap time series with contemporary sediment records may help assess potential alterations in the sedimentary cyst records caused by selective degradation and other factors, such as lateral transport or resuspension. Comparing the trap material with the sediment should be done cautiously, and the following must be accomplished for reliable comparison:

1) The sediment record must be well constrained chronologically to ensure cyst production and accumulation are compared over the same period, and that bioturbation did not affect the stratigraphy. This also requires a continuous sediment trap record and adequate sedimentation rates at the study site. For example, if a sediment trap is not operational for several weeks, such as a phytoplankton bloom and a significant cyst flux that would be recorded in the surface sediment, may easily be missed. This could lead to inconsistencies when comparing the two samples. In an open-ocean environment with low sedimentation rates, we cannot expect accurate comparisons between even a continuous annual or decadal sediment trap record and the surface sediments, as one centimetre of sediment can represent hundreds to thousands of years.
2) Both types of samples (sediment trap and surface sediment) must be processed using the same methods and preferably counted by the same individual to minimise potential cyst identification issues.

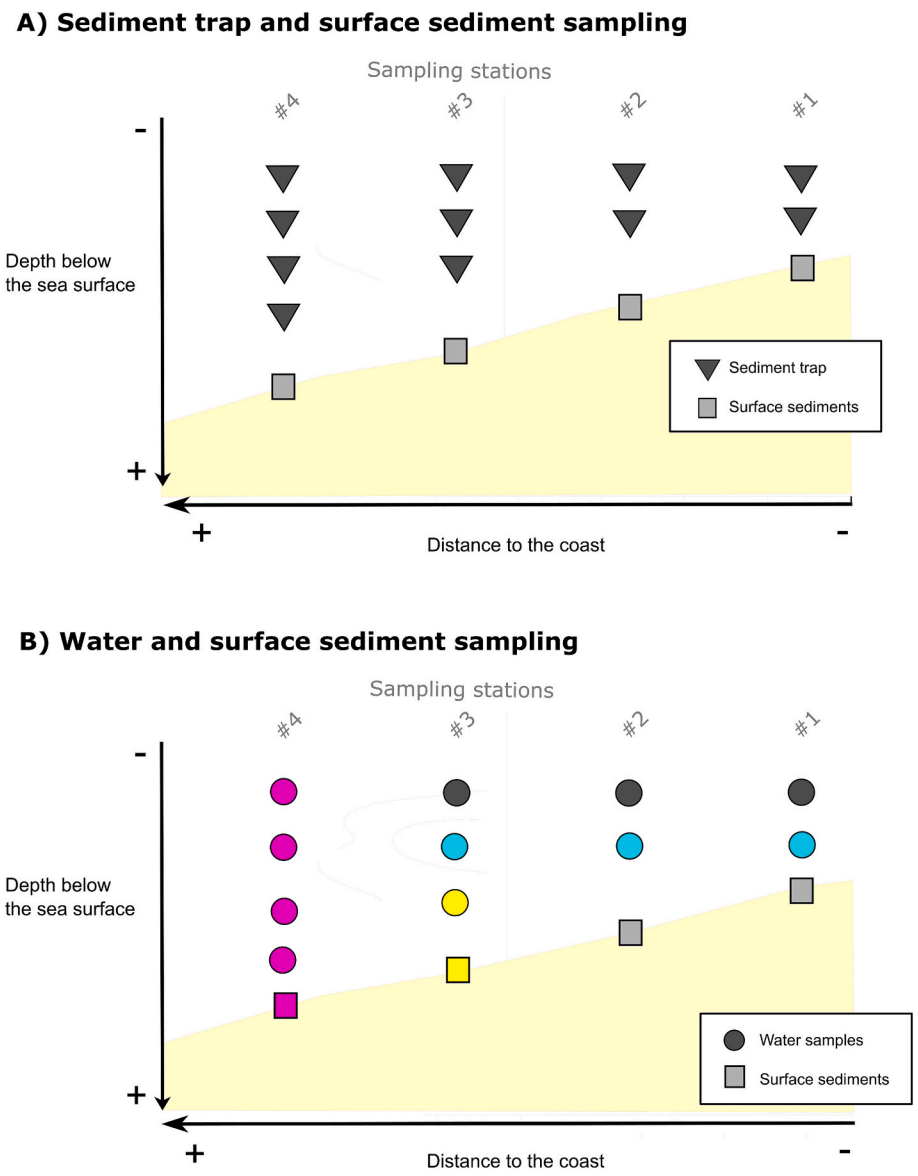

Fig. 6. Proposed sampling strategy using sediment traps (A) and water sampling (B) along a cross-shore transect to study lateral and vertical advection of dinoflagellate cysts. In panel B, similar colors indicate comparable dinoflagellate cyst assemblages: the pink samples indicate that vertical transport predominates over lateral transport, while the blue colour indicates a predominance of lateral transport; at station #3, different types of transport predominate depending on the depth in the water column (yellow, vertical transport; blue, horizontal transport). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3) To rule out lateral transport affecting the source-to-sink trajectory of cysts and allochthonous cysts influencing the sediment cyst assemblages, thorough knowledge of the hydrodynamics of the area is advisable. It might help to place the sediment trap as close to the seafloor surface as possible, but this might cause resuspension and should be done with caution. Analysing sediment traps located at different depths (in the same station) may enable assessing cyst transport in the water column and detecting possible allochthonous cysts in the sediments.

