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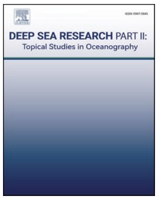

eDNA as a cornerstone for holistic long-term observations of Arctic marine biodiversity across trophic levels, habitats, and spatio-temporal scales

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ABSTRACT

Embedded in the interdisciplinary design of pelagic and benthic long-term observations at the Arctic long-term ecological research site HAUSGARTEN in Fram Strait (78°36,46′N - 79°56,63′N 10°50,91′E – 5°22,24′W; 250–5500 m), environmental DNA (eDNA)-based biodiversity studies span multiple habitats and trophic levels. These studies provide valuable insights into marine ecosystem functionality and carbon fluxes, including seasonal and interannual dynamics. Since 2009, eDNA studies of pelagic eukaryotic microbial communities have regularly been conducted. Recently, these studies have been expanded to cover the biodiversity of bacteria, archaea and metazoa such as zooplankton (including gelatinous taxa) and nekton (cephalopods and fish) alongside with microbial eukaryotes. The eDNA surveys have been coupled with measurements of physical and chemical properties, such as sea-ice coverage and water masses. By applying these approaches across spatial and trophic scales in a nested approach, we characterize the dynamics in biodiversity, its role in ecological processes, with a focus on current climate change. This is achieved by considering the complexity and interconnectivity of organisms, integrating information from different disciplines across scales and habitats, and focusing on functional processes including species composition. The resulting data improve our predictive capabilities for conservation and sustainable marine management in a rapidly changing Arctic. Here, we review the design of the first interdisciplinary Arctic eDNA long-term observatory and the results of more than ten years of method development and observations.

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1. Introduction

The Arctic Ocean is characterized by pronounced seasonality and variability in environmental parameters, such as solar radiation, temperature, sea ice cover and nutrient availability (Walsh, 2008). Currently, major parts of the Arctic system are undergoing rapid change; including rising temperatures and sea ice decline (Meredith et al., 2019). These changes will affect the biodiversity and functionality of Arctic marine environments, and eventually ecosystem services with relevance for the global climate and societies (Brandt et al., 2023). For example, boreal taxa have moved northwards (e.g. Kraft et al., 2013; Brandt et al., 2023; Husson et al., 2024) and primary production has increased in response to decreasing sea-ice cover (Arrigo and van Dijken, 2015). Such changes in the spatio-temporal distribution of species have cascading effects on species interactions and, thus, directly influence Arctic marine food web structure and biogeochemistry.

On a global scale, environmental variability and change have driven programs that monitor areas of particular ecological relevance and uniqueness to extend the understanding of the system and its vulnerability to disturbances (e.g. Wiltshire et al., 2010). The importance of monitoring programs to understand functionality and describe change of marine ecosystems has long been recognized, ultimately supporting the implementation of conservation and protection measures (e.g. Wassmann, 2011). While abiotic environmental data are routinely collected by autonomous standardized sensor-based methods worldwide, thorough sampling of marine biota diversity still relies mostly on manual methods and its synthesis is challenging, due to more complex and variable sampling and analysis techniques. This is particularly relevant for undersampled, remote and rapidly changing regions such as the Arctic Ocean. In 1999, the German Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research (AWI) established the Long-Term Ecological Research (LTER) site HAUSGARTEN in Fram Strait (Fig. 1), to detect and track the impact of environmental changes in the major transition zone between the northern North Atlantic and the central Arctic Ocean (Soltwedel, 2005). The LTER HAUSGARTEN was the first Arctic long-term observation site, located at the boundary between Atlantic and Arctic water masses in a region that hosts both, areas covered by sea ice year-round and, uniquely at this latitude, areas that are ice-free year-round. This area is characterized by a highly productive Marginal Ice Zone (MIZ) (Mayot et al., 2020), which allows studying the role of sea ice in shaping polar ecosystems in a comparably easy accessible area (Soltwedel et al., 2016). Since 2014, the observational program of LTER HAUSGARTEN has been extended by year-round automated assessments of physical, chemical, biological and biogeochemical parameters of seawater, sinking particles, and deep-sea benthos (Soltwedel, 2013). Microscopic analyses are key elements of the biological observation program to assess the biodiversity of planktonic and benthic communities based on morphology (e.g. Nöthig et al., 2015; Taylor et al., 2017). Yet, for many marine taxonomic groups, identification and enumeration using traditional methods such as cell or organism counts is difficult or impossible (e.g. Laakmann et al., 2020; Wollschlaeger et al., 2014) due to constraints related to the small size of the organisms and insufficient morphological features. Others, especially large pelagic organisms like macro zooplankton, fish and squid, cannot always be collected routinely as part of the annual expedition program. Moreover, many benthic and nektonic species have planktonic larvae, for which species identification is challenging due to lacking taxonomic expertise or even impossible due to missing diagnostic morphological features. This hampers comprehensive assessments of marine biodiversity, species interactions and thus understanding of ecosystem functionality in the Arctic Ocean.

However, over the past two decades, environmental DNA (eDNA)-based approaches have significantly advanced our ability to assess marine biodiversity and ecosystem functionality at different levels. Quantitative PCR (qPCR) has proven efficacious in enumerating single targeted species, while DNA metabarcoding has enabled high resolution

