RESEARCH ARTICLE

Pan–Arctic plankton community structure and its global connectivity

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The Arctic Ocean (AO) is being rapidly transformed by global warming, but its biodiversity remains understudied for many planktonic organisms, in particular for unicellular eukaryotes that play pivotal roles in marine food webs and biogeochemical cycles. The aim of this study was to characterize the biogeographic ranges of species that comprise the contemporary pool of unicellular eukaryotes in the AO as a first step toward understanding mechanisms that structure these communities and identifying potential target species for monitoring. Leveraging the *Tara* Oceans DNA metabarcoding data, we mapped the global distributions of operational taxonomic units (OTUs) found on Arctic shelves into five biogeographic categories, identified biogeographic indicators, and inferred the degree to which AO communities of unicellular eukaryotes share members with assemblages from lower latitudes. *Arctic/Polar indicator* OTUs, as well as some *globally ubiquitous* OTUs, dominated the detection and abundance of DNA reads in the Arctic samples. OTUs detected only in Arctic samples (*Arctic-exclusives*) showed restricted distribution with relatively low abundances, accounting for 10–16% of the total Arctic OTU pool. OTUs with high abundances in tropical and/or temperate latitudes (*non-Polar indicators*) were also found in the AO but mainly at its periphery. We observed a large change in community taxonomic composition across the Atlantic-Arctic continuum,

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supporting the idea that advection and environmental filtering are important processes that shape plankton assemblages in the AO. Altogether, this study highlights the connectivity between the AO and other oceans, and provides a framework for monitoring and assessing future changes in this vulnerable ecosystem.

Introduction

The Arctic Ocean (AO) is going through a rapid change due to anthropogenic warming, marked by the alarming rate of decline in the extent and volume of sea ice. Some models predict that by 2050 the AO will be ice-free in summer (Notz and SIMIP Community, 2020). Planktonic microorganisms are highly sensitive to climatic forcing (Hays et al., 2005); their population dynamics in the AO are tightly linked to sea ice-ocean interactions (Ardyna and Arrigo, 2020). In conjunction with changes in the Arctic icescape, major changes to the oceanography of the region are underway, from processes affecting local mixing and stratification to basin scale circulation (Timmermans and Marshall, 2020). The consequences of these effects on unicellular eukaryotic plankton are complex to delineate. Although future trajectories have been proposed for phytoplankton in general (Ardyna and Arrigo, 2020), ecological knowledge is still lacking at a fine taxonomic level, making predictions and the detection of shifts in these communities difficult.

In addition to environmental variations, plankton communities in the AO are influenced by the influx of Atlantic and Pacific waters that carry their physical and chemical signatures, as well as subpolar and temperate species, into the AO (Wassmann et al., 2015; Ardyna and Arrigo, 2020; Csapó et al., 2021). The transport of plankton by ocean currents (hereafter bioadvection) is now recognized as an important mechanism underlying the observed poleward expansions of some phytoplankton and zooplankton populations in the Barents Sea (Wassmann et al., 2019; Oziel et al., 2020; Greco et al., 2022). Unicellular plankton have high dispersal potential and broad geographic ranges, aided by high abundances, asexual reproduction and—in some cases—the ability to form dormant stages (Finlay, 2002). The success of advected species in establishing populations in the AO, however, depends on their ability to survive and reproduce under the extreme seasonality in day length and sea ice cover, as well as low temperatures and variable salinity. Thus, locally adapted species ought to outcompete or even take advantage of advected organisms from lower latitudes as a food source (Wassmann et al., 2019). As the warming of North Atlantic water continues and the sea ice volume that exits the Fram Strait decreases, the transport of Atlantic water into the AO is expected to intensify (Wang et al., 2020). In the Bering Strait, in situ mooring data already have documented a long-term increase (1990–2015) in the annual mean transport of Pacific water into the Arctic (Woodgate, 2018). Because the volume of Atlantic water that enters the AO through the Fram Strait and Barents Sea openings is about 10 times larger than the volume of Pacific water that

enters via the shallow and narrow Bering Strait (Timmermans and Marshall, 2020), the influx of Atlantic taxa is expected to be higher.

How changes in the current balance between bioadvection and local environmental filtering processes within the AO will affect plankton communities of microbial eukaryotes is a relevant and timely question. Efforts to compile published data sets from different regions of the AO have provided initial pan-Arctic inventories of the diversity of this phylogenetically rich group of microorganisms (Lovejoy et al., 2006; Bluhm et al., 2011; Poulin et al., 2011; CAFF, 2017; Rämä et al., 2017; Stoecker and Lavrentyev, 2018), but only a few of these studies have examined Arctic taxa in a global context. The biogeographic structure of these communities beyond the AO remains elusive. Based on microscopy records, the conclusion has been drawn that Arctic dinoflagellates form a coherent Arctic-boreal metacommunity, and that tropical-boreal and Antarctic-tropical-boreal species detected in the AO are allochthonous (Okolodkov and Dodge, 1996). An Arctic-boreal metacommunity was also suggested for the diatom order Thalassiosirales based on a molecular analysis (Luddington et al., 2016). A recent analysis of diatom communities from five Svalbard fjords showed that Arctic genotypes display a variety of biogeographic patterns, ranging from endemic to cosmopolitan distributions (Šupraha et al., 2022). These observations for selected taxa highlight the need for a more extended analysis of biogeographic patterns—on a pan-Arctic scale and across a wider range of Arctic taxa—to better understand the connectivity of AO communities with other oceans and the biogeographic processes that shape them. Such analysis could also help identify target species for monitoring and assessments of biotic responses to climate change.

Here, we have leveraged the globally collected *Tara* Oceans 18S rRNA gene amplicon sequencing data to study biogeographic patterns of operational taxonomic units (OTUs) from 75 deep-branching lineages that were recovered from the AO. OTUs were grouped into 5 biogeographic categories based on a statistical analysis of their abundance and occupancy patterns within and beyond the AO. These include *Arctic/Polar indicators*, *globally ubiquitous* OTUs, *non-Polar indicators*, and a group of less abundant OTUs that was further divided into a group that was only detected in AO samples (*Arctic-exclusives*) and a group of *background* OTUs with a broader range of distributions. Considering these groups, we asked the following questions: (1) What is the relative contribution of each biogeographic category to the contemporary pan-Arctic community and do taxa with high biogeographic specificity to the AO account for a higher proportion of AO

biodiversity? (2) Do the 75 deep-branching lineages differ in their biogeographic structure and are there lineages that are more enriched in a specific biogeographic category? (3) On a pan-Arctic scale, are taxa that show geographical preference to low latitudes more likely to be detected in the Arctic gateways compared to other regions of the AO?

Materials and methods

Data were collected during the *Tara* Oceans expedition; overviews of the expedition are provided in Sunagawa et al. (2020) and references therein. The analyses presented here are based on samples collected at 89 globally distributed stations, 18 of them located in the AO (TARA stations 158–209; Figure S1; Table S1). Here we provide additional details on the sampling program in the AO and the specific analyses performed in this study.

The Tara Oceans Polar Circle expedition: Environmental context and biological sampling

In June through October 2013, the *Tara* Oceans expedition circumnavigated the AO (**Figures 1A** and S1) using its standardized protocols to study plankton ecosystems (Pesant et al., 2015; Alberti et al., 2017). Contextual hydrographic parameters used here were obtained from daily deployments of a CTD rosette package that provided vertical profiles of temperature, practical salinity, chlorophyll fluorescence, and nitrate (Picheral et al., 2014; Pesant et al., 2015). Surface chlorophyll *a* concentrations were derived from fluorescence measurements (Wet Labs ECO sensor) that were calibrated against chlorophyll *a* concentrations obtained from high pressure liquid chromatography analysis. In situ measurements were augmented with remote sensing data of surface chlorophyll *a* and surface ice concentrations to produce dynamic maps (based on a 250-km latitudinal band) of their variations in the region and time of sampling (**Figure 1**). Satellite-derived chlorophyll *a* and sea ice concentration data were obtained, respectively, from the European Space Agency GlobColour project (http://www.globcolour.info) and the National Snow and Ice Data Center (https://nsidc.org). We used bottom depths from the National Oceanic and Atmospheric Administration (NOAA, USA) at 4-min spatial resolution from the R-package "marmap" (version 1.0.5). Additional environmental parameters used in the analysis included the mixed layer depth (MLD) that was calculated from our own potential density profiles following de Boyer Montégut et al. (2004); concentrations of iron, derived from the ECCO2-DARWIN ocean model (Menemenlis et al., 2008); and daylength, calculated from the astronomical applications of the U.S. Naval Observatory (https://aa.usno.navy.mil/data/index) at the sampling date and location. *Tara* Oceans expedition full contextual data are available at https://doi.org/10.1594/PANGAEA.875582.

Samples for DNA metabarcoding analyses were collected with Niskin bottles from 18 stations that encompass different continental shelf types (inflow, interior and outflow shelves; Carmack and Wassmann, 2006), hydrographic and nutrient regimes, and periods of melt and ice

formation (**Figures 1** and S2; a list of AO stations indicating sampling dates, locations, station depths and daylength is provided in Table S1). Most samples were collected in open water over Arctic shelves, with some stations coinciding with the marginal ice zone (approximately 30% sea ice cover) and slope waters. The sampling protocol was the same as for the global ocean (Pesant et al., 2015), including surface (5 m) and subsurface chlorophyll maxima (SCM) samples when the latter was detected with a fluorometer mounted on the CTD-rosette. Because of the low number of SCM samples from the AO (8 stations), we chose to focus the main analyses of this paper on surface samples. Seawater samples for DNA analysis were size-fractionated (Pesant et al., 2015). For the purpose of this study we have used the integrative fraction 0.8–2000 μm because it retrieves most functional groups and allows the characterization of the community across a wide range of cell sizes. Filters were immediately deep-frozen in liquid nitrogen for later DNA extraction and sequencing (Alberti et al., 2017).

Our analysis focuses largely on the pan-Arctic assemblage, but to address question #3 (Introduction) stations were grouped into 5 Arctic regions following the framework of the Arctic Marine Biodiversity Monitoring Plan (Gill et al., 2011; CAFF, 2017; **Figure 1A**): (1) Atlantic inflow shelf, which includes the Greenland and Barents seas (TARA stations 158, 163, 168 and 175); (2) inner Siberian shelves, which include the Kara, Laptev and East Siberian seas (TARA stations 173, 178, 180, 188 and 189); (3) Pacific inflow shelf, which includes the Chukchi Sea (TARA stations 191, 193, 194) and one station on the Beaufort Shelf (TARA station 196); (4) Canadian Archipelago/western Baffin Bay, a region characterized by a net outflow of modified Pacific and Arctic water (TARA stations 201 and 205); and (5) eastern Baffin Bay/Greenland fjord, an area influenced by the northward flowing West Greenland Current with an Atlantic water signature (Münchow et al., 2015; TARA stations 206, 208, 209).