Several studies have already used the above methodology and showed a good match between cyst assemblages found in sediment traps and those in well-dated cores or surface samples (both in cyst composition and abundances) (Pospelova et al., 2010; Price and Pospelova, 2011; Bringué et al., 2013; Heikkilä et al., 2016). This body of research suggests that selective cyst preservation and lateral transport do not pose significant issues in some environmental settings, such as coastal inlets, estuaries, or semi-enclosed basins like the Santa Barbara Basin and Hudson Bay. These observations suggest that the source-to-sink trajectory of cysts was not significantly altered and that the sediment records accurately represent local cyst production. In contrast, some studies found discrepancies between cyst assemblages in sediment trap and core samples that were interpreted as a result of selective preservation and lateral transport (Montresor et al., 1998; Harland and Pudsey, 1999; Zonneveld and Brummer, 2000; Prebble et al., 2013; Roza et al., 2024b). However, many of these studies were conducted in open, deep-sea settings where sedimentation rates are substantially lower, and a few time series lacked continuous records.

In summary, from the few observations made through the comparison of cyst records between sediment trap and surface sediments, we could hypothesise that in semi-protected environments with restricted water circulation, high sedimentation rates and lower oxygen content in the sediments, the degradation and lateral transport of cysts will be minimal, and therefore the local signal in the sediment is well preserved.

The main question of whether cysts in deep-sea sediments truly represent the local signal, i.e., the planktic dinoflagellate communities living in overlying waters, remains unresolved.

In addition to the suggestions above, there is a need for studies of living cyst-forming dinoflagellates (motile stages) from oceanic waters. Molecular methods applied to water samples or net tows may offer a more practical approach, though this would eventually need to cover an adequate time series, and cysts and motile stages would need to be differentiated.

10. Integrating cysts in studies of dinoflagellate bloom dynamics, including HABs

10.1. Harmful algal blooms and the ecology of encystment

Planktic dinoflagellates often exhibit seasonal to multiannual dynamics, with periods of low cell numbers followed by blooms during which a small number of species dominate the phytoplankton community, sometimes reaching impressive biomasses (e.g., more than 1300 mg chl $a \cdot m^{-3}$ for a bloom of *Lingulaulax polyedra* (formerly *Lingulodinium polyedra*), Wilson et al., 2022). Such high biomass blooms may cause abrupt changes in the physico-chemical properties of seawater, leading to hyper-oxygenation and low pH values during the day, and low oxygen at night, secretion of mucilage and other organic substances, or decomposition and formation of anoxic sediments when the remains of the bloom decay (e.g., Brownlee et al., 2005; Pitcher and Louw, 2021; Zingone et al., 2021). Additionally, toxins produced by some dinoflagellates can be accumulated by filter-feeding shellfish- and finfish, and transferred through the food web. When toxins in contaminated shellfish and fish exceed established regulatory levels, they become unsuitable for human consumption, and harvesting and fishing bans are enforced by health authorities.

