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LETTER

Seasonal patterns of microbial diversity across the world oceans

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Scientific Significance Statement

Marine microbes are essential for sustaining life in our oceans, making it crucial to monitor changes in their diversity to better understand and predict microbially driven ecosystem functions. Global oceanographic expeditions and basin-wide transects reveal positive correlations between microbial diversity and variables like temperature and productivity, but these studies often lack seasonal data and include few observations from high-latitude regions during winter. Our research shows that, despite differences in collection methods, DNA extraction protocols, targeted *16S rRNA* hypervariable regions, sequencing technologies, and bioinformatics pipelines, seasonal trends in microbial community richness and evenness remain consistent across time-series sites in both the northern and southern hemispheres.

Abstract

Understanding the patterns of marine microbial diversity (Bacteria + Archaea) is essential, as variations in their alpha- and beta-diversities can affect ecological processes. Investigations of microbial diversity from global oceanographic expeditions and basin-wide transects show positive correlations between microbial diversity and

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Data availability Statement: All data presented in this manuscript including detailed descriptions of methodologies and bioinformatic workflows are publicly available. The sequence data and associated metadata are deposited at institutional and international data repositories as outlined in Supplementary Materials and Methods. The code to reproduce and plot the figures presented in the manuscript is available at https://github.com/EricRaes/Time-series-Analyses.

A dedication to Paul Somerfield (1963–2023).

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either temperature or productivity, but these studies rarely captured seasonality, especially in polar regions. Here, using multiannual alpha-diversity data from eight time series in the northern and southern hemispheres, we show that marine microbial community richness and evenness generally correlate more strongly with daylength than with temperature or chlorophyll *a* (a proxy for photosynthetic biomass). This pattern is observable across time series found in the northern and southern hemispheres regardless of collection method, DNA extraction protocols, targeted *16S* rRNA hypervariable region, sequencing technology, or bioinformatics pipeline.

In terrestrial ecosystems, decreased species diversity can reduce central ecosystem functions (Tilman et al. 2014), such as primary productivity (Balvanera et al. 2006; Oehri et al. 2017), and disrupt ecosystem resilience and stability through time (Cardinale et al. 2011; Gross et al. 2014; Wagg et al. 2019). The relationship between microbial diversity and ecosystem functions, however, is complex, and remains poorly understood for oceanic environments (Sunagawa et al. 2020). At the base of the marine food web, Bacteria and Archaea (herein referred to as prokaryotes) are essential for ecosystem functioning (Falkowski 1997); alterations in their diversity and distribution could affect ecological dynamics (Horner-Devine et al. 2003; Hutchins and Feixue 2017; Cavicchioli et al. 2019). Untangling regional and global patterns in prokaryotic diversity across seasonal cycles is essential to understanding, modeling, and predicting microbially driven ecosystem functions (Hatosy et al. 2013; Vallina et al. 2014; Louca et al. 2016).

Global ocean research expeditions (e.g., Tara Oceans) or ocean basin-wide transects (e.g., GO-SHIP and Bio-GEOTRACES) have shown a positive correlation between bacterial diversity and either temperature (Ibarbalz et al. 2019) or primary production (Raes et al. 2018a, 2018b). Although basin-wide transects cover wide biogeochemical provinces, they do not systematically address seasonality. In addition, these programs collected few or no samples during winter in polar regions. Marine time series using an Eulerian sampling design (i.e., a fixed site) provide fundamental seasonal insights into the diversity patterns of marine microbes (Wiltshire et al. 2010; Fuhrman et al. 2015; Bryant et al. 2016; Marquardt et al. 2016; Brown et al. 2018; Buttigieg et al. 2018; Lambert et al. 2019; Auladell et al. 2022) and are complementary to basin-wide observations. In particular, highly resolved (fortnightly to monthly) seasonal observations from time series suggest that marine prokaryotic community diversity is strongly correlated with daylength (e.g., Gilbert et al. 2012; Bryant et al. 2016; Marquardt et al. 2016; Giner et al. 2019; Lambert et al. 2019; Raes et al. 2022).

Trends in archaeal and bacterial alpha-diversity have mostly been linked to (i) the kinetic energy hypothesis, that is, warmer temperatures increase metabolic reaction rates which in turn, affect genetic and evolutionary traits, ultimately resulting in higher alpha-diversities (Brown 2014); or (ii) the resource hypothesis, that is, a higher energy production can support more species through niche diversification Mittelbach et al. 2001. We utilized the established ecological temperature framework (Brown 2014) and the resources mechanism (Mittelbach et al. 2001) to predict the drivers behind shifts in prokaryotic diversity over time, with our primary focus on temporal fluctuations within a specific location, rather than spatial distinctions between different sites. Our rationale is based on the idea that the evolutionary timeline of prokaryotes within a given location or among various sites is likely to be similar. It is important to emphasize that prokaryotic evolution unfolds at a distinct pace compared to macrofauna, with prokaryotes demonstrating significant responsiveness to alterations in their environmental conditions, primarily due to their higher cell division rates (Hillebrand et al. 2022).

