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Sedimentary ancient DNA: a new paleogenomic tool for reconstructing the history of marine ecosystems

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Sedimentary ancient DNA (*seda*DNA) offers a novel retrospective approach to reconstructing the history of marine ecosystems over geological timescales. Until now, the biological proxies used to reconstruct paleoceanographic and paleoecological conditions were limited to organisms whose remains are preserved in the fossil record. The development of ancient DNA analysis techniques substantially expands the range of studied taxa, providing a holistic overview of past biodiversity. Future development of marine *seda*DNA research is expected to dramatically improve our understanding of how the marine biota responded to changing environmental conditions. However, as an emerging approach, marine *seda*DNA holds many challenges, and its ability to recover reliable past biodiversity information needs to be carefully assessed. This review aims to highlight current advances in marine *seda*DNA research and to discuss potential methodological pitfalls and limitations.

KEYWORDS

paleoceanography, *seda*DNA, marine sediment, metabarcoding, metagenomics, marine biodiversity

1 Introduction

Marine sedimentary archives are an important source of information for understanding the environment in which marine organisms lived over geological time scales. The analysis of these archives adopts a multidisciplinary approach, which requires the engagement of experts in geology, organic and inorganic geochemistry, geomorphology, paleoceanography, and micropaleontology, (e.g., Backman et al. (2009); Łącka et al. (2019); Łącka et al. (2020); Pawłowska et al. (2020a); Marino et al. (2022)). Records of past environmental change can be accessed by analyzing indirect sources of

information (so-called proxies) retrieved from marine sediment cores. These proxies can be fossil assemblages, indicator species, or geochemical proxies such as lipid biomarkers, pigments, or sedimentological properties. Such multidisciplinary approaches have greatly expanded our knowledge of marine paleo-communities and their physical and chemical environments, providing invaluable information for predictions on marine ecosystem response to future climate changes and anthropogenic pressures. However, our current view of past environmental changes and evolutionary responses of marine organisms has, until recently, been limited to selected groups of organisms whose remains are preserved in the fossil record. Examples of such fossilizing taxa are mollusks (Machado et al., 2018; Mcgann and Powell, 2022), coccolithophores (Jacques and Luc, 2007; Marino et al., 2022), foraminifera (Kujawa et al., 2021; Pados-Dibattista et al., 2022), diatoms (Oksman et al., 2017; Miettinen, 2018), and dinoflagellate cysts (Ellegaard et al., 2017; Hennissen et al., 2017; Gussone and Friedrich, 2018; Aubry et al., 2020). The compositional variation of these taxa reflects transformations in marine environmental conditions. Our current understanding of the past ocean is largely based on traditional proxies, such as foraminifera, for which oxygen isotope records provided detailed insight into the climate history during the Cenozoic (Zachos et al., 2008) and Mg/Ca ratios provided sea water temperature estimates (Mcclymont et al., 2020). However, these proxies are often used to infer a specific environmental variable (e.g., temperature, salinity) and do not provide an overview of biodiversity changes. Moreover, their taxonomic analysis is often labor-intensive and requires expertise that is not readily available making impractical their applications for long-term or large-scale assessments.

Over the last decade, advances in high-throughput DNA sequencing technologies and laboratory techniques for working with ancient DNA have offered richer, higher-quality analyses that better facilitate the reconstruction and understanding of paleo-communities. An initial study by Coolen and Overmann (1998) successfully used ancient 16S rDNA fragments from lake sediments and the carotenoid okenone to show that bottom-water anoxia and a sulfidic chemocline persisted in Mahoney Lake, Canada, during most of the Holocene. After this study, the number of sedaDNA-based publications remained relatively low until 2014. Since then, their number has been consistently increasing, yet studies of marine sediments remain less numerous than those of freshwater environments (Figure 1A). Early marine sedaDNA studies tested the burial of DNA and compared the microbial communities of sedaDNA and fossil assemblages exploring various marine habitats from coastal polar regions (Coolen et al., 2004; Boere et al., 2009; Pawłowska et al., 2014), to anoxic basins (Coolen et al., 2009; Boere et al., 2011; Coolen, 2011; Coolen et al., 2013) and abyssal plains (Lejzerowicz et al., 2013). An increasing number of studies is now combining sedaDNA analyses with other proxy data to gain insight into past oceanographic conditions, such as sea-ice cover (Boere et al., 2009; De Schepper et al., 2019; Pawłowska et al., 2020a; Zimmermann et al., 2020; Zimmermann et al., 2021), sea-surface temperatures and subsurface salinities (Zimmermann et al., 2021). As shown by the main keywords associated with sedaDNA publications, their main focus

so far has been: "paleoenvironments", changes in "biodiversity", "climate change" and "long-term dynamics" (Figure 1B).

This review aims to highlight the potential of sedimentary ancient DNA-based research for the characterization of past marine biodiversity and its response to environmental changes. We describe taphonomic or preservation processes and discuss key issues related to procedures for sampling, laboratory processing, and computational techniques involved in marine sedaDNA investigation. We focus on both planktonic and benthic microbial (prokaryotes and single-cell eukaryotes) and meiofaunal organisms deposited in marine sediments and discuss their potential in studying biodiversity changes across geological timescales.