The above-mentioned microalgal proliferations, with detrimental effects on ecosystems and human activities, are referred to as HABs (harmful algal blooms). Within the currently known cyst-forming dinoflagellates, toxic HAB-forming species mainly include yessotoxin- (*L. polyedra*, *Protoceratium reticulatum* and some species of *Gonyaulax spinifera* complex) and saxitoxin-producers (*Alexandrium* species (several), *Gymnodinium catenatum*, and *Pyrodinium bahamense*). Resting cyst formation (encystment) and germination (excystment) are crucial transitions in the life cycles of these species. The cysts produced by the motile phase in the water column can remain suspended for a time in the Benthic Nepheloid Layer (BNL) and ultimately accumulate on the seafloor. These living cysts, with the potential to germinate and produce new motile phases, form a seed reservoir that can be resuspended and feed new phytoplankton blooms (Anderson and Wall, 1978; Nehring, 1996; Pilskaln et al., 2014b). Therefore, encystment and excystment studies are highly relevant to understand the species-specific bloom dynamics.

Although the formation of resting cysts is tightly linked to sexual reproduction, it has been shown that some cyst-forming dinoflagellates can also reproduce sexually and form motile planozygotes that can divide and produce vegetative cells through meiosis without going through a maturation to hypnozygote and resting cyst phase (Figueroa et al., 2015) (Fig. 1). This led Lin et al. (2022b) to propose two different sexual reproduction pathways in dinoflagellates: “sex for proliferation” (i.e., without cyst formation) and “sex for encystment”. While the former seems to occur when conditions are favourable for vegetative growth, the latter appears primarily as a resistance strategy. For many dinoflagellate species, cysts are known primarily as a resting stage that enables organisms to survive periods of unsuitable conditions for vegetative growth, similar to seeds in annual plants (Anderson et al., 1983; Lopez et al., 2019).

Results from laboratory experiments suggest that encystment involves a modest fraction of the total population in culture, less than 40 % (e.g., Dale, 1983; Anderson et al., 1984; Anderson and Lindquist, 1985), although Olli and Anderson (2002) reported encystment rates near to 100 % in the species *Scrippsiella* cf. *lachrymosa*. Recent studies using continuous, in situ flow imaging recorders during an *Alexandrium catenella* bloom have shown that encystment rates in natural environments can be much higher than suggested in laboratory studies. Using an Imaging FlowCytobot (IFCB) deployed in a Cape Cod estuary, Brosnahan et al. (2015, 2017) were able to document the timing and extent of gametogenesis and planozygote formation, revealing a development phase of sustained vegetative division lasting ~three weeks, followed by the rapid formation of small gamete cells (three days), ultimately representing 80–90 % of all *A. catenella* cells. Thus, gametogenesis, the first step in the encystment pathway, was both concerted and nearly complete in its extent. The gametic period coincided with a spike in the frequency of fusing gametes and was followed by a zygotic phase (four days) dominated by swimming zygotes (planozygotes), which are the precursors to resting cysts. Interestingly, those planozygotes altered their diel vertical migration behaviour compared to vegetative cells, bringing them closer to the surface for more sunlight during the day, thereby facilitating population dispersal through the shallow inlet channel that otherwise retained the migrating vegetative cells which stayed deeper in the water column (Brosnahan et al., 2017).

Encystment has been linked to various stress factors, including nutrient depletion (e.g., Anderson et al., 1984; Figueroa and Bravo, 2005), temperature variations (e.g., Anderson et al., 1984) or salinity changes (e.g., Zonneveld and Susek, 2007), although some studies report no obvious stress (Anderson et al., 1983; Brosnahan et al., 2014). Conversely, other factors, such as turbulence can hinder mating and encystment (Smith and Persson, 2005). Some biological signals also seem to promote cyst formation, including the presence of specific bacteria (Adachi et al., 1999) or parasites like *Ameobophrya* (Chambouvet et al., 2011; Velo-Suarez et al., 2013; Brosnahan et al., 2015, 2017), although some bacteria might also inhibit encystment (Adachi et al., 2002). Interestingly, cyst formation seems to be an imperfect defence mechanism, as some parasites can subsist and remain dormant within resting cysts, successfully resuming infection after the germination of their hosts. The role of cysts in parasitic infections among dinoflagellates remains a topic of further inquiry. Additionally, the existence of chemical communication between dinoflagellate cells that could favour synchronised encystment still needs to be investigated, as there are suggestions of population density-driven encystment in field populations (e.g., Wyatt and Jenkinson, 1997; Brosnahan et al., 2015, 2017).