Metabarcoding analyses

DNA extraction and high-throughput amplicon sequencing protocols are described in de Vargas et al. (2015) and Alberti et al. (2017). For this work we used reads derived from the V9 region of the 18S rRNA gene, and compared our main results to data derived from the V4 region of the same gene (Table S2). For the latter, the utilized primers were TA-Reuk454FWD1 (5′-CCAGCA(G/C)C(C/T)GCGG-TAATTCC-3′, *S. cerevisiae* position 565–584) and TAReuk-REV3 (5′-ACTTTCGTTCTTGAT(C/T)(A/G)A-3′, *S. cerevisiae* position 964–981). In both cases, reads were grouped into OTUs using the following swarm-based pipeline: paired-end reads were merged with vsearch's --fastq_mergepairs command (version 2.15.1, allowing for staggered reads; Rognes et al., 2016), and trimmed with cutadapt (version 3.0; Martin, 2011), keeping only reads containing both forward and reverse primers. After trimming, the expected error per read was estimated with vsearch's command --fastq_filter and the option --eeout. Each sample was then de-replicated; that is, strictly identical reads were merged, using vsearch's command --derep_fulllength, and
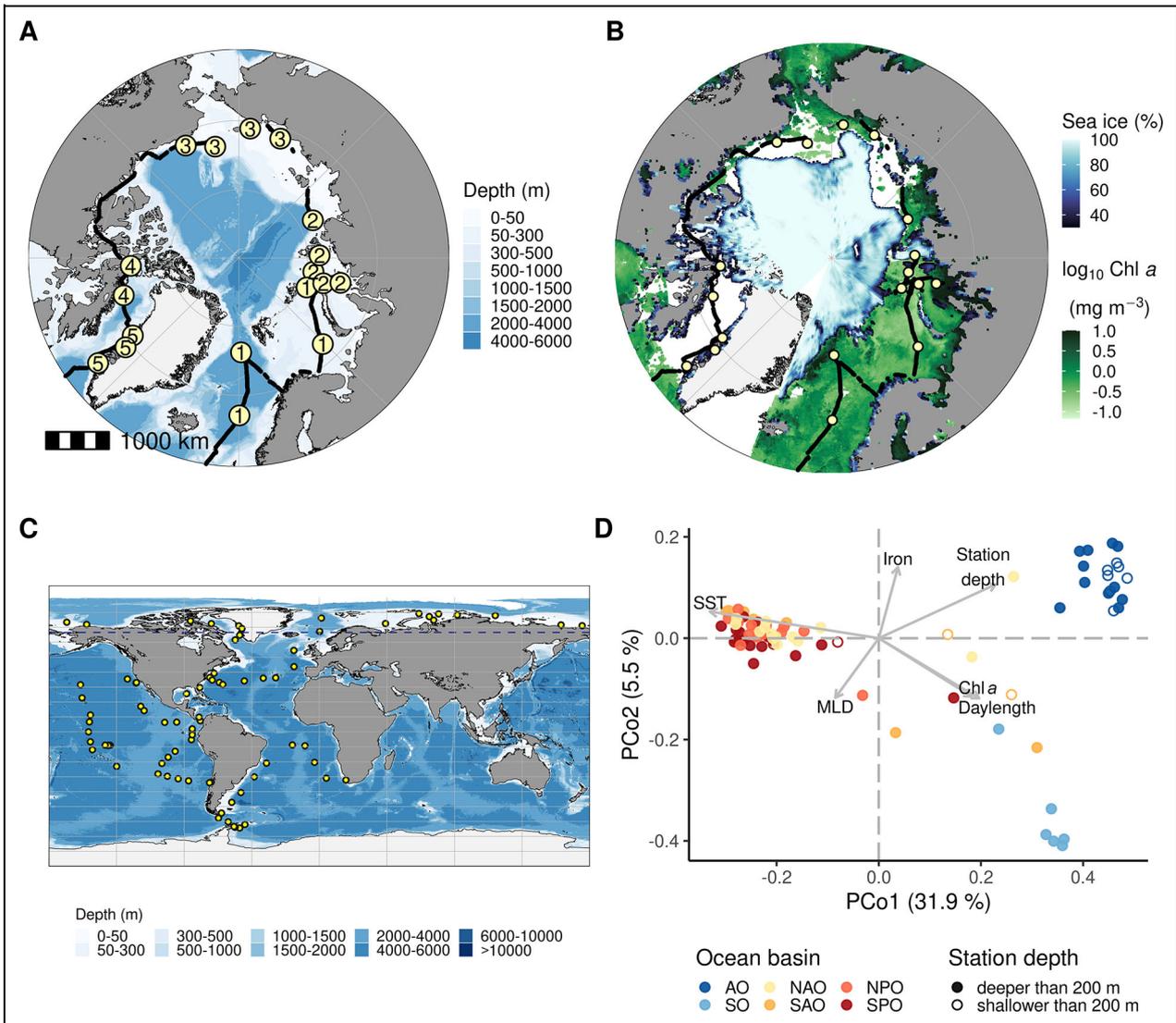
Figure 1. A global perspective of the pan-Arctic community of unicellular eukaryotic plankton. (A) North Pole-centered bathymetric map of sampling stations (yellow circles) during the *Tara* Oceans Polar Circle expedition. Numbers indicate station groupings based on the Arctic Marine Biodiversity Monitoring Plan (Gill et al., 2011; CAFF, 2017): (1) Atlantic inflow shelf, (2) Siberian shelf (inner), (3) Pacific inflow shelf, (4) Canadian Archipelago and West Baffin, and (5) East Baffin. (B) Dynamic map of contextual information on sea ice concentration (%) and chlorophyll a (mg m^{-3}) during the sampling period (derived from a 250-km latitudinal band following the timing and location of the cruise track). Black line represents the ship track; yellow circles, station locations. Satellite-derived datasets of chlorophyll and sea ice were obtained, respectively, from the European Space Agency GlobColour project (http://www.globcolour.info) and the National Snow and Ice Data Center (https://nsidc.org). For the Kara Sea and the Chukchi/Beaufort region, the actual ice-edge zone was south of that obtained via satellite. (C) Stations from the global *Tara* Oceans dataset (2009–2013) mapped on the world ocean bathymetry. (D) Principal coordinates analysis based on Bray-Curtis community dissimilarities for unicellular eukaryotes from the surface ocean, with proportion of variance on each axis (%). Each circle represents a community at a given sampling station (panels A and C), with colors indicating respective oceanic basins: North and South Atlantic Ocean (NAO and SAO), North and South Pacific Ocean (NPO and SPO), and Southern Ocean (SO). Filled versus open circles distinguish stations with depths below 200 m (filled) from stations shallower than 200 m (open). Six oceanographic variables were overlaid on the ordination through "envfit" function: sea surface temperature (SST), mixed layer depth (MLD), chlorophyll a (Chl a), station depth, daylength, and simulated iron concentration (statistics in Table S3). Arrows point toward the ordination space with maximal correlation; their length refers to relative strength of the correlation.

converted into fasta format. Clustering was performed at the sample level with swarm 3.0 using default parameters (Mahé et al., 2015). Prior to global clustering, individual fasta files (one per sample) were pooled and further

dereplicated with vsearch. Files containing per-read expected error values were also dereplicated to retain only the lowest expected error for each unique sequence. Global clustering was performed with swarm (using the fastidious

option). Cluster representative sequences were then searched for chimeras with vsearch's command --uchime_denovo using default parameters (Edgar et al., 2011).

Clustering results, expected error values, taxonomic assignments, and chimera detection results were used to build a "raw" occurrence table. Reads without primers, reads shorter than 32 nucleotides, and reads with uncalled bases ("N") were discarded. For a "filtered" occurrence table, non-chimeric sequences, sequences with an expected error per nucleotide below 0.0002, and clusters containing at least 2 reads were retained. As primer trimming is not perfect, some sequences can still contain primer fragments or be excessively trimmed. These sub- or super-sequences were identified using vsearch and merged with their closest, most abundant perfectly trimmed sequence. Finally, occurrence patterns throughout our sample collection were used to further refine the occurrence table. Clusters that contain sub-clusters with only a single-nucleotide difference but with different ecological patterns (defined here as uncorrelated abundance values in at least 5% of the samples) were turned into distinct clusters (https://github.com/frederic-mahe/fred-metabarcoding-pipeline). On the other hand, clusters with similar sequences that had correlated abundance values in at least 95% of the samples were merged using a re-implementation of lulu's method (Frøslev et al., 2017; https://github.com/frederic-mahe/mumu).

To ensure that the V9 and V4 data sets were comparable, we took into account differences in the number of samples and depth of sequencing. The V9 dataset had sequencing data for 18 surface samples and 8 SCM samples from the AO, while for the V4 dataset only 13 surface samples were available. The sequencing depth was approximately 10^6 reads per sample for the V9 region and approximately 10^5 reads per sample for the V4 region (Figure S3). These two aspects, together with the inherent differences related to the nucleotide sequence natural variation (e.g., GC content) and length that could affect steps such as the PCR or the subsequent construction of OTUs, motivated us to: (a) center our analyses on the V9 dataset and use the V4 for the validation of emerging patterns, and (b) exclude the very least abundant OTUs by keeping only those with at least one sample exhibiting a relative abundance of 0.001% in surface and SCM samples. We nevertheless recognize that rare OTUs are an important component of microbial communities, and the consequences of their removal were evaluated (Figure S4). From an Arctic perspective, the latter affected mainly the number of OTUs that were detected exclusively in the AO (Figure S4).

Both global datasets were rarefied at the Arctic minimum of 2.6×10^5, which was greater than the global minimum of 1.8×10^5, as a trade-off between reducing the effects of uneven sequencing depths for our ecological analyses and avoiding information loss from the Arctic plankton community. The slightly lower sequencing effort of certain samples from the non-Arctic ocean should be compensated by the higher number of non-Arctic stations (>3x). A sensitivity test was nevertheless performed by also rarefying at the global minimum (1.8×10^5), with no significant changes in the proportion of biogeographic categories.

A taxon name was assigned to each OTU by comparing its representative sequence (the most abundant one) against PR2_V9, a customized PR2 reference database (Guillou et al., 2013; de Vargas et al., 2015; http://doi.org/10.5281/zenodo.3768951), using vsearch --usearch_global command. OTUs classified as Bacteria, Archaea and Metazoa were removed from the analyses, as well as a few OTUs with low representation, pluricellular life-forms (Ulvophyceae, Phaeophyceae, Streptophyta, Fornicata, Glomeromycota, Parabasalia, Phytomyxea, and Rhodophyta, except for genus *Rhodella*) or nucleomorphs of both chlorarachneans and cryptophytes. OTUs with an identity matching <80% of a reference sequence were excluded as well. Trophic functions (photosynthetic, phagotrophic, parasitic, photosynthetic endosymbiont) were assigned to OTUs for which information is known from literature. The photosynthetic function refers here to the presence of a permanent chloroplast, based on a literature review (de Vargas et al., 2015), which does not exclude the possibility of mixotrophy. Altogether, the V9 region contained more deep-branching lineages than the V4 region. Mismatches to the primer set or the amplified fragment being longer than the sequencing capabilities (2×250 bp) explain why Diplonemida and Euglenida from the Excavata supergroup would be absent from the V4 data (Vaulot et al., 2022). Comparisons at the level of deep-branching lineages were performed on the 47 coinciding groups (Figure S5). These groups have consistent relative abundance regardless of the marker used (Spearman's rho = 0.93, p << 0.001). Raw reads of 18S rRNA gene metabarcoding are deposited at the European Nucleotide Archive (ENA) under projects PRJEB6610 and PRJEB9737.