2 Taphonomy and characteristics of marine sedaDNA

Marine sedaDNA research involves the analysis of genetic material preserved in marine sediments from organisms that once lived in the water column or on the ocean floor. Several investigations in different sedimentary basins shed some light on the taphonomy of sedaDNA in marine settings (Sunday et al., 2014; Kelly et al., 2018; Ellegaard et al., 2020) (Figure 2). The processes that regulate the accumulation and preservation of environmental DNA (eDNA) in marine environments are more complex than in the freshwater-terrestrial system. This is because the marine environment with its surface and bottom water currents, sinking water masses, lateral sediment transports, and sometimes very active benthic communities, is more dynamic than freshwater systems (Pedersen et al., 2015; Barrenechea Angeles et al., 2020; Allan et al., 2021).

The planktonic community, dominated by prokaryotes (Kallmeyer et al., 2012), protists (Vargas et al., 2015), and zooplankton (Murrell and Lores, 2004), is responsible for a large portion of the marine sedaDNA (Barrenechea Angeles et al., 2020). Several studies have described how planktonic DNA is deposited and preserved in sediments (Corinaldesi et al., 2011; Torti et al., 2018). As shown in Figure 2, after the death of planktonic organisms, their DNA has to travel through the water column for tens (shallow shelf) to thousands (open ocean) of meters to reach the sea floor (Smayda, 1971; Bach et al., 2016). During this journey, the planktonic DNA can be associated with organism remains or attached to particulate organic matter, skeletons, bound detritus, or inorganic mineral grains (Iversen and Ploug, 2010; Herndl and Reinthaler, 2013; Wood et al., 2020). Depending on the size of the sinking particles (Cael and White, 2020) and a range of physical and biological mechanisms (aggregation, downwelling and density inversion currents, packaging of cells in fecal pellets) in situ (Bach et al., 2016), the plankton sinking can take several days or even longer time to reach the seafloor (Bach et al., 2019; Nooteboom et al., 2019). The degree of planktonic DNA degradation depends on various factors such as organic matter load, temperature, pH, salinity, water depth, light intensity, and organismal activity through the water column (Corinaldesi et al., 2008; Torti et al., 2015; Andruszkiewicz et al., 2017; Collins et al., 2018; Mccartin et al., 2022). Some
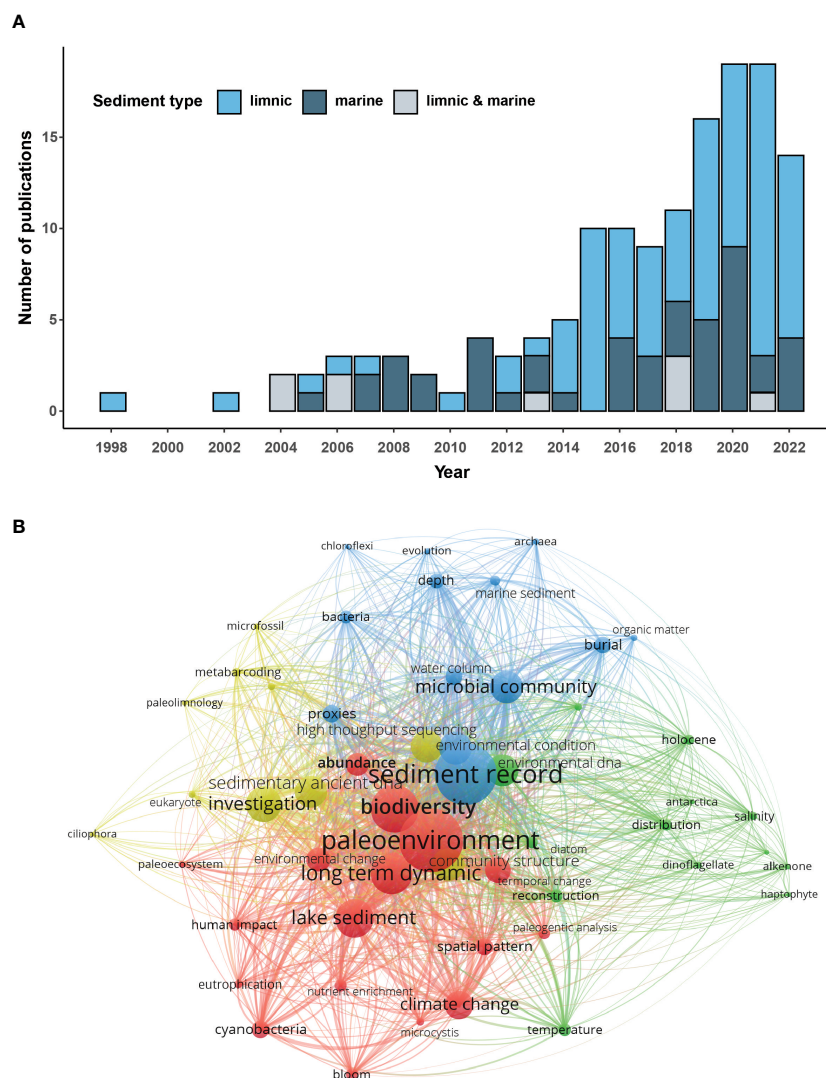
FIGURE 1
(A) Bar chart showing the annual number of published *seda*DNA research articles retrieved from Google Scholar and cross-checked with the literature database of the *seda*DNA scientific society (https://sedadna.github.io/). We queried for papers that (1) presented *seda*DNA data, and (2) targeted either bacteria, archaea, micro-eukaryotes (protists, fungi), meiofauna, or small zooplankton, and verified them manually. **(B)** Co-occurrence network map of keywords found in abstracts of *seda*DNA research papers. The network map was generated using the VOSviewer software (Perianes-Rodriguez et al., 2016). Size of the nodes and font are proportional to the eigenvector centrality; the nodes were colored to show different clusters. A total of 142 original studies on limnic and/or marine *seda*DNA were included in this review (Table S1).