The inducing factors and success rates, as well as other parameters related to cyst formation in cyst-forming dinoflagellates, remain poorly understood. They may also be highly variable among different species and regions. It is also unknown to what degree some or all of these parameters vary in nature compared to laboratory experiments under controlled environmental conditions. The development of new instruments for in situ observation of encystment dynamics, such as the aforementioned IFCB, and new molecular approaches mentioned in section 5, offers a unique opportunity to study the life cycle of dinoflagellates and hopefully will help fill the knowledge gaps on encystment dynamics.

10.2. Dormancy and excystment

Germination or excystment follows the dormancy period; however, the dormancy terminology must be used with care. The literature on seeds of higher plants defines ‘dormancy’ as the suspension of growth by active endogenous inhibition, and ‘quiescence’ as the suspension of growth by unfavourable environmental (i.e., exogenous) conditions (Anderson et al., 2003). Thus, dormant seeds cannot germinate, even under optimal environmental conditions, while quiescent seeds are competent to germinate but are inhibited by environmental factors. For dinoflagellate cysts, recent work (Fischer et al., 2018; Lopez et al., 2019; Brosnahan et al., 2020) has revealed two types of dormancy in several

species. The first, called mandatory dormancy, occurs immediately after cyst formation and is viewed as a maturation period required for cysts to germinate (e.g., Anderson and Morel, 1979). The second, called secondary dormancy, is a reversible state that underlies dormancy cycling and can recur many times within a single cyst's lifetime (Fischer et al., 2018; Lopez et al., 2019).

Laboratory experiments have shown that most dinoflagellate cysts need a mandatory dormancy from a few days to several months before germinating (Anderson, 1980; Blanco, 1990; Bravo and Anderson, 1994; Amorim et al., 2002; Figueroa and Bravo, 2005; Figueroa et al., 2008). Field observations indicate that the duration of the dormancy may be significantly variable within taxa. Comparisons of the abundances of cysts with and without cell contents in sediment traps at different depths in the water column, suggest that some cysts can germinate very fast—within a couple of days or even less—after their formation in the water column (Pospelova et al., 2010; Price and Pospelova, 2011; Zonneveld et al., 2022).

The mandatory dormancy period is followed by quiescence, then germination or excystment. The combination of temperature-based dormancy cycling control and exogenous (temperature- and oxygen-based) triggers for the germination of quiescent resting cysts ensures that germination is restricted to times of year and positions within sediments that are favourable for the development of new planktic blooms. Several conditions must be met for that germination (reviewed in Fischer and Brosnahan, 2022): i) cysts must be quiescent (Anderson and Keafer, 1987; Fischer et al., 2018); ii) oxygen must be present (Anderson et al., 1987; Kremp et al., 2018); and iii) temperature must be within a suitable range (Kremp and Anderson, 2000; Anderson and Rengefors, 2006; Fischer and Brosnahan, 2022). In some species, light is also needed (Binder and Anderson, 1986; Anderson et al., 1987; Kremp and Anderson, 2000). When these prerequisites are met, temperature is the primary determinant of the germination rate (e.g., Bravo and Anderson, 1994).

Recent work has shown that the duration of secondary dormancy in two dinoflagellates is regulated by temperature (Fischer et al., 2018; Lopez et al., 2019), with a quantifiable amount of cold exposure (chilling units) needed to transition the cyst from dormancy to quiescence. Similarly, warm temperatures, quantified as degree days (Brosnahan et al., 2020), can force the ungerminated cyst back into dormancy (hence "secondary dormancy"). This cycling between quiescence and dormancy can continue for many years if a cyst is located in sediments where conditions inhibit germination. Cysts of some species can remain in a resting state for long periods in anoxic sediments and still germinate from layers up to 100 years old, with constitutive mixotrophic species appearing to be preserved the longest (e.g., Lundholm et al., 2011). In diatoms, strains have been established from resting spores extracted from 7000 year old anoxic Baltic Sea sediments (Bolius et al., 2025). Nonetheless, losses of living cysts can be substantial during cyst dormancy, as Persson and Smith (2022) observed only one year after isolation in sediment bags. In their study, anoxic environments preserve living cysts much better than oxygenated ones.