Statistical analyses on surface samples
Community dissimilarity at global scale
OTU abundances were normalized by dividing each value by the total sum per sample, followed by a transformation using the "decostand" function. Bray-Curtis pairwise dissimilarities of samples were then calculated and used as input for a principal coordinates analysis. Differences between polar and nonpolar communities were assessed through a Permutational Multivariate Analysis of Variance (PERMANOVA) using the function "adonis." A selection of contextual variables (temperature, chlorophyll *a*, iron, mixed layer depth, daylength and station depth) was fit on the ordination with the "envfit" function to explore potential driving factors of community differences. A goodness of fit (R^2) and a p-value were retrieved from the function as a result from a permutative procedure (Table S3). This selection of contextual variables was chosen as general habitat descriptor and with the criterion of reducing collinearity (see multiple pairwise correlation analysis between all available habitat descriptors performed in Ibarbalz et al., 2019). Functions used for the above analyses are included in the R-package "vegan" (Oksanen et al., 2019) and were used with default parameters.

Biogeographic categories

OTUs were classified according to broad biogeographic distributions into 5 mutually exclusive categories. We used a species indicator approach to identify OTUs with strong affinity for the AO (De Cáceres and Legendre, 2009). This effort was performed with the function "multipatt" in the R-package "indicspecies" v.1.7.8 with parameter "IndVal.g." Specifically, an OTU was considered an indicator of the Arctic Ocean (s.Region$_{AO}$ = 1) and not of any other non-polar oceanic region (s.Region$_i$ = 0), when the association value was >0.7, and the p-value was <0.05, including false discovery rate correction for multiple comparisons. This association value threshold selected OTUs with at least 50% AO occupancy. Because many of these OTUs were also detected in the few samples of the Southern Ocean (n = 6), in the following text we refer to this group as *Arctic/Polar indicators.* Using the same approach, we defined *non-Polar indicators* by retrieving those OTUs with high affinity for regions below the Arctic circle (specifically, North Atlantic, South Atlantic, North Pacific or South Pacific Ocean; s.Region$_{AO}$ = 0, s.Region$_i$ = 1, same parameters). We emphasize that in these two categories the term "indicator" refers to a statistical definition based on their detection patterns throughout the world's oceans, in contrast with other ecological definitions related to particular functions or sensitivities (Siddig et al., 2016). We did not determine specific Southern Ocean indicators because of the small number of samples (n = 6). A third category was set for *globally ubiquitous* OTUs that were defined as OTUs having >50% occupancy at Arctic and >50% occupancy at non-Arctic stations, and were not defined previously as indicators. The remaining OTUs that were detected in the AO were found at relatively lower abundances. If they were only detected in the AO, they were considered *Arctic-exclusive*; otherwise, they were called *background. Background* OTUs were not differentiated by a degree of cosmopolitanism (i.e., a single detection outside of the AO was sufficient) given their overall low detection in samples.

OTU biogeographic annotations are available in the Appendix (http://dx.doi.org/10.17632/zb96mzvhv5.1). Estimates of the relative contributions of each biogeographic category to the pool of OTUs derived from the V9 variable region of the 18S rRNA gene were compared with estimates for the V4 region (Table S4). The circular panel delineating OTU distributions across taxa, biogeographic categories and Arctic regions (**Figure 4**) was done with R-package "circlize" (v. 0.4.10; Gu et al., 2014), where each biogeographic category of each lineage was sorted according to a model-based clustering obtained through functions "mclustBIC" and "Mclust" from R-package "mclust" (v. 5.4.6; Scrucca et al., 2016). A full version of **Figure 4A** is available at https://doi.org/10.6084/m9.figshare.14562606. We acknowledge the challenges and uncertainties of placing drifting (planktonic) organisms into biogeographic categories and use the term "biogeography" in a broad sense.

Gross changes in OTUs identity and dominance structure between North Atlantic and Arctic communities

Gross change in OTU identity and gross change in dominance structure or abundance were calculated for samples collected in the North Atlantic and Arctic oceans following the approach of Hillebrand et al. (2018). Briefly, in a pairwise comparison of samples, gross change in identity accounts for the sum of species that are not shared between samples, relative to the total number of species. This index corresponds to the Jaccard index. Gross change in abundance corresponds to a Simpson-based turnover index. Both indices vary between 0 and 1, with 1 meaning a complete change of community composition. Since gross change in identity can be sensitive to the sampling effort, we rarefied the data at the minimum sum among the subset of samples used prior to calculations (5 × 10^5 reads per sample; function "rrarefy" from R-package "vegan"). The effect of rare OTUs was evaluated by repeating the analysis starting from a lower OTU percentage cutoff (1 × 10^{-4}; Figure S4), allowing the number of rare OTUs to increase. This results in an increase in the average of gross change in identity by only 7%, with the overall patterns remaining the same.

Results and discussion

Environmental and taxonomic contextual information

Assemblages of eukaryotic plankton were sampled across heterogeneous conditions. The majority of the samples were collected in open waters at varying times since ice melt and varying distances from the seasonal ice edge (**Figure 1B**). Nitrate and chlorophyll *a* concentrations also varied greatly, reflecting different stages in the annual cycle of phytoplankton (**Figures 1B** and S2). Hydrographic profiles of salinity and temperature show the key water masses that were sampled during the *Tara* Oceans Polar Circle expedition (Figure S2). These included (i) the warm and saline Atlantic water that enters the AO through the Fram Strait and the Barents Sea and spreads across the Eurasian and Canada basins at intermediate depths, (ii) the relatively cold and fresh lens of surface water over the Siberian, Chukchi and Canadian shelves, (iii) the modified Arctic and Pacific waters (cold and fresh) that are advected southward along Baffin Island, and (iv) the warmer and saltier Atlantic water advected along western Greenland. Thus, while each station represented only a snapshot in time of a dynamic environment, their combination and the deep sequencing per site (>10^6 sequence reads per sample; Figures S3 and S4) captured a significant portion of the diversity of unicellular eukaryotes that occupy Arctic shelves.

An average of 934 (± 264) OTUs per station were recovered in the AO, resulting in a total of 3,082 different OTUs across the AO (for the V9 region; Figure S3; Table S2). These results were in good agreement with the numbers of OTUs derived from the V4 dataset (Table S2; Ibarbalz et al., 2019). The majority of the reads belonged to photosynthetic and phagotrophic organisms (Figure S6A), and likely included mixotrophic groups that can be both autotrophic and heterotrophic. Parasites and putative endo-photosymbionts were detected at lower abundances and mostly in regions associated with northward-flowing Atlantic water (regions 1 and 5; Figure S6A). Relative contributions of major photosynthetic and phagotrophic taxa

to the pan-Arctic pool are reported in Figure S6B–D to provide a general overview of the communities that were sampled during the *Tara* Oceans Polar Circle expedition.

In this study, we focused on the surface layer. Nevertheless, a relatively small number of available samples from the subsurface chlorophyll maximum (SCM, n = 8, V9 region) allowed us to explore how AO photic communities vary with depth, as previous studies have shown that SCM communities often differ from those in surface water (Monier et al., 2013; Ardyna et al., 2017). Our analysis suggests that variability due to geographic location of each station (as well as temporal variability due to the progression of the season during the circumnavigation) surpassed variations due to vertical zonation (Figure S7; PERMANOVA for surface versus SCM: $R^2 = 0.06$, not significant). Still, a fraction of low-abundant OTUs (32 ± 9% of OTUs per station, representing 1.9 ± 1.7% of read abundance) were only detected in the SCM, indicating that this layer contributes to AO biodiversity.

AO communities in a global context

When comparing community compositions of all *Tara* Oceans samples across the world's oceans, a clear pattern emerges, with AO communities clustering separately from most other communities (**Figure 1C–D**; see also Sommeria-Klein et al., 2021). Southern Ocean communities and some Atlantic Ocean communities, however, clustered close to AO samples along the first axis (31.9% of total variation). This pattern is consistent with previous reports for other groups of plankton such as bacteria (Ghiglione et al., 2012; Salazar et al., 2019), archaea (Galand et al., 2009a) and viruses (Gregory et al., 2019; Endo et al., 2020), as well as overall distinct plankton co-occurrence networks (Chaffron et al., 2021). Overall, community dissimilarities co-varied strongly with temperature and station depth, and to a lesser extent with other selected environmental parameters (**Figure 1D**; Table S3). The high proportion of samples collected over continental shelves in the AO introduces a bias in the analysis, as some of the differences from the rest of the predominantly oceanic *Tara* Oceans samples could be attributed to differences between shelf and oceanic communities. However, the clustering of all AO samples with each other, regardless of station depth (**Figure 1D**), and with oceanic samples from the Southern Ocean (station depth near 400 m for the two shallowest stations and between 2300–4100 m for the remaining stations; Table S3; PERMANOVA for "Polar" as factor: $R^2 = 0.3$, p < 0.001), implies that the more coastal nature of Arctic shelves is not the only driver of the observed dissimilarities.

Throughout the evolution of the modern Arctic, tectonic processes, such as the opening of the major Arctic gateways and glacial controls on sea level, combined with climatic changes have provided opportunities for species from the global ocean to establish populations in the AO. Contrarily, physical barriers for dispersal and isolation in sub-Arctic and Arctic refugia created during glaciation periods allowed genetic divergence in some populations (Hardy et al., 2011). These processes likely gave rise to a distinct mix of organisms, with different biogeographic histories, that is reflected in the contemporary pool of Arctic unicellular eukaryotic plankton. To further understand how the pan-Arctic community differentiates from and is influenced by communities from other oceans, we analyzed the biogeographic structure of the pan-Arctic community (**Figure 2A**).

Biogeography of Arctic unicellular eukaryotes: From a pan-Arctic to a global view

On a pan-Arctic scale, OTU abundance and occupancy correlated positively (**Figure 2B**), a pattern repeatedly observed across taxa in other environments (Gaston et al., 2000). The most abundant and widespread OTUs belonged to the *Arctic/Polar indicator* and the *globally ubiquitous* groups. As such, members of these groups likely play pivotal roles in the AO ecosystem, although accounting for only 9–12% and 6% of the pool of OTUs found in the AO, respectively (**Figure 2B**, Table S4). Winter samplings, in spite of a general decrease in biomass and changes in relative abundances, could determine if these OTUs are (as we think they are) still detected at most of the stations. Approximately half of the *Arctic/Polar indicators* (55–57%) were detected in our Southern Ocean samples (examples in **Figure 2C**). This result may indicate that a connectivity between populations of an OTU present in the two polar oceans existed, and perhaps still exists, or a difficulty to distinguish different ecotypes from their V9 or V4 rRNA gene sequence (Šupraha et al., 2022). This connectivity or difficulty may also be the case for the relatively few globally ubiquitous OTUs. Future strain isolations and single-cell sequencing could clarify these indications (Dorrell et al., 2022).