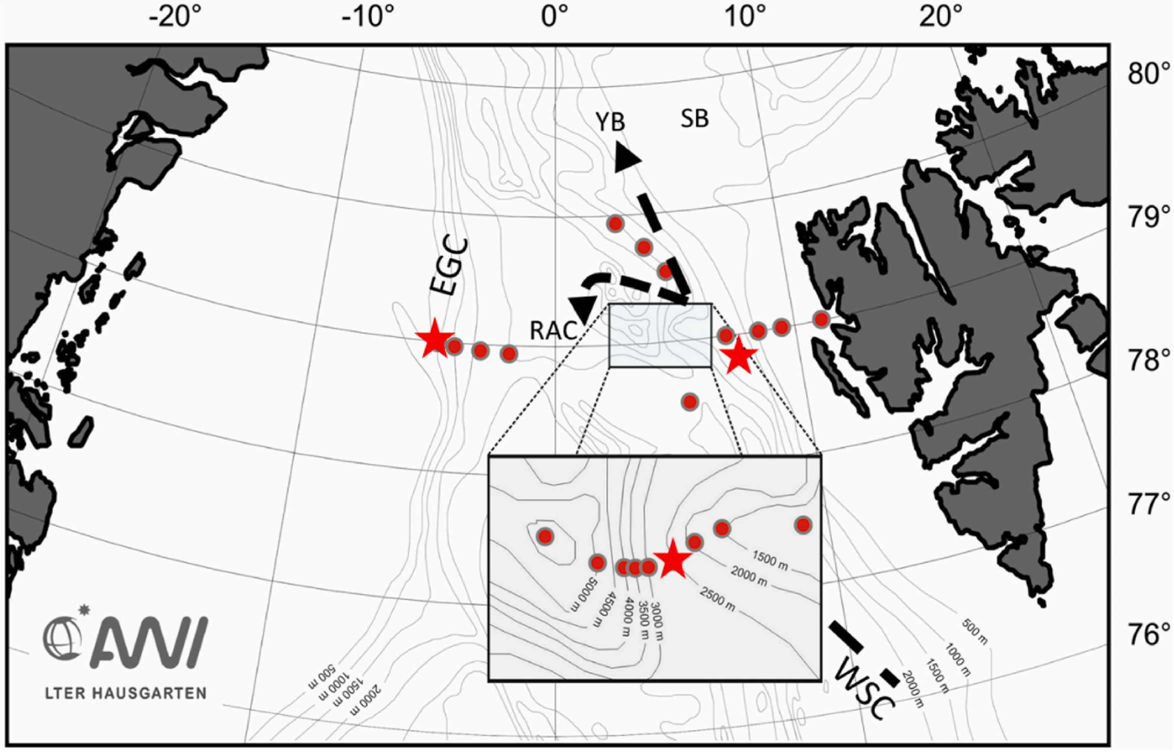

Fig. 1. Map illustrating sampling sites at LTER HAUSGARTEN. Red dots represent stations visited on annual basis during summer, red stars represent stations with long-term moorings, and ocean currents impacting the observation area are indicated as arrows (EGC: East Greenland Current; WSC: West Spitsbergen Current; RAC: Recirculating Atlantic Water (or Return Atlantic Current); SB: Svalbard Branch; YB: Yermak Branch). Isobaths from 500 m onwards are also shown. The map is modified after Soltwedel et al., (2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

profiling of communities to elucidate the relative composition of taxa (Kopp et al., 2023). Based on sequencing of the entire genetic content of a sample, metagenomic studies have provided unprecedented insights into the network and metabolic architecture of marine microbial communities (Acinas et al., 2021). While many current studies focus on method evaluation, selected environmental processes or spatial differences in community composition, the exploitation of eDNA analyses for biological long-term observations has started only recently (e.g. Käse et al., 2020; Krabberod et al., 2022).

Through nearly 25 years of observations at LTER HAUSGARTEN, we have significantly improved our understanding of linkages between the physical environment, biodiversity and ecological processes in the Arctic Ocean (Nöthig et al., 2015; von Appen et al., 2021; Ramondenc et al., 2025). Seasonal plankton variability in the upper photic zone was mainly derived from the composition of exported plankton and their biomass determined from microscopic information obtained from sediment traps mounted on long-term moorings at selected sites over several annual cycles (Ramondenc et al., 2023). However, the original program did not include assessments of bacterial and archaeal diversity, which were only added after 2009. Consequently, there are still significant knowledge gaps in characterizing the interactions and feedback mechanisms between seasonal factors, plankton biodiversity, and physical and biogeochemical processes in a region with highly variable sea-ice cover.

Understanding the impact of sea ice on biology and biogeochemistry is of critical importance to develop future scenarios of Arctic ecosystem functionality, enabling better integration of ecological impacts in climate models, and eventually improving conservation and management strategies. To meet these challenges, we accomplish coordinated and integrated eDNA studies across trophic levels and habitats at LTER HAUSGARTEN, addressing five overarching goals:

- Elucidate the impact of Arctic environmental change, including rising temperatures and melting sea ice, and resulting changes in stratification regimes, on pelagic and benthic communities.
- Characterize the biodiversity and biogeography of Arctic marine organisms across trophic levels, from microbes to vertebrates, and infer potential interactions.
- Decipher abundance and distribution patterns of Arctic marine species at various spatial and temporal scales as functions of environmental conditions.
- Determine linkages between biodiversity and ecosystem functions.
- Provide information to support conservation and sustainable marine management in the rapidly changing Arctic.

Here we review the strategic approach and provide a synopsis of first key results from more than ten years of eDNA observations at LTER HAUSGARTEN. Moreover, to address the knowledge gap on linkages between biodiversity and environmental change in polar ecosystems as outlined in the most recent IPCC reports (IPCC et al., 2023), we introduce a concept for a comprehensive eDNA long-term monitoring strategy, that embeds species distribution and abundance into environmental observations.

2. Methods and approaches

Variability in eDNA composition in Fram Strait has been studied on different horizontal and vertical scales, and along temporal scales ranging from months to decades. To evaluate the long-term observations in Fram Strait within a pan-Arctic context, we also applied the eDNA protocols developed at LTER HAUSGARTEN in the Central Arctic Ocean (CAO) during dedicated research cruises (e.g. Metfies et al., 2016), and more recently the during MOSAiC drift (Mock et al., 2022; Priest et al., 2023).

2.1. Sampling and preservation

Sampling – The automated filtration device AUTOFIM (Metfies et al., 2020), permanently installed in the bow of RV Polarstern, collects underway samples at a depth of ~11 m at defined intervals to resolve geographical variability in eDNA composition with a maximum resolution of up to ~2 km (Weiss et al., 2024). Water samples to capture the vertical and spatial variability at the 21 monitoring stations of LTER HAUSGARTEN have been collected via Niskin-bottles mounted on a rosette equipped with a CTD measuring oceanographic parameters, e.g. salinity and temperature (e.g. Metfies et al., 2016; Wietz et al., 2024). Seasonal variability in eDNA composition is addressed by combining automated water samplers and sediment traps attached to long-term moorings in the euphotic, meso- and bathypelagic zones; however at a coarser vertical and horizontal resolution than with CTD rosette deployments. Since 2016, we have deployed Remote Access Samplers (RAS; McLane, USA) in the euphotic zone at three mooring stations; this frequently includes the mixed layer or the deep chlorophyll maximum (DCM). These cover: (i) the Atlantic water in the WSC (mooring site "F4"), (ii) the transition zone between Atlantic water and polar water (mooring site "HG-IV"), which is regularly impacted by the MIZ, and (iii) polar water in the EGC (mooring site "HG-EG") (von Appen et al., 2021; Priest et al., 2023; Oldenburg et al., 2024). These moorings also carry long-term sediment traps at ~200 m below the surface and ~200 m above the bottom, collecting exported particles, including eDNA, over the seasonal cycle (Fig. 1). Finally, annually recurring sampling of the upper 1 cm of the deep-sea sediments at the monitoring stations of LTER HAUSGARTEN with a multicorer (MUC) allows to carry out studies of benthic eDNA studies and pelagic-benthic coupling in the area (Fig. 2).