Temperature-germination rate relationships are therefore fundamental to understanding cyst bed persistence because they control a significant component of the total cyst loss rate. Additionally, environmental signals that prevent excystment have been identified, including nutrient depletion (Rengefors and Anderson, 1998) and occurrences of chemical cues from herbivorous zooplankton (Rengefors et al., 1998).

10.3. Sampling and cyst study approaches

Cyst production by bloom-forming species can be studied by sampling or directly observing plankton in situ, using sediment traps or sampling the surface sediments. For some species (*Lingulaulax polyedra*, *Protoceratium reticulatum* and *Pyrodinium bahamense*), cysts are well-described and can be easily enumerated. For others, however, the identification and enumeration of cysts can be trickier, either because the descriptions of cyst stages corresponding to toxic motile forms are more ambiguous (e.g., *Gonyaulax. spinifera*, Mertens et al., 2015), or because cysts can rarely be identified morphologically at the species level (e.g., *Alexandrium*, Mertens et al., 2020a). In such complex cases, molecular techniques can help identify species (barcoding) and quantify the number of cysts of a species present in a sample, using quantitative PCR (qPCR) or digital PCR (dPCR) (Erdner et al., 2010; Bastianini et al., 2016).

Most studies on factors affecting cyst germination are based on controlled laboratory experiments. Ishikawa et al. (1995, 2007) have developed germination chambers to investigate in situ factors affecting excystment and germination rates in coastal environments. Other in situ trap methods have also been successfully used (e.g., Anglès et al., 2012). Despite the promising results of these methods, they have been rarely employed to date. The ongoing technological revolution in in situ systems, which enables automated imaging and analysis of plankton—such as the previously mentioned IFCB—will undoubtedly enhance our understanding of the underlying factors driving life-cycle transitions. However, these systems remain economically inaccessible to most phytoplankton laboratories.

Quantifying and mapping cyst production of a HAB species can help identify "seed banks" (or cyst beds) of resting cysts that are thought to have a critical ecological role in supplying seed populations for future blooms (e.g., Anderson and Wall, 1978). For this purpose, quantifying full cysts, with protoplasm, in surface sediments is needed. Ideally, the viability of these cysts (i.e., their potential to germinate) could be tested by culturing them in the laboratory. This knowledge can inform policies that limit activities disturbing the sediment, such as dredging and trawling in known cyst beds, thus reducing the risk of inoculating a bloom from human-driven resuspension of resting cysts (Mertens et al., 2023).

Efforts to unveil the driving factors for the cyst production of toxic dinoflagellates have employed several techniques. The most common and affordable method for quantifying cysts, including those affiliated with toxic species, involves studying cysts in surface sediments and linking their geographical distribution with local or regional environmental factors, such as nutrient availability, temperature, salinity, mixed-layered depth, etc. (e.g., Amorim and Dale, 1998; Vink et al., 2000; Marret et al., 2004; Pospelova et al., 2008; Radi and de Vernal, 2008; Bouimetarhan et al., 2009; Bravo et al., 2010b; Ribeiro et al., 2012; Mudie et al., 2017; Sala-Pérez et al., 2020; García-Moreiras et al., 2021, 2023a). However, the results do not provide insight into the species' bloom dynamics, such as their seasonal, annual, or interannual patterns, because, as already discussed, surface sediments may cover several to hundreds of years. Therefore, long, continuous, and high-resolution time-series datasets are required, which can be obtained using sediment traps or frequent surface sediment sampling (e.g., Bringué et al., 2013, 2019; Roza et al., 2024a).

Cyst records in sediment cores are a useful resource for studying past bloom dynamics. Several studies have reconstructed the historical dynamics of bloom-forming species (including toxic ones) and invasive species using cysts in dated sediment cores (Thorsen et al., 1995; Fjellså and Nordberg, 1996; McMinn et al., 1997; Kim et al., 2009; Ribeiro et al., 2012; Bringué et al., 2014). The quantification of cysts produced by bloom-forming species in sediment cores and their comparison with modern analogues allows inferences about past blooms, suggesting possible scenarios for future blooms (Dale, 2021). Moreover, recent molecular methods such as *sed*aDNA (see Section 8) offer new perspectives for analysing the sedimentary cyst record (Armbrecht et al., 2024). Molecular analyses of sediment cores can reveal large changes in the composition of the dinoflagellate community linked to significant anthropogenic disturbances (e.g., Siano et al., 2021). These approaches can help shed new light on the historical ecology of coastal ecosystems, including HAB dynamics. However, the degradation of cyst DNA can limit quantitative approaches by qPCR in sediments older than a few hundred years (Klouch et al., 2016).