authors suggested that macrobial *e*DNA degradation rates differ between marine, brackish, and freshwater systems (Thomsen et al., 2012; Collins et al., 2018). An experimental and comparative study by Collins et al. (2018) indicated the rate of decay to be 1.6 times faster in inshore waters than in offshore waters. Salinity seemed to be an important factor in steering decay rates, but it could also be related to microbial activities (Collins et al., 2018). In general, degradation rates of *e*DNA decrease in colder seawater (Okabe and Shimazu, 2007; Mccartin et al., 2022) with a higher pH (Collins et al., 2018), high dissolved organic carbon content, and low bacterial activity (Corinaldesi et al., 2008). However, very little is known about how the degradation of planktonic DNA that is going through the water column and deposited on the seafloor can impact the composition of

planktonic communities retrieved from *seda*DNA analyses (Morard et al., 2017; Barrenechea Angeles et al., 2020).

The physicochemical characteristics of the sediment in concert with environmental conditions are considered to play important roles in the preservation of *seda*DNA on the seafloor (Corinaldesi et al., 2008; Vuillemin et al., 2019). Early ancient DNA studies indicated that the sediment's characteristics such as high clay, borate, and organic content under cold/frozen and anoxic conditions facilitate optimal DNA preservation (Willerslev et al., 2004; Coolen and Overmann, 2007; Coolen et al., 2013; Furukawa et al., 2013; Torti et al., 2015). Indeed, it has been demonstrated experimentally that organic matter and clay increase the DNA adsorption capacity of sediment (Xue and Feng, 2018). In addition, the adsorption of DNA to sand is also well documented (Lorenz and
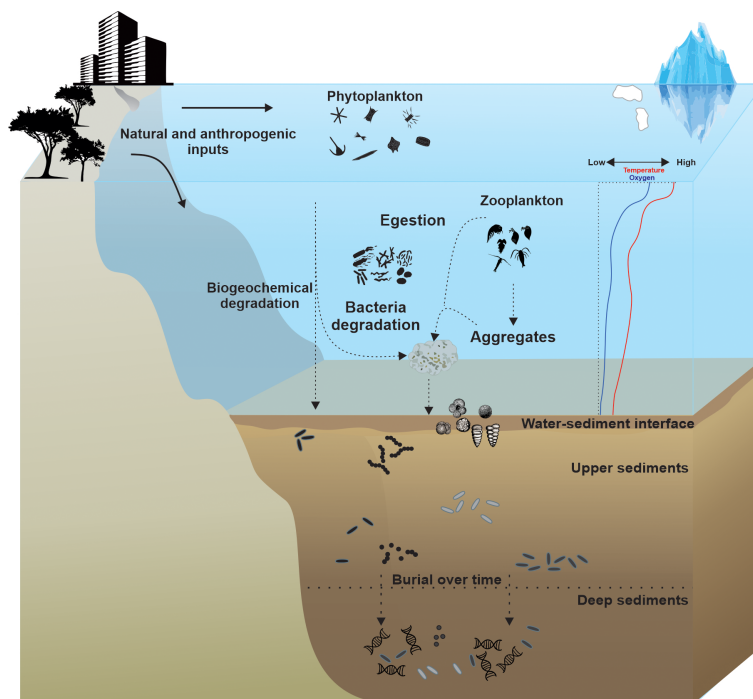
FIGURE 2
Schematic illustration of *e*DNA taphonomic processes in the marine environment. These processes involve *e*DNA distribution, degradation, and/or preferential preservation during the transition from the pelagic to the benthic zones, and from the water-sediment interface into subsurface sediment.

Wackernagel, 1987; Robert et al., 2005). However, overall, the relation between marine sediment characteristics and *seda*DNA preservation over time is poorly understood. Similarly, it remains unclear how bottom water temperature impacts *seda*DNA preservation. Since the bottom water temperature is remarkably stable and colder than 4°C below a depth of 700 m (Locarnini et al., 2018) it is possible that the influence of the bottom water temperature on the preservation of *seda*DNA may be comparable over large parts of the ocean. To date, the majority of *seda*DNA studies have been performed in high-latitude, cold environments, particularly the polar regions (Pawłowska et al., 2014; De Schepper et al., 2019), or deep-sea subsurface sediments (Corinaldesi et al., 2011; More et al., 2018; Armbrecht et al., 2021a). Warmer, shallow, or marginal seas and oceanic regions with strong seasonality were long assumed to be less favorable for the long-term preservation of *e*DNA. However, some studies show that *e*DNA can also be well preserved in temperate and tropical regions, beneath toxic water columns (Coolen et al., 2013; More et al., 2018), in well–oxygenated deep-sea sediments (Lejzerowicz et al., 2013), and tropical reef sediments (Del Carmen Gomez Cabrera et al., 2019).