Here, we use seasonal data from eight time series in the northern and southern hemispheres (from 79°N to 42°S) to test the hypothesis that, on a multiannual basis, marine prokaryotic alpha-diversity (richness and evenness) correlates more strongly with daylength than with temperature or productivity. Regardless of the various factors that can introduce variation in prokaryotic diversity studies, we demonstrate the generality of a recurrent yearly cycle in community structure.

Materials and methods

Selection of time-series sites for perspective on prokaryotic community diversity

16S ribosomal RNA gene (rRNA) metabarcoding data were retrieved from eight time series (Fig. 1; Table 1), alongside physical and biochemical metadata. These include (1) the Arctic FRAM observatory at the long-term ecological research (LTER) site HAUSGARTEN at F4 and HG-IV moorings; (2) the English Channel coastal L4 (ECL4) site; (3) the Compass Buoy Station HL0 in the Bedford Basin (BBNS), Canada; (4) the Blanes Bay Microbial Observatory LTER (BBMO), Spain; (5) the San Pedro Ocean Time Series (SPOT), California, U.S.A.; (6) Integrated Marine Observing System (IMOS) National Reference Stations (NRS) Yongala (YON), Australia; (7) NRS Rottnest Island (ROT), Australia; and (8) NRS Maria Island (MAI), Australia. Data obtained were generated from samples in the euphotic zone (shallower than 50 m depth) from polar, temperate, and subtropical climate zones. FRAM samples were collected autonomously using moored Remote Access Samplers (RAS; McLane), whereas all other samples were collected manually with Niskin bottles or a bucket (BBMO). The Supplementary Materials and Methods provide details on the selection criteria, discrete sampling depths at

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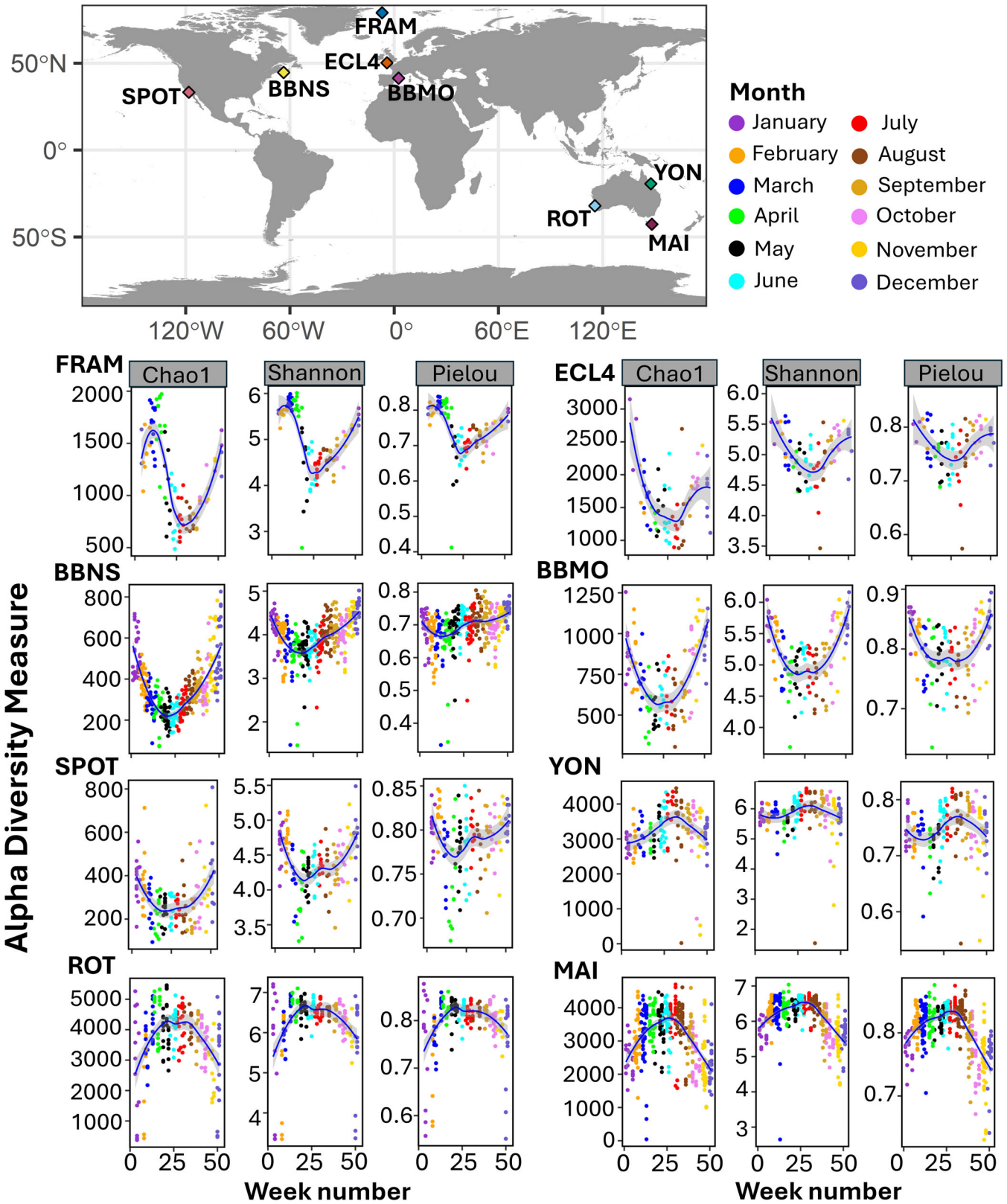