Sample preservation – Preservation and storage of eDNA samples is critical to create high-quality, meaningful and comparable molecular datasets. The standardized protocols used within our framework of long-term observations are based on thorough method evaluations. eDNA samples collected with AUTOFIM are preserved with a customized buffer (Metfies et al., 2020) and transferred to −80 °C within one week, while samples collected with the CTD rosette and using the MUC are processed directly after collection and subsequently frozen at −80 °C until isolation of genomic DNA in the laboratory in the home laboratories. Samples collected with RAS and sediment traps are preserved with mercuric chloride. A dedicated experimental study has shown that sample preservation in autonomous devices influences metabarcoding results, but preserved samples still reflect the original community (Wietz et al., 2022). Moreover, bacterial communities detected from fresh (via Niskin bottles) and preserved (via RAS) samples collected within 2 weeks at equivalent locations overlapped in the composition of major classes, with some overrepresentation of Alphaproteobacteria (especially Rhodobacteraceae) in RAS and Bacteroidota (especially Flavobacteriaceae) in Niskin samples respectively (Fig. 3).

2.2. eDNA approaches and taxonomic targets

Since their beginnings in 2009, eDNA analyses at LTER HAUSGARTEN included a set of molecular-genetic approaches (e.g. molecular fingerprints, quantitative PCR (qPCR) or metabarcoding) used in targeted studies or for long-term monitoring, depending on the individual scientific question addressed (Jacob et al., 2013; Wolf et al., 2014; Kilias et al., 2015). The portfolio has been regularly updated in line with the rapid advances in sequencing technology during the past decade. From 2009 to 2015, when metabarcoding was still costly, a combination of Random Amplified Fragment Length Polymorphism (RFLP) and 454 pyrosequencing provided valuable insights into the biodiversity and spatial distribution of Arctic marine eukaryotic microbes, with special emphasis on pico-eukaryotes (Kilias et al., 2014). Moreover, qPCR provided quantitative information on species abundances and their linkage to biogeochemistry (Engel et al., 2019). From 2015 onwards, the diversity of prokaryotes (bacteria, archaea) and microbial eukaryotes

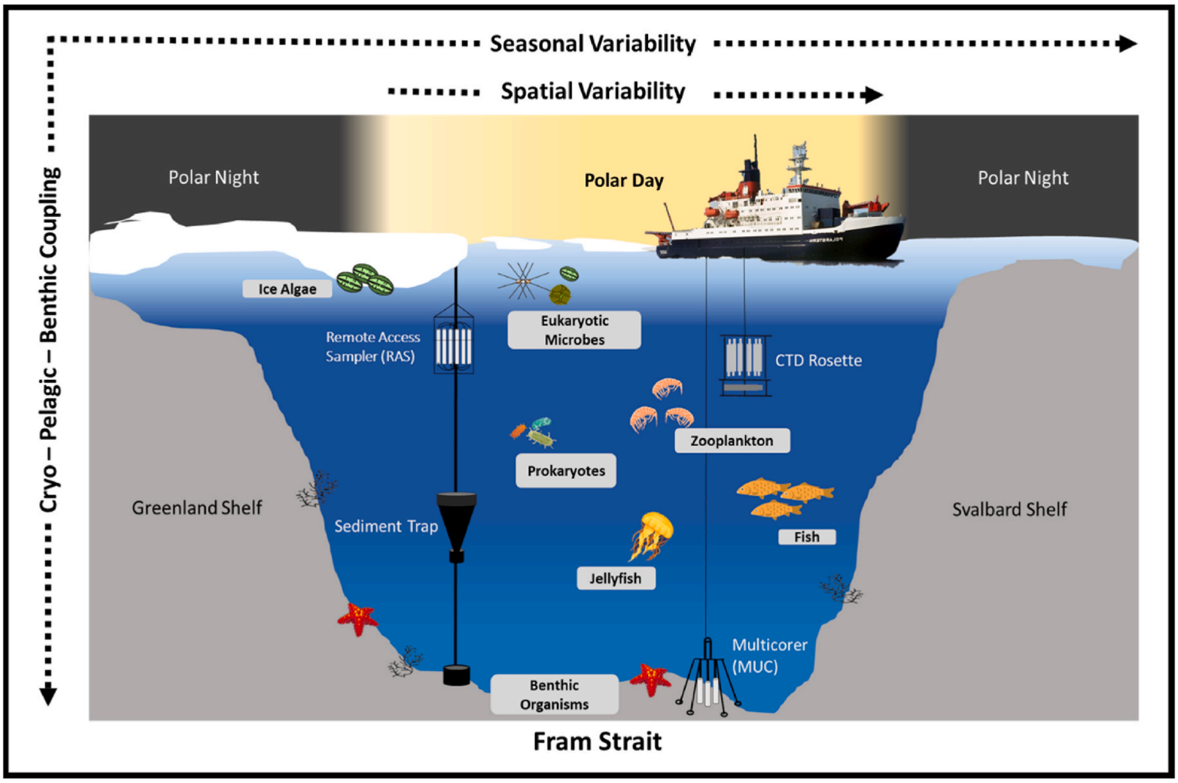

Fig. 2. Schematic drawing of the sampling strategy to collect eDNA targeting the respective organismic groups. During Polar Day, spatial variability across Fram Strait is captured on an annual basis via sampling with gear deployed during RV Polarstern transects (Niskin bottles mounted on a CTD rosette; underway filtration via AUTOFIM; MUC), while seasonal variability is studied in bi-weekly resolution year-round via automated water samplers and sediment traps deployed on long-term moorings. In this drawing, the mooring in EGC exemplifies our year-round sampling strategy of the different mooring-sites capturing eDNA at LTER HAUSGARTEN; it does not represent the exact location.