In comparison, *Arctic-exclusive* OTUs were less abundant, showed a more restricted distribution, and accounted for 10–15% of the OTU richness (significantly affected by the chosen abundance cutoff; see Methods; **Figure 2B**, Table S4). We cannot preclude the possibility that *Arctic-exclusive* OTUs might increase in abundance at certain times of the year not covered in this study, display interannual variations in population dynamics, or might simply exist at low abundances (Galand et al., 2009b; Ser-Giacomi et al., 2018). The small proportion of *Arctic-exclusive* OTUs that were found in this study is consistent with the notion, brought from microscopy observations, that true endemic planktonic species are few (Okolodkov and Dodge, 1996; Bluhm et al., 2011). However, their relatively low abundance, the limitations in the microbial species definition based on rRNA marker genes, and the difficulties in defining geographic boundaries for marine plankton preclude us from reaching firm conclusions about endemicity.

Non-Polar indicators were also present in low abundance and had restricted distribution within the AO (discussed below), yet their overall contribution to the observed richness was not negligible (16–24%; **Figure 2B**). These OTUs may represent a "newer" phase of the recolonization of the AO (on paleoclimatic time scales), with populations that are not fully established (and may never will). Finally, *background* OTUs contributed the most to OTU richness (48–54%; **Figure 2B**; Table S4). In light of
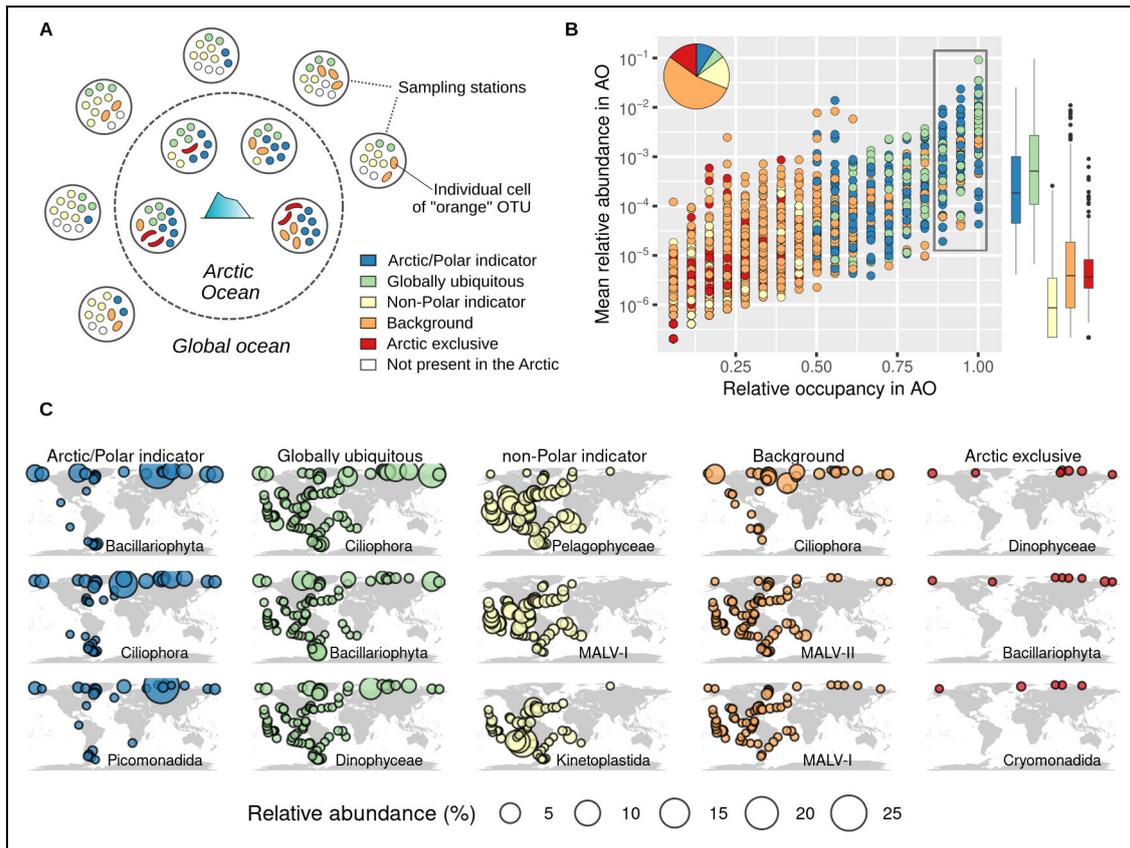
Figure 2. Globally contextualized biogeographic categories of Arctic OTUs and their distribution patterns. (A) Schematic representation of the different biogeographic categories where each shape represents an individual OTU colored by its biogeographic category. (B) Abundance-occupancy patterns of Arctic OTUs. Occupancy is scaled 0–1, with a value of 1 indicating that an OTU was present in all 18 stations. The rectangular frame encompasses OTUs that were present in ≥90% of the stations (a proxy for pan-Arctic distribution), which make up 6% of the total pool (Table S4). A log10-transformation of the y-axis is used for visual purposes. Each circle represents a single OTU, colored according to its biogeographic category. The inset pie chart shows the relative contribution of each biogeographic category to the total pool of Arctic OTUs; box plots show the median (and 75 percentile) abundance of OTUs for each biogeographic group (n = 18 stations). (C) Example global distributions of selected OTUs from each biogeographic category, with the name of the deep-branching lineage specified for each OTU. The size of each circle represents the relative abundance of the OTU. Data correspond to the V9 region of the 18S rRNA gene (see Methods).

their low detection in the global dataset, further investigation will be required to understand their biogeography (**Figure 2C**).

Taxonomic resolution of plankton biogeography and diversity patterns

An intriguing question that follows the previous discussion is how taxonomies and biogeographic categories relate to each other. Of the deep-branching lineages of unicellular eukaryotes represented in the global ocean V9 metabarcoding data set, 88% (75 out of 85) were detected in at least one AO station. A complementary analysis of the V4 data set produced a similar result (Table S2; Figure S5). Ten lineages from the global data set (V9) were not detected in our pan-Arctic sampling and, according to our analysis, their occurrence was found to be confined largely to low latitudes (Appendix). Overall, large variations were found in the representation of the different biogeographic categories among different taxa (**Figure 3A**; Appendix). Centrohelida, Picomonadida,

Mamiellophyceae, and the clades MOCH-1,2 were the lineages with the highest fraction of *Arctic/Polar indicator* OTUs (accounting for more than 25% of those OTUs). Conversely, *non-Polar indicator* OTUs made up high proportions (≥50%) of the OTUs associated with Prasinophyceae Clade 7 (Chloropicophyceae), RAD-A, MALV-IV and Collodaria. Highest proportions of *Arctic-exclusive* OTUs (>40%) were detected among Euglenida (mostly photosynthetic or mixotrophic), Dactylopodida (heterotrophic) and the parasitic lineage Ascetosporea, and fungi in the Chytridiomycota and Oomycota. *Globally ubiquitous* OTUs were detected in more than a third of the Arctic lineages, rarely exceeding 20% of the OTUs per lineage, while *background* OTUs were present in all lineages except one (Prasinophyceae Clade 7), with varying contributions per lineage (on average 58 ± 22%). Among the five biogeographic categories, variation in taxonomic and trophic composition was marked (Figure S8). Most notable were the higher proportions of OTUs assigned to MALV-I & II (parasites) and Diplonemida detected as *globally*
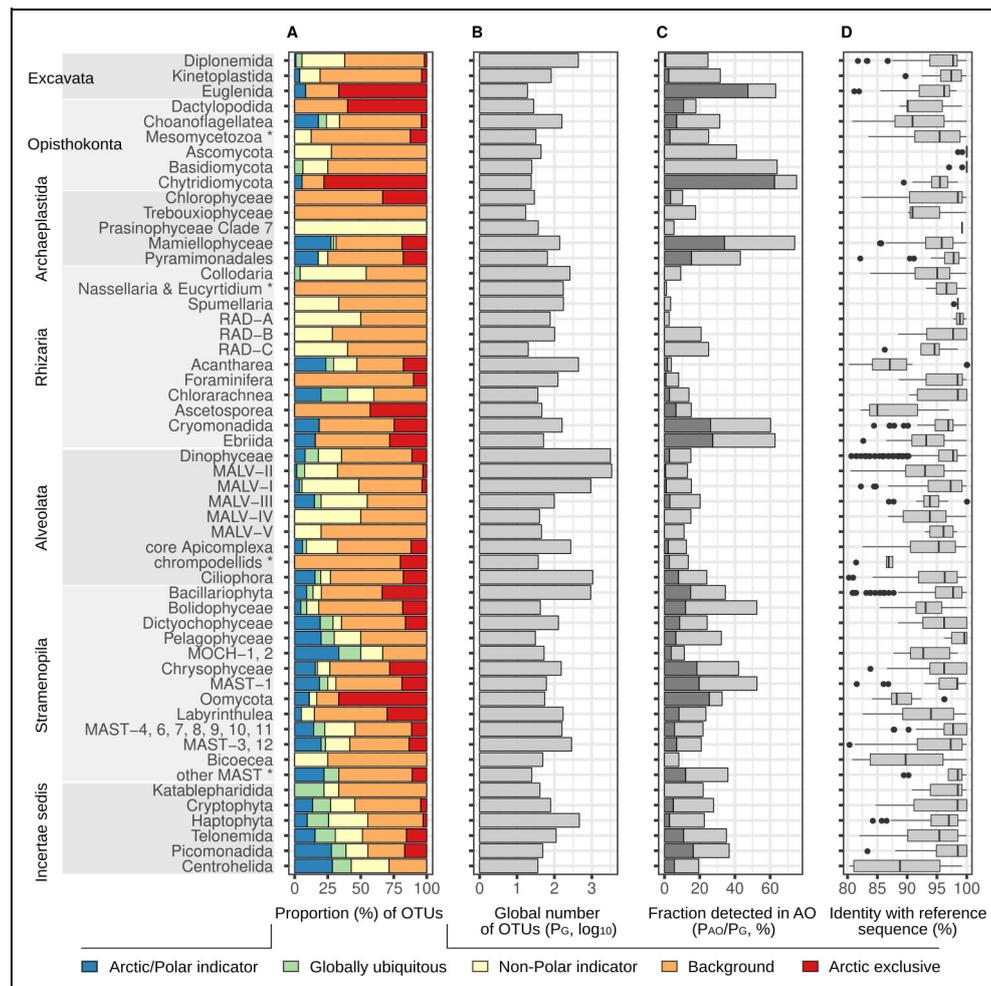
Figure 3. Biogeographic and diversity patterns across deep-branching lineages of Arctic unicellular eukaryotic plankton. For each lineage we determined: (A) proportions of OTUs associated with each of the 5 biogeographic categories; (B) total number of OTUs in the global *Tara* Oceans data base, which we refer to as the global pool (P_G); and (C) the fraction (%) of the global pool detected in the Arctic Ocean (P_{AO}). The dark gray color indicates the contribution of *Arctic/Polar indicators* and *Arctic-exclusive* OTUs to this fraction. (D) Box plots for percentage identity of OTUs with matching sequence from the reference database (see Methods). Data correspond to the V9 region of the 18S rRNA gene. Taxonomic groups are sorted by phylogeny (de Vargas et al., 2015), with lineages clustered in supergroups for visual purposes and with the caveat that classification of unicellular eukaryotes is under constant revision. Lineages with <10 OTUs were not included in the figure.

ubiquitous, *non-Polar indicator* and *background* compared to the two categories with higher affinity to the AO (*Arctic/Polar indicator* and *Arctic-exclusive*). For example, the relative contribution of MALV II to the *globally ubiquitous* OTUs is 16%, to the *non-Polar* indicator OTUs, 22%, and to the *Arctic/Polar indicator* OTUs, 2% (Figure S8). The relatively high contribution of OTUs associated with parasitic lifestyles within the *non-Polar indicators* and *background* groups points to the potential role of bioadvection in altering trophic dynamics in the AO, if those populations and their hosts become established, and calls for more in-depth investigation of parasitic interactions in the AO.