Although no accurate timeline predicting *seda*DNA preservation potential in various sediment types or geographical regions exists, marine *seda*DNA has been recovered back to the early Quaternary (Figure 3A). Micro-eukaryotic DNA has been recovered from 800-year-old fjord sediments (Pawłowska et al., 2014), 30,000-year-old deep-sea sediments (Lejzerowicz et al., 2013), 43,000-year-old oxygen-minimum zone sediments (More et al., 2018), and 100,000-year-old Greenland Sea sediments (De Schepper et al., 2019). Even longer preservation was documented in

sediments dating back to 1–1.4 Ma (Kirkpatrick et al., 2016; Armbrecht et al., 2022). Compared to modern sedimentary DNA, the *seda*DNA molecules are typically degraded into short fragments and may have extensive chemical damage (Armbrecht et al., 2020). However, some studies have shown that ancient DNA fragments longer than 500 base pairs (bp) can be recovered from subsurface sediments, for example, from the eastern Mediterranean Holocene and Pleistocene sapropels with aforementioned conditions for preservation (Coolen and Overmann, 2007; Boere et al., 2011) (see also Table S1; Figure 3A). This could be explained by the ability of some microbes such as bacteria and archaea (Vuillemin et al., 2019; Thomas et al., 2020; Capo et al., 2022), dinoflagellates, and diatoms (Ribeiro et al., 2011; Sanyal et al., 2022), to form dormant or resting stages for extended periods following sediment burial.

3 Marine *seda*DNA processing and analysis

The methods used in *seda*DNA processing and analysis have been reviewed by several authors, e.g. Epp et al. (2019); Fulton and Shapiro (2019); Capo et al. (2021). However, only a few papers concern specifically the marine environment, focusing on the collection, storage, and manipulation of marine sediments for *seda*DNA analysis (Armbrecht et al., 2019; Armbrecht et al., 2020; Selway et al., 2022). Here we will shortly discuss some of these methods with a special focus on challenges related to marine sediments.
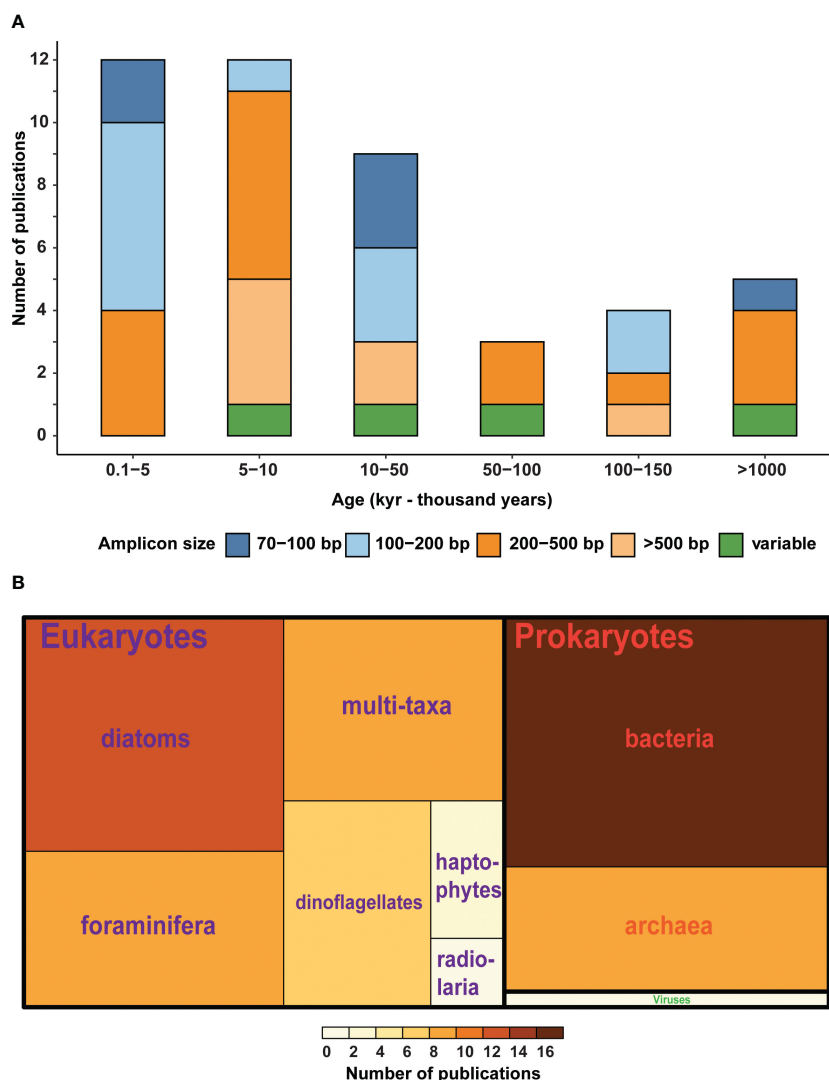
FIGURE 3

(A) Bar chart showing the number of published articles on marine *seda*DNA, indicating the age of the sediment and the fragment length of the analyzed amplicons, variable: a range of fragment sizes is obtained through metagenomics. **(B)** Treemap showing the number of published articles targeting different taxonomic groups of prokaryotes and eukaryotes in marine *seda*DNA. A total of 55 marine *seda*DNA studies were included in this figure (Table S1).