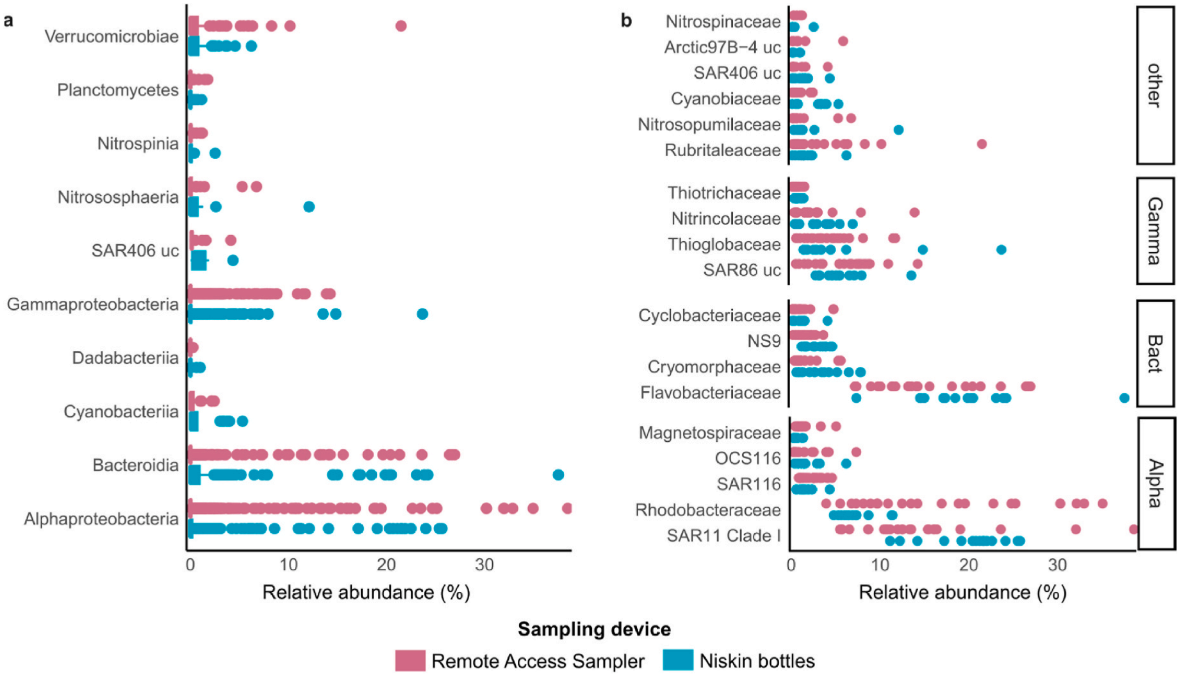

Fig. 3. Relative sequence abundance (16S) of bacterial orders (a) and families (b) comparing Niskin and RAS sampling in the same temporal and spatial dimensions (i.e. within 2 weeks at corresponding geographic locations; water depth range 5–35 m). Each dot relates to a distinct sample; hence illustrating the range of values across multiple time points, CTD casts and autonomous samplings. Alpha: Alphaproteobacteria; Gamma: Gammaproteobacteria; Bact: Bacteroidota; Other: other classes.

has been assessed by using Illumina 16S/18S metabarcoding (Wietz et al., 2024). Recently, these studies were complemented by metagenome studies based on sequencing long-reads via PacBio technology (Priest et al., 2023).

Although eDNA analysis of different trophic levels relies on the same principle (i.e., sequencing and/or quantification of specific marker genes), it still requires testing of genetic marker efficiencies and specific modifications of the protocols to capture the biodiversity of individual taxonomic groups as accurately as possible. This includes optimization of sample volumes, protocols for genomic DNA purification, selection of meaningful marker genes, specific primers and protocols for marker gene amplification, as well as selection and assembly of suitable and comprehensive sequence reference libraries for a reliable annotation of sequence data. In the following, we describe the details of the current approaches used to address individual target groups at LTER HAUSGARTEN via eDNA analyses.

Bacteria and archaea – At LTER HAUSGARTEN, we study the taxonomic diversity of bacterial and archaeal communities by metabarcoding of 16S rRNA genes across different ecosystem compartments. Based on performance assessment of different 16S rRNA primer sets on Arctic seawater, sea ice, sinking particles and seafloor samples (Fadeev et al., 2021a), we decided to use the V4-V5 primer 515F-926R (Parada et al., 2016). The eDNA from seawater is obtained by filtering 3–5 L per Niskin sample (depending on biomass) or 500–700 mL per RAS sample onto Sterivex cartridges followed by extraction using the PowerWater kit (Qiagen, Germany). eDNA from sinking particles and sediment, sampled by sediment traps or MUCs respectively, is obtained via DNA extraction using the PowerSoil kit (Qiagen, Germany). In addition, metagenome and metatranscriptome sequencing of eDNA characterize the functional diversity and expression of key genes, respectively.

Microbial eukaryotes – Single-cell eukaryotes, here summarized as microbial eukaryotes, play a critical role in Arctic marine ecosystem functionality, as they include the predominant primary producers, because planktonic cyanobacteria are rare (Vincent, 2000). In spite of their importance, our understanding of their biodiversity, biogeography and bloom phenology, is still limited for the Arctic Ocean. Genomic DNA for 18S metabarcoding originates from particles and cells in 2 L of seawater collected on polycarbonate filters via sequential filtration on 10 μm, 3 μm and 0.4 μm. This approach allows capturing eDNA from different plankton size fractions separately, keeping the opportunity to carry out size-fraction specific analyses. The eukaryotic microbial community composition is currently assessed by sequencing of a ~400 bp fragment of the 18S rRNA gene using a primer-set targeting the 18S-V4 region for initial amplification. The efficiency of this primer set was confirmed in comparison to microscopic counts (Käse et al., 2020; Metfies et al., 2020).

Fungi – Fungi are a hitherto neglected part of marine microbial communities. Only in the last decade, have marine fungi become the focus of intensive research showing that they are a very diverse, ubiquitously distributed group that can metabolize similar amounts of carbon as bacteria in both pelagic and benthic environments (Orsi et al., 2022). They also show high diversity in Arctic waters, occur in high abundances, and can accumulate ecologically relevant amounts of biomass (Hassett et al., 2019). However, the factors that influence their diversity and occurrence in Arctic waters are largely unknown. Furthermore, there is a lack of knowledge of the link of marine fungi to degradation processes in the Arctic microbial loop and of their place in the food web. To address these questions, we analyze the existing eukaryotic 18S metabarcoding datasets via our fungus-specific bioinformatics pipeline (Banos et al., 2020) and in combination with datasets of other taxonomic groups. This approach has proven successful because it allows the phylogenetic resolution of the evolutionarily oldest fungi versus sister groups, and the phylogenetic characterization of new, undescribed fungal clades (Yang et al., 2021).