While the diversity of many of the taxa mentioned here has been described previously in Arctic waters (Poulin et al., 2011; Terrado et al., 2013; Thaler and Lovejoy, 2015; Hassett et al., 2017; Šupraha et al., 2022), it was examined for a smaller subset of taxa and rarely placed in a global context. Generally, global trends show a decline in diversity toward the poles in many groups of organisms, including plankton (Ibarbalz et al., 2019). Impoverished richness (low P_{AO}/P_G; **Figure 3B** and **C**) is seen across all taxa, but is particularly evident among lineages within Alveolata and Rhizaria. Yet, if we consider *Arctic/Polar indicator-* and *Arctic-exclusive* OTUs as the specific contribution of the AO to global diversity, our analysis shows that the AO is an important source of biodiversity (**Figure 3B** and **C**). This importance is exemplified in lineages such as Euglenida, Mamiellophyceae, Crymonadida, Ebriida and Chytridiomycota, for which *Arctic/Polar indicator* and *Arctic-exclusive* OTUs constitute more than a quarter of their global biodiversity (**Figure 3C**). Given that the AO represents <5% of the global ocean's surface, this contribution to global plankton biodiversity is notable. While environmental sequencing data should be interpreted with
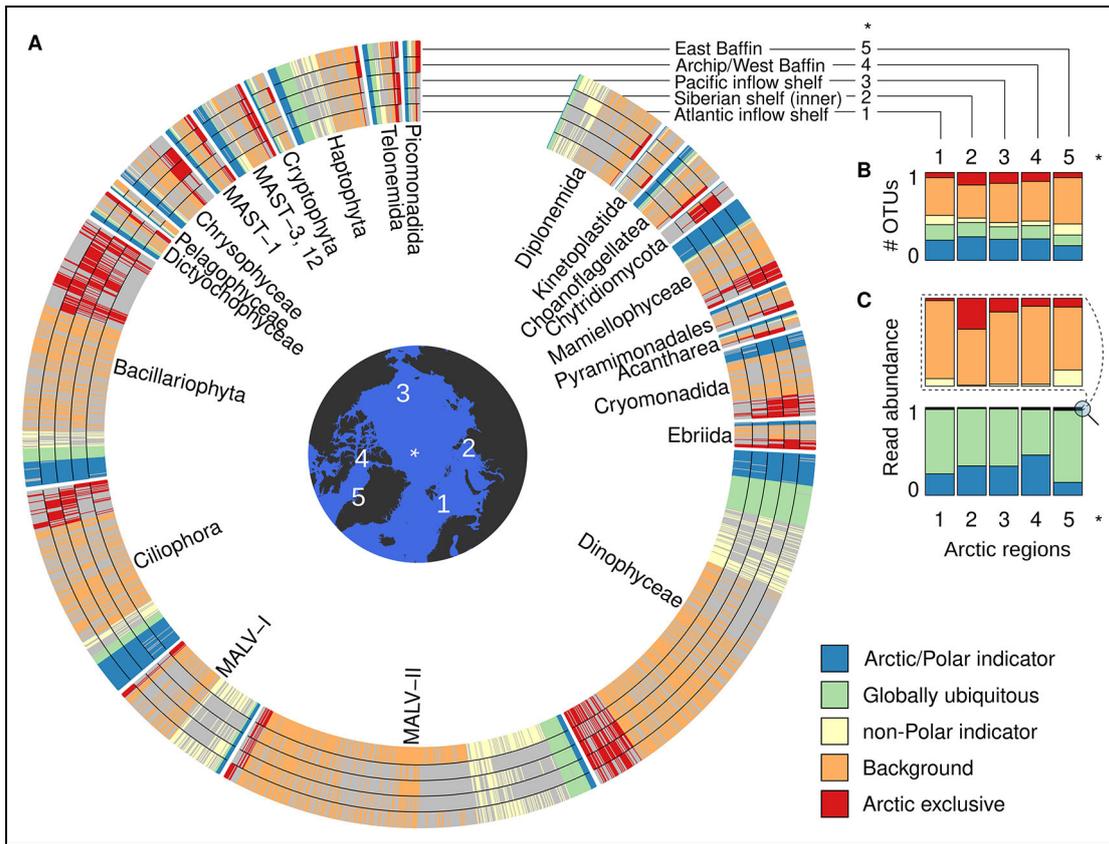
Figure 4. OTU occurrence pattern across Arctic regions. (A) Each circle band represents one of the 5 Arctic regions (see Methods). OTUs are split by lineage and colored according to their biogeographic category defined in the context of the global sampling. Gray color means absence. Only a selection of prominent lineages containing *Arctic/Polar indicators* are shown (see full panel at https://doi.org/10.6084/m9.figshare.14562606). (B) A summary of panel A depicting the contribution of each biogeographic category to the total number of OTUs detected in each Arctic region and (C) the relative read abundance per biogeographic category in each Arctic region (denoted by number code as in **Figure 1**). Panels B and C correspond to the complete dataset as compared to panel A. Because the relative abundance of *non-Polar indicators*, *background* and *Arctic-exclusive* OTUs are low, we have provided an insert that only includes these categories to better visualize their abundance patterns across the different regions of the AO.

caution (i.e., limited resolution of the DNA marker genes that may underestimate the number of Arctic species, and data that are not strictly quantitative), the high degree of coherence between the V9 and V4 datasets increases confidence in the ecological patterns presented here. The frequently observed low similarity to sequences from known species (**Figure 3D**) points to important gaps in the reference database and is a reminder that further work on microbial diversity (e.g., cultures or single cell isolations) is highly needed (Šupraha et al., 2022).

Arctic biodiversity and the interplay between bioadvection and environmental filtering

Concerns of climate change effects on Arctic biota often focus on loss of biodiversity. The large contribution of OTUs with broad biogeographic signatures (i.e., *non-Polar indicators* and *background*) to the pool of OTUs in the AO indicates a role for bioadvection in maintaining biodiversity. Annual exchange of Arctic surface water is on the order of 10% per year (Wefing et al., 2021), implying a continued influx of species from lower latitudes into the AO. Depending on the changing balance between

extinction and colonization rates, diversity of unicellular eukaryotes in the AO could maintain or even increase in the near future. Successful colonization, however, depends on the ability of species to adapt to the unique conditions in the AO. While warming could favor low latitude species, they may not be able to flourish under extreme conditions of seasonality in sunlight. We hypothesize that *non-Polar indicator* OTUs represent species with high dispersal potential, but physiologies that are not well suited for the current AO conditions. By mapping the distributions of all OTUs across the different regions of the AO, we observed that *non-Arctic* OTUs were more prevalent at the Arctic gateways compared to the inner Siberian shelves (**Figure 4**), a pattern indicative of the competing roles of advection (dispersal), environmental filtering, and/or biological interactions (Wassmann et al., 2015). This prevalence at the gateways was particularly noticeable among the lineages MALV-II and MALV-I, haptophytes, MAST-3,12, Diplonemida and Dinophyceae. The larger number of *non-Polar indicators* detected over the Atlantic inflow shelf compared to the Pacific inflow shelf is consistent with the significantly larger volume exchange at the Atlantic sector
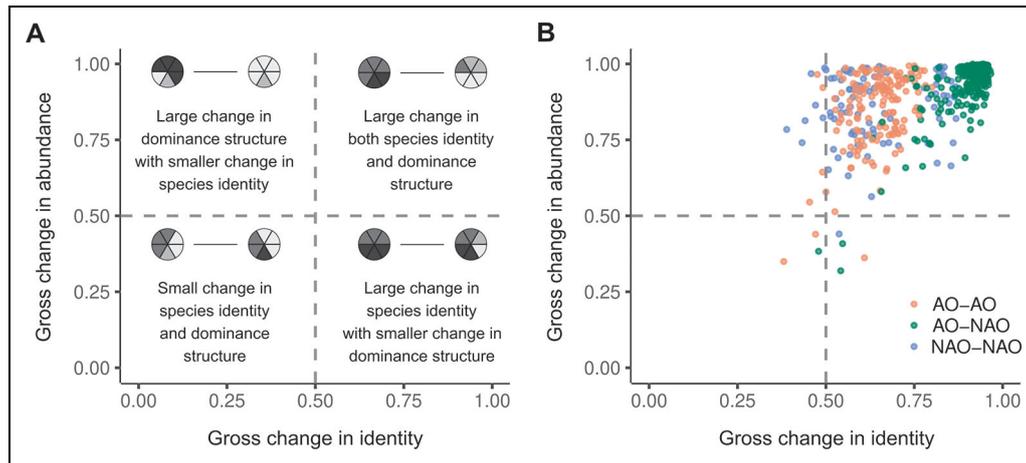
Figure 5. Gross change in species identity and dominance structure across the North Atlantic-Arctic domain. (A) Schematic representation of the analysis output interpretation per quadrant. (B) Comparison between and within North Atlantic and Arctic surface ocean communities of unicellular eukaryotes. Dots represent pairwise comparisons between samples and are colored by oceanic region combinations. See Table S5 for statistics supporting this analysis.

(Timmermans and Marshall, 2020). In contrast, *Arctic-exclusive* OTUs were generally less prevalent on shelves influenced by Atlantic water, although distribution patterns varied greatly among lineages (**Figure 4**). This reduced prevalence may point to a combination of habitat specificity and rarity within this category of OTUs, which could reflect highly specialized species with a narrow environmental niche or stochastic fluctuations in populations (Kunin and Gaston, 2012).

Indirect insights on environmental filtering can be gained from an examination of changes in community structure between the neighboring North Atlantic Ocean (NAO) and AO communities. In the absence of strong environmental gradients across the NAO-AO continuum, we may expect changes in species abundances (e.g., reflecting seasonal changes), but not necessarily a large shift in species identity. However, changes in both species abundances and identity would suggest a strong environmental filtering. We found large, concurrent changes in both species identity and relative abundances within and between the two oceans (**Figure 5**; see Methods). Although there are large spatial variations in community composition within each ocean basin, changes between AO and NAO communities were significantly greater than those within each basin (**Figure 5**; Table S5). These changes co-varied with changes in absolute richness (Figure S9), suggesting that the reduced biodiversity of Arctic plankton is contributing to the observed change in species identity. Overall, these results support the notion of environmental filtering at the North Atlantic gateway, a process that is also likely to occur at the Pacific inflow gateway and over outflow shelves (Kalenitchenko et al., 2019).