3.1 Sediment coring

The sediment core sampling strategy is the major difference between marine *seda*DNA and other studies involving ancient environmental DNA. In particular, sampling long cores (> 10-meter-long) from depths of hundreds to thousands of meters below the sea surface, while avoiding contamination is the main challenge of marine *seda*DNA. Depending on the functional mechanisms that ensure penetration into the sediment, the following coring methods are commonly used in marine *seda*DNA research: gravity corer (Coolen et al., 2013; Torti et al., 2018; De Schepper et al., 2019; More et al., 2021), piston corer (Zimmermann et al., 2021; Armbrecht et al., 2022), multicorer (Coolen et al., 2013; Lejzerowicz et al., 2013; De Schepper et al., 2019), and boxcorer (Coolen et al., 2006). The gravity and piston corers are used for obtaining sediment records of several meters in length to provide insights into past environmental

change over decades, centuries to millennia. Multicore systems, on the other hand, are typically used for short-term records of the seafloor and allow for simultaneous collection of 2, 4 or even 6 short cores (< 1 m).

Since collecting multiple gravity or piston cores in the marine environment can be problematic and costly, splitting the core lengthwise and taking multiple subsamples from the same core is usually the best way to obtain replicate samples for *seda*DNA analysis. Subsequent steps of *seda*DNA analysis should be performed in a sterile environment, ideally in a dedicated ancient DNA laboratory. Subsampling of sediment cores can be performed with sterile knives, spoons, and spatulas (Lejzerowicz et al., 2013; Hou et al., 2014; Szczuciński et al., 2016) or using mini-cores or cut-open syringes (Coolen et al., 2013; Capo et al., 2021; Talas et al., 2021; Armbrecht et al., 2022). The sampling intervals vary according to the objectives of each study, the sedimentation rates

in marine systems, and the weight/volume of samples required for further analysis. Subsampling for *seda*DNA should be conducted rapidly in cold, still-air conditions to avoid exposure to oxygen after the core is opened (Elbaum et al., 2006; Ogata et al., 2021). A recent study shows that although *seda*DNA can be obtained from cores that were split and stored in the dark at 4°C in plastic containers for several years, modern contamination from fungi and other eukaryotes are likely to be observed in such material (Selway et al., 2022). To avoid serious contamination issues, sediment cores should be transported and stored under cold, or even freezing temperatures. Alternatively, sediment cores for *seda*DNA analyses could be subsampled onboard the vessel or immediately upon arrival at the laboratory and stored frozen (Llamas et al., 2017; Selway et al., 2022).

3.2 *seda*DNA extraction

Due to the complexity of marine sediment composition and the wide range of target organisms to be analyzed, choosing a universally optimal *seda*DNA extraction method is challenging (Armbrecht et al., 2020; Murchie et al., 2020; Kang et al., 2021). Extraction of the highly degraded fragments of *seda*DNA has to ensure efficient removal of inhibitors, such as humic acids, while retaining a maximum amount of DNA in the solution. The efficiency of *seda*DNA extraction depends on the complex and variable mineral composition of the sediment (Lekang et al., 2015), and DNA extraction methods (Kang et al., 2021). Due to the interaction between DNA molecules and sediment colloids, different extraction methods can influence the final quantity and quality of total DNA and biodiversity assessments.

Commercially available spin column-based DNA extraction kits (e.g., Qiagen, MP biomedicals, Omega, etc.) are commonly used in marine *seda*DNA studies (Table S1). These products ensure a greater degree of uniformity and consistency than homemade solution-based protocols, especially when extracting DNA from a large number of samples. Yet, the latter, such as the phenol-chloroform method, have other advantages, including being cheaper than commercial kits, usually obtaining good quality and quantity of the extracted DNA, being easily optimized to the sample material, and preferentially recovering longer *seda*DNA fragments (Direito et al., 2012; Armbrecht et al., 2020). However, solution-based DNA extraction protocols can be quite laborious, since toxic chemicals are used and all steps are to be processed manually in a fume hood, which can be inconvenient in a clean laboratory.

It should be noted that using different DNA extraction methods can significantly affect DNA yield and quality and species assemblages (Deiner et al., 2018; Pearman et al., 2020; Kang et al., 2021; Brauer and Bengtsson, 2022). For example, the Qiagen DNeasy PowerMax Soil Kit that allows extraction of up to 10 g of material is recommended by some studies for eukaryote biodiversity surveys from the surface (Pearman et al., 2020; Kang et al., 2021; Pawlowski et al., 2022) and downcore (Epp et al., 2019) sediment

samples. The use of DNA-binding spin columns tends to selectively recover large DNA fragments (Armbrecht et al., 2020). Whereas non-column-based methods are more efficient for recovering smaller fragments, particularly when dealing with highly fragmented and degraded *seda*DNA (Armbrecht et al., 2020). Thus, when selecting a DNA extraction protocol, it is important to consider various factors such as the type and quantity of samples, the intended purpose of the study, the availability of equipment, and financial limitations.