Protistan parasites – In addition to true fungi, a range of other parasitic protistan taxa have been detected in Arctic waters including Fram Strait. These include cryptomonadids, perkinsids, Syndiniales and oomycetes (Hassett et al., 2019). The latter are associated with several diatom taxa such as *Chaetoceros* spp. and the ice algae *Melosira arctica* as well as in Arctic sediments. We also found diatom cells infected with parasites (oomycetes) at LTER HAUSGARTEN (Fig. 4). In general, the diversity of protistan parasites and in particular their host ranges and associated ecological functions in the Arctic Ocean remains to be established. This is mainly due to the complex life cycles of the taxa involved, and because some life stages are difficult to identify to species level due to a lack of morphological features (e.g. in the zoospore stages). The eDNA observatory at the LTER Hausgarten can play a pivotal role in the characterization of parasite communities.

Zooplankton – In recent years, target groups for eDNA studies have been extended beyond marine microbes to zooplankton. Zooplankton plays a central role in trophic interactions and biogeochemical cycles in marine ecosystems, linking primary production to higher trophic levels (e.g. Zeldis and Décima, 2020). At LTER HAUSGARTEN, the zooplankton distribution in summer has been studied using microscopy and image analysis of preserved samples since 2011 (Cornils et al., 2022, Dolinkiewicz et al., submitted, this issue). The metabarcoding approach using eDNA from water samples and bulk zooplankton from net-tows offers the opportunity to complement optical surveys. At LTER HAUSGARTEN, we target zooplankton with the primer set 528iF and 964iR used to capture eukaryotic microbes. It provides a first insight into zooplankton community composition and relative abundances are correlated to biomass (Weiss et al., 2024). However, it is not adequate for detailed biodiversity studies, as it resolves the zooplankton biodiversity to order, sometimes family, but not to species level (Laakmann et al., 2025.,). Furthermore, the 18S V4 metabarcoding does not target important taxonomic zooplankton groups such as Chaetognatha, Appendicularia and Amphipoda present in the image analysis. Therefore, complementary COI metabarcoding will be considered at LTER HAUSGARTEN in the future, as this method outperforms the 18S V4 (and V1-2, V9) biodiversity information (Murray et al., 2025). Moreover it identifies congeneric species that are morphologically similar and visually indistinguishable (Laakmann et al., 2020).

Gelatinous zooplankton – Within the zooplankton, gelatinous taxa are often overlooked in the Arctic (Geoffroy et al., 2018). The term gelatinous zooplankton combines taxa of different phylogenetic origin: cnidarians (hydrozoans and scyphozoans), ctenophores, and pelagic tunicates. They cover a wide range of body sizes and trophic roles, from grazers (e.g., appendicularians) to major predators that are able to control mesozooplankton biomass (e.g., scyphozoans and ctenophores) (Choy et al., 2017). Several of these fragile organisms are difficult to sample with traditional net catches (Remsen et al., 2004), leading to a lack of comprehensive baseline data in the region. To study the gelatinous zooplankton, eDNA analyses were applied using the Leray fragment (313bp) of the COI gene with the Leray-XT primers (Wangensteen et al., 2018). Samples are sequenced in the Illumina NovaSeq platform in order to achieve better sequencing depth to increase the detection of rare species (Murray et al., 2024). Ongoing and planned eDNA research includes the establishment of a time-series for monitoring changes in (gelatinous) zooplankton communities using multi-marker approaches, e.g. by targeting also the 18S v1-2 frament (Dischereit et al., 2024; Ruiz et al., 2024a,b; Ruiz et al. 2024, 2024).

Fish and cephalopods – Their high mobility and responsiveness to environmental conditions make Arctic nekton such as fishes and cephalopods good indicator species of communities facing global change. On relatively short time scales, these organisms locate optimal environmental conditions by actively adjusting their depth and geographic distribution. Here, eDNA represents a promising tool to monitor nekton at LTER HAUSGARTEN (Merten et al., 2023) and is especially well-suited for researching nekton which is known to avoid nets. To provide baseline information on Arctic nekton diversity, eDNA work focusing on fish and cephalopods is based on targeting the mitochondrial 12S rRNA gene for fishes (Valentini et al., 2016) and the nuclear 18S rRNA gene for cephalopods (de Jonge et al., 2021). In past studies, water samples originated from vertically stratified depths from 50 to

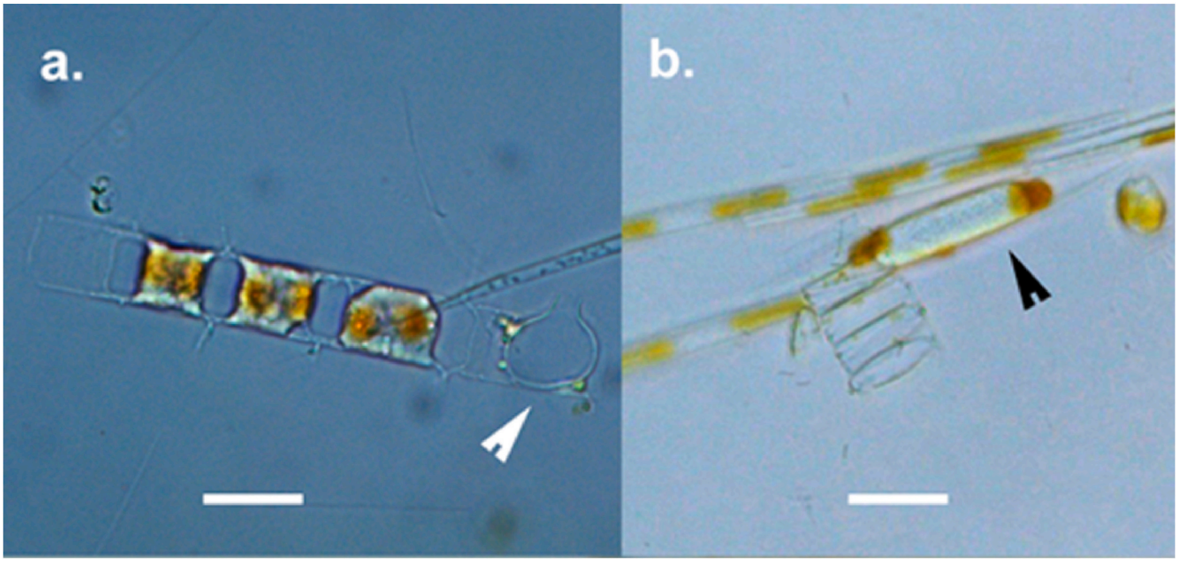

Fig. 4. Images of diatoms infected with parasites in field samples collected at LTER HAUSGARTEN. Arrows indicate parasite-infected cells.