10.4. Cyst toxicity

Another crucial question regarding the cysts of HAB-forming dinoflagellates is their toxicity. Dale et al. (1978) suggested that resting cysts of *Alexandrium catenella* are at least an order of magnitude more toxic than their equivalent motile cells, and Oshima et al. (1992) found that *Alexandrium* cysts can be six times more toxic than motile cells. On the contrary, Shankar et al. (2023) observed that *Pyrodinium bahamense* cysts exhibit lower toxicity and a distinct toxin profile compared to the corresponding vegetative stage. One possible explanation for this discrepancy relates to the impact of nutrient limitation (sometimes invoked as a trigger for sexuality) on toxicity. Anderson et al. (1983, 1990a, 1990b) demonstrated that phosphorus-limited *Alexandrium* cells can be 10 times more toxic than nitrogen-limited cells, suggesting that cysts formed from the fusion of two cells might differ in toxicity under each of these conditions. In contrast, recent work suggests that increasing nitrogen concentrations stimulate growth and the production of certain toxins in *Alexandrium tamarense* (Chen et al., 2024).

The toxicity of cysts remains poorly understood, with many questions still unanswered regarding the dynamics of intracellular toxins in cysts, differences in toxicity between strains of the same species, and the ecological role of cyst toxicity. These questions are particularly important due to the potential ecosystem and/or human health risks posed by toxic cysts (Dale et al., 1978).

In summary, we recommend a better integration of cysts within the study of dinoflagellate blooms, particularly in the case of HABs. Additionally, a more thorough understanding of the cyst physiology is required to further our understanding of their ecological roles. Research on chromosome dynamics within dinoflagellate cysts is still scarce (e.g., Bhaud et al., 2000). Transcriptomics offers a promising way forward, although it is not the only approach, to study cellular mechanisms at play during encystment, dormancy, quiescence and excystment, as already explored in ciliate cysts (Pan et al., 2019, 2021) and in the dinoflagellate *Scrippsiella acuminata* (syn. *Scrippsiella trochoidea*) (Deng et al., 2017; Guo et al., 2021).

11. Upcoming techniques and approaches

A significant portion of the workshop discussions focussed on emerging techniques and their applications in the study of dinoflagellate cysts. As some participants showed in their presentations during the oral sessions, some of these techniques are promising although they are still in their early stages of exploration. Below is a summary of these techniques, as presented by the workshop participants and co-authors of this manuscript:

- Recent research has demonstrated the utility of molecular techniques, such as metabarcoding (see section 8), for studying cyst biodiversity and its relationship with environmental gradients. While their application in palaeoclimatology and palaeoceanography remains in its early stages, combining them with classical microscopic techniques has the potential to enhance palaeoenvironmental reconstructions by increasing the number of identifiable cyst species.
- Proteomics can enhance the study of dinoflagellate cysts by identifying and quantifying proteins crucial for cyst formation, survival, and dormancy cycling. It provides insights into the biological functions of these proteins, such as stress responses and protective mechanisms. Proteomics can also help discover biomarkers for species identification and assess toxicity by studying proteins associated with toxin production. Additionally, it enables comparative studies of cysts under various environmental conditions, integrating with genomics and transcriptomics to provide a comprehensive understanding of cyst biology. This approach supports ecological monitoring and risk assessment of HABs.
- Transmission electron microscopy (TEM) of cysts has been applied, most notably by Jux (1968, 1971, 1976), to study cyst wall structure. Later work has used TEM to study internal structures in cysts, for *Ceratium* (Chapman et al., 1982) and *Alexandrium* (Kennaway and Lewis, 2004). The comparison of TEM images of modern dinoflagellate cysts with their fossil counterparts, could help identify differences in wall structure, chemical composition, and potentially even the mechanisms of wall formation. Although this method remains cumbersome and has been rarely applied, new techniques, such as focused-ion beam combined with scanning electron microscopy (FIB-SEM) have shown to be very useful in studying cells (e.g., Uwizeye et al., 2021) and hold promise for the study of cyst wall structure and the organisation of internal structures. Recently, cryo-electron tomography (cryo-ET) was used on flash-frozen *Karlodinium veneficum* cells, which were prepared as thin lamellae cell sections by focused-ion beam milling. Data analysis confirmed no additional membranes were added to the Kareniaceae plastid during serial endosymbiosis and that haptophyte-derived import processes were sufficient (Lewis et al., 2024).
- Functional groups—organisms sharing ecological and morphological traits—offer insights into biodiversity dynamics by highlighting how traits influence ecological roles (e.g., Swain et al., 2024). Applying this approach to dinoflagellate cysts could enhance understanding of their ecological roles and interactions. Grouping cysts based on shared traits may help track (palaeo)ecological changes (e.g., Atkinson et al., 2024), predict harmful algal bloom dynamics, and guide conservation efforts. By focusing on functional categories, researchers can better monitor environmental conditions and manage ecosystem stability, offering a broader perspective on cysts' impact on marine ecosystems. However, the role of the functional morphology of cysts remains largely unknown.
- New in situ instrumentation provides novel insights into dinoflagellate life cycle transitions and rates that are different from those obtained from culture studies (Brosnahan et al., 2015, 2017). For example, an imaging flow cytometer (e.g., IFCB) can be deployed subsurface where it samples the water three times every hour, continuously, obtaining hundreds of thousands of high-resolution images every day. It is now possible to observe and quantify the timing and rates of gamete production, gamete fusion, and planozygote production at a resolution that dwarfs anything possible in cultures. Moreover, these rates (as well as growth rates) are now seen to be much faster in natural waters than have been observed in cultures, bringing us closer to a more realistic understanding of the dynamics of these processes.
- Automatic scanning of palynological slides involves high-resolution cameras systematically capturing images of the slides. This process includes loading the slide into the scanner, capturing detailed images at various magnifications, and stitching them together to create a comprehensive digital representation. Such technology could significantly enhance the speed and efficiency of cyst identification and counting, enabling rapid digitisation of exhaustive slide collections, reducing manual labour and increasing data accessibility. However, it can be costly and may require specialised equipment. Machine learning algorithms can be used to analyse the digitised images, automating the identification and classification of palynomorphs. These algorithms learn from annotated datasets to improve accuracy and efficiency in palynological research.

12. Conclusions

During the round-table discussions held at the International Workshop on Dinoflagellate Cysts (18–21 June 2024, Vigo, Spain) progress in dinoflagellate cyst research was debated, priorities and challenges were identified, and solutions and future directions were proposed which are compiled in this paper. In recent years, new techniques have been developed that greatly contribute to cyst research and, in general, to the

study of marine biodiversity and marine ecosystems. We described in detail both classical and emerging techniques in the study of marine organic-walled dinoflagellate cysts, as well as new applications, that we believe will help both experts and those who want to start dinoflagellate cyst research to become up-to-date and design future studies.

Cyst extraction from sediments involves sonication and sieving. Moreover, the Bolch (involving heavy-liquid separation) and the palynological (involving digestion with strong acids) methods are the most widely used techniques for further cyst concentration, used by biologists and geologists, respectively. Cyst abundance can be measured either on volume (cm^{-3} of wet sediment) or weight (g^{-1} of dry sediment) basis, depending on the study's focus. Although extraction and quantification methods may vary to some extent depending on the sediment and study objectives, we believe that more efforts should be made to study the effect of methodological variations in cyst records, as this would help to standardise the process as much as possible, facilitating comparison between regions and studies.

Dinoflagellate cysts are valuable for quantitatively reconstructing sea-surface parameters like temperature, salinity, and productivity, using techniques such as transfer functions and analogue methods. Despite challenges such as limited regional data and calibration issues, standardised databases have improved the reliability of these reconstructions. New data collection in underrepresented regions and interdisciplinary approaches integrating molecular techniques, sedimentology, and biogeochemistry are critical for advancing palaeoenvironmental reconstructions and developing innovative proxies.