Concluding remarks

The use of consistent sampling protocols allowed us to examine assemblages of unicellular eukaryotic plankton in the AO from a global perspective. We have shown that, based on 18S rRNA gene amplicons of both V9 and V4

regions, AO communities consist of a mixture of unique and broadly distributed OTUs with a characteristic community structure. Among the shared OTUs, a considerable fraction (10–16%) have high affinity for lower, warmer latitudes, which could be a sign of change in progress. The importance of advected populations into the AO (Atlantic and Pacific gateways) has been examined primarily for mesozooplankton (Wassmann et al., 2015; Wassmann et al., 2019). Our results further demonstrate the strong connectivity of unicellular eukaryotic plankton communities with the global ocean. Surface velocities are increasing for the poleward-flowing North Atlantic current (Oziel et al., 2020), and the annual mean transport of Pacific water into the AO is also increasing (Woodgate, 2018). Together with other environmental changes over the AO shelves, they will likely alter the current dynamic of community assembly processes, with consequences for the structure and function of the AO ecosystem.

Results of this work are compiled in a resource table in which we provide the taxonomic and biogeographic affiliations for each OTU (Appendix). This resource could become a valuable framework for developing monitoring strategies of unicellular eukaryotic taxa. As an example, regarding the observed higher proportion of *non-Polar indicators* at the Atlantic inflow shelves, changes to their overall contribution to diversity, or more specifically to one of their deep-branching lineages (e.g., haptophytes; Figure S6; Ardyna and Arrigo, 2020; Egge et al., 2021) and/or corresponding OTUs (e.g., several assigned to haptophyte genera *Phaeocystis*, *Chrysochromulina* and the uncultured Clade D; abundance patterns not shown) could be monitored. Of socio-economic relevance, species implicated in harmful algal events are included in the resource table as well (e.g., *Dinophysis acuminata* and *Alexandrium* and *Pseudo-nitzschia* spp. among *Arctic/Polar indicators*; *Dinophysis acuta*, *Protoceratium reticulatum*, and *Margalefidinium polykrikoides*—previously *Cochlodinium polykrikoides*—, the haptophyte *Chrysochromulina leadbeateri* and the pelagophyte *Aureococcus anophagefferens* among

other biogeographic categories). Continued monitoring of target OTUs from this study, as well as an improved understanding of their physiologies and traits, could prove useful for predicting and detecting future changes in species ranges.

This work represents an extensive effort to map occurrence patterns among the 75 different deep-branching lineages that were retrieved from the AO. The majority of the samples in this study were collected from Arctic shelves, which account for 50% of the total area of the AO. Arctic shelf regions are affected most immediately by the decrease in the extent of summer sea ice (Onarheim et al., 2018) and the influx of allochthonous biomass from the neighboring oceans (i.e., the Atlantic and Pacific inflow shelves). In order to further understand the implications on the plankton community and the AO ecosystem, our biogeographic perspective should integrate the winter season and the central sector of the Arctic as well. Under-ice communities of microbial eukaryotes from the central Arctic are diverse and dynamic, with apparent exchanges between sea ice and water column communities (Hardge et al., 2017). The ice-associated taxa and mixotrophic plankton would likely contribute to our *Arctic/Polar indicator* or *Arctic-exclusive* categories. As the ice retreats beyond the shelf break, exchanges between shelf and central basin communities are expected to increase due to mixing processes at the shelf break (Charette et al., 2020), which will likely contribute to continued shifting of the AO plankton community.

Data accessibility statement

Raw reads are deposited at the European Nucleotide Archive (ENA) under projects PRJEB6610 and PRJEB9737 where they are publicly available (https://www.ebi.ac.uk/ena/browser/home).

Supplemental files

The supplemental files for this article can be found as follows:

Figures S1–S9. Tables S1–S5. PDF

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References

Alberti, A, **Poulain, J**, **Engelen, S**, **Labadie, K**, **Romac, S**, **Ferrera, I**, **Albini, G**, **Aury, JM**, **Belser, C**, **Bertrand, A**, **Cruaud, C**, **Da Silva, C**, **Dossat, C**, **Gavory, F**, **Gas, S**, **Guy, J**, **Haquelle, M**, **Jacoby, E**, **Jaillon, O**, **Lemainque, A**, **Pelletier, E**, **Samson, G**, **Wessner, M**, **Acinas, SG**, **Royo-Llonch, M**, **Cornejo-Castillo, FM**, **Logares, R**, **Fernández-Gómez, B**, **Bowler, C**, **Cochrane, G**, **Amid, C**, **Hoopen, PT**, **De Vargas, C**, **Grimsley, N**, **Desgranges, E**, **Kandels-Lewis, S**, **Ogata, H**, **Poulton, N**, **Sieracki, ME**, **Stepanauskas, R**, **Sullivan, MB**, **Brum, JR**, **Duhaime, MB**, **Poulos, BT**, **Hurwitz, BL**, **Pesant, S**, **Karsenti, E**, **Wincker, P**, **Bazire, P**, **Beluche, O**, **Bertrand, L**, **Besnard-Gonnet, M**, **Bordelais, I**, **Boutard, M**, **Dubois, M**, **Dumont, C**, **Ettedgui, E**, **Fernandez, P**, **Garcia, E**, **Aiach, NG**, **Guerin, T**, **Hamon, C**, **Brun, E**, **Lebled, S**, **Lenoble, P**, **Louesse, C**, **Mahieu, E**, **Mairey, B**, **Martins, N**, **Megret, C**, **Milani, C**, **Muanga, J**, **Orvain, C**, **Payen, E**, **Perroud, P**, **Petit, E**, **Robert, D**, **Ronsin, M**, **Vacherie, B**, **Bork, P**, **Boss, E**, **Follows, M**, **Gorsky, G**, **Hingamp, P**, **Iudicone, D**, **Karp-Boss, L**, **Not, F**, **Raes, J**, **Sardet, C**, **Speich, S**, **Stemmann, L**, **Sunagawa, S**. 2017. Viral to metazoan marine plankton nucleotide sequences from the *Tara* Oceans expedition. *Scientific Data* **4**. DOI: http://dx.doi.org/10.1038/sdata.2017.93.

Ardyna, M, **Arrigo, KR**. 2020. Phytoplankton dynamics in a changing Arctic Ocean. *Nature Climate Change* **10**(10): 892–903. DOI: http://dx.doi.org/10.1038/s41558-020-0905-y.

Ardyna, M, **Babin, M**, **Devred, E**, **Forest, A**, **Gosselin, M**, **Raimbault, P**, **Tremblay, J**. 2017. Shelf-basin gradients shape ecological phytoplankton niches and community composition in the coastal Arctic Ocean (Beaufort Sea). *Limnology and Oceanography* **62**(5): 2113–2132. DOI: http://dx.doi.org/10.1002/lno.10554.

Bluhm, B, **Gebruk, A**, **Gradinger, R**, **Hopcroft, R**, **Huettmann, F**, **Kosobokova, K**, **Sirenko, B**, **Weslawski, M**. 2011. Arctic marine biodiversity: An update of species richness and examples of biodiversity change. *Oceanography* **24**(3): 232–248. DOI: http://dx.doi.org/10.5670/oceanog.2011.75.

CAFF. 2017. State of the Arctic marine biodiversity report, Arctic Council. Conservation of Arctic Flora and Fauna International Secretariat, Akureyri, Iceland.

Carmack, E, **Wassmann, P**. 2006. Food webs and physical-biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. *Progress in Oceanography* **71**(2–4): 446–477. DOI: http://dx.doi.org/10.1016/j.pocean.2006.10.004.

Chaffron, S, **Delage, E**, **Budinich, M**, **Vintache, D**, **Henry, N**, **Nef, C**, **Ardyna, M**, **Zayed, AA**, **Junger, PC**, **Galand, PE**, **Lovejoy, C**, **Murray, A**, **Sarmento, H**, **Acinas, S**, **Babin, M**, **Iudicone, D**, **Jaillon, O**, **Karsenti, E**, **Wincker, P**, **Karp-Boss, L**, **Sullivan, MB**, **Bowler, C**, **de Vargas, C**, **Eveillard, D**. 2021. Environmental vulnerability of the global ocean plankton community interactome. *Science Advances* **7**(35). DOI: http://dx.doi.org/10.1126/sciadv.abg1921.

Charette, MA, **Kipp, LE**, **Jensen, LT**, **Dabrowski, JS**, **Whitmore, LM**, **Fitzsimmons, JN**, **Williford, T**, **Ulfsbo, A**, **Jones, E**, **Bundy, RM**, **Vivancos, SM**, **Pahnke, K**, **John, SG**, **Xiang, Y**, **Hatta, M**, **Petrova, MV**, **Heimbürger-Boavida, LE**, **Bauch, D**, **Newton, R**, **Pasqualini, A**, **Agather, AM**, **Amon, RMW**, **Anderson, RF**, **Andersson, PS**, **Benner, R**, **Bowman, KL**, **Edwards, RL**, **Gdaniec, S**, **Gerringa, LJA**, **González, AG**, **Granskog, M**, **Haley, B**, **Hammerschmidt, CR**, **Hansell, DA**, **Henderson, PB**, **Kadko, DC**, **Kaiser, K**, **Laan, P**, **Lam, PJ**, **Lamborg, CH**, **Levier, M**, **Li, X**, **Margolin, AR**, **Measures, C**, **Middag, R**, **Millero, FJ**, **Moore, WS**, **Paffrath, R**, **Planquette, H**, **Rabe, B**, **Reader, H**, **Rember, R**, **Rijkenberg, MJA**, **Roy-Barman, M**, **van der Loeff, MR**, **Saito, M**, **Schauer, U**, **Schlosser, P**, **Sherrell, RM**, **Shiller, AM**, **Slagter, H**, **Sonke, JE**, **Stedmon, C**, **Woosley, RJ**, **Valk, O**, **van Ooijen, J**, **Zhang, R**. 2020. The Transpolar Drift as a source of riverine and shelf-derived trace elements to the central Arctic Ocean. *Journal of Geophysical Research: Oceans* **125**(5). DOI: http://dx.doi.org/10.1029/2019JC015920.

Csapó, HK, **Grabowski, M**, **Węsławski, JM**. 2021. Coming home-Boreal ecosystem claims Atlantic sector of the Arctic. *Science of the Total Environment* **771**: 144817.

de Boyer Montégut, C, **Madec, G**, **Fischer, AS**, **Lazar, A**, **Iudicone, D**. 2004. Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. *Journal of Geophysical Research C: Oceans* **109**(12): 1–20. DOI: http://dx.doi.org/10.1029/2004JC002378.

De Cáceres, M, **Legendre, P**. 2009. Associations between species and groups of sites: Indices and statistical inference. *Ecology* **90**(12): 3566–3574. DOI: http://dx.doi.org/10.1890/08-1823.1.

de Vargas, C, **Audic, S**, **Henry, N**, **Decelle, J**, **Mahe, F**, **Logares, R**, **Lara, E**, **Berney, C**, **Le Bescot, N**, **Probert, I**, **Carmichael, M**, **Poulain, J**, **Romac, S**, **Colin, S**, **Aury, J-M**, **Bittner, L**, **Chaffron, S**, **Dunthorn, M**, **Engelen, S**, **Flegontova, O**, **Guidi, L**, **Horak, A**, **Jaillon, O**, **Lima-Mendez, G**, **Luke, J**, **Malviya, S**, **Morard, R**, **Mulot, M**, **Scalco, E**, **Siano, R**, **Vincent, F**, **Zingone, A**, **Dimier, C**, **Picheral, M**, **Searson, S**, **Kandels-Lewis, S**, **Acinas, SG**, **Bork, P**, **Bowler, C**, **Gorsky, G**, **Grimsley, N**, **Hingamp, P**, **Iudicone, D**, **Not, F**, **Ogata, H**, **Pesant, S**, **Raes, J**, **Sieracki, ME**, **Speich, S**, **Stemmann, L**, **Sunagawa, S**, **Weissenbach, J**, **Wincker, P**, **Karsenti, E**. 2015. Eukaryotic plankton diversity in the sunlit ocean. *Science* **348**(6237): 1261605(1:11). DOI: http://dx.doi.org/10.1126/science.1261605.