Fig. 1. Legend on next page.

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each site and protocols for physical and biogeochemical metadata.

DNA sampling, sequencing, and bioinformatics

Detailed information on sample collection dates, targeted *16S* rRNA gene hypervariable regions, primers, DNA extraction, sequencing technology, and bioinformatics are shown in Table 1 and correspond to the individual specifications of the original publications. No reprocessing of the sequencing data was conducted and the original ASV/OTU tables were used for statistical analyses except for SPOT and Bedford Basin, whose raw sequencing data were reprocessed identically as originally published (Raes et al. 2022; Yeh and Fuhrman 2022a). Details on bioinformatic workflows are shown in the Supplementary Materials and Methods. The V4–V5 and V6 *16S* rRNA regions target Archaea, Bacteria, and Eukarya (Lane et al. 1985; Weisburg et al. 1991; Lee and Gutell 2012; Parada et al. 2016), but eukaryotic information was not analyzed here.

Statistical analyses

Data analyses, visualization, and maps were generated with R (v4.2.2; R Core Team 2014) in RStudio (v.1.3.1093; see our GitHub). Statistical tests and correlations were conducted between sample points matching in time (i.e., alpha diversity, temperature, chlorophyll *a* (Chl *a*) concentrations and daylength at time x_1). To visualize changes in beta-diversity over time, pairwise Aitchison's distances were calculated between each possible pair of samples (Fig. 2, *y*-axis) and recorded over the time difference between those samples, in days (Fig. 2, *x*-axis); mean values and associated 95% confidence intervals are plotted for every 10-d interval (Fig. 2) using ggplot2 (v.1.3.2; Wickham et al. 2019). Centered log-ratio (CLR) transformations of non-rarefied ASV/OTU tables with an added pseudo-count of 1 for zeros and distances were calculated using the Vegan package (v.2.6.4; Oksanen et al. 2007). To evaluate the response of diversity to different predictors under the three hypotheses described here (daylength, temperature, Chl *a*), we tested four versions (model S1, model G, model S2, and model GS following Pedersen et al. 2019) of hierarchical generalized additive models (HGAMs) in R package mgcv (Wood 2017). HGAMs were tested with richness and Shannon's diversity as response variables. See Supplementary Section 3.7 for model details.

Results and discussion

Physical and biochemical seasonality

Seasonality of physical and bio-geochemical parameters is presented in Supplementary Fig. S8A–H. Daylength, as determined from latitude and time of year, exhibited the smallest and largest seasonal differences in the tropics (2.3 h) and in the Arctic (24 h), respectively. Overall, seasonality was apparent in the physical and biogeochemical parameters at all stations, except for YON, with oligotrophic conditions and low phytoplankton biomass throughout multiple years. Temperatures across the eight sites in the northern and southern hemisphere ranged from −1.7°C to 30°C. Dissolved inorganic nitrate and nitrite (NO_x) concentrations across all sites ranged from below detection limits (< 0.02 μmol L^{-1}) to 15 μmol L^{-1} at the ECL4. Highest NO_x concentrations occurred in the winter months, except at ROT (highest in summer) and YON (oligotrophic throughout the year). Chl *a* concentrations, a proxy for photosynthetic biomass, peaked in spring and autumn in BBNS (up to 40 μg L^{-1}), in early spring in SPOT (up to 19.8 μg L^{-1}), in spring and autumn in the ECL4 (up to 4.76 μg L^{-1}), in winter and spring in BBMO (up to 2.9 μg L^{-1}), and in summer in the FRAM (up to 2.9 μg L^{-1}). In the southern hemisphere, productivity was higher in spring at MAI (up to 1.6 μg L^{-1}) and in autumn at ROT (up to 0.9 μg L^{-1}). Low Chl *a* concentrations (< 0.5 μg L^{-1}) were recorded at YON throughout the year, though with a trend of relatively higher concentrations during the summer months.