5500 m. Additionally, sediment collected with a MUC, captured eDNA signatures of nekton derived from settling particles and preserved in surface sediments. For future sampling and establishment of a time series, the sedimentary eDNA analysis may be an integrative approach for nekton eDNA monitoring at HAUSGARTEN, since sampling and preservation procedures are fast and simple. However, it remains to be tested if all nekton species are equally well represented in sediment archives.

2.3. Data management and publication

In order to fully exploit the potential of our holistic eDNA observatory a reliable data management strategy is needed to make the HAUSGARTEN eDNA data **F**indable, **A**ccessible, **I**nteroperable, and **R**eusable according to the FAIR principles (Wilkinson et al., 2016). Within the Helmholtz Metadata Collaboration Project HARMONise ("Enhancing interoperability of biomolecular (meta)data across Helmholtz Centers"), members of the eDNA observatory team support the development of digital cultures by providing a framework for the high-quality and standards-compliant management of marine biomolecular data (Bienhold, 2024), which will enhance the findability, accessibility and interoperability of (meta)data from the molecular observatory. Relevant community standards pertinent to eDNA include: The "Minimum Information about any Sequence" (MIxS, Yilmaz et al., 2011) and "Minimum Information for the Publication of Quantitative Real-Time PCR Experiments" (MIQE, Bustin et al., 2009).

Currently, the sequence data for the different groups described above are deposited in the European Nucleotide Archive (ENA) or one of the other databases from the International Nucleotide Sequence Database Collaboration (INSDC). Collections of processed data are released in the PANGAEA World Data Center (Felden et al., 2023), and information on the analysis workflows are available on GitHub. Ribosomal metabarcoding and metagenomics data from the year-round studies are also publicly available under an ENA Umbrella Project (PRJEB43905). All bioinformatic code is deposited at GitHub, for instance describing the processing of metabarcoding reads from autonomous samplings (https://github.com/matthiaswietz/FRAM_eDNA). Such consistent documentation, linked to unambiguous sample IDs and ENA accessions throughout the analytic pipeline, ensures FAIR access. Furthermore, we have developed the interactive ShinyApp *polarDNAexplorer* (https://polardnaexplorer.awi.de) to visualize microbial metabarcoding data in their environmental context.

3. Results and case studies

Spatial patterns of microbial community composition in Fram Strait - LTER HAUSGARTEN is located in the hydrographically highly dynamic Fram Strait, the only deep-water connection between the North Atlantic and the Central Arctic Ocean (CAO). The West Spitsbergen Current (WSC) and the East Greenland Current (EGC), the two major currents in Fram Strait, harbor distinct bacterial, archaeal and eukaryotic microbial communities (Kilias et al., 2013; Fadeev et al., 2018), with pronounced seasonality especially in the WSC (Wietz et al., 2021). In the EGC, eukaryotic microbial communities, particularly the pico-plankton fraction, are highly similar to those in the Central Arctic Ocean (Metfies et al., 2016) probably due to advection processes facilitated by the transpolar drift. Besides major ocean currents, we found that small- and sub-mesoscale processes, such as eddy formation or sea-ice melt, alter community composition on a range of spatial scales, with seasonality of light, temperature and sea-ice coverage providing the fluctuating ecological baseline. This is particularly evident in the MIZ, which is a highly variable productive interface between an ice-free, often nutrient-limited, and an ice-covered light-limited ocean. Here, sub-mesoscale filaments characterized by a thin surface meltwater layer, coincide with distinct plankton composition, carbon export and primary production (Fadeev et al., 2021a). Combining high-resolution (~2 km) underway-sampling with physical underway measurements revealed that sub-mesoscale differences in eukaryotic microbiomes in surface waters of the MIZ were directly linked to differences in the physical environment, i.e. different water masses (Weiss et al., 2024). Furthermore, sea-ice cover significantly influences composition and functional diversity of microbial communities by shaping light availability and hydrography. The stratification caused by sea-ice melt drives microbial community composition and distribution, zooplankton composition, phytoplankton bloom phenology and carbon export (Fadeev et al., 2021a,b; von Appen et al., 2021; Priest et al., 2023; Oldenburg et al., 2024; Weiss et al., 2024; Fadeev et al., 2021a,b). Here, co-correlation networks of the concerted changes in microbial and zooplankton community composition in response to changing sea-ice conditions provide insights into potential trophic linkages between these taxonomic groups Oldenburg et al. (2024). In summer of 2010, melting sea ice in the ice-covered polar water of western Fram Strait increased the sequence abundance of pelagic sea ice-associated diatoms (e.g. *Fragilariopsis*), while heterotrophic dinoflagellates dominated the sequence assemblages in areas of the EGC associated with denser and thicker sea-ice. These communities contrast those of warmer, ice-free Atlantic waters of the WSC with pico-eukaryotic taxa, such as *Micromonas pusilla,* dominating the sequence assemblages in late summer (Kilias et al., 2013). Pico-eukaryotes, specifically the 0.4–3 μm size-fraction, are important contributors to Arctic eukaryotic microbial communities. During the summer of 2012, this size fraction accounted for 60–90 % of the Chl *a* biomass in Fram Strait and in the CAO. The highest pico-eukaryotic biomass occurred towards the end of the Polar Day in areas with higher light availability due to progressing sea-ice melt. Pico-eukaryotic diversity and community composition was linked to water mass distribution and nutrient availability (Kilias et al., 2014; Metfies et al., 2016), and specific co-occurring bacterial communities (Cardozo-Mino et al. 2021, 2023). Metabarcoding of the 16S rRNA gene has revealed contrasting bacterioplankton communities (members of the domain Bacteria and Archaea) in the WSC and EGC, with higher representation of SAR11 and SAR406 in ice-covered waters compared to Flavobacteria and Gammaproteobacteria in ice-free waters. These differences are underlined by differences in bacterioplankton abundances, with 10^5 cells mL^{-1} in ice-covered versus 10^6 cells mL^{-1} in ice-free waters. In addition to geographic patterns, communities vary with water depth (Cardozo-Mino et al., 2021). A recent survey of samples collected over five summers confirmed region and depth as key drivers of bacterial community structure in Fram Strait (Wietz et al., 2024).

In summary, water masses in the Arctic Ocean host distinct microbial communities, but mixing processes and other dynamics, such as eddy formation or sea-ice melt, can alter their composition across geographical scales, with seasonality of light, temperature and sea-ice coverage providing the framework for these change (Fadeev et al., 2021a,b; Kaiser et al., 2021; Weiss et al., 2024).