In combination with sediment surveys, cyst assemblages collected in the water column (mainly sediment traps) may help to study the distribution and dispersion of species and their spatiotemporal variability, as well as the environmental factors driving encystment and excystment dynamics, transport and preservation phenomena that affect the cyst accumulation in the sediments, providing key data to interpret the palaeoecological signals left by cysts in the sediment archive. Besides, examples and proposed sampling strategies were provided to investigate past and modern variability of bloom- and cyst-forming species (including toxin-producers). We highlighted a significant shortage of sediment trap records, particularly those for seasonal and multi-year periods. Given their relevance to understanding encystment and excystment dynamics and ecology of dinoflagellates, we strongly recommend that efforts be intensified and resources invested in obtaining seasonal and multi-year sediment trap records.

Furthermore, we explained how emerging techniques and upcoming approaches can help in species identification, phylogenetic studies, distribution studies and palaeoecological reconstructions using dinoflagellate cysts. These new techniques include Fourier Transform Infrared (FTIR) and Raman spectroscopy to study the chemical composition of cyst walls, metabarcoding data from ancient and modern DNA, automatic scanning of palynological slides to enhance the speed and efficiency of cyst identification and counting, proteomics to study cyst formation, survival, dormancy, and more.

While this paper reflects the current focus of funding and interest in the role of cysts in Harmful Algal Blooms (HAB), there remain exciting opportunities for research building on the rare, if not unique example of an important group of living organisms with a long-detailed fossil record (most likely with evidence of linkage to early eukaryotes). Future work should continue the traditional geologic/biologic joint research that launched (in the 1960s) the present interest in the dinoflagellate cysts. Molecular analysis should now target more cyst-forming species to improve phylogenetic trees, and morphology of fossil cysts and especially acritarchs should be re-evaluated to expose and use features other than the reflected thecal tabulation that is currently deemed definitive.

CRediT authorship contribution statement

Iria García-Moreiras: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Ana Amorim:** Writing – review & editing, Investigation, Conceptualization. **Vera Pospelova:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Karin Zonneveld:** Writing – review & editing, Investigation, Conceptualization. **Donald M. Anderson:** Writing – review & editing, Investigation. **Girish Beedessee:** Writing – review & editing, Investigation, Conceptualization. **Amy Dale:** Writing – review & editing, Investigation, Conceptualization. **Barrie Dale:** Writing – review & editing, Investigation, Conceptualization. **Ophélie David:** Writing – review & editing, Investigation, Conceptualization. **Anne de Vernal:** Writing – review & editing, Investigation, Conceptualization. **Eugenia Fatourou:** Writing – review & editing, Investigation, Conceptualization. **Emilie Folie-Boivin:** Writing – review & editing, Investigation, Conceptualization. **Javier Helenes:** Writing – review & editing, Investigation, Conceptualization. **María García-Portela:** Writing – review & editing, Investigation, Conceptualization. **Fang Gu:** Writing – review & editing, Investigation, Conceptualization. **Haifeng Gu:** Writing – review & editing, Investigation, Conceptualization. **Vincent Iratçabal:** Writing – review & editing, Investigation, Conceptualization. **Jan Janouškovec:** Writing – review & editing, Investigation, Conceptualization. **Audrey Limoges:** Writing – review & editing, Investigation, Conceptualization. **Fabienne Marret:** Writing – review & editing, Investigation. **Pjotr Meyvisch:** Writing – review & editing, Investigation, Conceptualization. **Yannick Nkouefuth Nfongmo:** Writing – review & editing, Investigation, Conceptualization. **Victor Pochic:** Writing – review & editing, Investigation, Conceptualization. **Beatriz Reguera:** Writing – review & editing, Investigation, Conceptualization. **Francesca Sangiorgi:** Writing – review & editing, Investigation. **Surya Eldo V. Roza:** Writing – review & editing, Visualization, Investigation, Conceptualization. **Nicolas Van Nieuwenhove:** Writing – review & editing, Investigation, Conceptualization. **Robert W. Williams:** Writing – review & editing, Investigation, Conceptualization. **Vincy Winifred:** Writing – review & editing, Investigation, Conceptualization. **Kenneth Neil Mertens:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

The AI tools *Jeni* and *ChatGPT* were used to improve the readability and synthesis of some sections, and to generate the highlights. *Grammarly* was used to check grammar and language usage. Furthermore, some pictures in the graphical abstract were created using *openArt.ai*. After using these tools, the authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

Declaration of competing interest

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Data availability

No data was used for the research described in the article.

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