Consistent patterns in seasonality regardless of sampling and metabarcoding methodology

Despite different amplification targets and different resolution (OTUs vs. ASVs), all sites showed significant seasonality in prokaryotic diversity (community richness and evenness; Fig. 1). Highest species richness and evenness were always recorded in the winter (2–3× greater than in summer), even at the tropical YON ($p < 0.05$ for all Wilcoxon tests between summer and winter). These trends remained regardless of rarefaction depths and were also observed when considering the rare microbiome (OTUs/ASVs composing < 1% community proportions; Supplementary Figs. S9–S16).

The choice of target *16S* rRNA variable region is tailored to specific research question and particular taxa (Choi et al. 2017), sequencing technology (Cruaud et al. 2014), and intercomparisons of results to other environments or older studies (Gilbert et al. 2009; Thompson et al. 2017; Brown et al. 2018). Considering the different PCR biases of primer sets, there is currently no perfect universal primer set for targeting variable *16S rRNA* regions across microorganisms (McNichol et al. 2021). Several studies have investigated how different primers capture true prokaryotic diversity (e.g., Bukin et al. 2019; Willis et al. 2019; Soriano-Lerma et al. 2020). Yet, here we show a consistent signal in seasonal

Fig. 1. Global seasonal trends in prokaryotic alpha-diversity. Top: World map illustrating the location of eight time series Fram Strait (FRAM), English Channel (ECL4), Bedford Basin (BBNS), Blanes Bay (BBMO), San Pedro (SPOT), NRS Yongala (YON), NRS Rottnest Island (ROT), and NRS Maria Island (MAI). For each site, individual panels show alpha-diversity trends across week number including richness (Chao1), Shannon, and Pielou metrics. Data points are colored by sampling month, with Loess regression lines (in blue with 95% confidence band in gray) fitted to the alpha-diversity metrics. The x-axis shows time in number of weeks, with one corresponding to the first week in January and 52 corresponding to the last week in December.

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Table 1. Time-series locations, climate zones, sampling schemes, and sequencing metadata.

Properties	Fram Strait, mooring F4	Fram Strait, mooring HG-IV	English Channel	Bedford Basin	Blanes Bay	San Pedro	Yongala	Rottnest Island	Maria Island
Acronym	FRAM	FRAM	ECL4	BBNS	BBMO	SPOT	YON	ROT	MAI
Latitude (N)	79°0.708′	79°1.380′	50°15′	44°41′37″	41°40′	33°30′	−19°18′	−32°0′	−42°36′
Longitude (E)	6°57.888″	4°15.708′	− 4°13′	−63°38′25″	2°48′	−118°30′	147°37′	115°25′	148°14′
Climate zone	Polar	Polar	Temperate	Temperate	Temperate	Temperate	Tropical	Subtropical	Temperate
Biogeochemical Province	Boreal polar/ Atlantic Arctic	Boreal polar/ Atlantic Arctic	Northeast Atlantic shelve	Northwest Atlantic shelve	Mediterranean Sea	Coastal Californian current	East Australian coast	West Australian coast	Tasman Sea
Depths sampled (m)	24–42	26–48	Surface	1, 5, 10	1	5	0, 10, 20, 26	0, 10, 20, 30, 40, 46	0, 10, 20, 50
Sampling frequency	Biweekly	Biweekly	Monthly	Weekly	Monthly	Monthly	Monthly	Monthly	Monthly
Sampling period	2016–2018	2016–2018	2003–2008	2014–2017	2004–2013	2005–2018	2015–2020	2015–2020	2012–2020
Total samples	46	47	72	191	120	147	54	58	89
16S rRNA region	V4–V5	V4–V5	V6	V4–V5	V4	V4–V5	V1–V3	V1–V3	V1–V3
Region length (bp)	∼ 410	∼ 410	∼ 68	∼ 410	∼ 435	∼ 410	∼ 490	∼ 490	∼ 490
Primers	515F + 926R*	515F + 926R*	967F + 1046R†	515F + 926R*	341F + 806RB‡	515Y + 926R*	27F + 519R§	27F + 519R§	27F + 519R§
Sequencing technology	Illumina MiSeq 2 × 300 bp	Illumina MiSeq 2 × 300 bp	454-pyro-sequencing	Illumina MiSeq 2 × 300 bp	Illumina MiSeq 2 × 250 bp	Illumina HiSeq 2500 PE250 (or PE300)	Illumina MiSeq 2 × 300 bp	Illumina MiSeq 2 × 300 bp	Illumina MiSeq 2 × 300 bp
Sequence denoising/ clustering (ASV/OTU)	ASV (DADA2)	ASV (DADA2)	OTU97 (DOTUR)	ASV (DADA2)	ASV (DADA2)	ASV (DADA2)	ASV (UNOISE 3)	ASV (UNOISE 3)	ASV (UNOISE 3)