Temporal patterns of microbial community composition in Fram Strait - Time-series observations of the plankton composition are critical for deciphering natural variability at seasonal, annual, and decadal scales - an important prerequisite for a process-based understanding of Arctic ecosystems, and for identifying transitions in communities in response to environmental change (Wassmann, 2011; Grebmeier et al., 2019). At HAUSGARTEN, moored automated water samplers and sediment traps have highlighted temporal patterns in the eDNA composition, but also the vertical variability and connectivity of plankton communities. In the upper water column, autonomous sampling with RAS elucidated the seasonality of microbial communities in the physicochemical context (Wietz et al., 2021). The community in the WSC clearly separated into a productive summer (dominated by diatoms and carbohydrate-degrading bacteria) and regenerative winter state (dominated by heterotrophic Syndiniales, radiolarians, chemoautotrophic bacteria, and archaea), with recurring patterns over consecutive years (Fig. 5). These shifts are included in the temporally controlled succession of distinct microbial groups (Oldenburg et al., 2024; Priest et al., 2025) and are connected to seasonally different metabolic regimes, with higher primary production and concentrations of labile organic matter in summer vs. autumn (von Jackowski et al., 2022).

A weaker seasonality and a stronger heterotrophic signature were found in the polar water masses of the EGC, at depth, and under sea ice. Densely ice-covered polar waters host a temporally stable, resident bacterial microbiome, with metabolic adaptations towards using inorganic and refractory organic substrates (Priest et al., 2023). These and further observations illustrate distinct effects of polar-vs. Atlantic-influenced conditions on the microbial loop and the biological carbon pump. We also found sea-ice related processes to alter community signatures and functions in the water column. Meltwater-derived stratification in vicinity of the MIZ leads to increased abundances of sea ice-related pelagic phytoplankton during the growth period and to changes in bloom phenology compared to an ice-free year (von Appen et al., 2021; Oldenburg et al., 2024). 18S metabarcoding analyses of samples collected with long-term sediment traps suggested decadal variability in the composition of exported communities in response to a warm anomaly (Metfies et al., 2017), leading to changes in POC export (Cardozo-Mino et al., 2023; Ramondenc et al., 2025). The integrated analyses of 15 years of benthic 18S metabarcoding data and a selected set of corresponding data from sediment traps identified the diatom

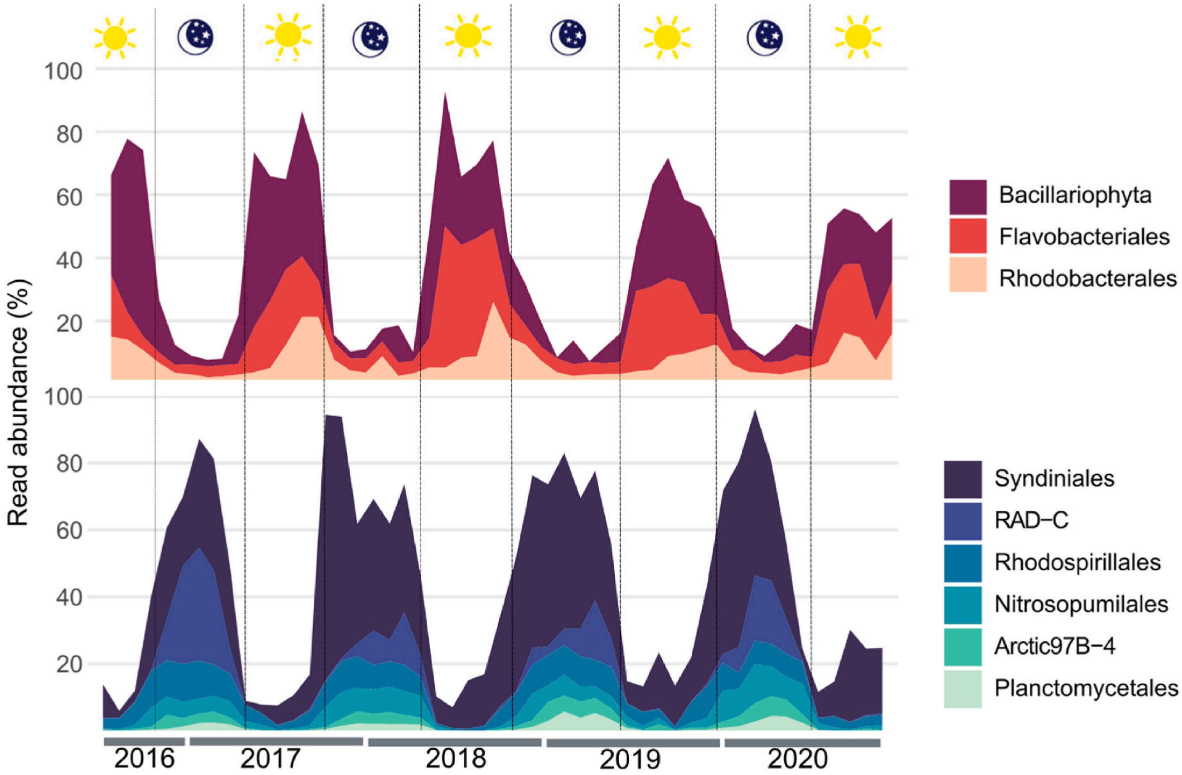

Fig. 5. Recurring microbial community succession over four annual cycles in the West Spitsbergen Current, showing the major bacterial, archaeal and eukaryotic taxa predominating during polar day (top; April–October) and polar night (bottom; November–March).

Chaetoceros socials as a critical component of the biological carbon pump in Fram Strait (Ramondenc et al., 2025). However, pico-eukaryotes, which are major contributors to chla a biomass in the Arctic Ocean (Metfies et al., 2016), might also contribute to carbon export. Sediment trap records suggest the highest exports of the pico-eukaryotes *Micromonas commoda* and *M. polaris* in Fram Strait in July (Bachy et al., 2022), while the details of its export mechanisms remain to be resolved. First insights into 18S meta-barcoding data from benthic samples collected in Fram Strait suggest that melting sea ice releases ballasting material that enhances the export of organisms with low sinking velocity, such as picoplankton (Swoboda et al., 2024).