3.3 Metabarcoding *vs* metagenomics

Most *seda*DNA studies to date have utilized metabarcoding approaches for the characterization of paleobiodiversity from sediment records. Metabarcoding consists of high-throughput sequencing of PCR-amplified marker genes, thus the success of DNA metabarcoding depends on the selection of an appropriate DNA marker. Ideally, such markers should have sufficiently conserved flanking primer-binding sites to minimize taxonomic biases during PCR amplification (Liu et al., 2020), distinguish targeted taxa, and possess a reference database for assigning taxonomy (Deagle et al., 2014). There are several marker genes commonly used for *seda*DNA metabarcoding studies, including nuclear ribosomal genes for eukaryotic organisms (Pawłowska et al., 2014; De Schepper et al., 2019; Thomas et al., 2019; More et al., 2021), prokaryotes (Torti et al., 2018; Vuillemin et al., 2019), the mitochondrial cytochrome oxidase I (COI) gene for animals (Coolen, 2011; Der Sarkissian et al., 2017), the chloroplast ribulose bisphosphate carboxylase large chain (rcbL) gene for diatoms (Zimmermann et al., 2020; Armbrecht et al., 2021a), and major capsid protein (MCP) for double stranded DNA viruses infecting algae (Coolen, 2011). Based on the research questions, the sequence length of DNA markers must be considered: longer fragments (e.g., 200 bp to 500 bp) usually provide a better ability to discriminate taxa, while shorter fragments (e.g. 100 bp or less) are more likely to be preserved in *seda*DNA (Figure 3A). In some cases, short fragments were also shown to provide effective taxonomic resolution (Meusnier et al., 2008; Pawłowska et al., 2014).

Currently, shotgun metagenomic sequencing is becoming more accessible and popular in marine *seda*DNA research (Armbrecht et al., 2021a; Armbrecht et al., 2021b; Armbrecht et al., 2022; Selway et al., 2022) because it allows detection of all genomic fragments preserved in the sediment independent of length and without the primer bias of metabarcoding (Armbrecht et al., 2021a). In addition, it preserves DNA damage patterns and thus allows for assessing *seda*DNA authenticity. On the other hand, the targeted group of organisms may constitute only a small portion of sequences in shotgun-sequencing samples, making this approach computationally challenging and costly. A recent study showed hybridization capture to be a promising compromise as it increases the yield of target eukaryote *seda*DNA while maintaining the possibility for ancient DNA authentication via damage patterns (Armbrecht et al., 2021b). Since metagenomics approaches allow

sequencing all DNA present in an ancient environmental sample, they have the potential to recover the full paleo-genetic record and provide the most holistic view of past marine biodiversity (Fellows Yates et al., 2021a; Armbrecht et al., 2022; Capo et al., 2022).

3.4 Bioinformatics challenges

The quality assessment and quality control of sequences produced by *seda*DNA metabarcoding-metagenomics studies are particularly challenging given the potential damage of DNA preserved in the sediments. It is critical to select a bioinformatic pipeline that addresses the challenges specific to the recovery of *seda*DNA signals. In the context of ancient environmental samples, ASV-based DADA2 (Callahan et al., 2019) may be more accurate than Operational Taxonomical Units (OTUs) for low abundance *seda*DNA containing damage patterns (substitution) as it allows to detect small variants (Callahan et al., 2019; Porter and Hajibabaei, 2020). It is also important to ensure that the taxonomic classification of *seda*DNA sequences is carried out using highly curated taxonomic reference databases. Although continuously updated (Guillou et al., 2012; Quast et al., 2012), such databases are largely incomplete, especially for marine meio- and microorganisms. The gaps in reference databases can be a key challenge associated with *e*DNA studies of both paleo- and modern communities since those are often dominated by taxonomically unassigned or unknown sequence fragments (Vargas et al., 2015; Cordier et al., 2022). The situation is also difficult in the case of metagenomic studies targeting marine eukaryotes as the number of reference genomes remains limited (Delmont et al., 2022).

In response to the rapidly growing production of ancient metagenomics data, new bioinformatics techniques have been developed to deal with the particular features of ancient DNA sequences. These techniques encompass a range of approaches, such as the integration of damage detection algorithms, e.g. in mapDamage (Jónsson et al., 2013; Kistler et al., 2017; Weyrich et al., 2017) and metaDMG (Michelsen et al., 2022). They also involve optimizing ancient DNA mapping through the analysis of cytosine residues deamination, utilizing algorithms such as BWA (Schubert et al., 2012; Weyrich et al., 2017), PyDamage (Borry et al., 2021). Furthermore, new tools have been developed to enhance the accuracy of taxonomic assignment of metagenomic reads (PIA, Cribdon et al. (2020), and for processing and analyzing ancient metagenomics shotgun data, specifically targeting ultra-short molecules, (e.g. Collin et al. (2020); Fellows Yates et al. (2021b); Pochon et al. (2022); Neuenschwander et al. (2023)). However, identifying ancient sequences is still a challenge due to the lack of standard bioinformatics pipelines to analyze DNA metabarcoding or shotgun metagenomics data. Using different bioinformatics procedures or genetic databases that lack consistent standards increases ambiguity and bias. Additionally, to ensure in silico reproducibility and facilitate further research, it is crucial to emphasize the need for publishing comprehensive bioinformatics analysis reports. The application and optimization of bioinformatics pipelines should be the focus of future research to accurately identify and authenticate marine microbiota in *seda*DNA.