Latitude and longitude in degrees minutes.
*Parada et al. (2016).
†Sogin et al. (2006).
‡Herlemann et al. (2011) and Apprill et al. (2015).
§Lane et al. (1985) and Weisburg et al. (1991).

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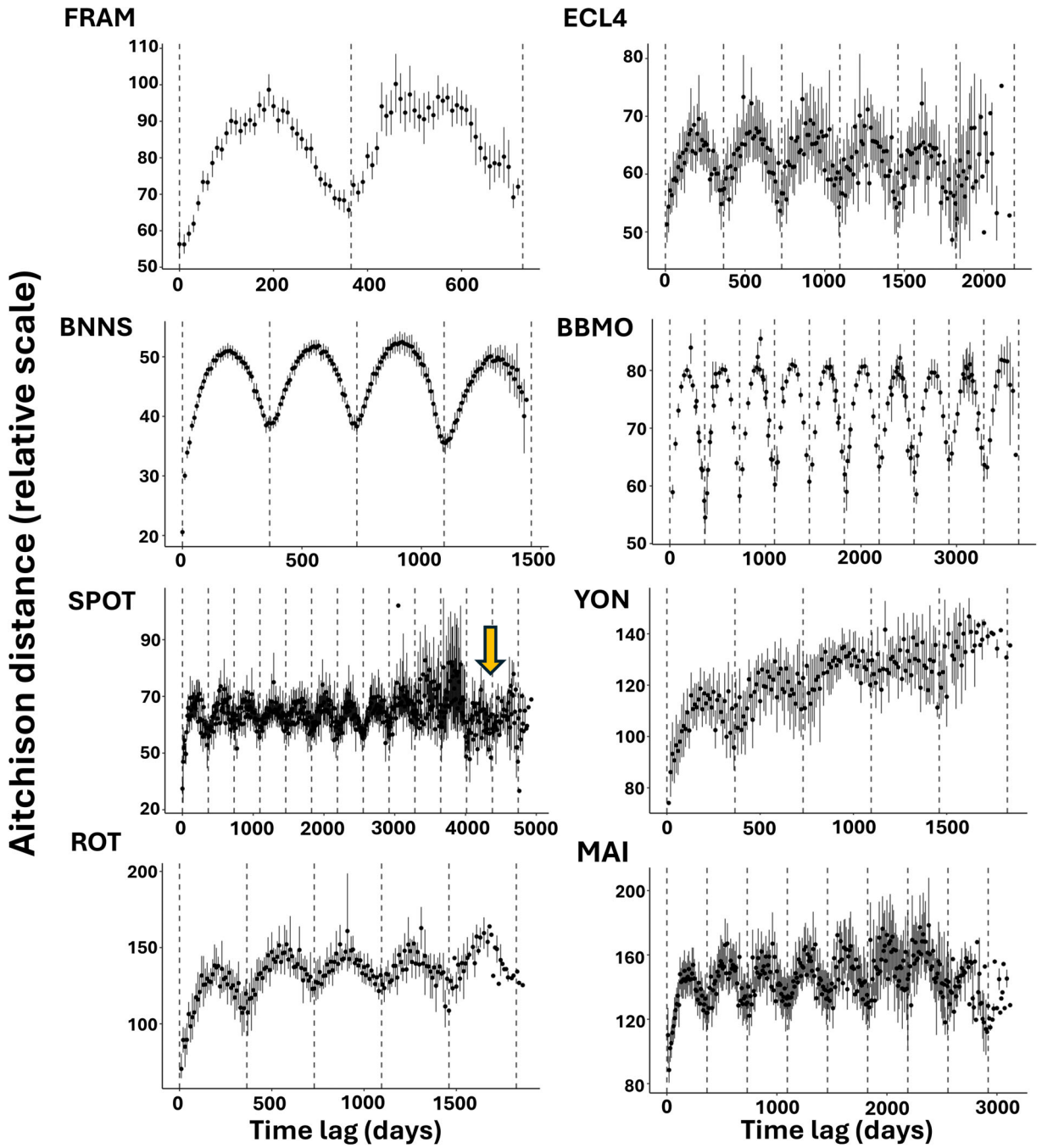