Zooplankton and Nekton - Recent inventories of the diversity of gelatinous communities in Fram Strait highlighted the importance of abiotic hydrographic parameters shaping their distributions and pointed towards several potential candidates that may benefit from Atlantification (Mańko et al., 2020). Furthermore, a spatio-temporal modeling study predicted an increase in gelatinous zooplankton abundances with further Atlantification (Pantiukhin et al. 2023, 2024). Hence, we can expect major changes in gelatinous biomass and diversity in the rapidly changing Arctic Ocean, which calls for an integration of this zooplankton group in monitoring studies at LTER HAUSGARTEN. The overall diversity of the nektonic fauna was relatively low in Fram Strait, e.g. compared to tropical regions, but after all, 12 and 7 cephalopod and 31 and 28 fish taxa could be detected in seawater and sediment, respectively (Merten et al., 2023). The highest relative read numbers for cephalopods were found for the squid *Gonatus* sp., an abundant and ecologically important cephalopod in the Arctic (Golikov et al., 2020; Snoeijs-Leijonmalm et al., 2022). Sequences of this cephalopod were present in most of the eDNA samples collected at LTER HAUSGARTEN. Also, the fishes *Mallotus villosus*, *Thunnus* sp. and *Micromesistius poutassou* and the squid *Histioteuthis* sp. were detected, all of which are taxa that usually occur further south and have not been found previously in this region. These results thus suggest potential range expansions (Merten et al., 2023), and may be early signs of Atlantification (Polyakov et al., 2023) in the Arctic nekton community. The analysis of sedimentary eDNA detected not only benthic but also pelagic fauna. Pelagic taxa found in the sediment can originate from feces of predators or scavengers, including fish and cephalopods, or derive from marine snow, shedded carapaces or carcasses. It remains to be further investigated, how reliably eDNA of sediments can archive the presence of nekton species.

4. Conclusions

More than a decade of eDNA-based observations at LTER HAUSGARTEN have significantly fostered our ability to characterize seasonal and interannual ocean-warming related variability in Arctic marine biodiversity, including so-far understudied groups such as eukaryotic picoplankton (e.g. *Micromonas sp.*, MALVs), fungi and gelatinous zooplankton. Autonomous samplers aided in the first full analysis of the seasonal succession of microbial communities and their role in carbon cycling. The LTER HAUSGARTEN has become a holistic Arctic marine observatory by including an eDNA observatory, to address biodiversity across trophic levels, time (weeks to decades), habitats (sea ice, water column, benthos), and spatial scales (sub-mesoscale to pan-Arctic).

Against the context of our scientific objectives, we have been able to demonstrate the following since 2009 in Fram Strait, extending our understanding of Arctic marine biodiversity and ecosystem functionality in response to environmental drivers:

- The biodiversity and biogeography of Arctic marine organisms across trophic levels, from microbes to vertebrates, are linked to polar versus Atlantic water masses and decadal variations, enabling the characterization of their distribution patterns and the inference of potential interactions. In future studies, appropriate methods must be used to show how many of the potential interactions are actual ecological relationships, such as predator-prey relationships, parasite-host relationships or symbioses and how they are impacted by environmental change.
- We deciphered the relative abundance and distribution patterns of Arctic marine species across spatial and temporal scales as functions of environmental conditions, noting significant seasonal variations in microbes, phyto- and zooplankton, and changes in peak carbon fluxes and biological pump signatures. Here, the composition of the microbial communities is subject to a recurring seasonal rhythm. In light of the expected progression of global change in the Arctic Ocean, ongoing long-term observations have to investigate how distribution patterns and seasonal phenology of organisms will be affected by environmental changes. It is also essential to determine whether all taxonomic groups are equally impacted and to assess the potential consequences for Arctic marine food webs, the carbon cycle, and overall ecosystem functionality.
- Our results suggest, that Arctic environmental change, including rising temperatures, melting sea ice, and altered stratification regimes, significantly affects pelagic and benthic communities, as evidenced by shifts in community composition across trophic levels and in different habitats driven by these environmental factors. The eDNA surveys reveal signs of Atlantification in the communities occurring in Fram Strait. Locally, sea ice coverage and stratification of surface waters, i.e. by ice melt, play an important role in shaping community composition over trophic levels. In respect to this, our long-term observations should put special focus on invasion of temperate taxa and the adaptive capacity of endemic taxa, and consequences of species loss or invasions for ecosystem functionality.

Leveraging state-of-the-art technologies and sampling approaches comprehensively capturing different scales, will allow to address the upcoming tasks and scientific questions of Arctic marine long-term observation. This includes, above all, elucidating multi-trophic interactions and the connection between biodiversity and ecosystem functionality. The combination of eDNA studies at LTER HAUSGARTEN with biogeochemical measurements, together with physical and chemical oceanographic measurements allow to assess change in ecological processes but also resilience of the system. Such system-oriented observational approaches are essential to improve our understanding of the patterns and processes underlying biodiversity variation and their implications for Arctic marine ecosystem functions. Ultimately, this interdisciplinary initiative will establish key insights into the dynamics and changes of Arctic marine ecosystems under the impact of rapidly advancing climate change. In addition, we will provide comprehensive datasets suitable for use with the latest AI and machine learning techniques to improve our understanding of the Arctic Ocean system and develop scenarios for its future functioning. This is an important contribution to the development of strategies for Arctic marine protection and management.

CRediT authorship contribution statement

Katja Metfies: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Christina Bienhold:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Astrid Cornils:** Writing – review & editing, Methodology, Investigation. **Charlotte Havermans:** Writing – review & editing, Methodology, Investigation. **Henk-Jan Hoving:** Writing – review & editing, Investigation. **Alexandra Kraberg:** Writing – review & editing. **Silke Laakmann:** Writing – review & editing, Methodology, Investigation. **Véronique Merten:** Writing – review & editing, Methodology, Investigation. **Barbara Niehoff:** Writing – review & editing. **Marlis Reich:** Writing – review & editing, Methodology. **Matthias Wietz:** Writing – review & editing,

Writing – original draft, Software, Methodology, Investigation, Formal analysis. **Kasper Skytte Andersen:** Writing – review & editing, Software. **Magda Guadalupe Cardozo-Mino:** Writing – review & editing. **Eduard Fadeev:** Writing – review & editing. **Kristin Hardge:** Writing – review & editing. **Lars Harms:** Writing – review & editing. **Ayla Murray:** Writing – review & editing. **Stefan Neuhaus:** Writing – review & editing. **Eva-Maria Nöthig:** Writing – review & editing, Conceptualization. **Ellen Oldenburg:** Writing – review & editing, Software. **Taylor Priest:** Writing – review & editing. **Josephine Z. Rapp:** Writing – review & editing, Investigation. **Marianne Rehage:** Writing – review & editing. **Ian Salter:** Writing – review & editing. **Julia Stefanschitz:** Writing – review & editing. **Sinhué Torres-Valdés:** Writing – review & editing. **Wilken-Jon von Appen:** Writing – review & editing. **Antje Boetius:** Writing – review & editing, Supervision.

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Declaration of competing interest

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

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