4 Current applications of the marine *seda*DNA approach

The main application of marine *seda*DNA is the reconstruction of past biodiversity in relation to environmental changes at geological time scales (Figure 4). In this context, the *seda*DNA approach provides a unique insight into the marine paleo-ecological communities. Its application allows reconstructing a detailed record of community changes from individuals to populations and species that occurred across time, increasing the accuracy of prediction models in anticipating how climate/environmental change affects biodiversity (De Schepper et al., 2019; Epp, 2019). Several studies have demonstrated the potential of *seda*DNA for screening genetic signals of multiple taxa (as in Figure 3B), including non-fossilizing organisms (Pawłowska et al., 2014; Selway et al., 2022; Barrenechea Angeles et al., 2023). Most studies focused on marine microbial and meiofaunal communities, revealing a huge and largely undescribed diversity of viruses (Coolen, 2011; Pratas and Pinho, 2018; Zheng et al., 2021), bacteria (Hou et al., 2014; More et al., 2019; Nwosu et al., 2021), archaea (Torti et al., 2018; Vuillemin et al., 2019), and protists (Lejzerowicz et al., 2013; Pawłowska et al., 2014; More et al., 2018; Zimmermann et al., 2020; Egge et al., 2021).

The aims of *seda*DNA studies vary from comparing the diversity of molecular and microfossil assemblages to analyzing the past diversity of non-fossilized taxa. Several studies demonstrated the lack of congruence between molecular and microfossil assemblages (Pawłowska et al., 2014; Barrenechea Angeles et al., 2020). This lack of congruence could be explained by difficulties in extracting DNA from hard-shelled, fossilized taxa, multiple copies of the target gene in the genome, PCR primers biases, or PCR inhibitors, e.g., in the case of several planktonic taxa (Barrenechea Angeles et al., 2020; Pierella Karlusich et al., 2023). Another possible explanation would be that the non-fossilized taxa are much more abundant, and their DNA dominates in sediment samples (Lejzerowicz et al., 2013). This could be the case for non-fossilized monothalamous foraminifera and the acantharian radiolarians that usually are more dominant in *seda*DNA datasets compared to fossilizing species of the same lineages (Lejzerowicz et al., 2013; Pawłowska et al., 2014). Indeed, they also dominate in modern sediment analyses (Lecroq et al., 2011; Pawłowska et al., 2014; Cordier et al., 2022). Despite this lack of congruence in community composition, the patterns inferred from metabarcoding and microfossil data are often similar. This was the case in one study of planktonic foraminifera microfossil and metabarcoding assemblages that exhibited congruent regional biogeographical patterns (Barrenechea Angeles et al., 2020). Similarly, *seda*DNA data of non-fossilized soft-walled foraminifera show comparable patterns as microfossil foraminiferal assemblage in 800-year-old fjord sediments (Pawłowska et al., 2014).
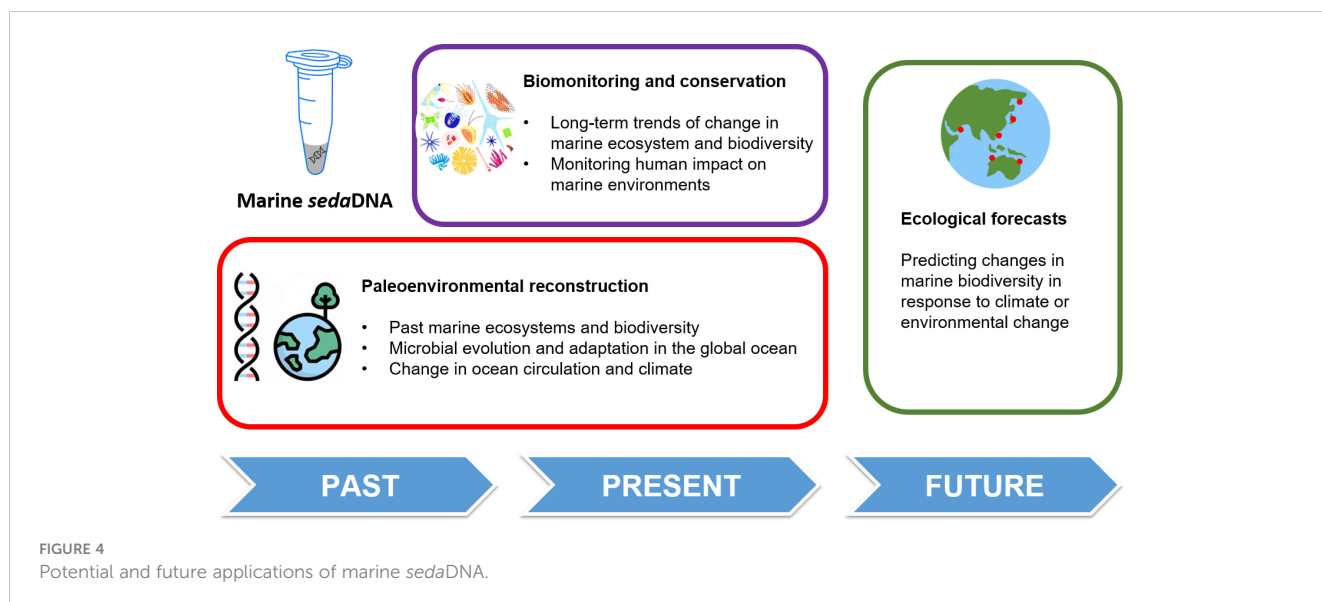
FIGURE 4
Potential and future applications of marine *seda*DNA.