Fig. 2. Global seasonal trends in prokaryotic community beta-diversity in the euphotic zone. Site-specific distributions of pairwise Aitchison distances between community compositions of each possible time difference (*x*-axis) between sample collections (95% confidence intervals around estimates of the mean every 10 d). Data from Fram Strait (FRAM), English Channel (ECL4), Bedford Basin (BBNS), Blanes Bay (BBMO), San Pedro Timeseries (SPOT), NRS Yongala (YON), NRS Rottnest Island (ROT), and NRS Maria Island (MAI) (panels from top to bottom, left to right, respectively). Dotted lines are shown every 365 d. The marine heatwave (the "Blob") is denoted by an arrow on SPOT between 2014 and 2015. Aitchison distance is the Euclidian distance calculated for the prokaryotic community compositon; it is based on read counts which were center logratio transformed.

alpha-diversity across sites, regardless of location or targeted *16S rRNA* gene hypervariable region (V1–V3, V4, V4-V5, V6), DNA extraction methodology, or even sample collection method (FRAM samples were collected autonomously and preserved with mercury chloride). Furthermore, our analyses display a recurring cyclical pattern in prokaryotic beta-diversity, with the strongest signal at the temperate and polar sites (Fig. 2; Supplementary Fig. S17). The only exceptions

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occurred at YON, where a "drifting" signal characterized the community as diversity became more dissimilar over time (Fig. 2). A possible explanation could be that biological interactions have a greater impact on that community as daylength, and oligotrophic conditions remain relatively constant year-round as is typical for tropical oceans. The recurring compositional cycle at SPOT was disrupted around 2014–2015 (Fig. 2; Yeh and Fuhrman 2022b), due to an anomalous major heating event across the northeast Pacific Ocean related to El Niño ("the Blob"), which impacted the whole marine food web (Cavole et al. 2016; Traving et al. 2021).

Kinetic energy, resource, and daylength hypotheses

Various environmental and ecological factors correlate with marine prokaryotic diversity (reviewed in Fuhrman et al. 2015; Ibarbalz et al. 2019). The kinetic energy and resource hypotheses provide mechanisms for changes in marine prokaryotic community diversity. The kinetic energy hypothesis postulates that elevated temperature leads to higher local diversity, through increased metabolic rates, accelerated physiological processes, shorter generation times, and ultimately producing a more diverse community. The resource hypothesis postulates that increasing productivity scales with expanding diversity due to the greater resource availability, which can support a greater number of species (Brown 2014; Ibarbalz et al. 2019). We used log-scaled Chl *a* concentrations, although it is notably not the best estimator of resource limitation for prokaryotes, particularly in very oligotrophic sites and during summer where a diverse bacterial component support pigment diversification (Auladell et al. 2022). Although the kinetic energy and resource hypotheses provide a framework to explain global marine biodiversity patterns, individual time-series observations have shown that prokaryotic richness and evenness are negatively correlated with daylength (Gilbert et al. 2012; Wietz et al. 2021; Raes et al. 2022; Doane et al. 2023).

In addition to linear correlations and multiple linear regression models (Supplementary Figs. S18–S23) we explored a form of hierarchical generalized additive models (HGAMs), which provide flexible predictions of nonlinear relationships (Hastie and Tibshirani, 1986). We show, using HGAMs, that the negative correlation between prokaryotic alpha-diversity and daylength persists on a multiannual basis across sites in both northern and southern hemispheres. The primary finding of the HGAMs indicates a prominent seasonality effect: knowing the month, site, and year of an observation accounts for > 80% of deviance explained (Fig. 3; Supplementary Table S1). Including daylength, temperature, and chlorophyll as fixed effects into HGAMs with global (model "G") and site-specific (model "S2") smoothers broadly reproduced similar patterns shown in linear regressions. Visualizing the partial dependence curves shows how model "G" captures a strong negative relationship between diversity and daylength, a positive relationship to temperature up to ~ 20°C—resembling a thermal performance curve—and a right-skewed relationship to chlorophyll with a peak at ~ 1 μg L^{-1}. Alternatively, model S2 allows variation using site-specific smoothers, yet only 1% additional deviance was explained compared to model G. Here, the relationship between diversity and temperature or chlorophyll are mixed across sites, although still significant, and a consistently negative relationship to daylength persists. Daylength emerges as a key statistical variable explaining patterns in prokaryotic diversity across multiple time series in the northern and southern hemispheres factor across the entire dataset, albeit with some variation at site level.