Dorrell, RG, **Kuo, A**, **Füssy, Z**, **Richardson, EH**, **Salamov, A**, **Zarevski, N**, **Freyria, NJ**, **Ibarbalz, FM**, **Jenkins, J**, **Karlusich, JJP**, **Steindorff, AS**, **Edgar, RE**, **Handley, L**, **Lail, K**, **Lipzen, A**, **Lombard, V**, **McFarlane, J**, **Nef, C**, **Novák Vanclová, AM**, **Peng, Y**, **Plott, C**,

Potvin, M, Rocha Jimenez Vieira, F, Barry, K, de Vargas, C, Henrissat, B, Pelletier, E, Schmutz, J, Wincker, P, Dacks, JB, Bowler, C, Grigoriev, IV, Lovejoy, C. 2022. Convergent evolution and horizontal gene transfer in Arctic Ocean microalgae. *Life Science Alliance* **6**(3). DOI: http://dx.doi.org/10.26508/lsa.202201833.

Edgar, RC, Haas, BJ, Clemente, JC, Quince, C, Knight, R. 2011. UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* **27**(16): 2194–2200. DOI: http://dx.doi.org/10.1093/bioinformatics/btr381.

Egge, E, Elferink, S, Vaulot, D, John, U, Bratbak, G, Larsen, A, Edvardsen, B. 2021. An 18S V4 rRNA metabarcoding dataset of protist diversity in the Atlantic inflow to the Arctic Ocean, through the year and down to 1000 m depth. *Earth System Science Data* **13**(10): 4913–4928.

Endo, H, Blanc-Mathieu, R, Li, Y, Salazar, G, Henry, N, Labadie, K, de Vargas, C, Sullivan, MB, Bowler, C, Wincker, P, Karp-Boss, L, Sunagawa, S, Ogata, H. 2020. Biogeography of marine giant viruses reveals their interplay with eukaryotes and ecological functions. *Nature Ecology and Evolution* **4**(12): 1639–1649. DOI: http://dx.doi.org/10.1038/s41559-020-01288-w.

Finlay, BJ. 2002. Global dispersal of free-living microbial eukaryote species. *Science* **296**(5570): 1061–1063.

Frøslev, TG, Kjøller, R, Bruun, HH, Ejrnæs, R, Brunbjerg, AK, Pietroni, C, Hansen, AJ. 2017. Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. *Nature Communications* **8**(1). DOI: http://dx.doi.org/10.1038/s41467-017-01312-x.

Galand, PE, Casamayor, EO, Kirchman, DL, Lovejoy, C. 2009a. Ecology of the rare microbial biosphere of the Arctic Ocean. *Proceedings of the National Academy of Sciences* **106**(52): 22427–22432. DOI: http://dx.doi.org/10.1073/pnas.0908284106.

Galand, PE, Casamayor, EO, Kirchman, DL, Potvin, M, Lovejoy, C. 2009b. Unique archaeal assemblages in the Arctic Ocean unveiled by massively parallel tag sequencing. *ISME Journal* **3**(7): 860–869. DOI: http://dx.doi.org/10.1038/ismej.2009.23.

Gaston, KJ, Blackburn, TM, Greenwood, JJD, Gregory, RD, Quinn, RM, Lawton, JH. 2000. Abundance–occupancy relationships. *Journal of Applied Ecology* **37**: 39–59. DOI: http://dx.doi.org/10.1046/j.1365-2664.2000.00485.x.

Ghiglione, J-F, Galand, PE, Pommier, T, Pedrós-Alió, C, Maas, EW, Bakker, K, Bertilson, S, Kirchman, DL, Lovejoy, C, Yager, PL, Murray, AE. 2012. Pole-to-pole biogeography of surface and deep marine bacterial communities. *Proceedings of the National Academy of Sciences* **109**(43): 17633–17638. DOI: http://dx.doi.org/10.1073/pnas.1208160109.

Gill, MJ, Crane, K, Hindrum, R, Arneberg, P, Bysveen, I, Denisenko, NV, Gofman, V, Grant-Friedman, A, Gudmundsson, G, Hopcroft, RR, Iken, K, Labansen, A, Liubina, OS, Melnikov, IA, Moore, SE, **Reist, JD, Sirenko, BI, Stow, J, Ugarte, F, Vongraven, D, Watkins, J.** 2011. Arctic Marine Biodiversity Monitoring Plan (CBMP-MARINE PLAN), CAFF Monitoring Series Report.

Greco, M, Werner, K, Zamelczyk, K, Rasmussen, TL, Kucera, M. 2022. Decadal trend of plankton community change and habitat shoaling in the Arctic gateway recorded by planktonic foraminifera. *Global Change Biology* **28**(5): 1798–1808.

Gregory, AC, Zayed, AA, Conceição-Neto, N, Temperton, B, Bolduc, B, Alberti, A, Ardyna, M, Arkhipova, K, Carmichael, M, Cruaud, C, Dimier, C, Domínguez-Huerta, G, Ferland, J, Kandels, S, Liu, Y, Marec, C, Pesant, S, Picheral, M, Pisarev, S, Poulain, J, Tremblay, JÉ, Vik, D, Acinas, SG, Babin, M, Bork, P, Boss, E, Bowler, C, Cochrane, G, de Vargas, C, Follows, M, Gorsky, G, Grimsley, N, Guidi, L, Hingamp, P, Iudicone, D, Jaillon, O, Kandels-Lewis, S, Karp-Boss, L, Karsenti, E, Not, F, Ogata, H, Poulton, N, Raes, J, Sardet, C, Speich, S, Stemmann, L, Sullivan, MB, Sunagawa, S, Wincker, P, Culley, AI, Dutilh, BE, Roux, S. 2019. Marine DNA viral macro- and microdiversity from pole to pole. *Cell* **177**(5): 1109–1123.e14. DOI: http://dx.doi.org/10.1016/j.cell.2019.03.040.

Gu, Z, Gu, L, Eils, R, Schlesner, M, Brors, B. 2014. Circlize implements and enhances circular visualization in R. *Bioinformatics* **30**(19): 2811–2812. DOI: http://dx.doi.org/10.1093/bioinformatics/btu393.

Guillou, L, Bachar, D, Audic, S, Bass, D, Berney, C, Bittner, L, Boutte, C, Burgaud, G, De Vargas, C, Decelle, J, Del Campo, J, Dolan, JR, Dunthorn, M, Edvardsen, B, Holzmann, M, Kooistra, WHCF, Lara, E, Le Bescot, N, Logares, R, Mahé, F, Massana, R, Montresor, M, Morard, R, Not, F, Pawlowski, J, Probert, I, Sauvadet, AL, Siano, R, Stoeck, T, Vaulot, D, Zimmermann, P, Christen, R. 2013. The Protist Ribosomal Reference database (PR2): A catalog of unicellular eukaryote small subunit rRNA sequences with curated taxonomy. *Nucleic Acids Research* **41**(D1). DOI: http://dx.doi.org/10.1093/nar/gks1160.

Hardge, K, Peeken, I, Neuhaus, S, Lange, BA, Stock, A, Stoeck, T, Weinisch, L, Metfies, K. 2017. The importance of sea ice for exchange of habitat-specific protist communities in the Central Arctic Ocean. *Journal of Marine Systems* **165**: 124–138.

Hardy, SM, Carr, CM, Hardman, M, Steinke, D, Corstorphine, E, Mah, C. 2011. Biodiversity and phylogeography of Arctic marine fauna: Insights from molecular tools. *Marine Biodiversity* **41**(1): 195–210.

Hassett, BT, Ducluzeau, ALL, Collins, RE, Gradinger, R. 2017. Spatial distribution of aquatic marine fungi across the western Arctic and sub-arctic. *Environmental Microbiology* **19**(2): 475–484. DOI: http://dx.doi.org/10.1111/1462-2920.13371.

Hays, GC, Richardson, AJ, Robinson, C. 2005. Climate change and marine plankton. *Trends in Ecology and Evolution* **20**(6): 337–344.

Hillebrand, H, **Blasius, B**, **Borer, ET**, **Chase, JM**, **Downing, JA**, **Eriksson, BK**, **Filstrup, CT**, **Harpole, WS**, **Hodapp, D**, **Larsen, S**, **Lewandowska, AM**, **Seabloom, EW**, **Van de Waal, DB**, **Ryabov, AB**. 2018. Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology* **55**(1): 169–184. DOI: http://dx.doi.org/10.1111/1365-2664.12959.

Ibarbalz, FM, **Henry, N**, **Brandão, MC**, **Martini, S**, **Busseni, G**, **Byrne, H**, **Coelho, LP**, **Endo, H**, **Gasol, JM**, **Gregory, AC**, **Mahe, F**, **Rigonato, J**, **Royo-Llonch, M**, **Salazar, G**, **Sanz-Sáez, I**, **Scalco, E**, **Soviadan, D**, **Zayed, AA**, **Zingone, A**, **Labadie, K**, **Ferland, J**, **Marec, C**, **Kandels, S**, **Picheral, M**, **Dimier, C**, **Poulin, M**, **Pisarev, S**, **Carmichael, M**, **Pesant, S**, **Babin, M**, **Boss, E**, **Iudicone, D**, **Jaillon, O**, **Acinas, SG**, **Ogata, H**, **Pelletier, E**, **Stemmann, L**, **Sullivan, MB**, **Sunagawa, S**, **Bopp, L**, **de Vargas, C**, **Karp-Boss, L**, **Wincker, P**, **Lombard, F**, **Bowler, C**, **Zinger, L.** 2019. Global trends in marine plankton diversity across kingdoms of life. *Cell* **179**(5): 1084–1097. DOI: http://dx.doi.org/10.1016/j.cell.2019.10.008.

Kalenitchenko, D, **Joli, N**, **Potvin, M**, **Tremblay, JE**, **Lovejoy, C.** 2019. Biodiversity and species change in the Arctic Ocean: A view through the lens of Nares Strait. *Frontiers in Marine Science* **6**: 479. DOI: http://dx.doi.org/10.3389/fmars.2019.00479.

Kunin, WE, **Gaston, KJ** eds. 2012. *The biology of rarity: Causes and consequences of rare–common differences.* Berlin, Germany: Springer Science & Business Media.

Lovejoy, C, **Massana, R**, **Pedrós-Alió, C.** 2006. Diversity and distribution of marine microbial eukaryotes in the Arctic Ocean and adjacent seas. *Applied and Environmental Microbiology* **72**(5): 3085–3095. DOI: http://dx.doi.org/10.1128/AEM.72.5.3085-3095.2006.

Luddington, IA, **Lovejoy, C**, **Kaczmarska, I**, **Moisander, P.** 2016. Species-rich meta-communities of the diatom order Thalassiosirales in the Arctic and northern Atlantic Ocean. *Journal of Plankton Research* **38**(4): 781–797. DOI: http://dx.doi.org/10.1093/plankt/fbw030.