The most promising application of *seda*DNA is to investigate past climates and their impact on oceanographic circulation and species migration. Until now, these studies were mainly based on macro- and microfossils, ignoring a large diversity of non-fossilized species, in particular those belonging to microbial and meiofaunal communities, which are essential for ecosystem functioning. This issue could be overcome by analyzing *seda*DNA from marine sediment cores. For example, changes in ocean circulation patterns were investigated by targeting *seda*DNA of non-fossilized foraminifera in cores collected east of Svalbard (Pawłowska et al., 2020a). Several studies integrate *seda*DNA data with geochemical proxies, including stable and radiogenic isotopes (More et al., 2018; Voldstad et al., 2020), and biomarkers (De Schepper et al., 2019). For example, through analysis of *seda*DNA and hydrogen isotopes of haptophyte-derived alkenones preserved in early Holocene oxygenated lacustrine and mid-to-late-Holocene anoxic coastal Black Sea sediments, planktonic community structures were reconstructed and associated with Holocene climate phases and transitions (Coolen et al., 2013). Paired analysis of *seda*DNA and the sea ice biomarker IP_{25} was used as a proxy for sea-ice reconstructions by targeting diatom *seda*DNA composition in the Fram Strait (Zimmermann et al., 2020), Subarctic North Pacific (Zimmermann et al., 2021), and to trace a sea-ice dinoflagellate east of Greenland (De Schepper et al., 2019). All of these studies provide complementary insights into ecosystem-climate histories, extending our current view of marine communities beyond the diversity found in modern populations and advancing our understanding of their past biogeographic patterns and adaptations to new environmental conditions.

At a shorter timescale, marine *seda*DNA studies also represent a promising complement to traditional biomonitoring surveys. Currently, modern sedimentary DNA metabarcoding is becoming a routine tool for monitoring the human impact on marine systems e.g., through construction, overexploitation, agriculture,

habitat loss, and pollution (Bálint et al., 2018; Cordier et al., 2021; Pawlowski et al., 2021). A few studies have shown that the *seda*DNA approach can be used to investigate the impact of anthropogenic activities on the ecosystem over the past century. One of these studies recovered the composition of marine plankton communities from hundred-year-old sediment samples and showed irreversible shifts after the cumulative effect of war and agricultural pollution (Siano et al., 2021). Another study demonstrated dramatic ecosystem changes resulting from a multi-level cascade effect of impacts associated with industrial activities, urbanization, water circulation, and land-use changes in one of the most polluted marine sites in Europe (Barrenechea Angeles et al., 2023). Both studies demonstrate the potential of *seda*DNA to elucidate the effects of human pollution on marine communities, contributing to the reconstruction of reference conditions and helping the conservation and management of marine and coastal ecosystems.

5 Future perspectives

Future developments in the marine *seda*DNA research field will make it easier to integrate paleogenetic signals preserved in the marine seafloor with other proxies (Figure 4). Based on the best understanding of each proxy, we can use the strengths of each approach to their best advantage (i.e., complementary patterns of DNA metabarcoding and morphology). The marine *seda*DNA allows recovering a wide range of organisms that will provide valuable material for searching for new paleo-bioindicators. These could include non-fossilized microbial and meiofaunal taxa that present various kinds of ecological characteristics, or the genotypes of fossilized species, the distribution of which can be used to detect paleo-environmental changes (Pawłowska et al., 2020b). In the future, *seda*DNA studies could also pay more attention to marine

mammals, fish, and macroinvertebrates, traces of which can be detected in sediment samples (Kuwae et al., 2020).

However, several technical challenges inherent to *seda*DNA research need to be considered for future developments in the field. First, incomplete reference databases are the major factor limiting the assignment of sequences to taxonomic names and might lead to divergent results (Balvociute and Huson, 2017). The continuous addition of new reference sequences from modern marine organisms to taxonomic databases is important to further complete the taxonomic picture of marine paleo communities. Second, marine *seda*DNA sampling and laboratory procedures may need further optimization (Armbrecht et al., 2019). In particular, the combination of amplicon sequencing (metabarcoding) with metagenomics through the further development of HTS technologies may improve the authentication of ancient signals in genetic data (Armbrecht et al., 2021a) and allow getting more diverse data from assembled sequences, at least for prokaryotes. Finally, more studies are needed to evaluate the limitations of the *seda*DNA approach, especially the time limits of DNA preservation in marine sediments. There is also a lack of evidence on which physicochemical characteristics of sediments are optimal for long-time DNA preservation.

Given the developments in the field, we foresee that the *seda*DNA approach will be rapidly integrated into routine paleoceanographic research. The approach is technologically mature, thus the costs of including a *seda*DNA module in research projects should continue to decrease, thereby increasing the feasibility of *seda*DNA as a regular inclusion in multi-proxy investigations. Even though there are still some challenging issues to be solved, the information provided by the *seda*DNA data is highly valuable. The DNA-based holistic overview of biodiversity changes through time is unique. Its various applications, from the studies of climate changes and water mass circulation at geological time scales to the monitoring of recent anthropogenic impacts, are of key importance to understanding the past and present state of marine ecosystems. Further development of the *seda*DNA field and its wider integration will not only help to improve our knowledge of past changes affecting the ocean and coastal ecosystems, but it will also help to establish and optimize strategies for their conservation and management.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1185435/full#supplementary-material

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