A clear example of site level variation is noticed for the tropical site YON, where annual variability in daylength is minimal (Fig. 3). Similarly, for the Arctic site FRAM, the absolute Pearson correlation coefficients between log(Chl *a*) and Shannon diversity was higher compared to the correlation coefficient between Shannon diversity and day length (Supplementary Fig. S19). In the Arctic, extreme seasonal shifts between summer and winter dictate changes in communities. Light triggers primary productivity, leading to lower prokaryotic diversity in summer and higher diversity in winter. In winter, prokaryotic niche diversity increases and a diverse group of prokaryotes contributes to nutrient replenishment in winter (Wietz et al. 2021). The only positive relationship with log(Chl *a*) concentrations was found for ROT (< 7% explained), with daylength still explaining between 15% and 24% of the trend in prokaryotic diversity (for Chao1 and Shannon, respectively; Supplementary Figs. S18, S19). A positive relationship between productivity and prokaryotic community richness has previously been noted by Raes et al. (2018a, 2018b) from a single transect along the Leeuwin Current flowing past Rottnest Island, explained by niche partitioning between nitrate-driven autotrophic and mixotrophic micro-eukaryotes. Multiple linear regression models (with temperature + log(Chl *a*) + daylength fitted last) corroborated our results (Supplementary Fig. S23). In a previous study we used Partial Mantel tests to separate the effects of day length and temperature on prokaryotic beta diversity. Despite the high temporal resolution of the Bedford Basin data (weekly over 4 years), it remained difficult to distinguish between light and temperature effects (Raes et al. 2022).

Studies at large spatial scales showed that temperature is the main (and positively correlated) explanatory variable for microbial community diversity in marine ecosystems (Fuhrman et al. 2008; Ibarbalz et al. 2019). Our analyses show that the relationship with temperature varied between sites; encompassing negative, positive, or no correlation with prokaryotic richness or evenness (Supplementary Figs. S6, S18, S19).

Our findings do not support the kinetic energy nor the resource hypothesis to explain the factors influencing prokaryotic diversity (Mittelbach et al. 2001; Ibarbalz et al. 2019). Instead, our analyses closely align with Ladau et al. (2013),

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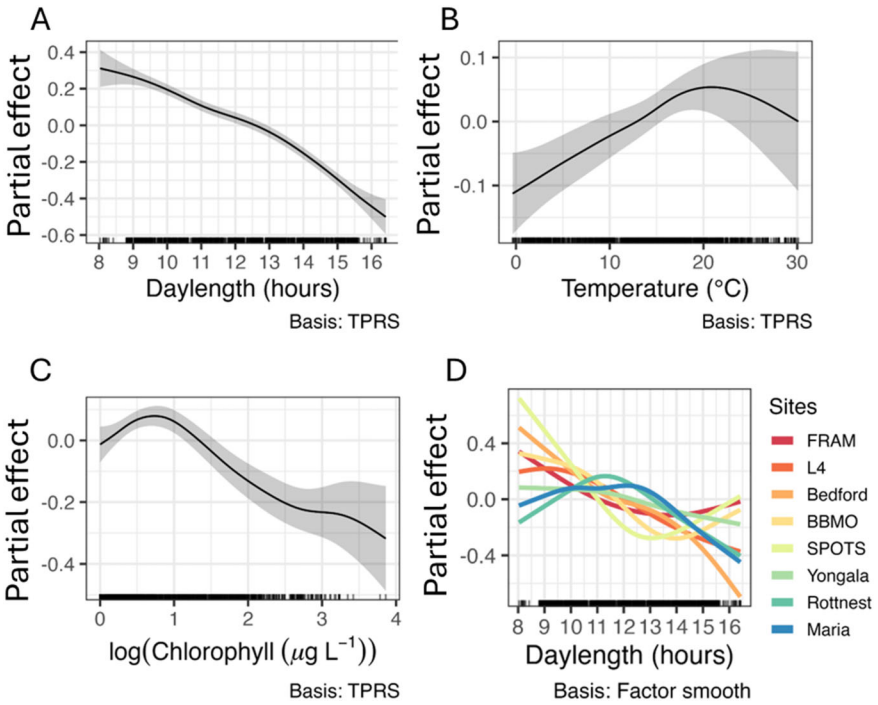

Fig. 3. Hierarchical generalized additive model plots (HGAM) showing the partial effects of explanatory variables: (**A**) daylength, (**B**) temperature, and (**C**) log (Chl *a*) on richness. The *y*-axis represents the contribution of a specific predictor to the response variable, after accounting for the effects of other predictors in the model (Supplementary Table S1). Positive values indicate an increase in the response variable, while negative values indicate a decrease. HGAM plots are shown for model G which uses global smoothers and random intercepts for sites (random effect). Gaussian quantiles for model G are shown in Supplementary Fig. S5. (**D**) Model S2 partial dependence curves for day length with site-specific smoothers and random intercepts for sites (random effect; *see* also Supplementary Fig. S6; Table S1. Global smoothers use default thin plate regression splines (TPRS) for each fixed effect covariate. Ticks are shown on each *x*-axis for the distribution of observed data points.