Mahé, F, **Rognes, T**, **Quince, C**, **de Vargas, C**, **Dunthorn, M.** 2015. Swarm v2: Highly-scalable and high-resolution amplicon clustering. *PeerJ* **3**: e1420. DOI: http://dx.doi.org/10.7287/peerj.preprints.1222.

Martin, M. 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet. Journal* **17**(1): 10. DOI: http://dx.doi.org/10.14806/ej.17.1.200.

Menemenlis, D, **Campin, J-M**, **Heimbach, P**, **Hill, CN**, **Lee, T**, **Nguyen, AT**, **Schodlok, MP**, **Zhang, H.** 2008. ECCO2: High resolution global ocean and sea ice data synthesis. *Mercator Ocean Quarterly Newsletter* **31**(October): 13–21.

Monier, A, **Terrado, R**, **Thaler, M**, **Comeau, A**, **Medrinal, E**, **Lovejoy, C.** 2013. Upper Arctic Ocean water masses harbor distinct communities of heterotrophic flagellates. *Biogeosciences* **10**(6): 4273–4286. DOI: http://dx.doi.org/10.5194/bg-10-4273-2013.

Münchow, A, **Falkner, KK**, **Melling, H.** 2015. Baffin Island and West Greenland Current Systems in northern Baffin Bay. *Progress in Oceanography* **132**: 305–317. DOI: http://dx.doi.org/10.1016/j.pocean.2014.04.001.

Notz, D, **SIMIP Community**. 2020. Arctic sea ice in CMIP6. *Geophysical Research Letters* **47**(10): e2019GL086749.

Okolodkov, YB, **Dodge, JD.** 1996. Biodiversity and biogeography of planktonic dinoflagellates in the Arctic Ocean. *Journal of Experimental Marine Biology and Ecology* **202**(1): 19–27.

Oksanen, J, **Blanchet, FG**, **Friendly, M**, **Kindt, R**, **Legendre, P**, **McGlinn, D**, **Minchin, PR**, **O'Hara, RB**, **Simpson, GL**, **Solymos, P**, **Stevens, MHH**, **Szoecs, E**, **Wagner, H.** 2019. vegan: Community Ecology Package. R package version 2.5-4.

Onarheim, IH, **Eldevik, T**, **Smedsrud, LH**, **Stroeve, JC.** 2018. Seasonal and regional manifestation of Arctic sea ice loss. *Journal of Climate* **31**(12): 4917–4932. DOI: http://dx.doi.org/10.1175/JCLI-D-17-0427.1.

Oziel, L, **Baudena, A**, **Ardyna, M**, **Massicotte, P**, **Randelhoff, A**, **Sallée, JB**, **Ingvaldsen, RB**, **Devred, E**, **Babin, M.** 2020. Faster Atlantic currents drive poleward expansion of temperate phytoplankton in the Arctic Ocean. *Nature Communications* **11**(1). DOI: http://dx.doi.org/10.1038/s41467-020-15485-5.

Pesant, SS, **Not, F**, **Picheral, M**, **Kandels-Lewis, S**, **Le Bescot, N**, **Gorsky, G**, **Iudicone, D**, **Karsenti, E**, **Speich, S**, **Troublé, R**, **Dimier, CC**, **Searson, S.** 2015. Open science resources for the discovery and analysis of *Tara* Oceans data. *Scientific Data* **2**: 150023. DOI: http://dx.doi.org/10.1038/sdata.2015.23.

Picheral, M, **Searson, S**, **Taillandier, V**, **Bricaud, A**, **Boss, E**, **Ras, J**, **Claustre, H**, **Ouhssain, M**, **Morin, P**, **Coppola, L**, **Gattuso, J-P**, **Metzl, N**, **Thuillier, D**, **Gorsky, G**, **Tara Oceans Consortium Coordinators (team)**, **Tara Oceans Expedition Participants (team)**. 2014. Vertical profiles of environmental parameters measured on discrete water samples collected with Niskin bottles during the Tara Oceans expedition 2009–2013. *PANGAEA*. DOI: http://dx.doi.org/10.1594/PANGAEA.836319.

Poulin, M, **Daugbjerg, N**, **Gradinger, R**, **Ilyash, L**, **Ratkova, T**, **von Quillfeldt, C.** 2011. The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: A first-attempt assessment. *Marine Biodiversity* **41**(1): 13–28. DOI: http://dx.doi.org/10.1007/s12526-010-0058-8.

Rämä, T, **Hassett, BT**, **Bubnova, E.** 2017. Arctic marine fungi: From filaments and flagella to operational taxonomic units and beyond. *Botanica Marina* **60**(4): 433–452. DOI: http://dx.doi.org/10.1515/bot-2016-0104.

Rognes, T, **Flouri, T**, **Nichols, B**, **Quince, C**, **Mahé, F.** 2016. VSEARCH: A versatile open source tool for metagenomics. *PeerJ* **2016**(10). DOI: http://dx.doi.org/10.7717/peerj.2584.

Salazar, G, Paoli, L, Alberti, A, Huerta-Cepas, J, Ruscheweyh, HJ, Cuenca, M, Field, CM, Coelho, LP, Cruaud, C, Engelen, S, Gregory, AC, Labadie, K, Marec, C, Pelletier, E, Royo-Llonch, M, Roux, S, Sánchez, P, Uehara, H, Zayed, AA, Zeller, G, Carmichael, M, Dimier, C, Ferland, J, Kandels, S, Picheral, M, Pisarev, S, Poulain, J, Acinas, SG, Babin, M, Bork, P, Boss, E, Bowler, C, Cochrane, G, de Vargas, C, Follows, M, Gorsky, G, Grimsley, N, Guidi, L, Hingamp, P, Iudicone, D, Jaillon, O, Kandels-Lewis, S, Karp-Boss, L, Karsenti, E, Not, F, Ogata, H, Pesant, S, Poulton, N, Raes, J, Sardet, C, Speich, S, Stemmann, L, Sullivan, MB, Sunagawa, S, Wincker, P. 2019. Gene expression changes and community turnover differentially shape the global ocean metatranscriptome. *Cell* **179**(5): 1068–1083. DOI: http://dx.doi.org/10.1016/j.cell.2019.10.014.

Scrucca, L, Fop, M, Murphy, TB, Raftery, AE. 2016. mclust 5: Clustering, classification and density estimation using Gaussian finite mixture models. *R Journal* **8**(1): 289–317. DOI: http://dx.doi.org/10.32614/rj-2016-021.

Ser-Giacomi, E, Zinger, L, Malviya, S, De Vargas, C, Karsenti, E, Bowler, C, De Monte, S. 2018. Ubiquitous abundance distribution of non-dominant plankton across the global ocean. *Nature Ecology and Evolution* **2**(8): 1243–1249. DOI: http://dx.doi.org/10.1038/s41559-018-0587-2.

Siddig, AAH, Ellison, AM, Ochs, A, Villar-Leeman, C, Lau, MK. 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in *Ecological Indicators*. *Ecological Indicators* **60**: 223–230. DOI: http://dx.doi.org/10.1016/j.ecolind.2015.06.036.

Sommeria-Klein, G, Watteaux, R, Ibarbalz, FM, Karlusich, JJP, Iudicone, D, Bowler, C, Morlon, H. 2021. Global drivers of eukaryotic plankton biogeography in the sunlit ocean. *Science* **374**(6567): 594–599. DOI: http://dx.doi.org/10.1126/science.abb3717.

Stoecker, DK, Lavrentyev, PJ. 2018. Mixotrophic plankton in the polar seas: A pan-Arctic review. *Frontiers in Marine Science* **5**. DOI: http://dx.doi.org/10.3389/fmars.2018.00292.

Sunagawa, S, Acinas, SG, Bork, P, Bowler, C, Eveillard, D, Gorsky, G, Guidi, L, Iudicone, D, Karsenti, E, Lombard, F, Ogata, H, Pesant, S, Sullivan, MB, Wincker, P, de Vargas, C. 2020. Tara Oceans: Towards global ocean ecosystems biology. *Nature Reviews Microbiology* **18**(8): 428–445.

Šupraha, L, Klemm, K, Gran-Stadniczeñko, S, Hörstmann, C, Vaulot, D, Edvardsen, B, John, U. 2022. Diversity and biogeography of planktonic diatoms in Svalbard fjords: The role of dispersal and Arctic endemism in phytoplankton community structuring. *Elementa: Science of the Anthropocene* **10**(1): 117. DOI: http://dx.doi.org/10.1525/elementa.2021.00117.

Terrado, R, Scarcella, K, Thaler, M, Vincent, WF, Lovejoy, C. 2013. Small phytoplankton in Arctic seas: Vulnerability to climate change. *Biodiversity* **14**(1): 2–18. DOI: http://dx.doi.org/10.1080/14888386.2012.704839.

Thaler, M, Lovejoy, C. 2015. Biogeography of heterotrophic flagellate populations indicates the presence of generalist and specialist taxa in the Arctic Ocean. *Applied and Environmental Microbiology* **81**(6): 2137–2148. DOI: http://dx.doi.org/10.1128/aem.02737-14.

Timmermans, ML, Marshall, J. 2020. Understanding Arctic Ocean circulation: A review of ocean dynamics in a changing climate. *Journal of Geophysical Research: Oceans* **125**(4). DOI: http://dx.doi.org/10.1029/2018JC014378.

Vaulot, D, Geisen, S, Mahe, F, Bass, D. 2022. pr2-primers: An 18S rRNA primer database for protists. *Molecular Ecology Resources* **22**(1): 168–179. DOI: http://dx.doi.org/10.1111/1755-0998.13465.

Wang, Q, Wekerle, C, Wang, X, Danilov, S, Koldunov, N, Sein, D, Sidorenko, D, von Appen, W-J, Jung, T. 2020. Intensification of the Atlantic Water supply to the Arctic Ocean through Fram Strait induced by Arctic sea ice decline. *Geophysical Research Letters* **47**(3): e2019GL086682.

Wassmann, P, Kosobokova, KN, Slagstad, D, Drinkwater, KF, Hopcroft, RR, Moore, SE, Ellingsen, I, Nelson, RJ, Carmack, E, Popova, E, Berge, J. 2015. The contiguous domains of Arctic Ocean advection: Trails of life and death. *Progress in Oceanography* **139**: 42–65. DOI: http://dx.doi.org/10.1016/j.pocean.2015.06.011.

Wassmann, PF, Slagstad, D, Ellingsen, I. 2019. Advection of mesozooplankton into the northern Svalbard shelf region. *Frontiers in Marine Science* **6**. DOI: http://dx.doi.org/10.3389/fmars.2019.00458.

Wefing, A-M, Casacuberta, N, Christl, M, Gruber, N, Smith, JN. 2021. Circulation timescales of Atlantic Water in the Arctic Ocean determined from anthropogenic radionuclides. *Ocean Science* **17**(1): 111–129.

Woodgate, RA. 2018. Increases in the Pacific inflow to the Arctic from 1990 to 2015, and insights into seasonal trends and driving mechanisms from year-round Bering Strait mooring data. *Progress in Oceanography* **160**: 124–154. DOI: http://dx.doi.org/10.1016/j.pocean.2017.12.007.

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