highlighting the primary impact of seasonality on regional, and potentially global, prokaryotic diversity. The true drivers for prokaryotic community diversity are difficult to identify with certainty as many parameters co-vary with daylength, and many potentially important parameters were not assessed here. Hence, it is not an "either/or verdict" for the hypotheses that were considered here, but rather a complex interplay of processes that dominate and differ when sampling at different spatial and temporal scales. We demonstrate that prokaryotic diversity patterns investigated locally, with seasonal resolution, are affected by different environmental drivers compared to large spatial studies, which usually do not account for temporal or seasonal variations. Our findings indicate that in high-latitude regions, diversity must be interpreted in the context of the particularly strong seasonal cycle, with highest diversity during the polar night. Hence, seasonality and local variation must be considered to understand marine prokaryotic community diversity, especially when comparing globally distributed sites.

The relevance of daylength has been described as a variable that integrates seasonal variability in temperature and stratification (Wietz et al. 2021). Shorter day length co-occurs with seasonal vertical mixing, thus the passive merging of surface (photic) and deep (aphotic) prokaryotic communities resulting in higher diversity (García et al. 2015). In addition, increased daylength and associated higher solar irradiance might have negative (bactericidal) effects on photosensitive microbes that are poorly adapted to high solar irradiance (Ruiz-González et al. 2013). Alonso-Sáez et al. (2006), for example, carried out experimental work that suggested that some groups of non-photosynthetic, heterotrophic bacteria may be negatively impacted by light, as they lack bacteriorhodopsin or other light harvesting photosystems as well as protective mechanisms against UV radiation.

A multiannual recurring state

Time-series data allow the description of long-term seasonal patterns and their associated variability, affording explicit tests for how changes in biological diversity impact ecosystem functions and ecological stability (Fuhrman et al. 2015; Benway et al. 2019). This advantage of time series is unique in comparison to larger-scale spatial studies (O'Brien et al. 2017) such as Tara Oceans, which cannot capture seasonality. Our analyses confirm clear boundaries for prokaryotic community variability over multiannual scales, from subtropic to polar oceans. While the kinetic energy or resource hypotheses are not mutually exclusive—temperature

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and Chl *a* covary—our findings and those from Fuhrman et al. (2015) show that daylength explains the largest variation in prokaryotic alpha- and beta-diversity. Daylength, as a variable, integrates various seasonal processes, including net heat flux, wind speed, total daily irradiance, stratification, depletion, and regeneration of nutrients, as well as the release of POC and DOC. These processes create a recurring pattern of changes in diversity that are not solely driven by temperature or Chl *a*.

Conclusions

Our results showed that daylength is statistically a strong variable accounting for prokaryotic diversity patterns across six of the eight independent prokaryotic time series. However, the inverse relationship between daylength and diversity is counterintuitive, and does not readily link to an underlying biological mechanism. Although physical mixing and seasonality in light-sensitive taxa are potential ecological mechanisms, other causal processes are possible, and a unifying mechanistic explanation still eludes formal description. Our study shows the necessity for considering the temporal dimension in both regional and global prokaryotic diversity analyses, as diversity trends are connected to our planet's seasonal rhythm. Diversity was up to threefold higher in winter across the majority of the eight time series analyzed. The highest variation was observed between the summer and winter months, with clear annually recurring seasonal beta-diversity patterns in polar and temperate waters. Notably, these patterns were independent of collection methods, DNA extraction chemistry, targeted *16S* rRNA hypervariable region, sequencing technology, resolution of taxonomic units, or bioinformatics pipeline. Our findings underscore the potential for improved global and networked observational initiatives by harmonizing methods so we can address comparisons of absolute diversity. This emphasizes the value in establishing standardized best practices for genomic data acquisition and reporting, encompassing the creation of a Minimum Information for an Omics Protocol, as recommended by Samuel et al. (2021). Such harmonization will promote data interoperability, facilitate collaborative research efforts, and promote comparisons of absolute diversity values between sites, which our work cannot address. Where climate changes do generate more frequent extreme events, this work highlights a potential, hitherto undescribed process whereby prokaryotic community fluctuations in response to an interference with the regular daylength-correlated cycles can be identified (*see*, e.g., the "Blob" 2-yr heatwave event Fig. 2e). We posit that based on the prokaryotic time series presented here, among the richest datasets yet available, the empirical evidence supports a primary role for daylength in explaining the seasonal diversity and ecological rhythm of prokaryotic microbes, the basal component of marine food webs, and warrants deeper investigation for causal processes.

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Conflict of Interest

None declared.

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